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PROJECT SUMMARY

Overview:

The Konza Prairie (KNZ) LTER program is an interdisciplinary research program, which aims to build a comprehensive understanding of ecological processes in grasslands, while contributing to synthetic and conceptual advances in ecology. KNZ also provides education and training (K-12 to postgraduate), public outreach, and knowledge to inform grassland management and conservation. Long-term, site-based research at KNZ focuses on tallgrass prairie, but cross-site and comparative studies extend the relevance of KNZ research globally. Proposed KNZ activities are integrated by a conceptual framework built around use of long-term studies to understand the sensitivity and resilience of grasslands to changes in historic and novel drivers. These changes occur over long time scales and require long-term study to detect, and long-term experiments to understand. Proposed activities expand the breadth and depth of KNZ LTER research, education of K-12 students and teachers, training of undergraduate and undergraduate students, and the impact of outreach to the public and natural resource managers.

Intellectual Merit:

This KNZ renewal proposal builds on a 30-vr foundation of decadal-scale experiments and measurements to understand ecological dynamics and trajectories of change in tallgrass prairie. Long-term watershed- and plot-level experiments at KNZ have altered critical grassland drivers (e.g., fire, grazing, climate, nutrient enrichment), providing important insights into their independent and interactive affects on terrestrial and aquatic grassland systems. Divergent responses to these manipulations have also created a template of varied ecological legacies and ecological states. The histories and trajectories under which these states and legacies developed are known, enabling use of long-term observations and experiments coupled with new treatments and complementary studies to (1) test and refine conceptual and theoretical models of community and ecosystem change, and (2) provide new insights into mechanisms underlying a broad range of ecological responses to important grassland drivers. Empirical and observational tests of mechanisms underlying the sensitivity and resilience of this grassland are proposed. These include long-term manipulation of key historic drivers, addition/alteration of novel drivers, and ceasing drivers in some long-term experiment to assess ecological legacy effects and feedbacks that affect ecological state. Fire and grazing studies will address fundamental questions regarding top-down and bottom-up controls of ecological processes, and effects of fire-grazing-induced heterogeneity on biodiversity and ecosystem processes. Studies of woody plant encroachment, climate change, and chronic N enrichment studies will address three of the most critical global changes occurring in grasslands worldwide. Restoration studies will test fundamental ecology theories on controls of plant diversity and community assembly, while building a foundation for more effective strategies for restoring grasslands and conserving grassland biodiversity. KNZ research is conceptually integrated through a common theme of sensitivity and resilience of grasslands to natural and anthropogenically-altered drivers. Regional, cross-site and synthetic studies will broaden the sphere of inference and applicability of KNZ results, and contribute to a more general and predictive understanding of grassland dynamics in a changing world.

Broader Impacts:

Grassland Conservation and Restoration: KNZ experiments inform conservation and test ecological theory relevant to grassland restoration. Fire and grazing are important components of grassland management, and KNZ research is relevant for designing improved management practices (e.g., patch-burn grazing) that sustain terrestrial and aquatic resources in grasslands. Restoration studies, a core part of the KNZ program, are particularly timely because human activities have resulted in widespread loss and degradation of tallgrass prairie and other temperate grasslands. Collectively, restoration studies at KNZ providing insights into the roles of abiotic and biotic variation on the restoration of prairie communities and associated ecosystem function. These studies will aid in developing more effective restoration approaches and enable us to better forecast the responses of restored grasslands to environmental change.

I. PROJECT DESCRIPTION: KNZ LTER VII: Long-Term Research on Grassland Dynamics – Assessing Mechanisms of Sensitivity and Resilience to Global Change.

A. INTRODUCTION. The Konza Prairie (KNZ) LTER program is an interdisciplinary research program with a long-term goal of building a comprehensive and detailed understanding of ecological processes in tallgrass prairie and other mesic grasslands, while contributing to broad synthetic and conceptual advances in ecology. KNZ also provides education and training (K-12 to postgraduate), public outreach, and knowledge to inform grassland management and conservation. Our long-term, site-based research focuses on tallgrass prairie, but cross-site and comparative studies extend the relevance of KNZ research globally (e.g., Melzer et al. 2010, Koerner et al. 2014). Since its inception, KNZ research has focused on fire, grazing and climatic variability as three key interactive drivers responsible for the origin, evolution, persistence and contemporary ecological dynamics of tallgrass prairie (Fig. 1) and grasslands worldwide.



Fig. 1. For more than 30-yrs, long-term research at KNZ has focused on the pervasive and interactive effects of *fire*, *grazing and climatic variability* on ecological patterns and processes in tallgrass prairie.

KNZ was in the first cohort of LTER programs funded in 1980 (Callahan 1984) and KNZ datasets, many spanning >30 yrs, encompass the five LTER core areas. The KNZ program has grown by building upon prior results, iteratively incorporating new questions and approaches, and expanding to include multiple ecological levels (genomic to landscape) and spatial and temporal scales. Early KNZ research addressed the effects of fire and grazing as influenced by a variable continental climate and heterogeneous landscape. LTER I (1981-1986) established long-term sampling sites and protocols, focusing on biotic responses to annual fire and fire suppression, topography and interannual climate variability. LTER II (1986-1990) encompassed a wider range of fire frequencies and broader spatial scales, and initiated studies on belowground processes. LTER III (1991-1996) incorporated bison and cattle treatments to understand how grazing interacts with fire across a landscape mosaic, all under a variable climate. In total, LTER I-III included studies of the major abiotic (climate, fire, topoedaphic gradients, hydrology) and biotic (herbivory, competition, mutualism) factors affecting mesic grasslands, and led to a dynamic, nonequilibrium perspective of ecological patterns and processes in grasslands (Knapp et al. 1998). In LTER IV (1996-2002), we used long-term studies to test theory and advance fundamental ecological knowledge (Blair 1997, Collins et al. 1998, Smith & Knapp 2003), while building a new focus on impacts of global change on grassland dynamics, with relevance to understanding, managing and conserving grasslands worldwide. Humans have long controlled grazing and fire, but we now alter other key drivers (nutrient inputs, atmospheric chemistry and climate) in grasslands. The impact of global changes on grasslands and grassland streams was the central theme of LTER V (2002-2008) and LTER VI (2008-2014). Research during these LTER cycles focused on responses to changes in land-use including altered fire and grazing regimes (Heisler et al. 2004, Towne et al. 2005, Powell 2008, Veen et al. 2008) and grassland restoration (Baer et al. 2003, 2004), changes in land-cover (Heisler et al. 2003, Briggs et al. 2005, McKinley & Blair 2008) and invasive species (Smith et al. 2004, Reed et al. 2005, Woods et al. 2009), climate change (Knapp et al. 2002, Heisler-White et al. 2009, Fay et al. 2011), and altered biogeochemical cycles (Johnson et al. 2003, Dodds et al. 2004, Bernot & Dodds 2005, Coolon et al. 2013).

Today, the rich history of research and current template of long-term experiments at KNZ provide new and unique opportunities for advancing ecological theory and addressing timely questions regarding grassland responses to multiple global changes. Our LTER VII proposal builds on a 30-yr foundation of research that includes decadal-scale experiments and measurements to understand ecological dynamics and trajectories of change in tallgrass prairie, with new complementary studies to investigate mechanisms underlying sensitivity and resilience of grasslands to global change (Fig. 2).

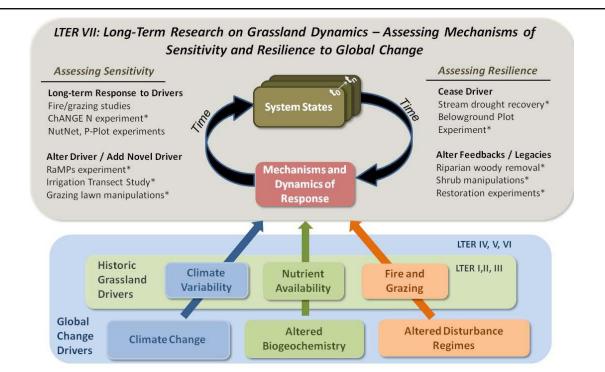


Fig. 2. Conceptual framework for KNZ LTER VII. New and continuing research builds upon LTER I-III (responses to fire, grazing, climate, and nutrient variability) and LTER IV-VI (responses to global change drivers) to understand the dynamics and mechanisms of grassland responses to changing drivers. New experiments or treatments are indicated by *. Mesic grasslands vary in their sensitivity and resilience to alterations in drivers, which can lead to changes in ecological states through time. In LTER VII, we propose a series of empirical and observational tests of potential mechanisms underlying sensitivity and resilience of this grassland, including continued long-term manipulation of drivers, addition/alteration of novel drivers, and ceasing experimental manipulation of drivers to assess ecological legacy effects and feedbacks. We define the terms in bold as follows: Ecological state — sets of unique abiotic and biotic conditions that occur under similar environmental conditions; may be stable (able to maintain identity in response to changes in drivers) or unstable (transient in space or time). Sensitivity — responsiveness of an ecological state to disturbance or a change in external drivers. Resilience — ability of a system to absorb and/or recover from disturbance or change in drivers and maintain a relatively constant ecological state. Legacy effects — historical changes in abiotic or biotic conditions that influences current or future ecological responses or states.

We address new research themes and questions in LTER VII, but our long-term overarching goal remains to further understand the interactive effects of key natural and altered drivers on grassland dynamics and to advance ecological theory through synthesis and integration of LTER data. Our long-term aims are to:

- 1. Build upon our core LTER experiments and expand datasets on fire, grazing and climate variability to deepen and refine our understanding of the abiotic and biotic factors and feedbacks affecting grassland structure and function;
- 2. Develop a mechanistic and predictive understanding of grassland dynamics and trajectories of change in response to natural and anthropogenic drivers using long-term experiments and datasets, coupled with complementary shorter-term studies;
- 3. Conduct new syntheses using KNZ data and results from other sites to advance ecological theory, and expand the inference of KNZ research to other grasslands and biomes;
- 4. Train the next generation of ecologists, educate the public, and provide outreach to increase the relevance of KNZ long-term research to society.

Background and Context. *Fire, grazing and climate variability* control ecological processes in tallgrass prairie and are ubiquitous features in most grasslands worldwide. *Fire* maintains tallgrass prairie (Anderson 1990) and altered fire frequency is a critical land-use change in grasslands (Bond & Keeley

2005, Bowman et al. 2009, Archibald et al. 2012). Fire influences light and soil conditions for emerging plants (Knapp & Seastedt 1986), plant phenology, physiology (Knapp et al. 1998, Nippert et al. 2011), demography (Dalgleish 2007), and interactions with microbial mutualists (Hartnett & Wilson 2002). Frequent fire increases aboveground net primary productivity (ANPP) (Briggs & Knapp 1995), decreases N availability (Blair 1997), favors perennial C_4 grasses while reducing abundance of C_3 plants (including woody species), occurrence of exotic species (Smith & Knapp 1999), and overall plant biodiversity (Collins et al. 1998). Differences in vegetation structure, composition, and tissue quality under contrasting fire regimes affect aboveground consumers (Kaufman et al. 1998, Joern 2005, Powell 2006), belowground invertebrates (Callaham et al. 2003, Jones et al. 2006, Jonas et al. 2007), and soil microbes (Jumpponen et al. 2005, Carson 2013). Fire suppression alters plant communities, and leads to woody plant encroachment and eventually conversion to forest, an ecosystem state change with immense ecological impacts (Briggs et al. 2005, McKinley et al. 2008, Twidwell et al. 2013). Grazers also play a crucial role in grasslands (Lemaire et al. 2000, Fuhlendorf et al. 2006, Frank 2007, Allred et al. 2011b) and changes associated with the management of large herbivores are another critical element of contemporary change in grasslands worldwide (Fuhlendorf & Engle 2001, 2004, McNaughton 2001, Walker 2001). Historically, tallgrass prairie was grazed by bison, but cattle have replaced large native grazers in the Flint Hills, as in many other grasslands globally. Grazers preferentially use recently burned grassland (Knapp et al. 1999, Allred et al. 2011a,b, Augustine & Derner 2014) and alter soil nutrient availability (Johnson & Matchett 2001, Veen et al. 2008), plant communities (Collins et al. 1998, Collins & Calabrese 2012) and vegetation structure. Grazers increase plant diversity by reducing cover of dominant grasses, increasing heterogeneity and altering the abundance and diversity of other consumers. *Climate* interacts with both fire and grazing (Koerner & Collins 2014) and determines the potential distribution, composition, and functioning of grasslands (Lauenroth et al. 1999). Inter- and intra-annual climatic variability drives both terrestrial (Sala et al. 1988, Fay et al. 2011) and aquatic dynamics (Bertrand et al. 2009) in grasslands.

Decades of KNZ research have produced a rich and detailed understanding of how these three drivers independently and interactively affect the structure and function of mesic grasslands (Knapp *et al.* 1998, Blair *et al.* 2013) and associated groundwater and streams (Dodds *et al.* 2004). The interplay of these drivers affects both abiotic conditions and biotic interactions in complex ways. While some ecosystems are constrained primarily by chronic limitations of a single resource (*e.g.*, water in arid sites), mesic grasslands are subject to multiple limiting resources (water, light, N, P) that vary spatially and temporally in response to fire, grazing, climate, site history and landscape position (Seastedt & Knapp 1993, Nippert & Knapp 2007a, Kaufman *et al.* 2012a,b). Variability in multiple limiting resources across a heterogeneous landscape leads to high species diversity and complex ecological dynamics, which are now affected by anthropogenically-driven changes in disturbance regimes, climate and resource availability. As a result, KNZ is ideal for addressing major global change phenomena, and testing fundamental ecological theory related to productivity-diversity and disturbance-stability relationships, top-down vs. bottom-up regulation of ecological processes, food web dynamics, and responses to environmental heterogeneity.

Research Site and Experimental Design. The core KNZ research site is the Konza Prairie Biological Station (KPBS), a 3487 ha temperate grassland with a continental climate. Mean annual precipitation is 835 mm yr¹, but is highly variable both among and within years. The climate is sufficient to support woody vegetation, making periodic drought, fire and grazing critical for maintaining grassland (Axelrod 1985, Anderson 1990). KPBS is topographically complex (320 to 444 m asl), and soil type and depth vary with topography. Soils are silty clay loams, formed from thick colluvial and alluvial deposits ≥2 m in lowlands, while hillside and upland soils are shallow (Ransom *et al.* 1998). Soils overlay alternating layers of limestone and shale, contributing to complex subsurface hydrology (Macpherson 1996, Oviatt 1998). Vegetation is primarily (>90%) native tallgrass prairie plants, dominated by perennial C₄ grasses. Numerous sub-dominant grasses, forbs and woody species contribute to high floristic diversity. The entire Kings Creek watershed, a USGS Benchmark Stream, is located on Konza. Hardwood forests occur along major stream courses. Several agricultural fields and restored prairies are located on site. Konza supports ~600 plant, 40 mammal, >200 bird, 34 reptile and amphibian, 20 fish, and >700 identified invertebrate species. Overall, the site is representative of native tallgrass prairie, with selected areas representing other contemporary land use practices (*e.g.*, agriculture, restored grasslands, cattle grazing).

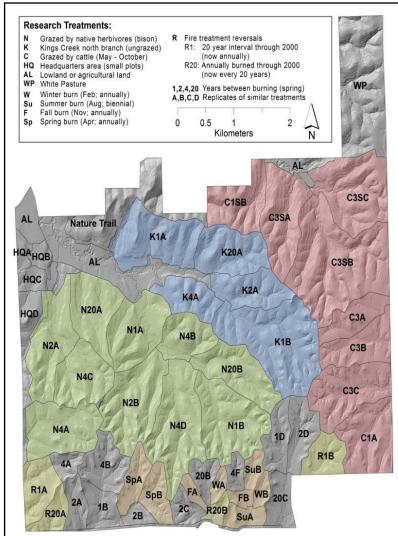


Fig. 3. The KNZ watershed-level experimental design. Watersheds grazed by bison ('N') are green, and cattle-grazed watersheds ('C') are red. Cattle-grazed treatments include both annual spring burning/season-long stocking and a 3-yr rotational patch burning-grazing treatment initiated in 2010. All other watersheds are ungrazed. Numbers designate fire return intervals for spring-burned watersheds. Watersheds subject to different seasons of fire (W=winter, F= fall, Sp= spring, Su=summer) are brown, and Fire Treatment Reversal ('R') watersheds are yellow. King's Creek watershed (USGS Benchmark Stream) is blue. The riparian woody removal experiment is located on watershed N2B. Stream gages are located on watersheds N2OB, N1B, N4D, N2B and lower Kings Creek, and groundwater sampling wells are located on N4D. Flux towers are located on 1D and 4B.

The foundation for KNZ research is a unique site-based, watershed-level fire and grazing experiment initiated in 1972 (Fig 3), with complementary long-term plot-level and streamreach experiments, and a network of sensors and sampling stations across terrestrial and aquatic systems. KNZ includes replicate watersheds burned at 1, 2, 4, or 20 yr frequencies, bracketing historic fire frequencies of ~4 yrs (Allen & Palmer 2011) and contemporary management extremes. Most watersheds are burned in spring, when large fine fuel loads and high frequency of lightning coincide, and when prescribed burning occurs regionally (Bragg 1995). Fires historically occurred at other times of year (Engle & Bidwell 2001), and in 1994 we incorporated replicate watersheds burned in spring, summer, fall or winter (Towne & Kemp 2003, 2008). In 2001, we began a long-term "fire treatment reversal" experiment (annual and 20yr fire treatments switched across replicate watersheds) to explore trajectories and rates of change in plants, animals and soil processes under varied fire legacies. We also manipulate fire in long-term plotlevel experiments on Konza, where detailed ecological responses and mechanisms underlying effects of fire and other manipulations are addressed (e.g., Callaham et al. 2003, Dell et al. 2005). Bison were reintroduced beginning in 1987 to a 1000-ha area including replicate watersheds burned at 1, 2, 4 and 20 yr intervals to address the role of grazers and interactions with fire (Hobbs et al. 1991, Johnson & Matchett 2001, Trager et al. 2004, Collins & Smith 2006). Studies of cattle grazing began

in 1992, and a large-scale experiment evaluating ecological responses to heterogeneous burning and cattle grazing (patch-burn rotational grazing) was initiated in 2010. In core LTER watersheds, long-term data on ANPP, plant species composition, plant and consumer populations, soil properties, and key above- and belowground processes are measured at permanent sampling stations stratified by treatment and topographic position. Effects of climate are addressed by long-term data collection under widely variable climatic conditions, and with studies that manipulate climate variables or hydrology.

Rationale for LTER VII. In 1980, at the start of the KNZ program, major vegetation types in similar landscape positions were comparable, reflecting a relatively uniform fire and grazing history. Decades of watershed- and plot-level manipulations of drivers coinciding with other environmental changes have yielded highly-divergent responses, ecological legacies, and a range of ecological states (Fig. 4), reflecting similar changes occurring in grasslands globally (Gibson 2009, Blair et al. 2013). Different ecosystem states at KNZ now include (see photos in Fig. 4) (a) high-productivity, low-diversity C₄-dominated grasslands (high fire frequency, no grazers), (b) high diversity C₃-C₄ co-dominated states (intermediate fire frequency or with grazers), (c) short-statured, high fertility grazing lawns (with and without wallows), (d) expanding shrublands (low fire frequency, deep soils), (e) expanding woodlands (deciduous riparian woodlands or mixed deciduous-conifer uplands with low fire frequency), and (f) others (e.g., exotic C_4 grass-invaded plots, multiple stages of restored prairie, and agricultural states). Legacy effects hypothesized to impact future responses vary from those that are highly apparent (e.g., shifts in dominant species [Collins et al. 2013] or life-form [Ratajczak et al. 2014]) to some that are less easily detected (e.g., changes in genetic structure of dominant grass populations [Avolio et al. 2013]). New KNZ research will capitalize on these different states and legacies. Because we know the histories and past trajectories under which many of these states and legacies have developed, we now are poised to use existing long-term observations and experiments, coupled with new treatments or complementary studies, to rigorously investigate the mechanisms underlying the sensitivity and resilience of grassland systems to the dominant natural and anthropogenic drivers of change.

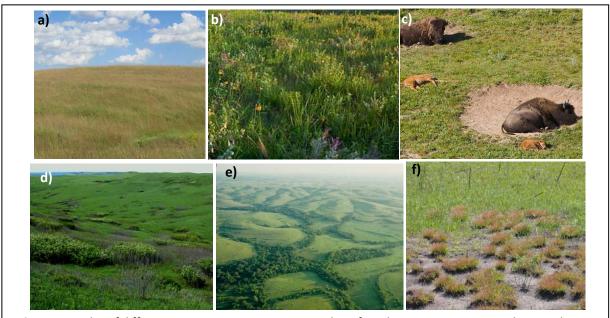


Fig. 4. Examples of different ecosystem states at KNZ resulting from long-term experimental manipulation of drivers (*i.e.*, fire, grazing) and other regional/global change drivers (*e.g.*, exotic species invasion, climate change). See text above for more detailed descriptions corresponding to photo labels. Other examples not pictured include legacies of long-term N addition and experimental water manipulations, agricultural fields in former prairie, and restored prairies at different stages of development.

LTER VII Theoretical Framework and Research Questions. Global changes and other alterations of ecological drivers in grasslands can modify resources and system responses in novel ways. Changes in drivers can be relatively discrete ("pulsed") events (e.g., periodic fire or drought), while others involve chronic and directional ("press") changes in resources or environmental conditions (e.g., increased N deposition, directional climate change) that may push ecosystems along trajectories and at faster rates of change than encountered in the recent past (Beisner et al. 2003, Rockstrom et al. 2009, Bestelmeyer et al. 2011, Bestelmeyer & Briske 2012). Various conceptual models have been proposed to describe effects of disturbance or change in drivers on ecological state changes. These state changes may be gradual, monotonic and reversible, or abrupt and non-linear (threshold responses). State-transition models (Fig. 5)

describe ecological state changes that can occur when response thresholds are crossed. (Scheffer 2009, Bestelmeyer et al. 2011). In some cases ('critical transitions' or 'regime shifts'), threshold responses may exhibit hysteresis as new stabilizing feedbacks are established, resulting in alternate states or attractors. In such cases, returning drivers to pre-transition conditions may be insufficient to return to a prior state. KNZ research has revealed evidence of thresholds, abrupt state changes and bi-stability in grassland-shrubland transitions in response to reduced fire frequency (Ratajczak et al. 2014). We will explore this

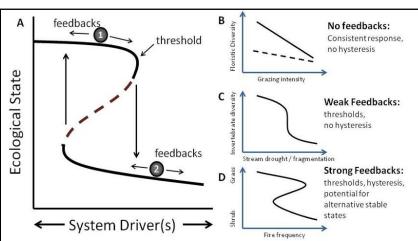
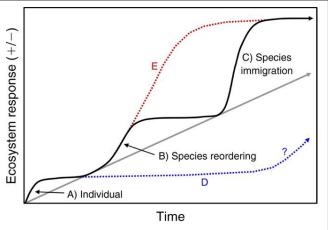


Fig. 5. State-transition model of responses to changing drivers. **Panel A** depicts a general relationship between feedbacks, critical thresholds and state changes that can lead to alternate stable states (1 and 2). The dashed brown line depicts an unstable state; **Panels B-D** illustrate how variability in feedback strength can affect ecological responses and lead to threshold responses and hysteresis, with examples relevant to KNZ long-term studies. Dashed and solid lines in Panel B indicate differential sensitivity.

further in LTER VII along with other potential state transitions. A complementary model – the Hierarchical Responses Framework (HRF) – was developed in response to long-term "press" resource manipulations at KNZ (Smith *et al.* 2009; Fig. 6). The HRF describes ecosystem responses as driven initially by individual-level responses and then by community reorganization in response to a chronic alteration in drivers. Long-term water and nutrient addition experiments at KNZ provided support for this model (Knapp *et al.* 2012a), but applicability to other drivers remains untested and is a fertile area for new KNZ research. The HRF hypothesizes mechanisms that can lead to ecosystem state changes consistent with state-transition models, although state transitions can also occur by other means. Testing and refining these and other models in response to a wider range of altered drivers is a major research emphasis in LTER VII. We also aim to identify mechanisms (*e.g.*, legacies and feedbacks) that influence the sensitivity of grasslands to different drivers, and that modulate the resilience and recovery of grassland when drivers are changed or removed.

Fig. 6. The hierarchical-response framework (HRF) postulates a hierarchy of mechanisms underlying non-linear ecological change (black line) in response to chronic resource alterations. Initially small ecosystem responses are driven by (A) individual-level (physiological/metabolic, mortality) responses to altered conditions. The magnitude and extent of this response is limited by the potential of resident species for acclimation and local adaptation. Larger responses may emerge with (B) reordering of species in the community, as some species are favored by changing conditions at the expense of others. Finally, (C) new species better suited for new resource levels may immigrate into the ecosystem, resulting in the further change in ecosystem response. In contrast



to this nonlinear series of responses, gradual linear change (gray line) in ecosystem response may occur if the magnitude and rate of change is similar for all three mechanisms. Lines D and E depict alternate trajectories of change. Ecosystems dominated by long-lived species that turnover slowly (e.g., forests), may appear to be resistant (D), with responses limited to physiological acclimation for decades or longer. Conversely, ecosystems where altered resources promotes invasion by exotic species or pests/pathogens may bypass physiological responses or community reordering and (E) and exhibit larger and more rapid changes. From Smith et al. 2009.

The variety of established long-term experiments at KNZ now will allow us to explore sensitivity of selected ecological processes to different drivers with comparative approaches and meta-level analyses. A preliminary synthesis using data from multiple KNZ studies identified N addition, supplemental water or drought, periodic fire, and ungulate grazers as the drivers eliciting the largest responses in ANPP (Fig. 7). These same drivers also alter the dominant plant life forms, a change that underlies many dynamics in this grassland (Fig. 7 inset; Smith & Knapp 2003, Baer *et al.* 2003, Knapp *et al.* 2008b, Avolio & Smith 2013), and which is a focus of new LTER VII projects. Recent KNZ research indicates that additional drivers affect other ecological responses. For example, insect herbivory affects productivity of forbs, an important component of plant diversity (La Pierre 2013). Although much LTER VII research focuses on fire, grazing, water and N, we also will address other drivers (*e.g.*, insect herbivory and stoichiometry), which are likely to yield new insights into controls of ecological processes in grasslands and other biomes.

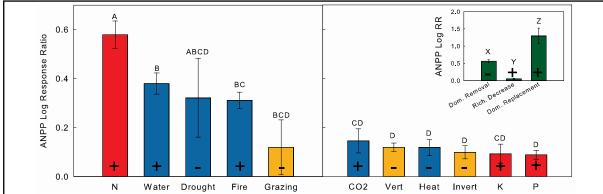


Fig. 7. Relative impacts of key drivers (*left panel*) and other abiotic and biotic factors (*right panel*) on above-ground net primary productivity (ANPP) based on data from multiple KNZ studies. Absolute relative change (log response ratio) is shown, with the direction of the effect indicated with a positive or negative sign. Red=nutrient manipulations; Blue=climate manipulations; Yellow=consumer manipulations. *Inset* Relative impacts of a 4-fold reduction (16 vs. 4 species) in plant species richness, loss of the dominant C_4 grasses (100% removal of *Andropogon gerardii* and *Sorghastrum nutans*), and a shift in life form from dominance by C_4 grasses to dominance by C_3 shrubs. (From Smith *et al. in prep*)

To accomplish our overarching goals, KNZ LTER VII research will address the following questions:

- 1. How do natural (fire, bison grazing, climate) and anthropogenic (altered disturbance regimes, climate change, altered biogeochemistry, cattle grazing) drivers affect grassland states and dynamics at multiple levels of ecological organization?
- 2. What are the long-term rates and trajectories (*e.g.*, directional, non-linear, threshold) of grassland response to altered drivers, and what mechanisms underlie, or constrain, observed responses? We focus explicitly on drivers that KNZ research has identified as having the greatest impact on ecological processes (Fig. 7) and thus the greatest likelihood of altering ecological states.
- 3. Do rates and patterns of change in this grassland, and the underlying mechanisms, conform to conceptual and theoretical models (*e.g.*, Scheffer 2009, Smith *et al.* 2009, Bestelmeyer *et al.* 2011)? The wide array of different structural and functional states resulting from KNZ long-term experimental treatments provides a unique opportunity to test complementary models.
- 4. What determines grassland resilience, and what legacies and/or feedbacks constrain recovery of system state and function following disturbance or when drivers change? Can recovery be facilitated based on ecological principles? The long-term experiments and datasets at KNZ provide a foundation for addressing these questions, by eliminating or altering chronic drivers in ongoing experiments and using data from natural experiments (*e.g.*, recovery from drought) to test for feedbacks and legacies that affect resilience and recovery.
- 5. What abiotic and biotic factors (filters) regulate community assembly and state changes in restored prairie? A variety of KNZ restoration experiments, including a sequential restoration experiment initiated in LTER VI provide a novel framework for testing theory (*e.g.*, community assembly) and our understanding of constraints on recovery and state change in restored prairie.

- **B. RESULTS OF PRIOR SUPPORT.** *Konza Prairie LTER VI: Grassland Dynamics and Long-Term Trajectories of Change.* Blair *et al.* 2008-2014. \$5,640,000. During LTER VI, KNZ scientist and students produced or contributed to 384 publications, including 305 refereed papers, 3 books, 13 chapters, 56 theses/dissertations, and 7 miscellaneous publications (complete list at *www.konza.ksu.edu*). KNZ publications include site-based, cross-site and network-level contributions in a mix of discipline-specific to high-impact journals. We leveraged additional grants (\$23M in new awards during LTER VI) to strengthen our research base and support studies complementary to KNZ goals. Below, we highlight results from **10 selected publications** and others that represent the breadth of research during LTER VI and provide a foundation for LTER VII.
- (i) Fire and grazing: Plant community / ecosystem response. Unraveling the effects of fire and grazing on populations, communities and ecosystems requires long-term study (Collins et al. 2008, Smith et al. 2009, Knapp et al. 2012c). In LTER VI, we documented multi-decadal responses to fire frequency, season of fire, and combinations of fire and grazing by native (bison) or domestic (cattle) ungulates. Grazing and fire have some comparable effects in grasslands (e.g., removal of aboveground biomass), but many community and ecosystem responses differ (Veen et al. 2008, Collins & Calabrese 2012). Spasojevic et al. (2010) analyzed 22 yrs of KNZ plant community data and found that communities burned every 4 yrs and those grazed by bison converged at the plant trait level. However, trait-based community responses to altered fire treatments (the 'Fire Reversal Experiment') were contingent on initial community state, demonstrating that treatment legacies and initial states affect trajectories of change. Other KNZ-led intercontinental comparisons provided a global perspective on grassland responses to fire and grazing (Buis et al. 2009, Koerner & Collins 2013, 2014, Eby et al. 2014, Koerner et al. 2014).

Grazer studies. Fire-grazing interactions create shifting mosaics of habitat and food quality that underlie responses of the grazers and other consumers. Bison are highly selective in habitat use and, during the growing season, disproportionately utilize areas recently burned in spring because food quality (*i.e.*, N content) is higher. They graze much less in unburned areas except in winter. Selection for burned areas is stronger when burned more recently, resulting in differential grazing pressure in responses to fire cycles of 1, 2 and 4 yrs. Bison also alter landscape vegetation patterns by physical disturbance (e.g., wallowing; McMillan *et al.* 2011). In addition to bison behavior, we studied herd genetics (Ungerer *et al.* 2013), maternal allocation to offspring (Hamel *et al.* 2012), effects of climate variability on bison performance (Craine *et al.* 2009, 2013), and differential use of available water sources by bison (Nippert *et al.* 2013).

Other consumer responses. Studies of small mammals, birds and grasshoppers revealed complex spatial and temporal responses to fire-grazing treatments, associated heterogeneity in resources, and altered land cover (Klug et al. 2010, Loaiza et al. 2011, Laws & Joern 2011,2012a,b). Joern & Laws (2013) synthesized data from multiple studies to show that arthropods play several important roles in grasslands, including contributions to biodiversity and ecosystem structure and function; however, arthropod responses to fire, grazing and climate are largely indirect and based on changes in resources, species interactions, habitat structure, and habitat heterogeneity. Small mammal populations and species assemblages are highly dynamic, responding to fire, grazing and weather, but in species-specific and often idiosyncratic ways (Kaufman et al. 2012a,b). In contrast, grasshopper feeding-guilds exhibit resource-based, density-dependent feedbacks and predictable population and community dynamics in response to these drivers at annual and decadal scales (Jonas & Joern 2007, 2008, Behmer & Joern 2012).

We addressed the potential for alternative fire and grazing management to enhance consumer diversity by promoting greater heterogeneity, as predicted by the habitat complexity and heterogeneity hypothesis. Species coexistence increased with resource and habitat heterogeneity for grasshoppers and spiders (Joern 2004, 2005). Bird populations also exhibit long-term variation in abundances and species composition in response to fire-grazing induced heterogeneity (Powell 2008, Rivers *et al.* 2010). Multi-season occupancy models of Greater Prairie Chickens revealed interactive effects of fire and grazing on local colonization (highest in grazed sites and decreased with woody encroachment) and extinction (inversely related to fire frequency at grazed sites) (McNew *et al.* 2012a). Population growth of this threatened species is depressed by low nest survival in sites managed for cattle production (McNew *et al.* 2012b). A landscape genetics approach revealed that land management and altered landscape connectivity also influenced the spatial dynamics and population genetics of snakes and lizards (Klug *et al.* 2011a,b, Blevins *et al.* 2011).

Stream response. We expanded studies of the impact of fire and grazers on grassland streams. Dissolved black organic C in streams was not unusually high relative to other biomes (Jaffé *et al.* 2012) despite the high fire frequency at Konza, and there was no relationship between fire frequency and levels of dissolved black organic C in KNZ streams (Ding *et al.* 2013), suggesting that black organic C cycles slowly in the soil and accumulates over long time periods. Studies of bison and cattle effects on stream water quality, sediment transport, and geomorphology (Larson *et al.* 2013a) revealed greater effects of cattle on nutrient and sediment transport relative to bison, which spend less time in stream and riparian areas.

(ii) Woody plant encroachment: Altered fire and grazing regimes are local drivers affecting grassland-woodland transition. Long-term KNZ data reveal patterns of community change consistent with a regime shift between alternative grassland and shrubland states, including critical thresholds that vary with fire frequency and topography (Ratajczak et al. 2014). Woody encroachment into tallgrass alters community structure and biodiversity (Ratajczak et al. 2012), ecosystem function (Knapp et al. 2008b, Barger et al. 2011), and ecohydrology (Brunsell et al. 2013). With 30+ yrs of data, we have begun to identify the interplay of fire (Briggs et al. 2005), soil moisture and water use (Nippert et al. 2013), and plant demographic feedbacks (Ratajczak et al. 2011) related to woody encroachment.

Woody encroachment is also occurring in riparian corridors, with cascading effects on stream metabolism and community structure (Riley & Dodds 2012, Reisinger *et al.* 2013). A comprehensive study of longitudinal patterns of in-stream primary (1°) and secondary (2°) productivity and food web structure revealed patterns consistent with a prairie stream continuum model (*e.g.*, greater 1° and 2° productivity in open-canopy headwaters), though top-down processes (*e.g.*, fish predation) may override some predicted responses to physical gradients (Whiting *et al.* 2011). We also removed woody riparian vegetation within 50-m on each side of two 100-m stream reaches (with controls). Removal stimulated gross 1° production in the stream and increased filamentous green algae growth and activity (Riley & Dodds 2012). This subsequently increased the abundance, biomass, and production of grazing stream invertebrates and total invertebrate production (Vandermyde & Whiles 2014). Riparian forest removal also increased denitrification in riparian soils by 50% (Reisinger *et al.* 2013).

(iii) Climate variability and change: Predictions of more frequent and extremes events (floods, drought, heat waves) combined with long-term directional climate changes (Petrie & Brunsell 2012, IPCC 2013) suggest new trajectories of ecosystem response to this driver. Over the past 30 yrs, we have investigated how climate variability and climate change (*e.g.*, CO₂, temperature, and precipitation regimes) affect ecological patterns and processes in tallgrass prairie (Owensby *et al.* 1993, 1999, Silletti & Knapp 2002, Knapp *et al.* 2002, Williams & Rice 2007, Williams & Xia 2009, Harper *et al.* 2005, Nippert *et al.* 2009).

Terrestrial responses. KNZ supports two of the longest running climate manipulation experiments (Knapp et al. 2012a,c) in the world: the 22-yr Irrigation Transect Experiment (ITE) and the 15-yr Rainfall Manipulation Plots (RaMPs) experiment. The ITE adds water as needed to alleviate growing season water stress and reduce interannual rainfall variability, and led to the development of the Hierarchical Response Framework (HRF) hypothesis (Fig. 6; **Smith** et al. 2009). Collins et al. (2012) and Knapp et al. (2012a found that plant community composition was relatively stable in the ITE over 20 yrs of irrigation. A notable exception was increased cover of the C₄ grass Panicum virgatum after 10 yrs, accompanied by a doubling of the ANPP response to irrigation (Knapp et al. 2012a). Both the observed lag period with modest ecosystem responses prior to community reordering, and the dramatic stepped increase in ecosystem function (i.e., ANPP) coincident with community change are key HRF predictions for ecosystems experiencing chronic resource alterations.

We also investigated responses to forecasts of an intensified hydrological cycle (larger storms, more extreme droughts; Mearns *et al.* 1990) within years as well as over decades. Since 1998, the RaMPs experiment has altered growing season rainfall patterns consistent with forecasts by increasing rainfall event size, reducing event number and increasing the length of dry intervals (by 50%) with no change in total rainfall relative to controls. A warming treatment is nested within rainfall treatments, but the effects of increased precipitation variability (*e.g.*, decreased photosynthesis, soil respiration, and ANPP) dominate responses (Fay *et al.* 2011). A related cross-site experiment altered precipitation event size and number in shortgrass steppe, mixed grass prairie, and at KNZ, and revealed that ANPP responses to increased

precipitation variability are contingent on mean annual precipitation, with ANPP in mesic sites decreasing and ANPP in semi-arid grasslands increasing (**Heisler-White** *et al.* **2009**). These results provided a test of a predictive framework for how extreme precipitation regimes alter soil water dynamics and ecosystem processes across a range of ecosystems (Knapp *et al.* 2008a). Other studies in the RaMPs yielded insights into mechanisms that alter soil C cycling and plant community responses. **Zeglin** *et al.* (2013) found that the drier soil conditions characteristic of a more variable precipitation regime altered soil microbial structure and physiology, and promoted traits (*e.g.*, microbial carbon use efficiency) that may decrease soil C loss and increase C sequestration. Avolio *et al.* (2013) found that more variable precipitation reduced genetic diversity of a dominant grass. Remaining genotypes were more distinct from one another, suggesting that genotypic sorting under a more variable climate results in niche differentiation and diversifying selection acting on key traits (**Avolio & Smith 2013**).

Stream responses. Climate change is predicted to increase floods and droughts, with impacts on stream ecosystems. KNZ experiments documented interactive effects of climate-driven disturbance (floods, droughts) and stream consumers on recovery of primary production and community assembly in prairie stream ecosystems (Gido et al. 2010). These studies are unique in that they established how food web diversity alters trajectories of ecosystem rates and structure following disturbances (**Murdock et al. 2010**). Grassland stream communities are dominated by grazing fish and crayfish that can delay the recovery of primary producer biomass and production following flood or drought (Bengston et al. 2008, Bertrand et al. 2009). These altered trajectories are likely to increase in importance as disturbances become more frequent. However, consumer communities have high spatial and temporal variability in biomass and species composition (Bertrand et al. 2013, Martin et al. 2013), making their influence on the trajectory of stream ecosystem change heterogeneous in space and time.

- (iv) Mechanisms driving plant dynamics: Plant recruitment in mesic grasslands derives primarily from below-ground buds (vegetative meristems) rather than from seed. Bud banks drive plant population dynamics (Dalgleish & Hartnett 2009, Ott & Hartnett 2011, 2012a) and may reduce invasibility (Sprinkle 2011, West 2012). Bud banks can mediate effects of herbivores, nutrient availability, and fire on plant populations (Dalgleish & Hartnett 2009), and bud banks reserves confer resilience to herbivory and fire (N'Guessan & Hartnett 2011). Bud banks can influence woody plant expansion (VanderWeide & Hartnett 2011). Our studies showed that differences in life history patterns and bud bank dynamics between C₃ and C₄ grasses can predict plant community responses to environmental change, and that bud dormancy and higher order bud production contribute to the high resilience of many perennial grasses (Ott & Hartnett 2011, 2012a, 2012b, VanderWeide 2013). We tested hypothesized controls on bud development and tillering, showing that light and N are key regulators of bud dormancy, outgrowth and tiller development in grasses, but that these controls differ significantly for C₃ and C₄ species (Williamson et al. 2012). Comparative studies with African grasses also showed that inter-specific differences in bud bank size and allocation to seed vs. vegetative reproduction may drive temporal dynamics of species composition and diversity (Dalgleish et al. 2012). Mycorrhizal symbioses also affect plant population dynamics, competition, species diversity, and responses to fire and grazing (Hartnett & Wilson 2002, Kula et al. 2005). Reinhart et al. (2012) used KNZ data on 95 plant species to demonstrate that mycorrhizal responsiveness and root colonization vary with phylogeny. Wilson et al. (2012) found that invasive grasses reduce mycorrhizal colonization and production of native prairie grasses, and McCain et al. (2011) showed that mycorrhizal symbioses may contribute to limited plant diversity in grassland restorations.
- (v) Biogeochemistry: Soil, microbial and consumer response to altered drivers. Climate changes and increased atmospheric N loading interact with fire and grazing to drive biogeochemical responses and feedbacks on KNZ. Soil N availability mediates grassland response to these drivers (Blair 1997, Collins et al. 1998, Johnson & Matchett 2001). The Belowground Plot Experiment (est.1986) showed that annual burning significantly increased soil C:N ratio and in situ CO₂ efflux, while decreasing ammonification and nitrification rates (Carson 2013), reflecting lower soil N availability with annual burning. Chronic N addition (10 g N m⁻² y⁻¹) reduced soil C:N ratio, microbial biomass, and potential C mineralization while increasing total soil N and nitrification and ammonification rates. N addition also altered microbial communities, by increasing bacterial biomass and reducing fungal biomass (Carson 2013). Coolon et al. (2013) used pyrosequencing to show that bacterial community structure varied with N enrichment, but not

P enrichment or fire. Chronic N enrichment significantly lowered bacterial diversity. **Wilson et al.** (2009) combined data on arbuscular mycorrhizal fungi (AMF), soil aggregate stability and soil chemistry from the Belowground Plot Experiment and other KNZ experiments to demonstrate that frequent fire and enhanced N-availability increase AMF abundance, glomalin-related soil proteins, and altered soil aggregate structure in ways that promote soil C and N sequestration. Collectively, these studies show that greater N availability alters soil N and C pools, microbial community structure, and microbially-mediated soil C and N transformations, with potential impacts on long-term C and N cycling and storage.

Ecosystem C flux. Eddy flux data were used to scale leaf-to-watershed C fluxes (Nippert et al. 2011), and to assess climate effects on growing season C flux (Petrie et al. 2012). We also addressed biogeochemical changes in ground and surface water. Shallow groundwater [CO₂] varies on an annual cycle and with precipitation events (Tsypin & Macpherson 2012), but also exhibited a directional increase of 20% from 1991-2005, much greater than the 7% increase in atmospheric [CO₂] over that period (Macpherson et al. 2008). Groundwater acidification and increased weathering is occurring as a result (Macpherson 2009). The impact of altered groundwater [CO₂] on the global C cycle will increase if the trend is widespread, because groundwater extraction and use releases CO₂ back to the atmosphere (**Macpherson 2009**). We observed substantial effluxes of CO₂ from headwater streams (~5-8 kg CO₂ m⁻² day⁻¹) on KNZ.

(vi) Restoration Ecology: KNZ restoration experiments inform conservation and test ecological theory. One experiment (est. 1998) is a long-term test of the 'environmental heterogeneity hypothesis' (Huston 1979). Variation in N availability influences dominance, diversity, and similarity of restored plant communities to native prairie (Baer *et al.* 2003, 2004, 2005). Mycorrhizae also contributed to dominance of grasses in restored prairie, and experimentally reducing abundance of the dominant grasses increased plant richness (McCain *et al.* 2010, 2011). Long-term data on plant and soil C and N pools and fluxes were used to test for the presence of positive feedback of soil N availability on plant productivity and subsequent N cycling rates in communities assembling under varying levels of N availability (Baer & Blair 2008). We found that plant-soil feedbacks under the non-steady state conditions of restored prairie differ from theoretical expectations. Positive feedback between enhanced soil N supply and plant productivity occurred, and may override progressive N limitation as C accrues in restored prairie. However, reduced N availability did not feed back to reduce ANPP, likely due to variable NUE of the dominant grasses and changes in plant functional group composition. Changes in plant communities and mechanisms underlying C and N dynamics in this experiment will continue during LTER VII.

We also investigated how genotypic structure (local vs. non-local seeds) and seed diversity affect community and ecosystem recovery (Carter & Blair 2012a, 2012b; Gibson *et al.* 2012, 2013; Baer *et al.* 2013, Klopf *et al.* 2013). Grassland restorations often use grass cultivars selected for seed productivity and viability, vigorous growth, etc. A multi-site, multi-year study of cultivars and local ecotypes revealed no differences in structure and function of restored prairie (Gibson *et al.* 2012, 2013; Baer *et al.* 2013). Klopf *et al.* (2013) further demonstrated that diversity of seed sources has a greater effect on community structure than the use of grass cultivars. Carter & Blair (2013) reciprocally seeded multi-species assemblages sourced from prairies along a north-south gradient into common gardens along the same gradient, and found no 'home site advantage' on performance of selected prairie species. However, another reciprocal common garden study along a longitudinal gradient provided evidence for local adaption in prairie restored under highly mesic conditions (Goad 2012, Mendola 2013).

(vii) Supplemental funding: NSF provided \$120K for the KNZ Schoolyard LTER program and \$62K to support 8 REU students. International supplements (2 totaling \$30K) supported collaborations of KNZ scientists and students with counterparts in South America and Africa. Equipment supplements (\$50K) were used to upgrade sensors and dataloggers, and modernize a stream gauging network. Social science supplements (\$38K) supported participation in the cross-site Maps And LocalS (MALS) project, which identified patterns and anthropogenic drivers of landscape change at 11 LTER sites (York *et al.* 2011). Supplements for Information Management (IM) (\$185K) were used to upgrade infrastructure and support undergraduate and graduate student programmers. IM activities focused on updating KNZ data and metadata to newer EML standards and formats to ensure the accurate and timely harvest of KNZ data and metadata into the LTER Network Information System (see *Information Management* for details).

- (viii) Broader impacts: *Education* KNZ provided support for >56 graduate students from KSU and 11 other institutions, 8 REU students, and facilitated student activities in the KSU site REU site and Undergraduate Research Mentoring programs. The KNZ Schoolyard LTER program engaged > 1000 students yr¹ in realistic and relevant site-based science activities. *International activities* KNZ supported collaborations with U Botswana (N'Guessan & Hartnett 2011, Dalgleish *et al.* 2012, Hartnett *et al.* 2012, 2013), U Pietermarizburg/South African National Parks (Buis *et al.* 2009, Knapp *et al.* 2012b, Koerner *et al.* 2014), and with both the South Africa and Botswana ILTER networks. We developed a KSU study-abroad course on African savannas (18 students to date), supported graduate field experiences in southern Africa (10 students to date), and hosted two international symposia. We supported reciprocal visits of KNZ scientists with Aarhus U (Denmark) (Riis *et al.* 2012), an avian conservation group in Uruguay, and grassland scientists in China. *Conservation and management* KNZ research was communicated through KS Extension and regional NGOs to inform land management and conservation practitioners and policy makers on improved grazing and fire management, conservation of grasslands, improved burning and air quality issues, and grassland restoration. In 2013, KSU and the National Wildlife Federation jointly hosted the 2nd America's Grasslands Conference, attended by >200 participants.
- (ix) Synthesis, cross-site and LTER network-level activities: Cross-site and synthetic *BioScience* articles explored unexpected insights provided by LTER data (Dodds *et al.* 2012) and the value of long-term experiments (Knapp *et al.* 2012c). KNZ contributed to multi-site syntheses of plant responses to precipitation variability (Cleland *et al.* 2013), N enrichment (Cleland *et al.* 2011, Gough *et al.* 2012), and climate change impacts on soil N cycling (Brzostek *et al.* 2012). KNZ scientists participated in syntheses of woody plant expansion (Barger *et al.* 2011, Ratajczak *et al.* 2012), and in LINX II cross-site studies of stream function (Bernot *et al.* 2010, Beaulieu *et al.* 2011). KNZ scientists led and participated in numerous Network-level activities and working groups (Climate Change, Experiments within the LTER Network, EcoSeRE and others). Blair chaired the 2011 Science Council Planning Committee, presented at the 2011 NSF Mini-Symposium, and served on the LTER Executive Board (2011-2014). Knapp chaired the publications committee, Briggs served on the Network Information System Advisory Committee and Communication Committee, and Hartnett served on the US ILTER committee.

Table 1. KNZ LTER VI publications selected to highlight research breadth. *graduate student author

- 1. Avolio*, M.L. and M.D. Smith. 2013. Mechanisms of selection: Phenotypic differences among genotypes explain patterns of selection in a dominant species. **Ecology** 94: 953-965.
- 2. Baer, S.G. and J.M. Blair. 2008. Grassland establishment under varying resource availability: A test of positive and negative feedback. **Ecology** 89: 1859-1871.
- 3. Heisler-White*, J.L., J.M. Blair, E.F. Kelly, K. Harmoney, and A.K. Knapp. 2009. Contingent productivity responses to more extreme rainfall regimes across a grassland biome. **Global Change Biology** 15: 2894-2904.
- 4. Joern, A. and A. Laws. 2013. Ecological mechanisms underlying arthropod species diversity in grasslands. **Annual Review of Entomology** 58: 19-36.
- 5. Macpherson, G.L. 2009. CO₂ distribution in groundwater and the impact of groundwater extraction on the global C cycle. **Chemical Geology** 264: 328-336.
- 6. Murdock*, J.M., K.B. Gido, W.K. Dodds, K.N. Bertrand* and M.R. Whiles. 2010. Consumer return chronology alters recovery trajectory of stream ecosystem structure and function following drought. **Ecology** 91: 1048-1062.
- 7. Ratajczak*, Z., J.B. Nippert and T.W. Ocheltree*. 2014. Abrupt transition of mesic grassland to shrubland: evidence for thresholds, alternative attractors, and regime shifts. **Ecology** dx.doi.org/10.1890/13-1369.1
- 8. Smith, M.D., A.K. Knapp, and S.L. Collins. 2009. A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. **Ecology** 90: 3279-3289.
- 9. Wilson, G.W.T., C.W. Rice, M.C. Rillig, A. Springer, and D.C. Hartnett. 2009. Soil aggregation and carbon sequestration are tightly correlated with the abundance of arbuscular mycorrhizal fungi: results from long-term field experiments. **Ecology Letters** 12: 452-461.
- 10. Zeglin, L.H., P.J. Bottomley, A. Jumpponen, C.W. Rice, M. Arango*, A. Lindsley, A. McGowan*, P. Mfombep*, and D.D. Myrold. 2013. Altered precipitation regime affects the function and composition of soil microbial communities on multiple time scales. **Ecology** 94: 2334-2345.

C. NEW AND CONTINUING RESEARCH FOR LTER VII. Our conceptual framework (Fig. 2) reflects development of the KNZ program over time, and explicitly recognizes that the key drivers of ecological processes in grasslands are directly (land use and management) and indirectly (climate change and nutrient inputs) altered by human activities. Our goal in LTER VII is to understand the dynamics and trajectories of responses to global change, with new studies to evaluate mechanisms of sensitivity and resilience of grasslands. The temporal extent of KNZ data provides great value for assessing the dynamics of ecosystem responses to global change and relationships to ecological theory. Multi-decadal research coupled with new initiatives analyzing sensitivity and resilience of ecological patterns and processes will enable us to better understand long-term rates and trajectories of change, including non-linear dynamics, thresholds, and the role of ecological legacies. KNZ LTER VII research will advance fundamental ecological knowledge, and provide a more comprehensive and predictive understanding of the consequences of global change in grassland ecosystems.

Grasslands are ideal for developing and testing of ecological theory. KNZ data have been used to test hypotheses relating species richness and ecosystem function (Baer *et al.* 2003, Adler *et al.* 2011), plant traits as modulators of response to altered resources or disturbance regimes (Hartnett & Wilson 2002, Dalgleish & Hartnett 2006, Tucker *et al.* 2011), plant-soil feedbacks (Baer & Blair 2008, Nippert *et al.* 2012), mechanisms of grasslands sensitivity to climate variability (Knapp *et al.* 2008, Nippert *et al.* 2011, Hallett *et al.* 2014), effects of N saturation on stream N transport (Mulholland *et al.* 2008), and effects of intraspecific variation on community assembly (Carter & Blair 2012a, Klopf *et al.* 2013). KNZ studies contributed to development of a novel theoretical framework describing hierarchical ecological responses to chronic changes in resource availability (Smith *et al.* 2009), and were used to test for the presence of bistability and alternate attractors in the transition from grasslands to shrublands (Ratajczak *et al.* 2014).

Grasslands are also subject to a wide array of global change drivers, which can create novel conditions with no historical analog (Williams & Jackson 2007). Predicting ecological responses under novel conditions requires mechanistic understanding of system behaviors, including sensitivity and resilience. Grasslands can serve as tractable model systems for assessing the impacts of many global changes, including responses to chronic N enrichment (Baer & Blair 2008, Coolon *et al.* 2013), climate change (Hartman & Nippert 2013, Brunsell *et al.* 2014, Hoover *et al.* 2014), and altered land use and land cover (Dodds & Oakes 2008, Ratajczak *et al.* 2011). The sensitivity and responsiveness, modest generation times of key organisms, and relative ease of manipulative experiments in grasslands makes them attractive experimental systems. As a result, KNZ studies continue to provide important mechanistic and predictive insights into ecological responses of grasslands to a changing world (Fay *et al.* 2011, Dodds *et al.* 2012). This information is increasing important for conserving and restoring grassland ecosystems.

KNZ LTER VII research is organized in 4 thematic areas related to major global change drivers in grasslands to foster integration across disciplines, biological levels of organization, and temporal and spatial scales of study: (1) <u>LAND-USE AND LAND-COVER CHANGE</u>, including (a) impacts of changing firegrazing regimes and (b) patterns, causes, and consequences of grassland-shrubland/woodland transition; (2) <u>CLIMATIC VARIABILITY AND CLIMATE CHANGE</u>; (3) <u>ALTERED BIOGEOCHEMICAL CYCLES</u>; and (4) <u>RESTORATION ECOLOGY</u>. Activities within these research themes are coordinated within and across research groups (see *Project Management*), and include datasets encompassing the original five LTER core areas as well as specific research foci outlined in this proposal. Although we present research activities in these thematic areas separately, many linkages exist among research groups, and short-term and plot-level experiments are integrated with core KNZ experiments and long-term data. This facilitates synthesis among research groups and allows results from one thematic area to support others.

C1a. LAND-USE AND LAND-COVER CHANGE: FIRE AND GRAZING. Fire and grazing studies contribute data in multiple core LTER areas, including primary productivity, nutrient cycling, population and community dynamics, and disturbance. Plants, microbes and consumers in tallgrass prairie track a shifting landscape of habitat and resources initiated by fire-grazing interactions and variability in precipitation (Knapp *et al.* 1999, Plumb *et al.* 2009, Augustine 2010, Allred *et al.* 2011a,b, McNew *et al.* 2013). Thus, it is essential to understand the mechanisms that generate and maintain heterogeneity, and how heterogeneity affects species' responses and influences community and ecosystem resilience.

Spatio-temporal heterogeneity in soils, habitat characteristics, resource availability and environmental conditions at the landscape level underlie many hypotheses on the origin and maintenance of species diversity and distributions (Augustine & Frank 2001, Winnie et al. 2008, Joern & Laws 2013, Xi et al. 2014). Large grazers, including bison and cattle, preferentially use recently burned patches (Allred et al. 2011a,b, Augustine & Derner 2014), reducing plant biomass and altering vegetation structure, which in turn affects fuel loads and future fire return intervals. We hypothesize that the differential responses of species to the shifting mosaic of habitat resulting from fire-grazing interactions promote diversity across the landscape. This spatial 'heterogeneity-diversity hypothesis' has significant implications for understanding population and community dynamics (Amarasekare 2003, Chesson et al. 2004, Seabloom et al. 2005, Armstrong et al. 2010) and for management and conservation (Fuhlendorf & Engle 2004). In LTER VII, we will evaluate the consequences of spatial and temporal heterogeneity for: (1) generation and maintenance of plant and consumer diversity in response to fire-grazing-generated patch mosaics, and (2) relationships between landscape heterogeneity, plant nutritional quality, and grazer distributions. Questions about habitat heterogeneity, disturbance and connectivity in aquatic systems (section C2) parallel this theme. Related fire and grazing studies in LTER VII will assess (3) demographic processes driving grassland responses, (4) rates and trajectories of community changes, and (5) food web dynamics.

We will extend long-term studies of fire and grazing on plant species composition (Collins & Calabrese 2012), reproductive effort (La Pierre *et al.* 2011), bud bank dynamics (Dalgleish & Hartnett 2009, Ott & Hartnett 2012a, b), and consumer populations (Jonas & Joern 2007). New research will assess effects of fire and grazing on species interactions and communities at multiple scales, and test current theories on community structure and the contributions of biotic interactions. We will address: (a) whether the 'heterogeneity-biodiversity hypothesis' explains consumer diversity and its distribution in tallgrass prairie; (b) whether self-reinforcing feedback mechanisms constrain reversibility of community and ecosystem trajectories to altered fire-grazing regimes, and if so which variables are irreversible; and (c) whether bud banks constitute a storage effect (Warner & Chesson 1985, Chesson 2000) that increases vegetation resilience to environmental change. Our research will assess rates and trajectories of change, and relate these to mechanisms and ecosystem processes as outlined in the next 3 sections.

- 1. Core Long-Term Studies: Consumer responses to fire/grazing and spatio-temporal heterogeneity. KNZ long-term studies focus on grasshoppers, fish, birds and small mammals – important grassland consumers that differ in trophic level, size, metabolic capabilities, habitat, and vagility. We will continue long-term measurements of these groups to assess directional changes and spatial heterogeneity in key resources and habitat structure that influence consumer dynamics under different fire-grazing treatments. Long-term KNZ data reveal strong species-specific consumer responses to changing fire, grazing and weather or habitat disturbance (Powell 2006, Jonas & Joern 2007, Reed et al. 2007), and indicate the need for new mechanistic studies to link organism responses to spatial and temporal heterogeneity and to better incorporate trophic interactions. These studies will enable better predictions of consumer responses to future environmental change or to feedbacks resulting from consumption across trophic levels or combinations of trophic functional groups. Another effect of consumer responses fire/grazing heterogeneity is related to spatial distribution of grazers. Activities of large grazers influence hydrology, geomorphology and terrestrial/aquatic linkages. Bison have modest effects on sediment and nutrient levels in stream channels (Kemp and Dodds 2001, Larson et al. 2013a) but do influence stream invertebrates locally (Fritz and Dodds 1999). In contrast, preliminary KNZ results indicate much greater influence of cattle on stream geomorphology and water quality in tallgrass prairie. We will continue to monitor water quality and survey stream geomorphology in bison grazed and ungrazed watersheds to assess the influence of native grazers on aquatic-terrestrial linkages.
- 2. Continuing Studies Initiated in LTER VI: (a) Landscape heterogeneity, nutritional quality, and bison distributions Ungulate grazing in response to fire creates heterogeneity that influences future grazing patterns and other grassland processes across multiple scales (Hobbs 1996, Laca et al. 2010, Collins & Calabrese 2012,). Grazers make foraging decisions within a nutritionally heterogeneous landscape (Senft et al. 1987, Wilmshurst et al. 1999, Drescher et al. 2006, Verweij et al. 2006, van Langevelde et al. 2008, Winnie et al 2008, Courant & Fortin 2012). We will expand an ongoing study using GIS technology and field surveys to document spatial patterns of bison distributions and grazing

activity with respect to forage quality, habitat heterogeneity, water availability, and plant community sensitivity and resilience to grazing. Ten bison will be fitted with GPS collars each year, and data will be used to analyze spatial variation in distribution and grazing intensity at multiple scales (Sasaki et al. 2008). Resource selection functions and logistic regression models (Boyce et al. 2002) will be used to determine effects of time since fire and other potentially important environmental factors (e.g., plant nutritional quality, topography, past grazing use, etc.). We will use spatial patterns of bison distribution and grazing intensity to inform studies of plant community sensitivity to grazing. Predictive spatial models of plant biomass and forage quality across the landscape will be developed for KNZ using remotely-sensed data (Fig. 8; Ling 2013). Protein content will be estimated

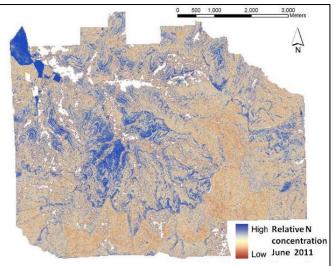


Fig. 8. Spatial distribution of plant N concentrations on KNZ derived from hyperspectral imaging in June, 2011. Cooler colors are higher plant tissue [N]. Note high [N] in recently burned bison (center) and cattle (far right) units, as well as in agricultural fields (upper left).

from hyperspectral data on [N] using models developed by Ling (2013). We will expand studies on how fire-induced heterogeneity in forage quality and vegetation structure influences grazer foraging decisions, using broadband and hyperspectral remote sensing vegetation indices and GIS data on bison activities.

Patch Burn Grazing (PBG) Experiment – We will continue the long-term rotational PBG experiment initiated in 2010 to determine how spatio-temporal dynamics of fire-grazing interactions create heterogeneity in a managed grassland context, and to assess resulting consumer responses. This experiment includes two large replicate cattle grazing units, each encompassing a mosaic of three watersheds (patches) subject to asynchronous fire regimes (Fig. 3). Each PBG unit is comprised of three watersheds equally accessible to cattle (no cross fencing), with one watershed burned each year in a 3-yr rotation. In any year, each unit includes patches at 0, 1 and 2 yrs since fire. These units are stocked at a moderate density (4 ha animal⁻¹) comparable to the bison units. Like bison, cattle preferentially use recently burned areas, resulting in a shifting mosaic of grazing intensities. Each PBG unit is paired with a more uniform annually-burned cattle-grazed unit (traditional cattle management) for comparison. We will test the hypothesis that a shifting habitat mosaic in the PBG units will modulate population and community responses and increase plant and consumer diversity at the unit level, while community composition among component watersheds will change more rapidly due to species-specific habitat requirements. Plant species composition, ANPP, soil nutrients, and consumer responses (i.e., arthropods, small mammals, birds) will be measured using standard KNZ protocols. Distance sampling methods and Program Mark (Sandercock 2006) will be used to evaluate vertebrate abundance and demographic data, and cattle weight gains and body condition will be measured. Species diversity in each landscape type will be quantified with species/area accumulation and species diversity (H') curves; spatial heterogeneity will be assessed using estimates of variation (e.g., CV) in responses along transects. Quantitative similarity indices will be calculated, and mean dissimilarity among watersheds will be used as an index of beta diversity. Ordination will be used to assess patterns of diversity and community similarity among patches and landscape types for all organismal groups, and to extend a recent analysis of the scale dependency of fire and grazing effects on community heterogeneity (Collins & Smith 2006). We will also continue to assess effects on stream geomorphology and water quality responses (dissolved organic C, total N and P, and sediment export) by comparing streams draining PBG landscape units to comparable streams draining bison-grazed areas. Detailed geomorphological surveys of stream channels will document changes in patch burn, ungrazed and bison grazed watersheds.

3. New Questions/ Experiments/ Measurements/ for LTER VII: Alternate vegetation states in response to bison grazing – Grazing lawns are patches of low-stature vegetation of high nutritional quality that support heavy grazing, potentially maintained by positive feedbacks between herbivory and soil nutrient status (Archibald 2008, Cromsight & Olff 2008). These lawns represent a putative multi-trophic alternate stable state to tall-canopy ungrazed or lightly grazed grassland. A central question we aim to answer is whether these patches/states require a consistent "press" (bison activity) to persist, or do they become selfsustaining due to internal feedbacks? If so, what feedback mechanisms are involved (e.g., reduced fire, repeated activity of grazers, soil feedbacks)? Important effects of repeated grazing on lawns may include: (a) shifting plant architecture and species composition, (b) maintaining forage in a continually "young" high nutrient state, (c) altering soil nutrient concentrations, and (d) depleting bud banks over time. We hypothesize that all, or a combination of these may affect reversibility to the tallgrass state after cessation of grazing. Changes in foliar quality also can influence the use of grazing lawns by other herbivores, possibly further affecting plant species composition. We will test hypotheses on grazing lawns as alternate stable states and the nature of feedbacks that may maintain them. A state-transition model of patch selection by bison with respect to feedbacks between fire-grazing interactions and patch reuse in time and space will also be developed and parameterized to understand the transition to, maintenance, and significance of grazing lawns in time and space (Winnie et al. 2008). To test this, we propose to "prime" lawns using a fully factorial combination of mowing and fertilization (each with two levels: + and -). We will also establish exclosures (some full growing-season, some half season) on 16 existing lawns to examine resilience and reversibility, and quantify putative positive feedback mechanisms and assess potential thresholds (Hughes et al. 2012). Comparisons of vegetation, microbial and soil processes on and off lawns will help identify state variables and mechanisms. Experiments on grazing lawn initiation (including mowing replicate plots frequently after green-up, with and without addition of NPK fertilizer) will be performed near existing lawns to measure new grazing lawn establishment in response to plant height and soil nutrient addition. Plant species composition, grass demography, architecture and bud bank densities will be measured on and off grazing lawns. Potential belowground mechanisms to be evaluated include mycorrhizal colonization, fungal and bacterial abundance (PLFA), and N mineralization. This will enable us to examine relationships between grazing intensity and plant community responses with respect to fire-grazing-soil nutrient interactions, and to identify linear or non-linear responses. This experiment will increase our understanding of the role of plant-herbivore interactions on grassland dynamics, and inform management and conservation by identifying critical thresholds of change.

Effects of non-ungulate herbivores – Invertebrate (Coupe & Cahill 2003, Schadler et al. 2008, Blue et al. 2011, Allan & Crawley 2011) and non-ungulate vertebrate herbivores (Edwards & Crawley 1999, Howe et al. 2002, Bakker et al. 2006) can have strong effects in grasslands, with insect herbivore outbreaks capable of causing state-dependent shifts in plant communities (Karlsen et al. 2013). However, feedbacks from small herbivores on plant community composition and ANPP are poorly understood. We will examine the relative impacts of different herbivore groups to assess the importance of these potential of these groups in top-down control of grassland structure and function. A recent 5-yr KNZ experiment indicates that insects increase forb diversity, but depress forb biomass and responses to nutrient addition (La Pierre 2013). To date, small vertebrate removals have not affected plant species composition or ANPP. However, the responses and relative strengths of different herbivore groups at KNZ remain largely uncharacterized with respect to fire-grazing interactions, topography or climate.

Nutrient availability alters plant quality and species composition, and can affect invertebrate herbivore abundances, trophic structure, and behavior (Joern & Mole 2005, Cleland *et al.* 2004, Hartley & Jones 2004, Jonas & Joern 2008, Blue *et al.* 2011). Manipulating plant stoichiometry increased grasshopper herbivory on plots fertilized with N, but not P (Loaiza *et al.* 2011), consistent with predictions based on grasshopper feeding trials (Jonas & Joern 2008, 2013, Joern *et al.* 2012). We will expand an experiment begun in 2009 to assess long-term impacts of small mammal and insect herbivory on plant communities and ANPP at low and high soil nutrient levels crossed with fire frequency. Small vertebrate herbivores will be eliminated with fine mesh skirts (open-plot control) crossed with insecticide applied twice monthly during the growing season to reduce insect herbivory (water-only control). Herbivore removal will be crossed with NPK addition using 2m x 2m plots arranged in a full factorial experimental design. Three

blocks of each treatment combination will be established in each watershed burned at different intervals (1, 2, 4 y). Plant species composition, biomass and estimates of foliar herbivory will be measured in August using standardized KNZ sampling methods. Insect removals will also be conducted in a restoration experiment (*see Section C4*) to assess top-down effects on assembling communities.

Demographic processes of plant responses to changing fire/grazing regimes: the role of bud banks — KNZ plant population studies seek to link organismic through ecosystem-level phenomena, and elucidate mechanisms underlying plant community and ecosystem responses to environmental change. Belowground bud banks and meristem limitation drive perennial grass population dynamics across heterogeneous landscapes and grassland ecosystems (Knapp & Smith 2001, Dalgleish et al. 2008, Dalgleish & Hartnett 2009, Ott 2009, Ott & Hartnett 2011, 2012a), and there are strong differences in patterns and controls of bud bank dynamics in C₃ and C₄ species (Ott & Hartnett 2011, 2012a, 2012b, Williamson et al. 2012). We hypothesize that these differences drive differential sensitivity or population stability of perennial grasses, and can aid in predicting grassland plant community dynamics and responses to environmental change. For example, reduced bud bank densities under grazing may reduce the 'storage effect' and vegetation resilience to drought. We will develop demographic models for perennial grasses (C_3 and C_4 species) and forbs to test the meristem storage effect hypothesis and improve predictions of shifts in relative abundance of plant functional groups with environmental change. Resource storage (e.g., rhizome biomass) also provides a mechanism for restoring grassland vegetation structure and function following disturbance. We hypothesize that long-term fire and grazing treatments will create legacy effects by altering bud bank size and resource storage to affect resilience of tallgrass prairie to environmental change. Feedback effects (e.g., grazing-induced changes in plant architecture that reduce defoliation intensities) and thresholds (e.g., effects of disturbance intensity or extent on recruitment) may create and maintain patches in different states (e.g., grazing lawn vs. tall canopy or low vs. high diversity patches), influencing heterogeneity at the landscape scale. Since rhizome biomass is an excellent predictor of bud bank size (VanderWeide 2013), we will measure grass and forb rhizome biomass (g m⁻²) at 3-yr intervals across selected fire x grazing treatments as a proxy for bud bank density and an estimate of belowground resource storage. Variation in grass, forb, and total rhizome biomass among treatments will be analyzed and relationships between rhizome biomass and resistance of ANPP and plant species composition to change (from co-located LTER transects) will be examined via regression models.

Trajectories of plant community change – We will use the long-term plant species composition data to calculate species and patch type replacement probabilities under various fire x grazing regimes over the past 30 yrs. Coupled with ongoing measurements during LTER VII, data from this new analysis will be used to populate species and patch-type transition and sensitivity matrices to predict future patterns and trajectories of plant community change, and identify potential leading indicators of imminent change in system trajectories or dynamics. Assessing the relationship between bud bank density and rhizome storage and the rates and trajectories of community change under alternate disturbance regimes will also provide tests of our hypothesis that these belowground traits confer a demographic buffering capacity, increasing vegetation resilience to environmental change. These proposed studies will build upon studies testing the influence of other belowground mechanisms driving aboveground dynamics in tallgrass prairie (Hartnett & Wilson 2002, Nippert and Knapp 2007a,b, Wilson et. al. 2009, Hartnett et al. 2013).

Food web studies and network analyses – We propose new studies on arthropod food web properties in response to fire-grazing interactions using an interaction network analysis (Pascual & Dunne 2006). This conceptual framework for understanding trophic structure responses to heterogeneity in grassland addresses current ecological and complex systems theory and underscores the importance of species interactions. We will characterize networks at KNZ to assess the role of compartmentalization and nestedness (Thebault & Fontaine 2010) for system persistence and resilience. Theory predicts that compartmentalization is the most important structural property stabilizing trophic networks and may result from a variety of sources, including body size (Gotelli & Ellison 2002), habitat (Pimm & Lawton 1980), top predators (Rezende *et al.* 2009), phylogenetic constraints (Cattin *et al.* 2004), and coevolution (Thompson 2006). Compartments in trophic webs may lead to stability through reduced connectivity that diminishes the spread of perturbations. Nestedness is most important in stabilizing mutualistic networks. Food web structure will be compared among watersheds with different fire (1, 2, 4, 20 yrs) - grazing (+/-)

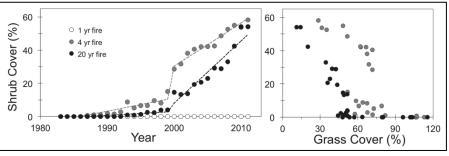
combinations. These studies will complement and extend recent KNZ field experiments assessing trophic cascades and indirect interactions in plant-grasshopper-spider food webs under different nutrient and temperature conditions (Laws & Joern 2012a). The structure of empirical networks will be evaluated using statistical methods described by Almeida-Neto *et al.* (2008), Thebault & Fontaine (2010), and Zhang *et al.* (2011). Pollinator-plant and trophic food web relationships will be determined by quantitative sampling of watersheds over a range of fire-grazing treatments using standard sampling protocols (replicated sweeping, bee bowls, transect counts, standardized observation, and DNA bar-coding to link herbivore diets with plants). Network analyses will use computational methods of Bascompte *et al.* (2003), Joppa *et al.* (2010), Almeida-Neto *et al.* (2008), and Zhang *et al.* (2011). For mutualistic networks, we hypothesize increased heterogeneity resulting from fire x grazing interactions will increase species richness and compartmentalization (decreased nestedness). Understanding the causes of stability of mutualistic networks is increasingly important as pollinators are declining globally (Burke *et al.* 2013).

We will use model networks constructed from KNZ data to test the following hypotheses: (a) Nested communities are more robust than randomly-assembled networks to habitat loss and local extinction (Fortuna & Bascompte 2006, Memmot *et al.* 2004); (b) Phylogenetic relationships limit interactions of pollinators or insect herbivores resulting in non-random network structure (Rezende *et al.* 2007); (c) The asymmetry of specialist and generalist species will allow rare species to persist because the species they interact with are maintained by generalists (Jordano 1987) and will be sensitive to the removal of the most connected species (Sole & Montoya 2001); (d) Functionality of links has a larger effect than the number of links on a network's stability (Allesina *et al.* 2009); and (e) Specialist species are more susceptible to extinction than generalists (Ashworth *et al.* 2004, Kunin 1993).

C1b. LAND-USE AND LAND-COVER CHANGE: WOODY PLANT EXPANSION. Woody plant expansion in tallgrass prairie, including grassland-shrubland/woodland transitions, reflects changing land-use, particularly fire suppression (Briggs *et al.* 2005, Ratajczak *et al.* 2014), and may be exacerbated by climate change (Kulmatiski & Beard 2013) and increasing atmospheric [CO₂] (Higgins & Scheiter 2012). Although increased woody plant cover in prairie due to fire suppression has been long recognized (Gleason 1913), the consequences of more moderate reductions in fire frequency are not well understood, nor is the potential for restoring grasslands after transition to shrub/tree dominance. KNZ long-term datasets provide a synoptic perspective of the transition from grassland to shrubland or woodland, and offer a unique opportunity to identify drivers of this important change, mechanisms affecting sensitivity and resilience to woody plant expansion, ecological consequences, and potential for recovery.

1. Core Long-Term Studies: We will continue to collect and analyze long-term data on species composition and cover of herbaceous and woody vegetation across a range of fire and grazing treatments in a topographically heterogeneous landscape. Relevant KNZ datasets include transect-level plant species composition and cover, ground-based GPS maps of shrubs and trees on core LTER watersheds, historical and current aerial photographs, and remote sensing imagery. These datasets will be used to quantify continuing trajectories and rates of change in cover, frequency, and species composition of woody plants under different fire frequencies, grazing regimes, and in landscape positions that vary in soil depth and water availability. Analyses of these datasets indicate ongoing non-equilibrium dynamics of grasses and trees under all but annual and 2-yr fire frequencies. During LTER VI, we began testing theories based on competition, alternate attractors, positive feedbacks, and the identification of critical thresholds. We identified temporal bimodality of shrub cover and abrupt shifts in shrub cover corresponding with gradual declines in C₄ grass cover (Fig. 9; Ratajczak *et al.* 2014). KNZ woody cover increased non-linearly over 3





decades in watersheds burned at intervals ≥ 4 yrs, with topographic position, fire frequency, and grazing history all affecting rates of change. Increases in shrub cover were abrupt and exhibited positive feedbacks (reduced fuel load and fire intensity, increased shrub survival/growth, greater grass suppression). These changes suggest thresholds between states, and provide mechanistic support for alternate stable states in this system (Ratajczak *et al.* 2011). Using KNZ LTER data, Ratajczak *et al.* (2014) identified thresholds of grassland and shrubland cover on KNZ that precede regime shifts between states, which can be used as a management template to avoid crossing critical thresholds that may be difficult to reverse. We will expand KNZ studies of the sensitivity and resilience of tallgrass prairie to woody encroachment. We expect the sensitivity of state transitions will be highly variable across KNZ fire and grazing treatment legacies and topography (Ratajczak *et al.* 2014). We will combine KNZ data on species composition and tree/shrub distribution with new experiments to identify demographic and physiological mechanisms underlying encroachment (*see below*).

2. New experiments for LTER VII: Shrub responses to altered water availability - Differential use of water resources by depth facilitates grassland-shrubland transitions, but how reduction in growing season rainfall amounts or changes in seasonal distribution will alter transitions is unknown. We will manipulate growing season rainfall and water availability for individual shrub islands to refine our understanding of vertical niche partitioning as a key mechanism promoting clonal shrub expansion, and to link studies of shrub expansion to potential climate change (Section C2). We will implement three rainfall treatments using shelters built over replicate shrub islands (~5m dia.): (1) control (ambient rainfall), (2) 50% growing season reduction to simulate moderate-severe drought, and (3) 50% growing season reduction + 25% non-growing season increase, to simulate a predicted shift in seasonal rainfall distribution and test if this seasonal shift offsets effects of summer drought alone by recharging deep soil water. Rainfall reductions will be implemented using passive shelters that intercept and redirect a fixed percentage of precipitation (Yahdjian & Sala 2002). Water additions will be applied using portable water tanks. Shelters will be erected in lowland locations with a 4-yr burn frequency, with and without bison (n=6/trt and controls). Response variables will be monthly LAI, litter accumulation, clonal stem production, ramet population growth rates, and source-water use (3x per summer via stable isotopic analyses). We hypothesize that alteration of event size and seasonal distribution of rainfall will favor shrub growth over co-occurring C₄ grasses, similar to results observed in savanna (Kulmatiski & Beard 2013).

Plant population studies – We will initiate new studies to identify demographic mechanisms underlying expansion of dominant shrub populations in tallgrass prairie. Field-based studies of growth, reproduction, bud bank dynamics and survivorship of *Cornus drummondii* and *Rhus glabra* and development of size-structured matrix models will aid in predicting rates of expansion and providing insight into population dynamics. We ask: how does seed and vegetative reproduction influence rates and patterns of shrub expansion? Do interspecific differences in bud banks and belowground storage drive differential rates and patterns of expansion among woody species? Do legacy effects of prior management influence species sensitivity or resilience?). Together, these data can identify the relative contribution of complex demography and feedback mechanisms.

Forecasting state change with leading indicators – Theory postulates that dynamical temporal and spatial behavior may predict imminent state transitions (Peters et al. 2004, Hastings & Wysham 2010, Dakos et al. 2012), but this requires further development and testing, especially in terrestrial systems. We will use long-term KNZ plant species data to look for increases in spatial autocorrelations and cross-scale species interactions that precede critical transitions. Preliminary analyses revealed negative cross-correlations between grass and shrub cover that increased in magnitude prior to grassland-shrubland transitions. We will explore this relationship further, and apply these concepts to a wider suite of metrics of ecosystem structure and function. These analyses will test applicability of developing ecological theory (Scheffer et al. 2009, Dakos et al. 2012) and may inform management of woody plant expansion.

Riparian woody plant removals – Woody expansion in tallgrass prairies includes riparian forests along stream corridors (Briggs et al. 2005). Historically, the vegetation of headwater and low order streams in these landscapes was predominantly grassland. Transition to forest alters stream hydrology, energy inputs, communities and biogeochemistry. LTER VI experiments that removed woody plants from 100 m stream segments showed shifts in algal and macroinvertebrate communities (Vandermyde & Whiles 2014) and

altered ecosystem functions (Riley & Dodds 2012, Reisinger et al. 2013). We initiated a wholewatershed tree removal experiment in 2011 to assess the cumulative effects on hydrology, geomorphology, and in-channel energy and nutrient processing using a Before-After Control-Impact design (Stewart-Oaten et al. 1986, 1992). We hypothesize that riparian woody expansion would decrease water yield, alter stream geomorphology, and shift stream and riparian sediment communities. We cut or girdled all trees and shrubs from within 30 m of the main channel and 10 m of side channels along the entire 4.8 km stream systems draining watershed N02B (Fig. 10). We will continue to remove any regrowth biennially coincident with burning, through LTER VII. Responses in water chemistry, stream metabolism, discharge, sediment transport and geomorphology will be measured. Preliminary results of woody removal indicate large pulses of NO₃ (Fig 11) and other nutrients (likely from reduced plant demand), increasd sediment transport, reduced stream roughness and altered hydrology. New analyses will investigate the legacies of tree removal from patterns of seasonal and interannual climate variability. Longterm results may vary from initial responses, as the first few years following woody plant removal were extremely dry, and unexpected results often occur in long-term experiments (Dodds et al. 2012). We will conduct a new study of source-water use by riparian tree species in unmanipulated reference areas using stable isotope analyses (sensu Nippert et al. 2013) to understand effects of woody plants on hydrology. We will compare stream food webs before and after removal with data on stream invertebrates, benthic organic matter, and riparian insect inputs (Stagliano & Whiles 2002, Whiting et al. 2011). We will assess plant communities in removal areas, forested controls, and grassland areas. Differences in soil and stream microbial communities among removal, forested and naturally grass-covered riparian areas will be characterized using molecular and bioinformatic methods (Wang et al. 2007, Schloss et al. 2009, Caporaso et al. 2012).

C2. CLIMATE VARIABILITY AND CLIMATE

CHANGE. Anticipated climate changes, particularly those that alter water availability, will impact ecological processes in tallgrass prairie at multiple



Fig. 10 Watershed N02B before (upper image) and after (lower image) removal of riparian woody vegetation from 4.8 km of stream channel (dashed oval). The middle stream channel was treated, while the ones to the left and right were not. Note the stream bed is visible after removal.

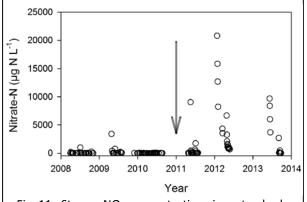


Fig. 11. Stream NO_3 concentrations in watershed NO2B before and after riparian woody removal (arrow). Spikes in NO_3 coincided with increases in other nutrient and sediment concentrations, and did not occur in a control watershed or in the prior 20 years in N20B. Gaps in data represent dry periods without stream flow.

ecological scales across aquatic and terrestrial environments. Predictions for the Central Plains include increased temperatures and temporal variability in rainfall (*i.e.*, larger storms and longer intervening dry periods; Easterling *et al.* 2000, Polley *et al.* 2013), with temporal variability predicted to impact grasslands more than changes in precipitation quantity alone (IPCC 2013). Precipitation variability affects ANPP in grasslands more than in other biomes (Knapp & Smith 2001, Knapp *et al.* 2008a), and floods and drought

have large impacts on streams (Dodds *et al.* 2004). At KNZ, analyses of long-term data have linked natural variation in climate to ecosystem responses (Knapp *et al.* 1998, Nippert *et al.* 2006, La Pierre *et al.* 2011), and current manipulative experiments are revealing how grasslands and streams respond to more extreme climate patterns (Fay *et al.* 2011, Bertrand *et al.* 2013, Zeglin *et al.* 2013, Polley *et al.* 2010).

1. Core Long-Term Studies/Measurements: KNZ core data cover a broad range of climatic conditions over 30+ yrs. The approach of linking long-term climate variability with ecological responses is especially valuable for studying aspects of ecosystem that are not amenable to experimentation - such as whole watershed C flux or ecohydrologic responses to climate variability (Petrie et al. 2012, Nippert et al. 2013). In 2011-12, we experienced a strong drought that led to the longest continuous drying of stream channels since 1988, resulting in extended isolation of upstream pools from downstream flowing reaches. For the first time in 30 yrs, portions of lower Kings Creek were comprised of isolated pools connected only by subsurface flow. This extreme event (sensu Smith 2011) had unexpected consequences: (1) sediment accumulation in pools and riffles, transforming benthic habitat dominated by limestone cobble to one dominated by muddy and silty substrate; (2) channel narrowing in headwater streams via vegetation invasion; (3) woody vegetation colonization of gravel bars formerly void of permanent vegetation; and (4) establishment of emergent macrophytes in downstream channels, which widened and dammed stream riffles, similar to changes in aridland streams upon cessation of grazing (Sponseller & Fisher 2006). We hypothesize that large floods are required to re-set the system. We will: (1) use 15 yr photographic records of gravel bars to quantify in-stream of woody cover, (2) continue geomorphological stream channel surveys initiated during the drought, and (3) continue in-channel surveys of emergent aquatic vegetation and vegetation cover transects on gravel bars. Ongoing monitoring of fishes and stream invertebrates will be used to assess changes in food webs (e.g., shifts toward species dependent upon allochthonous versus autochthonous food sources), which will be linked to data on precipitation, hillslope hydrology, groundwater levels, and stream discharge. A fundamental understanding of watershed hydrologic responses will help predict timing of material and solute export, temporal and spatial fragmentation of biological communities, thermal regimes, the distribution, population and metapopulation dynamics of fishes, and the substrate composition in stream channels. We hypothesize that modest floods will reverse in-channel changes, but that decade-long return time floods will be required to completely change riparian cover to its prior state. This natural experiment is an excellent opportunity to assess the stability of the altered ecological state post-drought, and the resilience of the stream biota to this state change.

The 30+ yrs of data on climate variability and ecosystem responses at KNZ are complemented by long-term climate change experiments, such as the RaMPs (15+ yrs) and the Irrigation Transect Study (20 yrs) (see *Prior Results* and below). These experiments provide new opportunities to combine experimental and observational data to determine if sensitivity of grasslands to climate variability is altered in response to long-term changes in hydroclimatic conditions (Ponce-Campos *et al.* 2013), and to identify potential mechanisms of altered sensitivity. Initially, we will focus on evaluating changes in ANPP-precipitation relationships under: (1) chronically dry conditions (annually burned grassland in shallow-soil uplands; Knapp *et al.* 1993), (2) long-term increased soil moisture variability (RaMPs; Fay *et al.* 2011), and (3) long-term increased soil moisture availability (ITS; Knapp *et al.* 2012a). Analyses to date suggests that sensitivity in ANPP has changed dramatically in the latter experiment (Knapp *et al.* 2012a), consistent with the HRF model (Fig. 6, Smith *et al.* 2009). To test this, we will assess the role of changes in community composition in altering sensitivity. This will improve forecasts of ecosystem responses to future climates, and the sensitivity of ANPP responses to interannual variability in precipitation.

2. New Experiments/ Measurements/ Questions for LTER VII: Climatic changes can broadly be characterized as: (1) directional and chronic (e.g., warming temperatures, regions becoming wetter or dryer), or (2) more extreme and episodic (e.g., increased frequency and intensity of droughts, floods). These represent the "press" and "pulse" of climate change, respectively (Collins et al. 2011). Press climate changes may lead to gradual and cumulative increases or decreases in resources (e.g., soil moisture or N) accompanied by shifts in community structure and ecosystem function, while extreme climate events often are discrete and abrupt (traditionally studied as disturbances, Smith et al. 2009), and can rapidly alter biotic structure and generate resource pulses. Historically, droughts have been the most important climatic extreme impacting central US grasslands (Albertson & Weaver 1944, Woodhouse & Overpeck 1998).

Intensification of the hydrological cycle is forecast (Mearns *et al.* 1990, Marvel & Bonfils 2013) and is expected to increase both droughts and floods (key drivers of aquatic systems).

New Irrigation Transect Study and RaMPs treatments - Two KNZ terrestrial climate change experiments – the 22-yr Irrigation Transect Study (ITS) and the 15-yr Rainfall Manipulation Plot (RaMPs) experiment – focus on how long-term changes in the mean and variability of precipitation, respectively, impact grassland structure and function. Over time, they have revealed surprising ecological responses to these chronic climate changes (see Results from Prior Support section), and today they represent legacies effects of these treatments (sensu Yadjidan & Sala 2006) that differ markedly from controls. Viewed from a state transition model perspective, grasslands exposed to these climate legacies now exist in a different structural and functional state relative to control plots. We hypothesize that responses to (1) future changes in key drivers or (2) climate extremes (the pulse of climate change) will differ from predictions based on current responses. These differences in responses represents a potential interaction between pulse/press climate changes likely to occur in the future (IPCC 2007), but about which we know little because most climate change experiments to date have primarily focused on one or the other (Kreyling et al. 2008, Xu et al. 2012). By modifying the ITS and RaMPs long-term climate change experiments, we have the unique opportunity within LTER VII to significantly advance an understanding of how legacies of press climate changes may alter ecosystem sensitivity to future climate change in grasslands. After

more than 20 yrs of experimentally increasing growing season precipitation amounts and documenting community and ecosystem responses (Collins et al. 2012, Knapp et al. 2012a), we will now use this well-replicated (30 irrigated, 30 control plots in transects that span upland to lowland topoedaphic gradients) template to address new questions relevant to future grasslands. Specifically, climate change forecasts of "wetter regions becoming wetter and drier areas drier" combined with an increase in climate extremes (IPCC 2013) suggests that mesic grasslands may experience increases in mean annual precipitation but also more extreme periods of drought. However, grassland sensitivity to predicted changes in precipitation relative to historic conditions remains to be tested. We will modify the ITS to address this issue by maintaining a subset of plots under their current long-term treatments (ambient rainfall and supplemental irrigation averaging a 30% increase in growing season precipitation to minimize soil water limitations), while assigning another subset of plots with a history ambient and irrigated treatments to

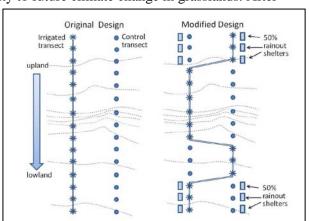


Fig. 12. Original (left) and modified (right) experimental design of the KNZ Irrigation Transect Study, showing treatment designations on one of two replicate transect pairs. Each transect is ca. 140 m long with 15 sampling locations each. Irrigated plots receive sufficient water to minimize growing season water stress, while control plots receive ambient precipitation. Passive rainout shelters will reduce rainfall by 50%.

new precipitation treatments – a 50% reduction in ambient growing season rainfall, ambient rainfall, and irrigation (Fig. 12). The fundamental relationship between precipitation inputs and ANPP has changed over time (Knapp *et al.* 2012) and these new treatments will allow us to test the legacy effects of 22 yrs of supplemental water, and determine the sensitivity of tallgrass prairie to future alterations in a key driver.

Long-term climate change experiments, particularly those that modify multiple global change drivers, are critical for understanding ecosystem responses to global change (Luo *et al.* 2011). Such experiments are uncommon, however, in part because of their expense. The RaMPs experiment (Fig. 13), one of the longest running multi-factor climate change experiments in the world, has been supported by LTER and other grants. Continuing this successful model of co-support, we will modify the long-term RaMPs experiment to specifically assess the interaction between the press (15 yrs of increased precipitation variability and 10 yrs of experimental warming air temperatures) and pulse (an extreme 2-yr drought) of climate change. We will impose an extreme 2-yr drought (66% reduction in growing season rainfall) in all

plots to assess how the history of altered precipitation patterns and warming (all combinations of these two forecast climate change treatments) will influence sensitivity of this grassland to a climate extreme. This will allow us to address the hypothesis that the cumulative ecological effects of chronic climate changes (i.e., the legacy effects of the RaMPs experiment) will alter the resilience to a period of extreme drought. This hypothesis is based on past measurements that show that the RaMPs press treatments have led to a chronic reduction in soil water availability along with altered genetic diversity and genotypic identity of the dominant C₄ grass A. gerardii (Avolio et al. 2013) - specifically, an increase in genotypes with more drought tolerant phenotypes (e.g., increased root:shoot ratio and rooting depth, and decreased canopy leaf area; Avolio & Smith 2013). We hypothesize that these

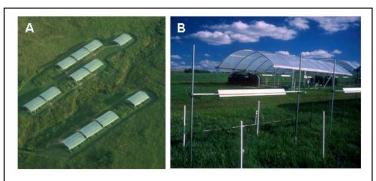


Fig. 13. A) Aerial view of the RaMPs experiment at the KNZ. B) View of a RaMP rainout shelter (background) with heating lamps in unsheltered plot in the foreground. The RaMPs experiment has imposed **15 years** of chronic increases in variability in growing season rainfall patterns (fewer, but more intense storms and longer dry intervals, with no change in total amount) and **10 years** of continuous 1.5-2°C warming. We now have a set of large (36 m²) replicated plots with documented responses to these chronic 'press' treatments, from genes to ecosystems. In LTER VII, we will alter the RaMPs experiment to assess how the legacy effects of long-term climate change influence the sensitivity and resilience of tallgrass prairie to a severe, 2-year drought. This research is co-funded by an NSF Ecosystem grant, which will be extended with LTER support.

genotypic changes combined with other more subtle alterations (changes in soil N content, microbial community structure and activity) will decrease the sensitivity (or increase resistance) of this ecosystem to an extreme drought.

Avian demography and migration phenology – Climate change is altering species distributions and seasonal phenologies (Cotton 2003, Jonzen et al. 2007, Both 2010, La Sorte & Jetz 2010, Bellard et al. 2012, Dunn & Møller 2013), although the factors affecting the pace and synchrony of change among species and locations are poorly understood. We propose new KNZ bird monitoring focused on demographic and phenological responses of migratory birds to climate change. These efforts will extend past KNZ studies (Augustine & Sandercock 2011, McNew et al. 2012a,b) by employing mark-recapture methods to identify the consequences of variation in climate and other drivers on bird populations. We focus on phenology as a key response of migrants to changing climates in the understudied central flyway. Mechanistic studies examining responses of consumers to variation in climate, grazing, and fire and new studies of physiological underpinnings of behavioral processes will complement our new longitudinal sampling protocol and benefit from proposed repeated capture of individuals. These new efforts will strengthen efforts to understand sensitivity and resilience of vertebrate communities to climate change and other drivers from the individual level up to the community level. Our proposed sampling plan consists of four discrete sampling events during the winter period to estimate overwinter survival rates (Sandercock & Jaramillo 2002), and more intensive sampling during spring migration. We will capture birds monthly over 3 consecutive days from December to March, and weekly over 2 consecutive days from April to early May. This sampling scheme permits demographic parameters to be estimated using robust capturemark-recapture models that account for detectability in estimating survival (Sandercock 2006).

C3. ALTERED BIOGEOCHEMICAL CYCLES. Altered biogeochemical cycles are both a cause and consequence of global change (Schlesinger 1997), with feedbacks that affect community structure and ecosystem processes, atmospheric chemistry, and water quality. KNZ biogeochemical studies will continue to focus on (1) quantifying rates of nutrient input, export and internal dynamics, (2) evaluating effects of fire and grazing, woody plant expansion, and climate change on biogeochemical processes, (3) assessing short- and long-term responses to nutrient enrichment, and (4) linking changes in nutrient cycling to ecosystem and community responses.

1. Core Long-Term Studies/ Measurements: Nutrient inputs and outputs – Long-term data on nutrient inputs are essential for constructing nutrient budgets, calculating weathering rates, and for assessing interannual variability and directional changes in nutrient loading (Blair et al. 1998). In collaboration with the National Atmospheric Deposition Program, we will document inputs of NO₃, NH₄⁺, SO₄⁼, PO₄⁼, H⁺ and major cations in wetfall, with complementary KNZ measurement of N and P in bulk precipitation. In collaboration with CASTNet (www.epa.gov/castnet), we will continue measuring N- and S-containing aerosols, and initiate new direct measurements of the larger particulate component of dry deposition using passive aerosol collectors. We will also continue long-term measurements of groundwater chemistry and stream nutrient export, which are integral to many KNZ experiments listed previously and in this section.

P Addition Experiment (2002-present) – Nitrogen strongly controls plant productivity at KNZ (Fig. 7) and elsewhere, but P limitation can affect plant community structure and alter ecosystem processes (Elser et al. 2007). Most prairie plants are mycorrhizal-dependent (Hartnett & Wilson 2002), with arbuscular mycorrhizal fungi (AMF) mediating P uptake and competitive interactions (Smith et al. 1999, Hartnett & Wilson 2002). As atmospheric N inputs increase, we hypothesize that P limitation and plant-AMF interactions will become more important, and species able to efficiently acquire P will be favored, altering plant diversity and community dynamics. To test this hypothesis, we will continue to add P at 0, 2.5, 5, and 10g P m⁻² crossed with N at 0 and 10g m⁻² (n=6/combination), and document changes in ANPP, plant species composition, plant-available N and P, and AMF colonization. Adding P alone had minimal effects, even after 10+ yrs, while P+N altered plant community composition more than either P or N alone, lowering C₄ grass dominance and increasing non-N-fixing perennial and annual forbs (Avolio et al. in review). Altered species composition correlated with reduced ANPP as grass cover declined and forb cover increased. Community heterogeneity (dissimilarity among plots) also increased in high P+N plots. We also saw significantly lower AMF colonization with added P, and higher colonization with added N. In LTER VII, we will continue to document longer-term responses to N and P treatments, and analyze results from a 2-year drought manipulation in a subset of plots to assess nutrient enrichment x drought interactions.

The Nutrient Network Experiment (2007-present) – The Nutrient Network (NutNet) focuses on the extent to which multiple resource limitations and bottom-up vs. top-down controls affect plant community

structure and function. NutNet is a globally distributed network that includes >60 sites (www.nutnet.org). At KNZ, NutNet experiments manipulate N, P and K and herbivores (using exclosures), while collecting data on plant community structure, productivity and soil nutrient availability using identical methodology (Borer *et al.* 2013). In LTER VII, we will continue NutNet studies of relationships of nutrient availability and herbivory on plant diversity, ecosystem function and stability, and belowground responses to address site-specific questions and to contributed to multi-site NutNet papers (*e.g.*, Adler *et al.* 2011, Lind *et al.* 2013, Hautier *et al.* 2014, Firn *et al.* 2011, Seabloom *et al.* 2013.

Landscape C/H₂O fluxes – To quantify landscape-scale spatial variability in plant-soil relationships and C and H₂O flux (Fig. 14), we established sensor and sampling transects across topographic gradients in two 1- and 4-yr burned watersheds (including 2 watersheds with flux towers). Sensors record microclimate (PAR, VPD, air and leaf temperature) and soil (moisture and temperature) data at 30 min intervals. At each sensor location, bi-weekly biomass (grass, forb, dead), leaf area index, and canopy height of dominant grasses will be measured to link spatial and temporal patterns of plant growth and gas exchange to micro-climatic variability. This research is essential for modeling landscape C and H₂O exchange under varying climate scenarios (sensu Morales et al. 2007). In conjunction with the sensor networks,

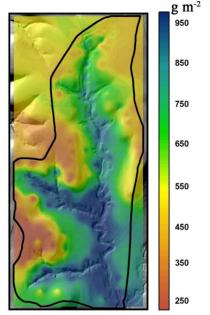


Fig. 14 Watershed-level pattern of ANPP (g m⁻² yr⁻¹) derived from a digital elevation model parameterized with data collected from a transect across watershed 01D (Nippert et al. 2011).

two eddy flux towers provide data to assess larger-scale fluxes of C, H₂O and energy in relation to fire frequency (Brunsell et al. 2014). These towers are located in an annually- and 4-yr burned watershed, with the latter undergoing grassland-shrubland transition. Co-located towers and sensor/sampling transects facilitates scaling of leaf and soil processes to watershed scales, and allows comparisons of contrasting land-use and land-cover on energy and water exchange (Brunsell et al. 2011a,b). Watershed- and regionallevel scaling is also facilitated by a large aperture scintillometer on KNZ (Brunsell et al. 2008), and two additional (non-LTER) flux towers at drier and wetter locations across a regional precipitation gradient. We will use eddy flux data for further model development and calibration, with an initial focus on (1) assessing discrepancies in land surface models induced by surface patchiness related to woody encroachment, as a function of spatial scale, and (2) relative impacts of microclimatic and regional-scale influences (Brunsell & Anderson 2011). Based on tower-measured differences in C and H₂O flux, we expect strong effects of boundary layer processes with increased woody cover (Brunsell et al. 2011b). We will explore potential regional effects of changes land-cover on precipitation processes in the context of global climate model simulations using the Weather Research and Forecasting (WRF) model (www.wrfmodel.org). We hypothesize that increased evaporative fluxes due to regional land cover change will alter surface energy partitioning, moist static energy, and downwind precipitation processes.

Groundwater hydrology and geochemistry—We will extend long-term datasets on groundwater levels and geochemistry with the goals of (1) identifying mechanisms behind ongoing increases in [CO₂] in groundwaters (Macpherson 2009),9(2) linking groundwater processes to increases in-stream [NH₄⁺], and (3) understanding trends of declining groundwater levels in some strata. We will sample groundwater

chemistry monthly, and use automated (5-minute) recording of groundwater levels to establish timing of aquifer recharge and discharge to streams in relation to precipitation patterns. We will coordinate groundwater and stream chemistry measurements to link subsurface weathering and stream chemistry in relation to groundwater recharge and discharge patterns. We hypothesize that precipitation (and temperature) affects soil pore-space [CO₂], which in turn controls groundwater [CO₂] and weathering rates. We expect that groundwater discharge to streams will deliver increasing levels of solutes, due to increased weathering rates. We will expand assessment of groundwater chemistry and linkages to stream baseflow and stream water chemistry by identifying groundwater discharge points in stream channels using thermal imaging, and analyzing long-term data on groundwater temperatures (2005-present) to understand aguifer recharge timing and patterns.

3. New Measurements/ Experiments for LTER VII: Improving estimates of dry deposition – Both wet and dry deposition of N is increasing in Central Plains grasslands. Since 1983, [NH₄⁺] in wet deposition at KNZ has increased by ca. 6.5% yr⁻¹ (Fig. 15; NADP 2013) while [Ca²⁺] has increased and [H⁺] has decreased substantially. Increasing atmospheric deposition of Ca²⁺ has been attributed to dust transport from increased aridity and changing agricultural practices in the Midwest (Brahney et al. 2013). The acid-neutralizing capacity of Ca-bearing minerals is consistent with observed decreases in rainfall [H⁺] at KNZ. Long-term records of atmospheric deposition are critical for understanding and interpreting changes in soil, stream and

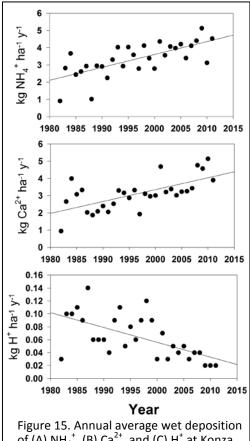


Figure 15. Annual average wet deposition of (A) NH₄⁺, (B) Ca²⁺, and (C) H⁺ at Konza Prairie LTER (site KS31) from 1983 - 2013. Source: NADP.

groundwater biogeochemistry. We have data on wetfall chemistry, but dry deposition rates of N, Ca²⁺, and other constituents are poorly constrained. New direct measurements of dry deposition flux are needed,

particularly in light of evidence that dry deposition has increased due to climate and land use changes (Neff *et al.* 2008). Changes in wet and dry N deposition also may contribute to observed changes in stream water [NH₄⁺] (*see below*). We will add weekly collection with a dedicated wet/dry collector with inserts to minimize air turbulence designed to collect "vertical" deposition.

Long-term changes in stream chemistry – KNZ stream chemistry data indicate multi-decadal changes in the balance of inorganic N forms, with several-fold increases in $[NH_4^+]$. These changes may be linked to altered organic C transport. New research on NH_4^+ and dissolved C dynamics will aid in understanding changes in stream biogeochemistry. Increased stream water $[NH_4^+]$ may be driven by several interactive processes: (1) decreased stream and groundwater pH, linked to increased groundwater $[CO_2]$ (see above), may reduce nitrification, (2) increased N deposition may directly increase in-stream $[NH_4^+]$ and via dissolved N transport from soils, and (3) increased woody riparian cover and terrestrial C inputs to streams may enhance heterotrophic activity and ammonification. We will investigate mechanisms of change with (1) expanded monitoring and characterization of dissolved organic matter (DOM) using optical spectroscopy to determine if changing sources of organic matter are linked to altered N cycling, (2) expanded assays of nitrification and denitrification in stream channels and riparian soils in forested and grassy riparian areas, and (3) assessment of pH effects on nitrification and denitrification to link groundwater observations to stream N cycling.

We also propose new studies of stream DOM using optical spectroscopic techniques to determine if changes in organic matter source are linked to altered N cycling. We expect the chemistry of DOM to vary over space and time, with increases in woody riparian cover contributing to a more terrestrial DOM signature, independent of change in DOM concentration. We hypothesize that increased woody riparian vegetation alters the composition and seasonality of inputs, with greater terrestrial organic C inputs during autumn leaf fall compared to grass-dominated riparian zones. We will extend spatial water sampling to stream reaches in areas with and without increased woody cover and upstream/downstream of groundwater sources, and conduct temporal sampling of surface water, springs, and groundwater to capture wet and dry periods. We will characterize DOM using indices from UV-vis absorbance spectroscopy, including specific UV absorbance as an indicator of aromaticity (Weishaar *et al.* 2003), and spectral slope data to determine molecular size and microbial and/or photochemical transformations (Helms *et al.* 2008). We will also use fluorescence indices to describe DOM source, freshness, and humification (McKnight *et al.* 2001, Parlanti *et al.* 2000, Zsolnay *et al.* 1999), and quantify changes in fluorophores of interest (*e.g.*, amino acid-like fluorescent components that are associated with DOM bioavailability) using parallel factor analysis modeling (Stedmon & Bro 2008).

Assessing feedbacks and resilience following chronic N enrichment – Since 1986, research in the Belowground Plot (BGP) Experiment has focused on above- and below-ground processes and responses

to fire, nutrient enrichment (N, P or N+P) and mowing (Fig. 16). The BGP has provided important insights into effects of N enrichment and interactions with fire. Long-term N enrichment (10 g N m⁻² y⁻¹) significant altered above- and belowground community composition and ecosystem structure (Garcia & Rice 1994, Collins et al. 1998, Wilson et al. 2009, Coolon et al. 2013). After 28 yrs, plots under different fire-N treatments have vastly divergent plant communities, available N levels, and soil microbial communities and processes (e.g., loss of diversity and shift in dominant species in burned +N plots; transition to woody vegetation in unburned plots; greater soil aggregation and associated C and N storage in Nfertilized treatments; changes in microbial community composition). During LTER VII, we will end is experiment in its current form, and



Fig. 16. BGP treatments include burning (annually burned or unburned, plots with yellow borders in image), aboveground biomass removal (annually mowed or unmowed until 2004), and long-term nutrient additions (N only, P only, N+P, and control. N-enriched plots show up as darker green here.

initiate a new long-term N gradient experiment (see below) to address new questions. However, the contrasting ecological states developed in response to long-term BGP fire-N treatments provide opportunities for new research on legacy effects, feedbacks, and resilience following cessation of N additions. For example, 20 yrs after cessation of N enrichment at the Cedar Creek LTER site, species richness recovered from low-to-moderate N enrichment, but diversity remained depressed in high N plots despite a return to pre-treatment soil N levels. This suggests that chronic high N enrichment can lead to alternative stable states (Isbell et al. 2013a,b), but this has not been tested in more nutrient rich soils and under different fire regimes. We will cease N (and P) enrichment in the BGP experiment to test if longterm chronic N enrichment has created legacy effects (e.g., altered plant-soil feedbacks) that maintain current ecological states, and how (or if) annual burning mediates the return of above- and below-ground community structure and function to reference grassland states (control plots). Several mechanisms may have affected N accumulation in this experiment, including: (1) fire-induced N loss via volatilization, (2) N stabilization in soil aggregates in fertilized plots, (3) fire suppression increasing N accumulation via establishment of woody vegetation. Accumulated N may buffer changes in composition and ecosystem processes after N additions cease, depending on the mechanisms in play. We hypothesize legacy effects of N addition will be strongest in unburned plots, contributing to slower recovery of communities and processes (e.g., N mineralization). We will measure ANPP, belowground biomass C and N, soil C and N pools and transformations, and plant and microbial community structure following cessation of N fertilization.

ChANGE: Chronic Addition of Nitrogen Gradient Experiment – Chronic N additions can significantly alter plant communities in tallgrass prairie (Isbell et al. 2013) and other grasslands (Stevens et al. 2004, Bai et al. 2010, Cleland & Harpole 2010). Current and predicted rates of N deposition are lower than 10 g N m⁻² y⁻¹, with predicted N deposition in grasslands expected to remain under 5 g m⁻² (Galloway et al. 2004). This begs the question of whether grassland responses will be more gradual with lower rates of N addition, and if responses to increased N loading will be monotonic or exhibit thresholds. In acidic soil grasslands across Great Britain, N deposition of 1.7 g m⁻² yr⁻¹ led to a 23% loss of richness. At the Cedar Creek LTER site, 1 g N m⁻² yr⁻¹ reduced species richness by 17% (Clark & Tilman 2008). We will use a range of N addition rates (0, 2.5, 5, 7.5, 10, 15, 20, or 30 g m⁻² as time-released urea) to assess sensitivity and thresholds. To isolate the effect of N alone from changes in relative N and P limitation, we will add P in appropriate stoichiometric balance with N in a subset of plots. Plant community composition, ANPP, belowground biomass (2-3 root ingrowth cores/plot) and soil N availability (resin bags and soil cores) will be measured annually. ChANGE will (1) test if nutrient thresholds exist for plant species and functional groups, and if exceeding these thresholds drives plant community change, and (2) determine what factors underlie observed threshold responses (e.g., nutrient saturation, mycorrhizal loss, insect herbivory). With separate funding, ChANGE will also be implemented at a shortgrass steppe site in Colorado and at 3 grassland sites in Inner Mongolia to provide comparative data on grassland responses to N additions, and whether thresholds vary with precipitation, ambient soil nutrient availability, and species identity/composition. ChANGE will allow us to address the following questions: (1) At what level of N does plant community change occur, and over what timescales? Is community change gradual/monotonic or abrupt? (2) Do thresholds vary for different plant species or functional types? (3) Are total mass or flux rate of N deposition more important? (e.g., does 5g m⁻² for 6 yrs create similar response as 30g m⁻² for 1 yr or 15g m⁻² for 2 yrs?); (4) Is decreased light availability due to increased ANPP the primary determinant leading to community shifts (e.g., Stevens et al. 2004), or do other factors determine change in community composition and structure (e.g., invertebrate herbivory or loss of AM fungi)? (5) Does reduced niche dimensionality (Harpole & Tilman 2007) with multiple nutrient additions (N and P) reduce species diversity further than N additions alone? (6) How do tolerance thresholds for N enrichment, above which community composition changes, vary among grassland types? We have designed ChANGE as a longterm experiment that will attract additional investigators over time with new research questions.

Woodland periodical cicada study – During LTER VII, we will have a unique opportunity to study the biogeochemical effects of a potentially expanding population of woodland periodical cicadas at KNZ. Cicada Brood IV (17-year periodical cicadas) will emerge on KNZ in May 2015. At the last emergence in 1998, GIS maps of emergence densities were used to estimate energy and N flux (Whiles *et al.* 2001).

Deposition of cicada carcasses can significantly increase soil N and microbial biomass (Yang 2004). Sampling in 2015 will reveal if the riparian woodland expansion on KNZ has increased spatial extent of emergence and the associated resource pulse. We will partner with an undergraduate institution, Simpson College, for cicada sampling, building on connections with a former KNZ graduate student. We will use emergence trap arrays (Callaham et al. 2000) to quantify material and energy fluxes. Individuals will be measured for size, mass, and nutrient content, and to assess potential long-term changes in body sizes. Decreasing body sizes of many species have been linked to climate warming (Daufresne et al. 2009, Sheridan & Bickford 2011), but studies have focused on aboveground and aquatic species with rapid generation times. How slow-growing insects that inhabit a thermally buffered environment respond to climate change is unknown. Through the KSU Entomology Museum, we have access to specimens of 17year cicadas from KNZ and adjacent areas encompassing 5 emergence events since the 1930s. We hypothesize that body size has declined, with consequences for fitness as body size and egg production are positively related in insects (Vannote & Sweeney 1980). A related opportunity provided by this emergence event will be to examine the affect of the associated resource pulse aboveground foodwebs. Periodical cicadas at KNZ have a distinctive ¹³C and ¹⁵N isotopic signatures (Callaham *et al.* 2000), allowing us to follow the pulse of C and N resources into riparian and grassland foodwebs. We will collect arthropod consumers of live and dead cicadas (e.g., spiders, ants, millipedes) and analyze tissues to determine trophic effects of periodical cicada biomass. We will collect consumer taxa in spring and early summer of 2014 to establish baselines for stable isotope signatures, and compare those to samples collected during the 2015 emergence to evaluate the impact of cicada derived C and N in the diets of consumers.

C4. RESTORATION ECOLOGY. Conversion of tallgrass prairie to agriculture, forest, and exotic grasses can result in state changes and abiotic or biotic ecological legacies (abiotic or biotic) that inhibit return to a grassland state and now require human intervention (restoration) (Hobbs et al. 2011). For example, longterm cultivation eradicates most prairie species from the soil seed bank (Willand et al. 2013), degrades soil structure, depletes soil C and N pools, reduces microbial diversity and biomass, and elevates soil nutrient availability (Baer et al. 2010, Bach et al. 2010). Reconstructing prairie from this state must overcome dispersal limitations, and consider agricultural legacies (Baer et al. 2003, Baer & Blair 2008), diversity and sources of propagules (Carter & Blair 2012a,b, Klopf et al. 2013) and higher trophic levels. Invasion of grassland by exotic herbaceous or woody species can result in state changes with feedbacks that make it difficult to restore grassland with natural drivers: feedbacks that prevent fire in the case of woody expansion (Briggs et al. 2005, Ratajzak et al. 2014) and positive feedback in response to fire as with invasion by functionally similar grasses (Reed et al 2005). The riparian woody removal study (described in C1b. Land-Use and Land-Cover Change), connects 'ecosystem restoration' and 'woody plant expansion' themes. Restoration can require considerable knowledge of plant-soil feedbacks (Heneghan et al. 2008, Baer et al. 2012, Wilson et al. 2012) because invasion of tallgrass prairie by nonnative grasses can alter belowground microbial communities. Inoculating soil with arbuscular mycorrhizal fungi (AMF) can increase restoration success (Wilson et al. 2012). AMF also influence plant invasions (Pringle et al. 2009) and alter plant-soil feedbacks. AMF exhibit host-specific growth responses (Bever 2002), which vary with AMF identity (Johnson et al. 2010, Hoeksema et al. 2010). Non-native invasive plant species can alter the density and/or composition of AMF communities, which can feedback on invasion (Bever 2002, 2003; Reinhart & Calloway 2006). Changes in AMF may also affect soil aggregate stability and soil C storage (Wilson et al. 2009).

KNZ restoration research will investigate constraints to restoring tallgrass prairie with the goal of revealing legacies and feedbacks that constrain restoration to ecological state representative of extant lowland KNZ prairie. Ecological legacies can result from deterministic (predictable changes to the environment resulting from disturbance) or stochastic (historical legacies resulting from priority effects) processes (Fukami 2010). Multiple field experiments are underway to investigate deterministic factors influencing community assembly and recovery of ecosystem processes through manipulations of soil heterogeneity (initiated in 1998; ongoing and currently funded by NSF-LTREB), propagule sources (initiated in 2005 and 2008), and diversity (initiated in 2005). In LTER VI, we began sequentially restoring prairie in an agricultural field to reveal the relative importance of stochastic events (interannual

variability in climate) and deterministic factors (herbivory by deer) on community assembly and ecosystem function. During LTER VII we will: (1) continue the sequential restorations (performed every other year), and add a new treatment to exclude insect herbivores, and (2) initiate a new investigation of the role of plant-soil feedback (microbial legacies) on restoration of prairie invaded by a functionally equivalent non-native warm-season grass. A chronosequence of restored prairies created by multiple past and present studies will continue to serve as a platform to assess longer-term (decadal-scale) rates of change and model recovery of ecosystem properties.

New and Continuing Research: Sequential prairie restoration experiment. – In 2010, we initiated a unique, long-term study of the effects of stochastic processes (inter-annual variation in environmental conditions) and herbivory (deer) on community assembly and recovery of ecosystem processes. We are sequentially restoring replicate blocks of prairie in an agricultural field over multiple years using the same species, seeding rates, and restoration techniques (Fig. 17). The overarching hypothesis is that community

assembly is largely deterministic over the long term, despite stochastic influences on the initial structure and functioning of restored communities. We further hypothesize that inter-annual variability in climate will cause short-term variation in communities and ecosystem processes and herbivory by ungulates and insects will structure plant communities with consequence for ecosystem function. Three restoration blocks (each with 4 replicate 400-m² plots) were established in LTER VI and we propose to restore 3 additional blocks in LTER VII. When complete, this will result in a 12-yr chronosequence. We continuously collect seeds from KNZ, and analyze for % live seed to ensure the same number of live seeds per species are sown each year. In 2012, fences were erected to exclude browsing by deer in two subplots within each plot in block 2. In all blocks, we measure plant species composition (n=16 per block/yr) and ANPP (n=32 per block/yr). Preliminary data indicate high divergence in



Fig. 17. Portion of the KNZ Sequential Prairie Restoration Experiment in the 2nd growing season after sowing. The full experiment will comprise a 12-year chronosequence sown with identical methods, but under variable initial conditions.

initial plant community composition and ANPP under highly contrasting rainfall conditions and in response to deer exclusion. In 2014 and coinciding with the restoration of Block 3, we will initiate a new treatment to assess the role of insect herbivory in prairie community assembly. Insecticide (diluted Spectracide® Triazide® Insect Killer Once & Done®) or water (control) will be applied biweekly during the growing season in 2m x 2m experimental units within each subplot, and results will be compared over multiple years. Insecticide treatments will allow us to assess the cumulative role of insect herbivory in vegetation establishment and plant community development during early restoration periods among years and with different weather patterns at initiation (an initial conditions hypothesis).

Role of plant-soil feedbacks in restoring invaded grassland – Invasion of grassland by exotic species results in a state change and represents a strong biotic filter that can limit recovery of native prairie species (Baer et al. 2009). We propose a new experiment to assess if invasion by an exotic C₄ grass alters soil microbial communities and plant-soil feedbacks in ways that limit recovery of prairie composition and function. We will conduct this study in a subset of the Belowground Plot Experiment, where a past mowing treatment facilitated invasion of a C₄ exotic grass (Caucasian bluestem, Bothriochloa bladhii). We will establish 12 replicate 2m x 2m plots in areas with 95-100% invasive grass cover and in adjacent non-invaded sites. In each replicate plot, we will assess AM fungal communities, with both traditional methods (spore identification, quantifying extra- and intra-radical hyphal abundance) and molecular techniques, including phospholipid and neutral lipid fatty acid analyses (PLFA, NLFA) and rDNA sequences from field-collected roots and rhizosphere soil. We will also quantify pre-treatment species composition soil aggregate stability. Following pre-treatment assessment, we will eradicate exotic grasses through applications of Glyphosate in early spring, followed by solarization by securing black UV-

resistant polyethylene sheets across each plot. Previous research has indicated a 6 month period of solarization is required to eradicate the non-native grasses. We will then evaluate potential legacy effects of altered soil microbial communities, and influence of inoculation with native soil communities, on *B. bladhii* re-establishment, native plant establishment, and restoration of ecosystem function. We will inoculate each formerly-invaded plot with 1 of 3 treatments: fresh soil collected from native prairie, AMF-inoculated nurse plants (*Andropogon gerardii*, *Lespedeza capitata*, and *Ratibida pinnata*), and a non-inoculated sterile control. We will test if inoculated nurse plants allow native AMF to colonize adjacent non-inoculated plants. After planting nurse plants, each plot will be sown with a diverse mix of native grasses and forbs. In each plot, we collect data on nurse plant size and density, plant species composition, and AMF composition, soil aggregate stability and soil C. We will test the spread of the inoculated AMF by quantifying gradients in density of unique AMF taxa observed in the DNA approach with distance from nurse plants, and document bulk soil microbial community composition, including AM fungi.

D. CROSS-SITE AND REGIONALIZATION. We will continue regional, cross-site, and cross-biome comparative studies and synthetic activities to advance the intellectual merit and broader impacts of KNZ research. A few examples of current cross-site activities by KNZ investigators include: (1) MASS loss – a decomposition meta-analysis that will broaden the context of KNZ stream litter decomposition studies, (2) the EcoSeRE working group evaluating ecosystem sensitivity to rainfall across sites, (3) an international working group on ¹⁵N tracers and stream food webs, and (4) a working group to evaluate ecosystem sensitivity to winter climate anomalies. KNZ investigators lead two NSF Research Coordination Networks: Drought-net (Smith) and the Stream Resilience Network (Whiles & Dodds). With KNZ VII there are exciting opportunities for cross-site syntheses, testing of existing theory, and developing new theory related to ecological state transitions, as this is becoming an important theme across sites (e.g., KNZ, SEV, JOR, CDR, VCR, and others). Documenting and understanding state transitions requires both long-term data and supporting mechanistic studies, which LTER sites are well positioned to provide (Peters et al. 2013, Bestelmeyer et al. 2011). We will seek opportunities to integrate results from KNZ studies with those at other LTER sites to broaden the generality of this research. Other NSF-funded studies that expand our ability to meet KNZ objectives and extend the inference of our research include: (1) EDGE – Extreme Drought in Grassland Experiment, (2) the Savanna Convergence Project, and (3) SCALER - Streams Consumers and Lotic Ecosystem Rates, Many of these efforts involve international participants and most involve other LTER sites. We have strong ties to grassland researchers in other countries, notably China, Brazil, Botswana, and South Africa. KNZ and KPBS will continue to encourage and support visiting international scientists and land managers.

E. SYNTHESIS. In LTER VII, the KNZ program will continue to grow in breadth and depth of research questions and expertise of KNZ scientists (Intellectual Merit), and training K-12 students and educators. graduate and undergraduate students, and the general public through outreach activities (Broader *Impacts*). A fundamental mission of the KNZ program, and the LTER program (Callahan 1984), is to provide comprehensive site-based research and long-term data to build a general understanding of the structure and function of ecosystems, and a baseline from which to assess change. The KNZ program will continue to support long-term research to advance ecological knowledge and provide a deeper understanding of tallgrass prairie responses, at all levels of ecological organization, to natural and anthropogenic change. Our LTER VII conceptual framework is based on using long-term studies to understand the sensitivity and resilience of tallgrass prairie to changes in historic and new drivers. Many of these changes occur over long time scales (decades or more) that require long-term study to detect, and long-term manipulations to reveal mechanisms resulting in change in structure and function. Assessing potential feedbacks, legacies, and interactions among drivers will provide important new insights for state changes and resilience. We propose a combination of new and continuing long-term experiments and observations, coupled with shorter-term complementary studies that will (1) test the applicability of conceptual and theoretical models of community and ecosystem change, and (2) provide new insights into the mechanisms underlying a broad range of ecological responses to important grassland drivers. Temperate grasslands are among the most endangered ecosystems on the planet (Hoekstra et al. 2005). Threats to the spatial extent and biodiversity of grasslands include conversion to crop agriculture (including biofuel production [Fargione et al. 2008, Hartman et al. 2011a,b]), expansion of woody

species, and invasion by exotic species (Baer et al. 2009). New and continuing KNZ research will contribute to the sustainable management, conservation and, when necessary, restoration of this and other grasslands globally. This application of KNZ research forms one dimension of the *Broader Impacts* of our LTER program.

Integration and synthesis at KNZ is facilitated by the theme-based organization of our research, with interdisciplinary research groups addressing multiple facets of complex ecological questions that cross spatial and temporal scales and levels of biological organization. Interactions among research teams are promoted by monthly meetings of local researchers and non-local researchers (via teleconferencing). We also promote interaction, integration and synthesis at our annual KNZ meeting, with rotating themes based on major KNZ VII objectives and outside scientists invited to present fresh perspectives. We will continue to lead, and participate in, synthesis workshops at the LTER All Scientists Meeting, and follow-up working group activities. At the Network-level, KNZ PI's and senior personnel will continue to provide leadership and service on key committees, including Blair – Executive Board; Briggs – NISAC and Communication Committee; Knapp – Chair, Publication Committee; Hartnett – International LTER Committee (see *Prior Results* p. C-12 for examples of past synthesis and network-level activities).

II. RELATED ESSENTIAL RESEARCH PROJECTS. Many complementary projects on KNZ support research related to core LTER questions (e.g., ecological effects of climate change, land cover change, food web dynamics) or that provides insight into mechanisms that underlie long-term changes in the structure and function of natural(e.g., plant population genetic and genomic studies) and restored (e.g., the role of environmental heterogeneity) prairie. These studies are valuable and synergistic with KNZ core research, but most are not essential for meeting KNZ core objectives. Examples of two related projects that directly contribute to core LTER goals are NSF grants that supports activities in the RaMPs climate change experiment and in the 'environmental heterogeneity' restoration experiment. The RaMPs grant provides funding to address population-level genetic changes that are one hypothesized source of the legacy effects we are testing in that experiment. The 'environmental heterogeneity' LTREB grant provides support for studies of plant traits in relationship to environmental heterogeneity. Two Macrosystems Biology grants aid in extending the range of inference and generality of KNZ research. One (SCALER) addresses scaling of stream reach studies to whole stream systems. The other (EDGE) includes cross-site studies and modeling of grassland responses to extreme drought, and extends the inference of our climate change research. Other research programs that provide data essential data for interpreting long-term dynamics are the USGS stream monitoring on Kings Creeks (hydrology integrating several smaller gauged watersheds on KNZ), the NADP program (wetfall chemistry), and the EPA Clean Air Standards Network (CASTNET) monitoring station (atmospheric aerosols and associated dry deposition).

III. EDUCATION AND OUTREACH ACTIVITIES. KNZ education and outreach activities form the second dimension of our *Broader Impacts*, and can be divided into 4 focal areas: (1) K-12 education, (2) post-secondary education, (3) community outreach and engagement, and (4) grassland conservation and restoration.

K-12 Education: Konza Environmental Education Program (KEEP) is led by Jill Haukos (Director of Education) with assistance from Hallie Hatfield (www.ksu.edu/konza/keep). KEEP offers diverse educational experiences including Schoolyard LTER (SLTER), with >1,000 students participating annually. Students participating in KEEP collect, enter, analyze, and interpret data using methods developed for SLTER, and compare responses from SLTER databases over time. K-12 research specific to KNZ includes: grasshopper surveys, evaluating effects of fire on vegetation, measuring geomorphological changes in stream channels and stream macroinvertebrates, and assessing plant diversity under varying watershed treatments. An annual Summer Teacher's Workshop provides training for, and opportunities for feedback from, teachers. Participants are encouraged to return with their students to participate in SLTER activities. KEEP supports community education through collaboration with the Kansas Association for Conservation and Environmental Education, Flint Hills Discovery Center, Manhattan Boys and Girls Club, and United School District 383. For the past 15 years, KNZ has hosted a local high school summer field biology course - the KSU Girls Researching Our World (GROW) program. This KSU program, funded by NSF, exposes middle school girls to careers in STEM fields using environmental stewardship as a theme (www.ksu.edu/grow/).

Undergraduate, Graduate, Postdoctoral Education: Undergraduate and graduate student training is a core activity of the KNZ LTER program. KPBS serves as an outdoor educational laboratory for university classes and visiting field courses from numerous institutions each year with tours typically led by senior KNZ scientists. A Konza Prairie site-based REU program (www.konza.ksu.edu/general/reu.html) supports ~ 10 undergraduates per year in addition to several LTER- and other grant-supported REU students. In a 5-yr period (2009-13), 29 scientists served as mentors for 59 REU student participants. REU participants were recruited from 44 institutions in 37 states (including Puerto Rico), and included 37 women and 20 students from racial/ethnic groups that are historically underrepresented in science (1 Native American, 12 Hispanic, 5 African-American, and 2 multiracial). During LTERVI, REU participants published 24 papers in national peer-reviewed journals. Several REU participants have completed senior honors theses and/or presentations at national meetings based on their KNZ research. KNZ contributes significantly to graduate student training, with 56 graduate student theses and dissertations completed during LTER VI from 10 institutions: Kansas State U (31), Southern Illinois U (6), Colorado State U (2), Oklahoma State U (3), U of Kansas (5), Yale (3), and 4 others (6).

Community Outreach and Engagement: Both KNZ scientists and trained volunteer docents engage the public. Docent training includes ornithology, entomology, mammalogy, herpetology, botany, ecology, climatology, geology, and interpretation. Training lectures are viewable at The Konza Prairie Channel on YouTube (www.youtube.com/user/TheKonzaPrairie). KNZ scientists, students, and docents host a biennial "Visitor's Day" (~1500 people/yr), featuring LTER research and education programs. KNZ scientists also provided scientific expertise and advice on the creation of the Flint Hills Discovery Center (FHDC), a natural history museum in Manhattan, KS (opened in 2013). The mission of the FDHC is to "serve as a principal place for learning and understanding about the tallgrass prairie and the Flint Hills eco-region in particular; to assure its long-term preservation." In 2012, the book "Fire and Form on the Konza Prairie" was published and contains an article by J.M. Briggs (Director of KBPS), photos and commentary by KSU emeritus Professor of Art Edward Sturr, and an essay and poetry by KSU English Professor, Elizabeth Dodd. Work by Sturr and Dodd was featured in the Ecological Reflections Exhibit at NSF in 2013. KNZ scientists and students deliver numerous presentations and talks each year to various civic groups as well as educational, professional, and conservation organizations and agencies (e.g., The International Grassland Congress, Grassland Society of Southern Africa, The Nature Conservancy, The National Wildlife Federation, National Parks Conservation Association, National Bison Association, KS Dept. of Wildlife & Parks, Kansas Agricultural Experiment Station, Kansas Natural Resources Conference, and other public education events). During LTER VI, we hosted several professional meetings, and workshops, including The Nature Conservancy's Grassland Working Group, Tallgrass Legacy Alliance, The Kansas Grazers Association and the KS Rural Center. KNZ scientists sponsored the international symposium "Grasslands in a Global Context" from Sept. 12-14, 2011. The symposium hosted speakers from South Africa, Netherlands, Australia, China and North America who discussed generalities and differences in the structure and function of global grassland and savanna ecosystems, while identifying significant research gaps (many of which are proposed for study in LTER VII). We also co-hosted a conference with the National Wildlife Federation with the theme of "America's Grasslands: The Future of Grasslands in a Changing Landscape." This conference hosted >200 participants from a variety of occupations including researchers, natural resources professionals, farmers and ranchers, policy experts and conservationists.

Grassland Conservation and Restoration: KNZ experiments inform conservation and test ecological theory relevant to grassland restoration. Fire and grazing are important components of grassland management, and KNZ research is relevant for designing improved management practices (e.g., patchburn grazing) that sustain terrestrial and aquatic resources in grasslands. Restoration studies, a core part of the KNZ program, are particularly timely because human activities have resulted in widespread loss and degradation of tallgrass prairie and other temperate grasslands. Collectively, restoration studies at KNZ providing insights into the roles of abiotic and biotic variation on the restoration of prairie communities and associated ecosystem function. These studies will aid in developing more effective restoration approaches and enable us to better forecast the responses of restored grasslands to environmental change.

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Facilities, Equipment and Other Resources

The 3,487-ha Konza Prairie Biological Station (KPBS), located in the Flint Hills of NE Kansas, is the core research site for the KNZ program. In addition to providing the watershed-level fire and grazing treatments, agricultural fields, restored prairie, stream network and weirs, KPBS includes several buildings in the headquarters area that support LTER research. The on-site Ecology Laboratory (2,400 ft²) includes (1) a wet/dry lab with sinks, fume hood, refrigerators, balances, etc., (2) two large multi-purpose work rooms with bench space and sinks for processing samples, drying ovens, refrigerators and freezers, and equipment storage, and (3) and a large researchers' shop equipped with a variety of tools and field supplies. Other station buildings include a fire station and maintenance building, a large storage building for equipment, and a residence occupied by the site foreman year round. The 4,650-ft² Hulbert Center

houses a library/conference room, administrative offices, classroom and teaching laboratory (used primarily for K-12 activities), reference herbarium and animal collections, and a kitchen and dormitory-style housing for 15 visitors. Two small guest cottages (each with 2-bedrooms living room, bath, kitchen, and laundry facilities), can accommodate up to 5 persons/cottage. A larger cottage, built in 2012, can accommodate up to 12 guests, expanding the capacity of on-site accommodations to 37 visiting researchers.



With support from an NSF Field Stations and Marine Laboratories (FSML) grant, Kansas NSF EPSCoR, the Kansas Agricultural Experiment Station, KSU, and private foundations, several major site improvements and building renovations were completed during LTERVI. These include new housing for visiting students and scientists (included above), an on-site meeting and conference center, and improved Internet capabilities. With funding from an NSF-FSML grant and additional support from KSU and a

private donor, an historic limestone barn at the KPBS headquarters was transformed into a multipurpose meeting facility for on-site conferences, workshops, and educational programs. The historic stone barn was renovated in 2008 and has the Cortelyou Lecture Hall (1,750 ft²) with a seating capacity of ~100 persons fully equipped with A/V equipment and wireless internet. An additional large multi-purpose room (1,850 ft²) is designed as flexible space for varied uses including additional meeting space, workshops, scientific posters and other research displays, social gatherings, and education programs for large groups.



All lab and office buildings at KPBS have T1 Internet connectivity to the KSU campus. In addition, there is a wireless link to KPBS from campus with multiple wireless access points (802.11abg) that provide coverage to >60% of the 3,487-ha site. Current users include: KNZ LTER (sensor networks in several locations, meteorological stations, eddy flux towers, stream discharge loggers), USGS, University of Kansas, Colorado State University, and KPBS (visiting scientists lodging). Network upgrades to increase both coverage and throughput are possible.

Other LTER infrastructure, maintained by KPBS, includes the outside perimeter fence (29.8 km), the interior bison management area enclosed by 16.4 km of "New Zealand" fence, 98 small (25-m²) grazing exclosures, 11.7 km of fence for cattle research, 26.4 km of access roads and 61 km of fireguards separating the experimental watershed units. KPBS maintains several general-purpose vehicles on-site, as well as specialized equipment (tractors, fire trucks, mowers, soil augers, etc.). KPBS makes staff and equipment available to assist with KNZ research activities, including mowing fireguards, installing equipment, soil coring, etc. KPBS staff also coordinates the fire management plan and implementation of prescribed burning of watersheds and experimental plots, and the management of bison and cattle herds for KNZ grazing treatments. The headquarters area include a corral and handling facilities for managing

the bison herd (hydraulic chute, electronic scales, etc.), which is essential for LTER grazing studies. Other field equipment and instrumentation on site includes the main KNZ weather station, a network of 11 rain gauges, two eddy flux towers for quantifying ecosystem-level C and water vapor flux, four weirs and associated stream gauging equipment (updated in 2012 to Sutron Constant Flow Accubar® bubble gages and recorders with wireless connectivity), 46 wells for measuring groundwater levels and chemistry, numerous TDR probes, neutron access tubes and tension lysimeters for soil water measurements. Related equipment co-supported by other programs includes a USGS stream monitoring station, a NASA CIMEL Sun Photometer, 2 seismometers (USGS), an aerosol and ozone monitoring facility (CASTNet), and a NOAA Climate Reference Network (CRN) weather station. These facilities add significantly to data for LTER research and education programs, and for regional and cross-site studies. KPBS is also a core site for National Ecological Observatory Network (NEON), which will begin construction of major research infrastructure in summer 2014. NEON will provide additional unique measurement capabilities and data at KPBS, which will complement many KNZ LTER studies.

In addition to facilities at KPBS, a wide-range of modern laboratory facilities are available on the nearby KSU campus approximately 15 km from KPBS (e.g., Analytical Chemistry Labs, Stable Isotope Lab, Center for Ecological Genomics, Core Sequencing and Genotyping Facility, Lipodomics Center, Gene Expression and Microarray Facility, a BioSafety Level 3 Facility for invasive species and infectious disease studies, etc.). The majority of core 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, and these specimens are now electronically databased and georeferenced. Some specific equipment and facilities available for LTER research are located within other Departments (Agronomy, Biological and Agricultural Engineering, Plant Pathology, Geography), reflecting the interdisciplinary nature of our research. Some major analytical instruments available for KNZ investigators include: 2 Alpkem autoanalyzers (FlowSolution IV) for liquid samples, Carlo-Erba 1500 automated C/N analyzer for solid samples, Shimadzu TOC 500 analyzer for dissolved C, a Hitachi U2900 automated dual-beam spectrophotometer, several gas chromatographs with electron capture, flame ionization and thermal conductivity detectors, a Nikon compound microscope with epifluoresence and video imaging capabilities, 4 LiCor 6400 Portable Photosynthetic Systems, 2 LiCor 8100 systems dedicated for soil CO₂ flux measurements, a LiCor 1600 null-balance porometer for stomatal conductance, and 3 pressure chambers (PMS model 1000) for measuring plant water potential, 4 Tektronix cable testers (model 1502B) coupled to Campbell CR10 data loggers for TDR soil moisture measurements, 2 Troxler (model 3221) neutron probe gauges for soil moisture determinations, a back-pack mounted minirhizotron (Bartz Technology Co) camera system, and Trimble GPS units. Eight multi-parameter sonds (YSI 6000) are used for monitoring oxygen and temperature in 3 watersheds. 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 instruments (balances, microscopes, etc.) are available in individual investigator laboratories.

Presently, KNZ has general use four pickup trucks, ranging in model year from 1993-2001, and two newer trucks for transporting people and materials between campus and the field station, and for work on site. Because a reliable 4-wheel drive vehicle is necessary for prescribed burning and bison management, we are requesting funds to replace one 4-wheel drive vehicle during LTER VII.

Other KSU Facilities

KNZ co-PI Nippert is the Director of the KSU Stable Isotope Mass Spectrometry Laboratory (SIMSL). The laboratory, housed in the Division of Biology, is dedicated to the stable isotopic (‰) and elemental (%) analysis of carbon (C), nitrogen (N), and oxygen (O) in organic and inorganic phases (solids, liquids and gases). SIMSL is a hands-on teaching facility for the students (undergraduate and graduate) at Kansas State University, and a regional research facility for stable isotope users. SIMSL

operates a Finnigan Delta-plus IRMS, and sample introduction peripherals including a Costec elemental analyzer and Thermo gas bench. Additionally, SIMSL operates a Picarro isotopic water analyzer and a Picarro isotopic CO_2 analyzer. SIMSL is equipped to process samples using Wiley mills, ball mills, small-sample amalgamators, soxhlet, and has a vacuum extraction line to cryogenically extract water from plant and soil samples.

The KSU GIS Spatial Analytical Laboratory (GISSAL) was established in 1990 as a multidisciplinary center supporting spatial research, education, and outreach activities at Kansas State University. GISSAL was recognized as a National Center of Digitizing Excellence by the USDA Natural Resource Conservation Service and key contributor to the 2005 ESRI Special Achievement in GIS Award for Agriculture awarded to KSU. GISSAL combines faculty expertise and trained graduate and undergraduate student technicians with advanced geospatial technology and sophisticated spatial analysis capabilities. GISSAL offers a modern computing infrastructure, access to state-of-the-art data visualization tools, and the most powerful GIS, satellite remote sensing, digital mapping, database, and statistical analysis software packages. Although primarily a research facility, GISSAL also offers contract services including GIS database design and construction, digital cartographic support and production, web-servable maps, distributed geographic information services, and customized GIS workshops and software training.

Computer Software and Hardware

Most laboratories, all PI offices, and KPBS buildings contain computers linked to a local area network managed by the KNZ LTER program. All Konza servers are housed in a separate climate controlled facility with clean power, and managed by the KSU Physics Computer Support Center through a contractual arrangement. The KNZ IMS includes a local area network that supports IM access, data entry workstations, over 80 KNZ user accounts, shared software and storage resources. This network is managed for KNZ use, and is separate from other KSU campus networks. IMS hardware includes: 1 dual quad core blade, domain controller; 2 dual quad core blade servers, each with 32 GB of RAM, divided into a total of 12 virtual servers. The IMS includes a Storage Area Network (SAN) with mirrored 300 GB SAS for VMs and 8.5 TB storage in RAID 5 arrays. Backups of KNZ file are done daily, with backup stored off site on a monthly basis. The KNZ IMS also supports a wireless network at the Konza Prairie Biological Station, with direct linkages to the KNZ servers on campus. The KNZ LTER Program supports individual and site licenses for several software packages for use by KNZ researchers, including the suite of ESRI GIS software, SigmaPlot, SAS, MS Office, Adobe Acrobat, Photoshop, and ERDAS and ENVI software for image processing.

KSU Institutional Support

Kansas State University has a long history of providing support for the KNZ LTER program, which will continue during the LTER VII funding cycle and which includes leveraged support of the overall infrastructure and programmatic needs outlined in the LTER VII application. KSU is in the process of completing a major upgrade of the computer network in, and Internet connectivity to Bushnell Hall. KSU will provide computer server and network support through a partnership between the KNZ LTER program and the KSU Physics Computer Support Center, where KNZ network servers are housed. KSU will provide support for operation of the Environmental Chemistry Laboratory in Bushnell Hall, which is used for LTER water sample analyses. KSU will also provide support in the form of available assistantships for graduate students conducting KNZ research.

Information Management

Information management continues to be a priority for the Konza Prairie LTER (KNZ) program, even as we went through several recent changes in IM personnel, as noted below. The (KNZ) Information Management System (IMS) includes people, hardware, and software to store, manage and deliver scientific information that will facilitate interdisciplinary research and scientific discovery. The overarching KNZ IMS goals are to:

- 1. Assure the accuracy, integrity and long-term security of all KNZ data;
- 2. Ensure that KNZ data and metadata adhere to LTER standards, to enhance data accessibility and usability for current and future generations of scientists and students;
- 3. Facilitate efficient data discovery and ready access to data and metadata to support local, network, and other research and education activities
- 4. Proactively communicate with researchers and students in the research design phase, so that they understand and follow information management best practices

As one of the initial LTER sites, KNZ has a long history of development, leadership and participation in ecological information management. At its beginnings in the early 1980's, the KNZ information manager (IM) and support staff worked to develop and implement a base-level research data management plan to allow researchers to archive, locate, interpret and use KNZ data. The original KNZ IMS plan was designed using guidelines established by Gorentz *et al.* (1983) and documented by Gurtz (1986) The development of the original KNZ IMS has been summarized by Briggs and Su (1994) and Briggs (1998). John Briggs served as KNZ IM from 1984-1998 and continues to consult on KNZ IMS issues while serving as Director of Konza Prairie Biological Station. Over time, the KNZ IMS has evolved from s primarily a site-based system serving local researchers, to providing LTER data and related information to a much broader and more diverse clientele, including a multi-disciplinary team of KNZ investigators from numerous universities, researchers at other LTER sites, the broader scientific community, and others One important metric of success of the KNZ IMS is the large and growing number of publications, by KNZ scientists and by others not affiliated with the KNZ program, that use KNZ data.

During LTER VI, we made major upgrades to our IMS hardware, software, and our database structure, while transitions through changes in our IMS personnel. At the start of LTER VI, we transitioned to a new IM (Adam Skibbe) from outside the LTER network, but with significant GIS and computer skills. Adam's arrival coincided efforts to transition from an ASCII text-based IMS to one based on SQL Server. Following SQL training, Skibbe helped complete the development and implementation of a new SQL database system and a new KNZ website. These were major accomplishments. During LTER VI, we also worked to adopt newer LTER database and website standards and best practices, and ensure compatibility of the KNZ data and IMS with the developing Network Information System (NIS). This required editing all existing KNZ metadata, creating new metadata for some datasets, and updating EML from version 2.0.1 to 2.1. We hired additional programming help to assist with these tasks and to improve website functionality. We also hired a parttime IM assistant and archivist, to oversee scanning and archival of both digital and hard copies of old data, field notes, program code and many photographic records. We began to develop workflows to automatically export and store harvestable CSV files for direct downloadable access by the NIS on our website. However, in December 2013, Skibbe left to accept a GIS position elsewhere. We were fortunate to quickly hire a new IM, and Yang Xia arrived in January 2014. Yang had five years of experience as a research and database assistant at the SEV LTER site, and nearly four years of experience as an IM and database administrator at the national LTER Network Office in New Mexico before joining the KNZ program. She has a background in ecology (MS in Ecology with minor in statistics) combined with strong computer and technical skills. She has specific skills in Ecological Metadata Language and SQL database analysis and design, and is thoroughly familiar with all the requirements and skills expected of LTER

Information Managers. In short, she is an ideal fit for our IM position. Although she has only been in the KNZ IM position for a short time, she made tremendous progress in coming up to speed with our hardware and software, and learning our database system. Her knowledge of the LTER network databases has been a real asset as she works to complete the transfer of KNZ data to the NIS. She completed migration of most of our former ASCII-based data files to our SQL database and to the NIS, with additional conversions and transferred planned. She has also been working to update aspects of the KNZ website to improve functionality, data discovery and data access. During LTER VII, she will oversee continued migration of remaining digital datasets and metadata for incorporation into the NIS, create new datasets as needed, and improve the KNZ website with LTER standards and best practices in mind. Yang will also work with KNZ investigators to optimize KNZ IM practices, including data collection and processing, and data accessibility through KNZ internal servers, the KNZ website, and the LTER NIS.

Our continued goal for LTER VII is to make all new LTER data available on-line as soon as possible, as well as working towards filling in any gaps in our digital holdings (e.g., converting archived hard copy data to digital form, duplicating any paper copies or images into digital format, incorporating LTER-related "orphan data sets" that from research not funded by but relevant to KNZ into the formal LTER IMS). On-line KNZ data will continue to be made available to outside investigators without restriction, and we will continue to offer data downloads via a variety of search and browse options in the "Data" section of our website. We will continue to edit our metadata and update procedural protocols to ensure any changes in technique or structure of our datasets are accounted for. Our data catalog (metadata), methods manual (techniques) are available online, and we will complete revisions of our data entry procedural handbook. We are also committed to helping KNZ-related researchers develop data management plans for related NSF research.

Hardware and Software

The KNZ IMS includes a local area network that supports IM access, data entry workstations, over 80 KNZ user accounts, shared software and storage resources. This network is managed for KNZ use, and is separate from other KSU campus networks. IMS hardware includes:

- Servers
 - 1 dual quad core blade, domain controller
 - 2 dual quad core blade servers, each with 32 GB of RAM
 - Running 12 virtual servers
- SAN
 - Mirrored 300 GB SAS for VMs
 - 8.5 TB storage in RAID 5
- Backup
 - Daily backup with monthly offsite storage
- Wireless
 - Direct link from KPBS to campus

The virtual servers provide a number of different functions, including: a domain controller, a SQL 2008 Database server, a Konza Web server, a GIS data server, a dedicated server for the KPBS weather station, terminal services (32- and 64-bit), print services, and others. All Konza servers are housed in a separate climate controlled facility with clean power, and managed by the KSU Physics Computer Support Center. This frees our IM from maintaining server hardware and software, and allows her to concentrate efforts on providing access to data and metadata to support local, network, and other research and education activities.

Data processing and archiving

There are currently 194 individual datasets included under 101 major datasets, collected and managed by the KNZ program. Our goals are to provide on-line access for all our data updated as soon as possible, and KNZ investigators are committed to this goal. Although LTER guidelines are within two years of data collection, we generally strive to do this within one year of data collection, processing and appropriate quality control. A few historical data sets have not yet been incorporated into our online database, and these offline data are stored on the centralized KNZ IMS and available upon request. Non-digital data (*e.g.*, historic photos, field notes, etc.) are also documented, archived, and available by request to the IM.

Data quality assurance /quality control are essential for data integrity and management. The KNZ IM offers advice and expertise in data collection, storage, and archival issues where needed, particularly as new studies begin Investigators, technicians, and students who collect the data are responsible for documentation to IM, with a key investigator assigned responsibility to each dataset. The IM encourages researchers to submit their data as comma delimited ASCII files or, in cases where data were digitally-collected, the native file format. The error-checked dataset is then returned to the responsible investigator-of-record, who provides a final data check and approval before they are placed on the internal web server An additional automatic error check, including a data validation step using preset thresholds to limit data to an acceptable range are conducted by the KNZ IMS.

Some of our data stream directly from field-based electronic sensors (*e.g.*, flux tower data, temperature arrays, stream discharge) and these also go through a preliminary range-check with alarms if sensors are out of range. Currently these routines are managed through SAS programs which then convert the data to formats for input into the IMS. For field data that are collected by hand, we have initiated procedures to electronically log samples and follow their processing until analyzed. For example, water samples are logged in a tracking database when collected, with any comments associated with those samples. The samples are then subsampled and filtered and labeled vials are frozen and stored in specific locations. Control sheets and procedures are then used to insure data and sample flow and accounting.

Once those steps are completed and final data are obtained, the IM will load data into existing datasets or create new project datasets in our SQL database. Datasets are associated with a research project or core area code that allows for efficient tracking and association with research methods in our Methods Manual. During LTER VI, we migrated our KNZ database and all data from SQL Server 2000 to SQL Server 2008. We established an improved workflow for data processing (from field data collection through entry, QA/QC, and query), to support prompt data entry and updates. We will continue to improve and build on these workflows to enhance the efficiency with which we handle increasing data throughput as the KNZ program grows.

Spatial data from the KNZ site are stored locally in a file geodatabase format. These data are available for download through our web server in zipped Shapefile (SHP) or Keyhole Markup (KML) formats. Larger remotely-sensed images, such as satellite images, are stored with CDs and DVDs. If required, the images can be downloaded from our web server through arrangement with the IM, although with the largest data sets simply copying the DVD and mailing is most efficient. We created an online KNZ spatial data portal for accessing these data and metadata which includes interactive mapping capabilities built on the Google Earth API: http://www.konza.ksu.edu/knz/map/index.html. In doing so, we moved our online spatial database beyond its prior role as a simple map visualization and query tool, to a more powerful data analysis tool that is integrated with our web pages. The KNZ program has continued to work towards increasing our spatial data offerings, both in historic data as well as newly collected data, digitizing and rectifying a series of historic aerial photographs, and developing a detailed GIS of past and current research plot locations. Using high-resolution GPS units, we georeferenced over 95% of sampling locations related to LTER dataset collections and have developed protocols for non-KNZ scientists to georeference their study sites assist them in archiving that data.

An additional important IM activity is the organization and digitization of all original field data, including many field notes and maps dating back to the beginning of the LTER program. We created copies and stored them separately from original field data in a storage room in a separate building. We cataloged and scanned all original field notes and data, and we can now provide digital scans (.pdf) to complement SQL and ASCII version of the data for every available dataset. Our intent was to make these scans internally available, so those interested in cross checking data or viewing original datasheets can have access without having to visit the archives. However, these files are available to others upon request.

Non-electronic materials, including samples (plant and soil specimens, documents, and photographs) are stored in various locations on the KSU campus and at KPBS, as appropriate. For example, voucher plant and insect specimens are stored in the KSU Herbarium or the KSU Museum of Prairie and Arthropod Research, respectively which maintain an on-line access system (http://biodis.k-state.edu/). The Konza IM provided expertise on data management for both of these facilities, and has been instrumental in efforts to database and improve electronic access to specimen information.

Management of Metadata

Ecological Metadata Language (EML) is the metadata standard adopted by the LTER Network. We recently updated KNZA metadata to EML 2.01. This was a significant undertaking, as many of the specific metadata requirements for EML 2.1 were not included in the previous version of EML (2.0) that we were using, and some of our datasets did not yet have EML-based metadata. For these later datasets, we created new metadata. One of our goals for LTER VII is to update metadata as standards change. We are devoted to making all KNZ data PASTA-compliant with a focus on EML 2.1 integration, including updating any KNZ datasets that have not yet been brought up to NIS standards, and making sure that new datasets are NIS-compliant as they are created.

Content Management

General information about the KNZ projects, field station, site descriptions, past proposals and annual reviews, personnel info, and publications are stored in our internal server and SQL server database. In 2011, we designed and deployed an internal content management system (CMS) to better manage our web content, personnel and publications databases. This system has resulted in a much more user friendly and reliable website as well as the ability to make prompt future updates to web content. We can now regularly and easily update personnel, publication, project, and web content through this web portal. Web content and navigation are controlled by XML with connection to the database, and are dynamically loaded when pages are browsed.

Website

The Konza LTER web site provides an access data catalog that is widely used by the scientific community for research and education. In 2012, Konza launched a redesigned website: http://www.konza.ksu.edu, supported by information architecture in a relational database management system Metadata and data are queriable and downloadable. The KNZ IMS includes a web-accessible, upto-date database of all KNZ publications, including journal articles, conference proceedings, books and book chapters, theses and dissertations, and electronic publications supported by KNZ program. The bibliography module includes both a search interface for the general user as well as a web portal interface for citation entry over the web The list is searchable by key words, author name, and date. We have linked personnel with publications through a dynamic connection with our SQL Server database, making it easy for users to find specific personnel information and related publications.

We continue to maintain an open data access policy as we always have, and our on-line data continue to be made available to outside investigators without restriction. We will continue to offer data downloads via a variety of search and browse options in the "Data" section of our website (https://www.konza.ksu.edu/knz/pages/data/knzdata.aspx).

LTER Network Activities

KNZ will continue its participation and contributions to several LTER and related data networks, including the LTER Data Portal, Site and Network bibliography, Personnel DB, SiteDB, and ClimDB/HydroDB. We will continue participation in the All-LTER Network annual meeting, and collaboration with other LTER Information Managers.

Future Directions

Enhancements and continued improvements to the Konza IMS are planned for LTER VII, including:

- 1. Continuing to ensure data quality, data integrity, and data availability, using the latest LTER standards and updating these as soon as necessary;
- 2. Developing workflows and QA/QC procedures to streamline and automate, where feasible, the collection and processing of selected LTER data (e.g., climatic data, stream hydrology, etc.);
- 3. Complete some reorganization and housekeeping of the KNZ SQL database, and improve documentation of procedures;
- 4. Updating the KNZ website as needed to meet LTER standards, as well as working to improve site-based data and metadata discovery and access.
- 5. Continuing to work with researchers to develop tools to more efficiently process, quality check, integrate and publish their data with high integrity;
- 6. Improving and upgrading our EML metadata based on "best practices" data-enabling integration, and submitting more data packages to PASTA to enhance KNZ data availability to the broader scientific community;
- 7. Exploring new methods to improve KNZ IMS, including developing a web-based EML editor;
- 8. Continuing to develop, and add to, an online KNZ photos archive;
- 9. Continuing to support IM training to insure the latest IM methodology and software can be used and support travel of the IM to LTER network IMS meetings to keep contact with IM's at other sites:
- 10. Moving toward direct electronic logging of field notes and electronic data transfer wherever possible:
- 11. Upgrading IMS hardware by adding two additional blade servers, a new high-speed switch, and additional storage to accommodate the additional workload of the above activities, and to enhance the reliability and security of the IMS.

KNZ PROGRAM MANAGEMENT

The KNZ administration and management model is based on shared intellectual input, distributed leadership and group decision-making. The PI coordinates group interactions and manages the overall execution of activities within this framework. Although participants and specific organizational themes have changed over time, this model has served KNZ well for 30+ years. Our governance and organizational structure for LTER VII, as depicted in Table S1, is built around the current roster of PIs and the major themes for our proposed LTER VII activities. John Blair will continue to serve as PI-ofrecord and primary KNZ LTER point-of-contact at the local (University), LTER Network and NSF levels. The PI is responsible for overall scientific leadership, coordination of KNZ activities, fiscal oversight, timely reporting to NSF, and communication and other interactions with the LTER Network Office. The PI works closely with an Executive Committee comprised of the four signatory co-PIs to manage the project. Day-to-day administrative decisions are handled by the PI. The Executive Committee provides input on matters that require significant LTER resources (e.g., support for new investigators, reallocation of funds, etc.) or decisions that could significantly affect KNZ research groups or the program as a whole. For decisions requiring broader input and coordination, we have a KNZ LTER Scientific Steering Committee, consisting of the Executive Committee plus other key senior personnel. The Steering Committee meets for strategic planning following our annual research meeting, and as needed during the year to make decisions regarding scientific direction of the KNZ research program. Konza LTER researchers are clustered into Research Groups, based on common themes and/or questions, with designated leaders for each group (Table S1). Group leaders help coordinate activities and projects within, and across, thematic areas. Group leaders are consulted as needed regarding decisions about research areas/projects, allocation of LTER resources, or when specific requests for information or collaboration are received. Ultimately, authority for decisions regarding allocation of resources rests with the PI. LTER staff members are evaluated annually by an LTER Personnel Committee comprised of KNZ co-PIs and Senior Investigators, with the intention of defining individual responsibilities, evaluating annual performance, and setting goals for the upcoming year. The Personnel Committee reports to the PI, who makes decisions regarding reappointment and any merit-based salary increases.

In addition to fostering participation in KNZ project management, our administrative model seeks to maximize the involvement of KNZ investigators in LTER Network activities. Blair serves as the KNZ representative to the LTER Science Council, with other KNZ investigators attending and participating in Science Council meetings as appropriate. Minutes from these meetings and other Network correspondence are distributed to the entire KNZ group as appropriate. Individual participation in other LTER workshops is encouraged and supported whenever possible, especially for the LTER All Scientist Meeting. A large proportion of our KNZ investigators and graduate students attend this meeting.

We encourage collaboration and promote scientific and programmatic interactions among KNZ LTER investigators using multiple avenues for information sharing. All investigators (at KSU 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 the lead PI or "site-exec" are routinely forwarded to the KNZ Executive or Scientific Steering Committees or, if appropriate, to all KNZ investigators. In addition, a Konza listsery (Konza-l) provides a means of broadcasting announcements and disseminating information to all Konza researchers. During the academic year, we hold monthly meetings for all Konza scientists and graduate students, with off-campus participants joining by teleconference (e.g., Zoom). General announcements and research presentations comprise the format of these meetings, in addition to LTER planning or discussion of issues directly related to local or network-level LTER activities. On an annual basis, we host a Konza Prairie LTER Workshop. Offcampus researchers, local scientists, students, KNZ support staff, K12 educators, and docents attend these all-day workshops. Faculty, post-docs, graduate and undergraduate students are invited to present research results as oral or poster presentations, with ample opportunities for informal interactions, as well as a formal planning meeting for the Scientific Steering Committee and other senior personnel. The KNZ program has been very successful at attracting new investigators, from both KSU and other institutions,

and we will strive to expand our institutional and scientific diversity during LTER VII. The availability of KNZ resources and LTER data have been invaluable in attracting both KSU and non-KSU investigators. In addition to engaging new faculty members with LTER interests recently hired in Biology (Jesse Nippert 2007, Alice Boyle 2012, Lydia Zeglin 2014), we continue to engage, and support when possible, faculty members in other departments at KSU (John Harrington, Geography; Stacey Hutchinson and Trisha Moore, Bio/Ag Engineering; Natalie Mladanov, Civil Engineering; Chuck Rice, Agronomy) and from other institutions (Sara Baer and Matt Whiles, Southern Illinois University; Melinda Smith and Alan Knapp, Colorado State; Gail Wilson, Oklahoma State; Nate Brunsell and Gwen Macpherson, U Kansas; and Tim Crews, The Land Institute). We will continue to encourage use of the Konza site and KNZ LTER data by additional investigators as opportunities arise through a variety of mechanisms, including: on-site research support, support for new graduate students, opening the process of applying for LTER supplements to new researchers, providing LTER "seed money" to researchers that get involved during the course of LTER VII and, if feasible, more formal subcontracts. We will also continue to make an effort to engage junior faculty (e.g., Lydia Zeglin as leader of the Biogeochemistry Research Group) and to promote institutional diversity and gender equity in KNZ leadership positions (e.g., new co-PI role for Sara Baer).

The Konza Prairie LTER has been a successful model of the LTER Program goal of facilitating long-term, site-based research programs with a relatively stable funding base that 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, established experiments, and data collection efforts of the LTER sites (Callahan 1984). A group of KSU faculty led by G. Richard Marzolf initiated LTER I (1981-1986), implemented 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 Knapp, John Blair and Briggs, with co-PIs Hartnett, Kaufman, Walter Dodds and Loretta Johnson. Blair assumed administrative responsibilities at the midpoint of LTER IV, and served as lead PI of LTER V, with Knapp, Briggs, Hartnett, Johnson, Dodds and Kaufman as Co-PIs. Blair led LTER VI with Dodds, Anthony Joern, Hartnett and Jesse Nippert as Co-PIs. Briggs re-joined the KSU faculty in 2008 as Professor and Director of the Konza Prior Biological Station, a new position created to support continued growth of the Konza site and research base.

Research during LTER VII will continue to be led by Blair as PI, with Sara Baer (SIU), Dodds, Joern, and Nippert as co-PIs. An important reason for the continued scientific success of the KNZ LTER program has been shared intellectual leadership, and continuity of former PIs as Co-PIs with substantial advisory roles. Our current plans are to transition leadership of the Konza LTER Program from Blair to a new lead PI in the next funding cycle. We will work diligently to provide leadership training for this transition. We anticipate that a current co-PI will assume PI responsibilities for the next cycle. We expect to integrate younger, incoming faculty members to leadership roles by the next funding cycle, with at least one individual assuming the position co-PI. This approach has the advantage of broadening input into overall management decisions by including researchers at different career stages and research expertise, preparing a group of individuals to provide a logical succession of leadership for the future, and expanding diversity within the KNZ LTER Executive and Scientific Steering Committees. For example, a likely candidate to assume future leadership responsibilities is Lydia Zeglin. Lydia will join the KSU Biology faculty in Aug. 2014. She completed her graduate degree within the LTER network (SEV), and has had experience with KNZ LTER prior to arrival in a faculty position. Her tenure-track position was secured to add expertise in microbial ecology for our LTER program, and she brings significant talents in this regard. Our current plans are to integrate Lydia into the KNZ program while she develops her research program as a faculty member working towards tenure in the Division of Biology at KSU, and then provide opportunities for increased KNZ leadership roles in a logical and timely fashion.

Table S1 - Organizational structure of the Konza Prairie LTER Program

Executive Committee (PIs)

J. Blair, S. Baer, W. Dodds, A. Joern, J. Nippert

Scientific Steering Committee (in addition to PIs)

J. Blair, S. Baer, J. Briggs, W. Dodds, D. Hartnett, J. Haukos, A. Joern, A. Knapp, J. Nippert, M. Smith, L. Zeglin, Y Xia

Konza LTER Staff

Yang Xia (Information Manager); Amanda Kuhl (Field Coordinator); Rosemary Ramundo (Chemist/Lab Coordinator); Jeff Taylor (Research Assistant); Gene Towne (Plant Sampling and Fire/Bison Management); Jill Haukos (KEEP Director & Schoolyard LTER Coordinator)

Konza LTER Research groups

Primary affiliations are indicated, but most researchers participate in several groups. Bold font indicates group leaders/co-leaders. Asterisks indicate new LTER participants.

Fire/ grazing	Woody plant	Climate	Biogeo-	D4 4	Education &
studies L DI:	<u>expansion</u>	<u>change</u>	<u>chemistry</u>	Restoration	Outreach
J. Blair	J. Blair	J. Blair	J. Blair	S. Baer	J. Blair
A. Boyle*	J. Briggs	Alice Boyle*	M. Daniels*	J. Blair	J. Briggs
J. Briggs	W. Dodds	N. Brunsell*	W. Dodds	S. Collins	W. Dodds
S. Collins	D. Hartnett	M. Daniels*	A. Jumpponen	T. Crews	J. Harrington
T. Crews*	A. Knapp	W. Dodds	G. Macpherson	G. Wilson	J. Haukos*
W. Dodds	J. Nippert	K. Gido	N. Mladanov*		E. Horne
D. Hartnett	B. Sandercock	J. Harrington	C. Rice		B. Snyder
E. Horne		D. Hartnett	M. Smith		
W. Jensen		S. Hutchinson	M. Whiles	Synthesis	
A. Joern		A. Joern	L. Zeglin*	S. Baer	
A. Knapp		A. Knapp		J. Blair	
J. Nippert		G. Macpherson		J. Briggs	
B. Sandercock		N. Mladanov*		S. Collins	
M. Smith		T. Moore*		W. Dodds	
E. Towne		J. Nippert		D. Hartnett	
M. Whiles		C. Rice		A. Joern	
G. Wilson		B. Sandercock		A. Knapp	
L. Zeglin*		M. Smith		J. Nippert	
C		G. Wilson		M. Smith	
		L. Zeglin*		Y. Xia*	
				L. Zeglin*	