

Konza Prairie LTER Site Review

September 6-8, 2017

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

Assessing Sensitivity

Long-term Response to Drivers

Fire/grazing studies
ChANGE N experiment*
NutNet, P-Plot experiments

Alter Driver / Add Novel Driver

RaMPs experiment*
Irrigation Transect Study*
Grazing lawn manipulations*

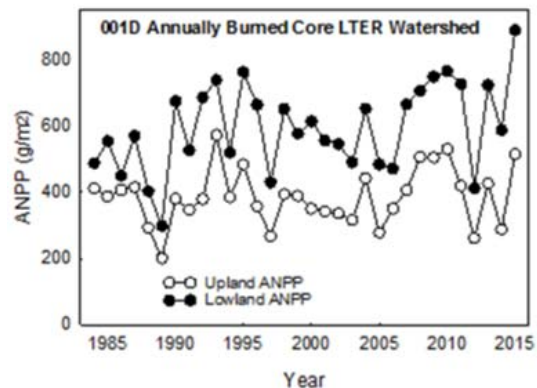
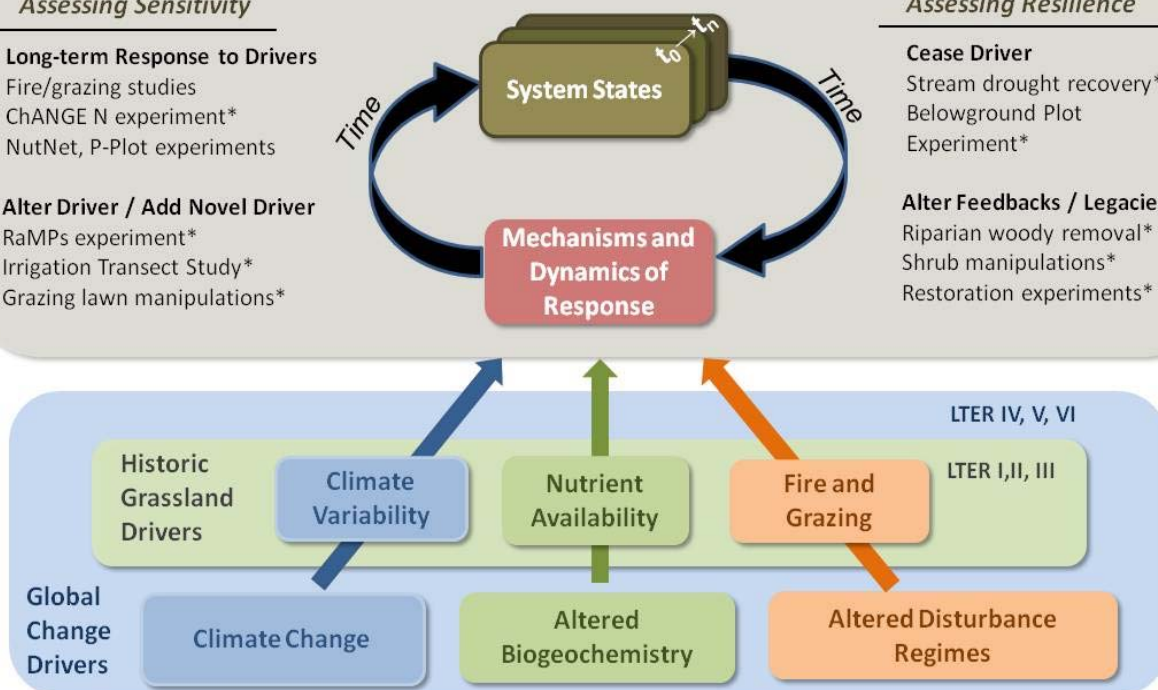
Assessing Resilience

Cease Driver

Stream drought recovery*
Belowground Plot
Experiment*

Alter Feedbacks / Legacies

Riparian woody removal*
Shrub manipulations*
Restoration experiments*





Research Treatments:

- N** Grazed by native herbivores (bison, year-round)
- K** Kings Creek north branch (ungrazed)
- C** Grazed by cattle (May - October)
- HQ** Headquarters area (experimental plots)
- AL** Lowland or agricultural land
- WP** White Pasture (leased for cattle grazing)
- 1,2,4,20** Years between burning (spring burns)
- A,B,C,D** Replicates of similar treatments
- W** Winter burn (Feb; annually)
- Su** Summer burn (Aug; every other year)
- F** Fall burn (Nov; annually)
- Sp** Spring burn (Apr; annually)
- R** Fire treatment reversals
- R1** 20 year interval through 2000, now annually burned
- R20** Annually burned through 2000, now every 20 years



----- Gravel Roads (Brown Dashed)

Revised August, 2017



White Pasture

[Pre-meeting: Aug. 30, 10:00-12:00; IM Technical Review]

Day 1 – Sept 6

7:40: Van pick-up at Fairfield Inn and transport to Konza Prairie

8:00: Overview presentations and discussion on selected LTER VII research foci (~18-20 minute talks to provide background and context for discussion; open question/discussion time after each talk).

Moderator - John Blair

SPEAKER	TOPIC
John Blair	Introduction & Overview of KNZ LTER Program
Tony Joern	Fire-Grazing Interactions and Landscape Heterogeneity
Jesse Nippert	Causes and Consequences of Woody Plant Encroachment
	--break / informal discussion--
Melinda Smith	Grassland Responses to Climate Variability and Climate Change
Walter Dodds	Aquatic Ecology and Biogeochemistry
	--break / informal discussion--
Lydia Zeglin	Soil Microbial Responses
Sara Baer	Grassland Restoration Ecology

Lunch: 12:00-1:00 Posters will be up for informal noon-time interactions. Brief tours of KPBS facilities (bison handling facilities, fire house, Hulbert Center) if desired.

1:00 – Field Trip to Selected Research Sites on KNZ Experimental Watersheds

[handouts provided with key findings, figures and references for each stop. See map for Stop # locations]

Stop	LOCATION	SPEAKER	TOPIC
1	WS N2B	Joern; Hartnett Dodds	Fire-Grazing studies Woody Removal Exp.
2	WS R1A/R20A	Briggs, Ratajczak	Fire reversal; LU/LCC legacies
3	WS 4B	Nippert, Ratajczak O'Connor, Taylor Brunsell	Woody encroachment Browsing project Eddy flux studies; C3/C4
4	WS 2C	Avolio; La Pierre	P-plots / NutNet / V-IV removal
5	WS 20B	Briggs, Nippert	Woodland state; fire effects
6	WS 1D/20C	Knapp Koerner Boyle	Freq. fire & ANPP GhostFire Grassland bird studies
7	WS K2A/C3SB	Joern, Briggs, Olson Santos	Patch-burn grazing experiment Iso-flux study
8	WS N4D	Dodds Macpherson, Sullivan Gido; Whiles	Stream studies Groundwater/hydrology studies Stream consumer dynamics

5:00 – Site Review team meeting (closed activity)

6:30 – 8:00 Group dinner at KPBS meeting hall (w/ Provost April Mason and KS TNC reps Rob Manes [State Director] and Brian Obermeyer [Landscape Programs Manager]) **followed by informal discussion and Q&A with KSU/TNC representatives; transport to Fairfield Inn afterwards**

Day 2 – Sept 7

7:40 Van pick-up at Fairfield Inn and transport to Konza Prairie

8:00 Field trip to selected HQ are experiments. See map for stop locations

Stop	LOCATION	SPEAKER	TOPIC
1	Belowground plots	Zeglin, Blair Wilson Smith	N enrichment effects Bothriochloa invasion/recovery ChANGE
2	Irrigation transect	Blair	Climate change legacies
3	CEE	Smith, Knapp	Extreme drought responses
	RaMPs	Knapp, Smith	Altered rainfall effects
4	Restoration expts.	Baer	Restoration dynamics

Break

10:45 – 12:00 Presentations/discussions on KNZ IM, education, and outreach

<i>SPEAKER</i>	<i>TOPIC</i>
Yang Xia	KNZ Information Management
Jill Haukos	Schoolyard LTER / KEEP activities
John Briggs	KPBS outreach

12:00- 1:00 Lunch (*informal discussions with investigators, staff, and students*)

1:00 – 2:00 Meeting with KSU administration representatives - Vice President for Research Peter Dorhout, College of A&S Dean Amit Chakrabarti, College of Agriculture Assoc. Dean Ernie Minton

2:00-3:30 Poster session and discussion with LTER graduate students / post-docs

3:30-5:00 Short (15 min) presentations on specific recent/new LTER VII research activities

Moderator – Jesse Nippert

<i>SPEAKER</i>	<i>TOPIC</i>
Alice Boyle	Avian studies
Andrew Hope	Small mammals; host-parasite interactions
Ellen Welti	Grassland consumer network responses to fire and grazing
Kim La Pierre	Synthesis across long-term Konza experiments
Zak Ratajczak	Thresholds and tipping points in grassland-woodland transitions
Nate Brunsell	Modeling atmospheric dynamics and landscape processes

5:00-6:00 Wrap-up and Synthesis

John Blair	KNZ Program Management, Integration and Training
Jesse Nippert	Synthesis, Cross-site and Network Contributions, and Future Directions

Review team transported to town for working dinner; dinner on your own for KNZ investigators

Day 3 – Sept. 8

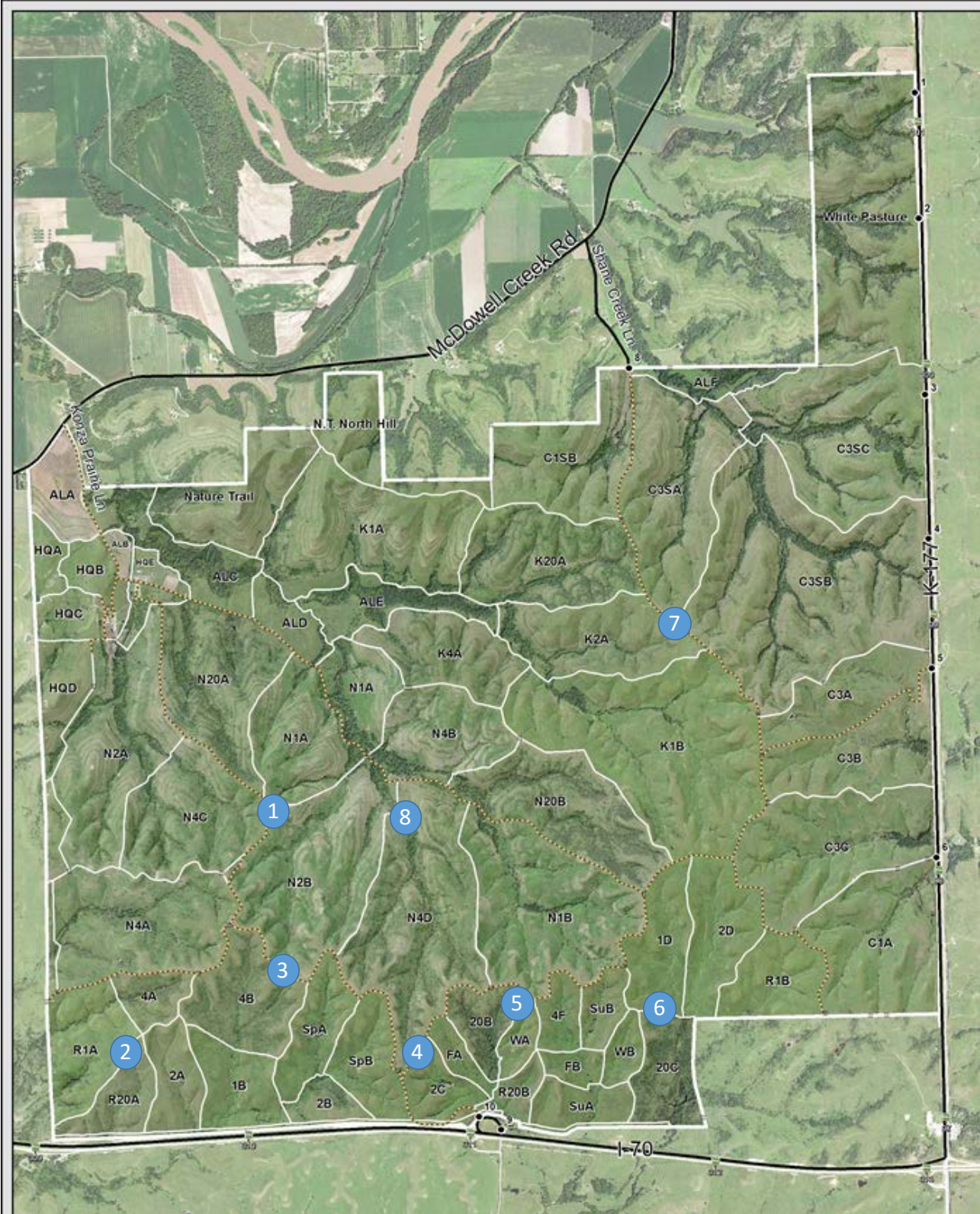
7:40 Van pick-up at Fairfield Inn and transport to Konza Prairie

8:00-12:00 Review Team finalizes site review and report (Hulbert Center)

12:00-1:00 Review team presentation of final report at Konza Meeting Hall

1:00 Transport back to town for lunch / meetings / departure

Day 1: Field Trip Stops – see schedule for topics and presenters



Day 2: Field Trip Stops – See Schedule for Topics and Presenters

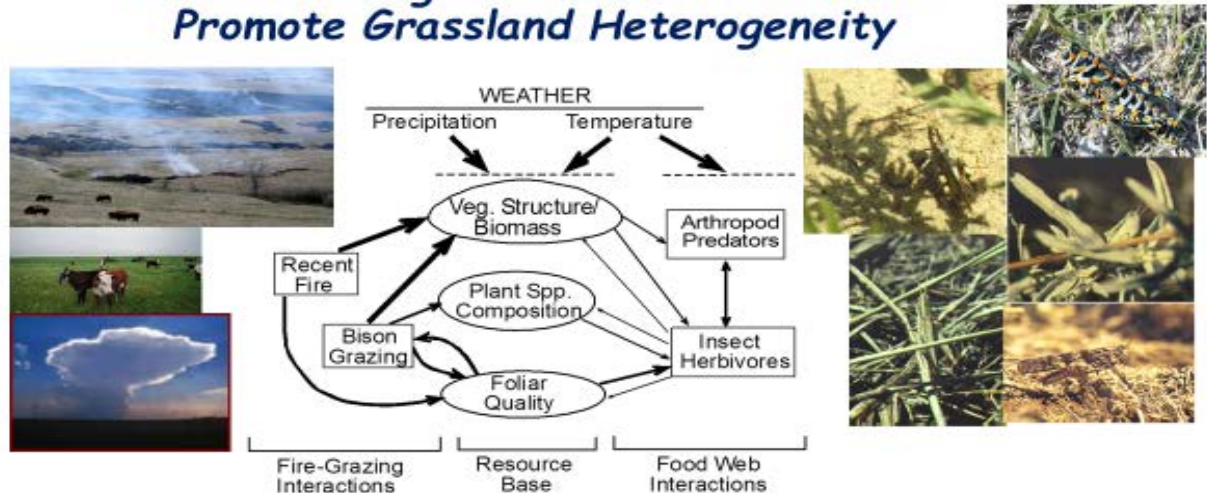


Spatial Heterogeneity and Bison/Fire Interactions; Arthropod Community Responses to Fire/Grazing Interaction (Grasshopper & Spiders)

Investigators: Anthony Joern, Doug Goodin, Angela Laws, *Ellen Welti, *Edward (E.J.) Raynor, *Jesus E. Gomez, *Bohua Ling *former graduate students

Motivation and Rationale – Fire-grazing interactions lead to a watershed-level template that shifts in time and space (climate impacts). These changes affect distributions, species diversity and abundances of most organismal groups examined (plants, grasshoppers, spiders, small mammals, birds).

Fire - Grazing - Climate Interactions Promote Grassland Heterogeneity



Basic Questions and Hypotheses:

- (1) How do burning, topography and weather affect resources and combine to determine bison distributions among watersheds? How does the addition of grazing to fire responses alter habitats for arthropod consumers?
- (2) How do fire-grazing interactions and climate variability manifest themselves in terms of vegetation structure and heterogeneity (habitat for consumers)?
- (3) Does arthropod community diversity increase with habitat structure and/or heterogeneity, and do communities shift across the landscape in time and space?
- (4) Does community network structure (trophic plant-herbivore and plant pollinator) vary in response to variable fire-grazing interactions?

Bison Patch/ Watershed Selection

- Recent fire activity determines the distribution of foliar [N] hotspots
- Recursive relationship with time delay: fire enhances grazer feeding / fire carries best without grazing
- Results of burning range from homogeneous with high biomass to patch with low biomass
- Bison respond directly to forage quality, measured as foliar [N], & bison distribution during growing season reflects distribution of foliar protein across watersheds



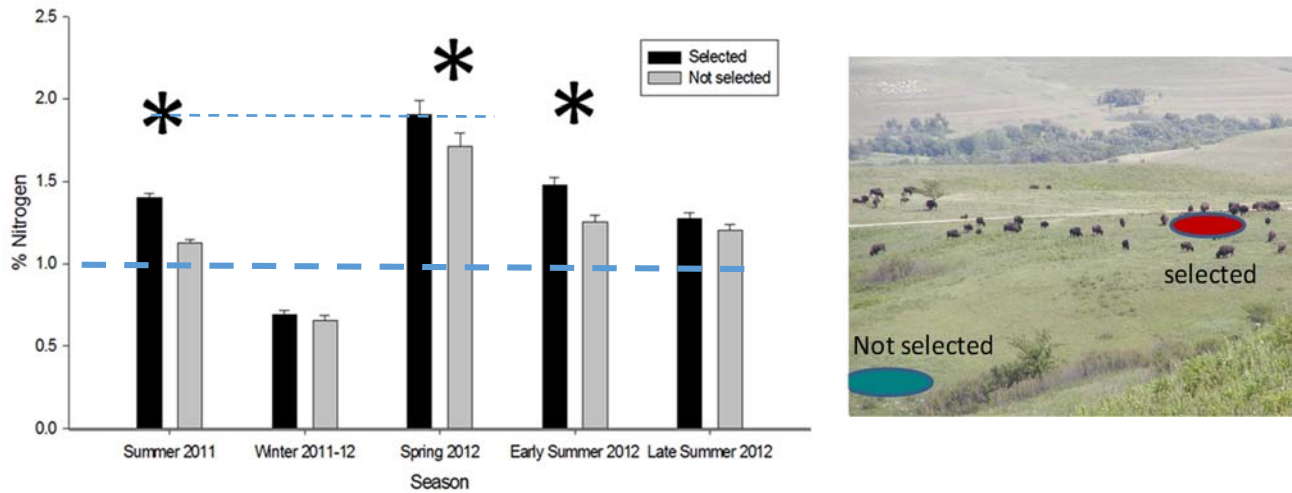


Fig. 1. Hierarchical foraging responses (e.g., Senft et al. 1987) result following burns, with impacts ranging from immediate feeding stations to seasonal watershed selection.

Arthropod Community Responses to Effects of fire & Grazing (Figures 2-5)

- Multiple habitat factors affect arthropod species diversity
- Arthropod diversity increases with habitat heterogeneity
- Vegetation used as consumer habitat responds to fire-grazing interactions as a shifting mosaic. Increased habitat diversity leads to increased arthropod community diversity
- Community taxonomic composition changes in response to vegetation (poster session: Gomez & Joern)



(Gomez & Joern. In revision. Ecological Entomology)

Fig. 2. Spider Diversity and Density

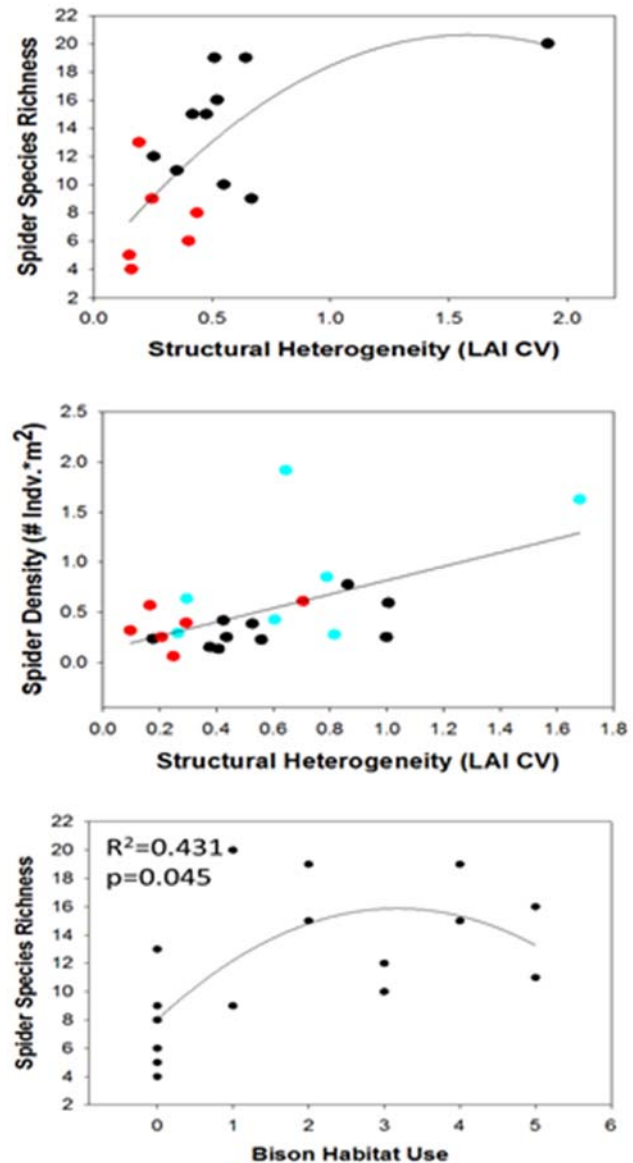
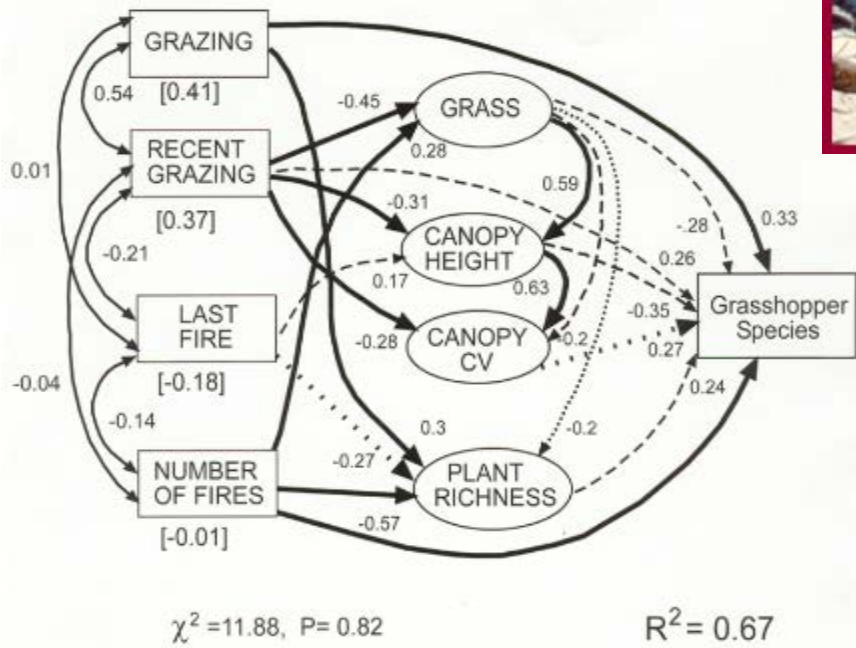


Fig. 3. Grasshopper Species Richness



Figs. 3-4. Structural equation models of spider diversity responses to fire and grazing for grasshoppers (Fig. 3, unpub.) and spiders (Fig. 4, Gomez & Joern, in revision, Ecological Monographs)

Fig. 4. Fire-grazing effects on spider species diversity.

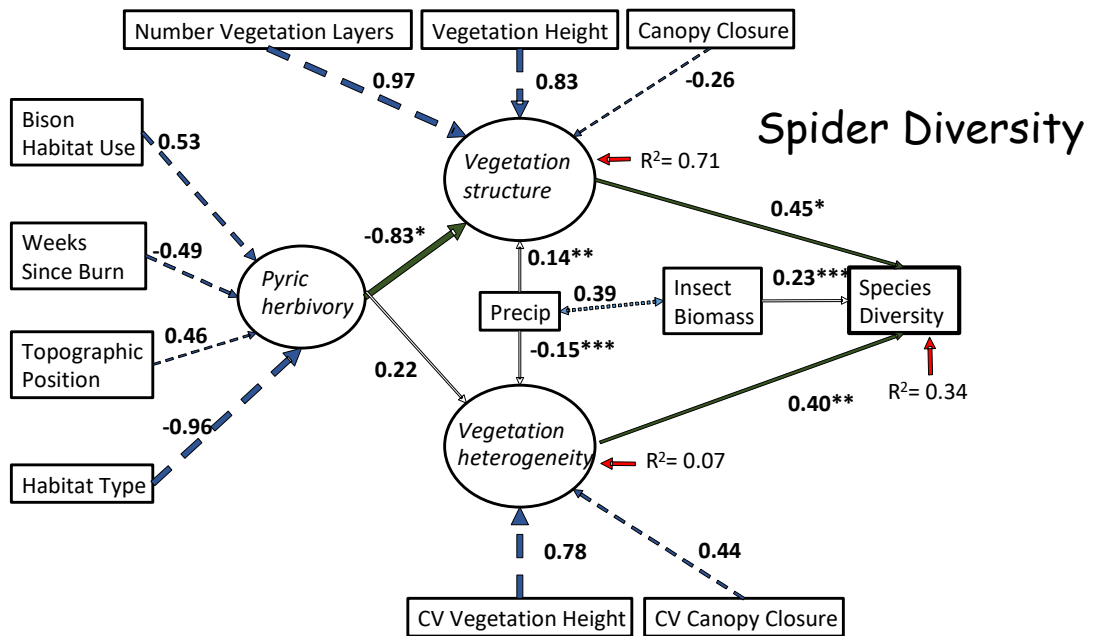
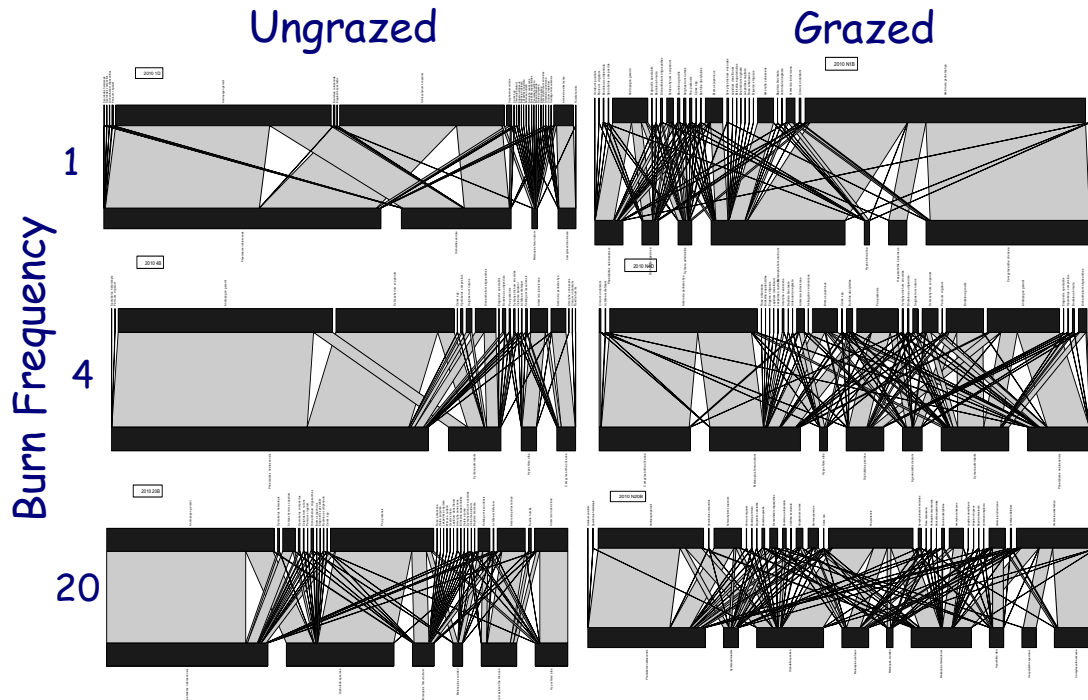


Fig. 5. Grasshopper Community Trophic Networks



Konza Grasshopper - Food Plant Networks

- Community network structure of grasshopper-plant interactions responds to fire-grazing interactions with consequences for the modularity, generalism and robustness (stability) of the community (Welti 2017 KSU Dissertation).

Representative References

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- Laws, A. and A. Joern. 2015. Predator-prey interactions in grassland food chains are context dependent. *Environmental Entomology* 44 (3): 519-528.
- Laws, A., J.L. Jonas, J. Gomez, and A. Joern. In review. Grasshopper community responses to fire, grazing, and nutrient addition in tallgrass prairie. *Range Ecology and Management* (in revision).
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- Raynor, E.J., A. Joern, and J. Briggs. 2015. Behavioral mechanisms of bison in response to fire and drought in nutritionally heterogeneous grassland. *Ecology* 96: 1586-1597.
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- Raynor, E.J., A. Joern, J. Nippert, and J.M. Briggs. 2016. Foraging decisions underlying restricted space-use: fire and forage maturation effects on large herbivore nutrient uptake. *Ecology and Evolution* 6:5843-5853.
- Raynor, E.J., A. Joern, A. Skibbe, M. Sowers, J.M. Briggs, A.N. Laws, and D. Goodin. 2017. Temporal variability in large grazer space use in an experimental landscape. In press - *Ecosphere*. doi: 10.1002/ecs2.1674.
- Russell D.M., B. Grudzinski, M. Daniels, W.K. Dodds, M.D. Daniels, A. Skibbe, and A. Joern. 2013. Blazing and grazing: influences of fire and bison on tallgrass prairie stream water quality. *Freshwater Science* 32: 779-791.
- Welti, E.L. and A. Joern. 2014. Structure of trophic and mutualistic networks across broad environmental gradients. *Ecology and Evolution* 5: 326-334.
- Theses: Gomez (2017), Raynor (2016) & Welti (2017)**
- KNZ Dataset: CGR02**

Plant Population and Community Response to Fire and Grazing: Grazing Lawn Studies

Investigators: David Hartnett, Anthony Joern, *Monica Shaffer, #Samantha Grieger

*graduate student; #undergraduate student

Rationale: Konza LTER data have shown that interactions between fire and grazing create a dynamic landscape mosaic of alternate vegetation states. High (annual) fire frequency alone reduces diversity and heterogeneity whereas bison grazing offsets these effects and increases floristic diversity and patch diversity and dynamics. Grazing lawns are patches of low-stature vegetation that support heavy grazing, potentially maintained as an alternate state by one or more positive feedback mechanisms (Archibald 2008, Croomsight and Olf 2008, Veldhuis et al. 2014) (Fig. 1,2). Because high grazing frequency/intensity on lawns results in minimal fuel loads, bison grazing lawns also represent a unique patch type of de-coupled fire x grazing interactions. Little is known about the initiation, maintenance, and ecological consequences of grazing lawns in temperate grasslands (Coppock et al. 1983) compared to well-studied grazing lawns in tropical grasslands and savannas (e.g. Bell 1971, McNaughton 1984, Bonnet et al. 2010, McIvor et al. 2005, Arnold et al. 2014). One central question we are addressing is whether bison grazing lawns are alternative stable states in tallgrass prairie maintained by internal positive feedbacks, or do they require a consistent “press” (bison activity) to persist.



Questions and Hypotheses: We are currently addressing several key questions using field and laboratory studies (begun in November 2015, and a grazing lawn “priming” experiment to begin in May 2018). Specifically:

(1) What feedback mechanism(s) maintain grazing lawns? We are testing the hypothesized nutrient-based pathway, demographic-structural change pathway, water-based pathway, and plant-soil microbial feedback pathway (Figs.1,2)

(2) What are the distinguishing characteristics of

vegetation on tallgrass prairie grazing lawns? We are testing the alternative hypotheses that differences in characteristics between grazing lawns and tallgrass swards are due to: a) differences in plant species composition (Veblen 2012), and/or b) intraspecific variation in plant traits (Arnold et al. 2014).

(3) How do grazing lawns affect plant species diversity at different scales? We hypothesize that the additive or synergistic effects of multiple bison activities generates hotspots of floristic diversity on grazing lawns relative to other patch types on the tallgrass prairie landscape

(4) How resistant/persistent are grazing lawns? Once established, do grazing lawns remain spatially static, or do they migrate/expand/contract over time? Is there a threshold frequency of use that leads to degradation or to an alternate state? Are there threshold levels of vegetation traits that lead to lawn abandonment? (Fig.7)

(5) Does the soil bud bank confer resiliency to intense/frequent defoliation on grazing lawns? Our ongoing studies have shown that plant population dynamics on tallgrass prairie are strongly driven by belowground bud bank dynamics rather than aboveground seed reproduction (e.g. Benson et al. 2004, Ott and Hartnett 2012a,b) and we hypothesize that the maintenance of a belowground bud bank is a key trait explaining the high resilience of grassland plants to high grazing frequency on grazing lawns and lawn persistence.

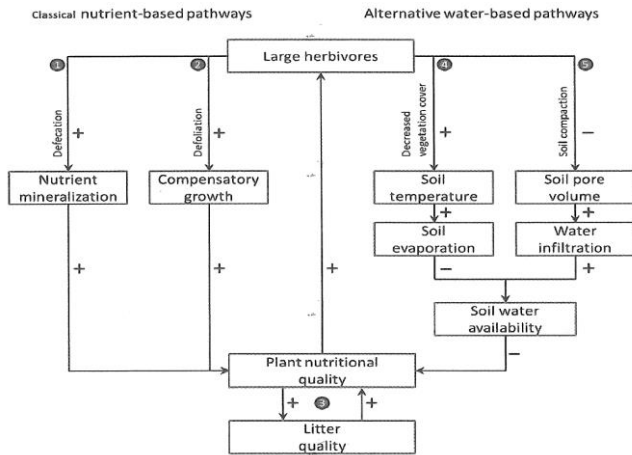


Fig. 1 – Hypothesized nutrient-based and water-based positive feedback mechanisms maintaining grazing lawns.

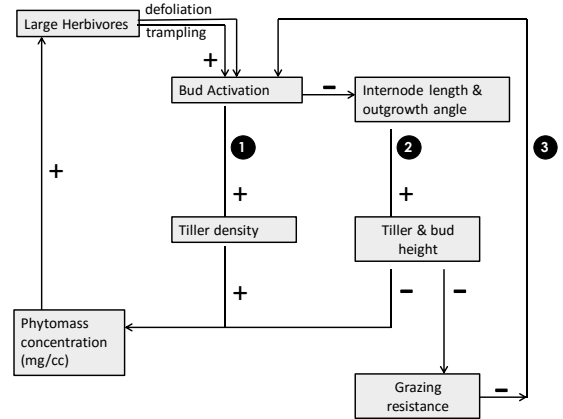


Fig. 2 – Positive feedbacks through plant architectural/demographic shifts that increase foraging efficiency

Representative Results to Date

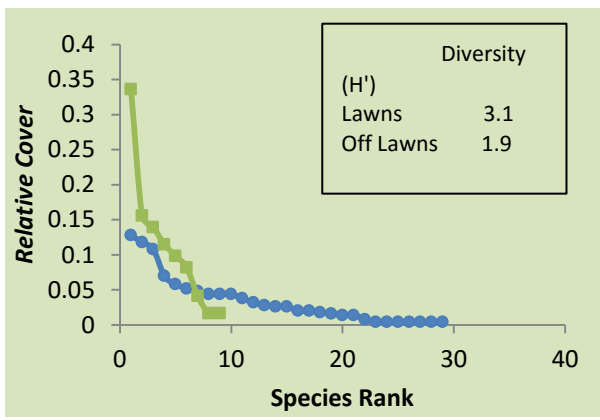


Fig. 3– Lawns have higher species diversity, richness and evenness; and distinct species assemblages.

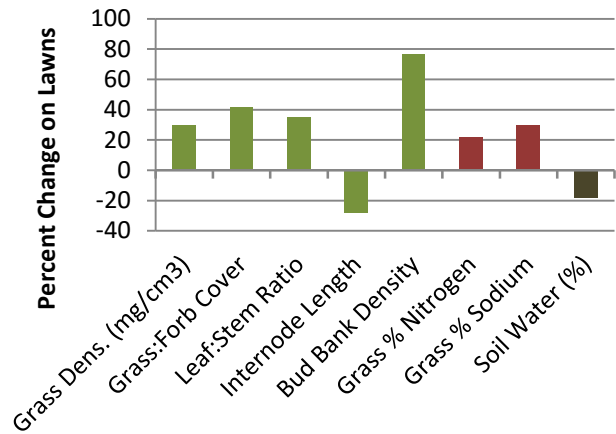


Fig. 4 – Lawns have distinct vegetation and soil characteristics, with strong evidence for positive plant-grazer feedbacks.

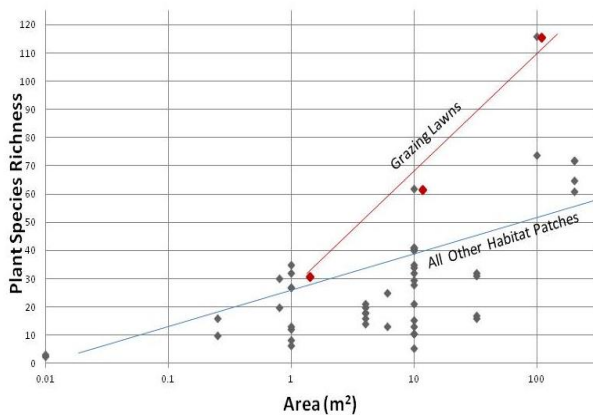


Fig. 5 – Grazing lawns are hotspots of floristic diversity on the tallgrass prairie landscape.

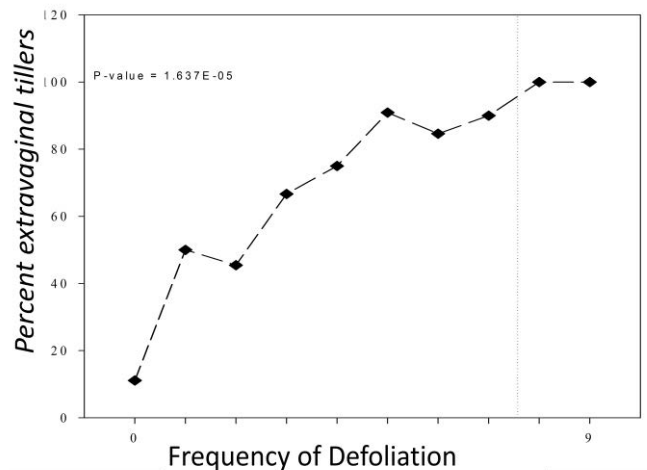
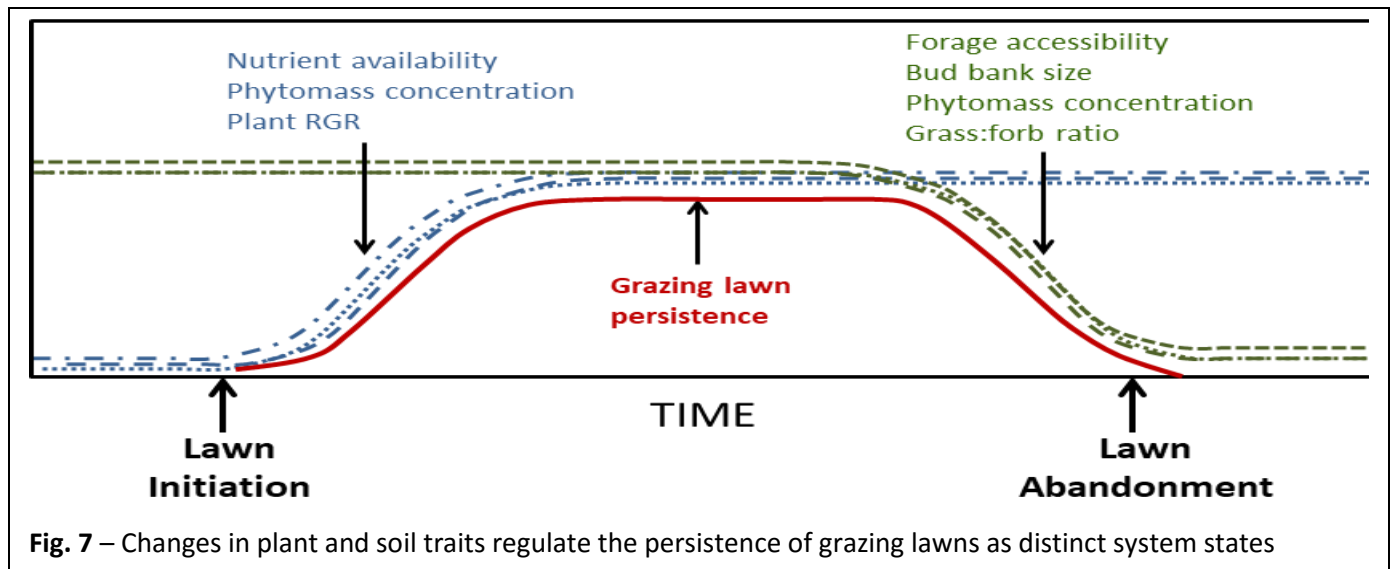


Fig. 6 – High defoliation frequency on grazing lawns results in plant architectural shifts that increase foraging efficiency.



Citations and Selected References:

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- Arnold, S.G., T.M. Anderson and R.M. Holdo. 2014. Edaphic, nutritive, and species assemblage differences between hotspots and matrix vegetation: Two African case studies. *Biotropica* **46**: 387-394.
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- McIvor, J.G., S. McIntyre, I. Saeli and J.J. Hodgkinson. 2005. Patch dynamics in grazed subtropical native pastures in south-east Queensland. *Austral Ecology* **30**: 445-464.
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- Schrama, M., G.F. Veen, E.S. Bakker, J.L. Ruifrok, J.P. Bakker and H. Olff. 2013. An integrated perspective to explain nitrogen mineralization in grazed ecosystems. *Perspectives in Plant Ecology, Evolution and Systematics* **15**: 32-44.
- Veblen, K.E. 2012. Savanna glade hotspots: Plant community development and synergy with large herbivores. *Journal of Arid Environments*. **78**: 119-127.
- Veldhuis, M. P., R. A. Howison, R. W. Fokkema, E. Tielens and H. Olff. 2014. A novel mechanism for grazing lawn formation: large herbivore-induced modification of the plant-soil water balance. *Journal of Ecology* **102**: 1506-1517.

Woody Riparian Vegetation Removal Experiments

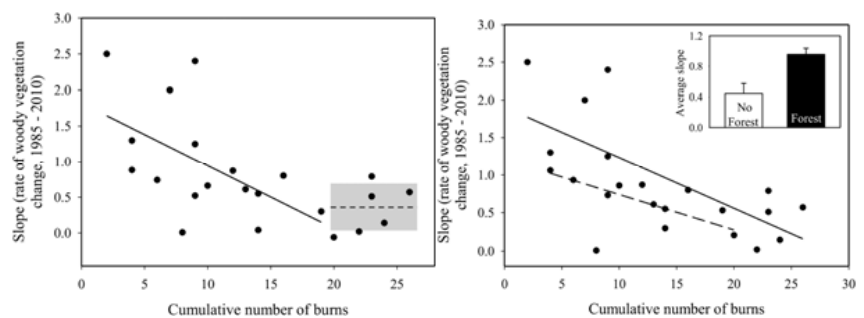
Investigators: Walter Dodds, Jesse Nippert, Matt Whiles, *Bartosz Grudzinski, *Danelle Larson, *Allison Veach, #James Guinnip *former graduate students; #current graduate students

KNZ Data sets: ASD02, ASD04, ASD05 for discharge; ASW01 stream suspended sediments, and NWC01 stream nutrients.

Rationale: Tallgrass prairie streams are among the most endangered ecosystems in North America. Tallgrass prairie has been reduced to a few percentages of its former extent, but an even smaller portion of the remnants encompass whole watersheds. While scientists have produced many publications on forested streams, far fewer studies have been done on streams in other biomes, including grasslands and wooded grasslands (Dodds et al. 2004, 2015). Though the streams of grasslands originate in relatively dry habitats, they cover almost 1/3 of the terrestrial area on Earth and are responsible for around 1/5 of global runoff. Woody vegetation is a major threat to grasslands, and has been increasing along riparian corridors on Konza since at least the 1930's (Fig 1). Our central hypothesis is that woody vegetation expansion fundamentally alters grassland stream communities and ecosystem processes by shifting the primary base of the food web from autochthonous to allochthonous carbon sources. Our large-scale vegetative removal experiment is an expansion on previous LTER work where we compared naturally forested, open grassland stream or experimentally removed woody vegetation along smaller areas (30 m stream length, 30 m on each side).

Woody removal allowed streams to approximate naturally open reaches including stream metabolism and algal and macroinvertebrate communities (Riley and Dodds 2012, Vandermyde and Whiles 2015). Woody removal stimulated riparian and benthic denitrification (Resinger et al. 2013). These experiments could not show the whole-watershed effects of woody expansion such as stream chemistry and discharge influences.

Figure 1. Rate of woody riparian expansion from 1985-2010 on Konza (Veach et al., 2014). A threshold occurred at about a 2-year burn return time, left. Same data with sites that were forested in 1985 contrasted to those with little woody riparian vegetation.



Basic Questions:

(1) Does woody expansion increase the probability of stream drying? Days of stream drying each year have increased over the last 30 years, without any substantial directional change in total precipitation, temperature, or evapotranspiration. Woody vegetation can decrease stream flow is controversial (e.g. Huxman et al. 2005, Wilcox et al. 2005), but our initial hypothesis was that discharge would decrease. (2) What are the biogeochemical consequences of removing woody riparian growth?

We predicted an increases in nutrient export as woody vegetation buffers intercept nutrients entering stream channels. This hypothesis is based on whole-watershed vegetation removals from deciduous forests (Likens 2013). We did a before-after control-impact (BACI) whole-watershed woody removal experiment to explore these questions. For impact, woody vegetation was cut for 30m on each side of the main channel and 10m on each side of the smaller channels in watershed N02B. A total of 4.8 km of stream channel were treated. About half of the stream riparian areas are re-cut every winter to maintain the treatment (Fig. 2).

Figure 2. Before (left) and after (right) woody riparian removal in watershed N02B



Representative Results to Date:

In general, we saw little influence on stream discharge but this response may not be detectable with such high variance. Isotopic data (unpublished) indicate woody riparian vegetation relies on different water sources (deep soil moisture) that is disconnected from the stream water sources. We observed very large increase in sediments and nutrients for the first few years after the removal then a return to control levels (Figs. 3&4). As expected, the removals caused shifts in soil microbial communities; Cyanobacteria, Ascomycota, Chytridiomycota and Glomeromycota relative abundances were greater in removal areas (Veach et al. 2015). Pre-measurements were made of channel geomorphology and these will be repeated in two years.

Figure 3. Sediment increases and nitrate associated with woody removal. BACI confirms a significant treatment effect (Larson et al. submitted, A-D).

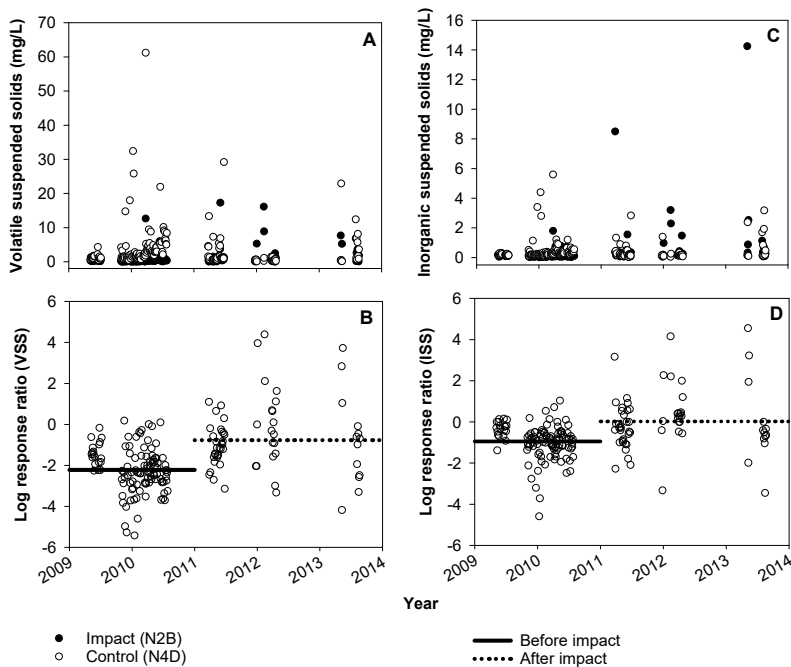
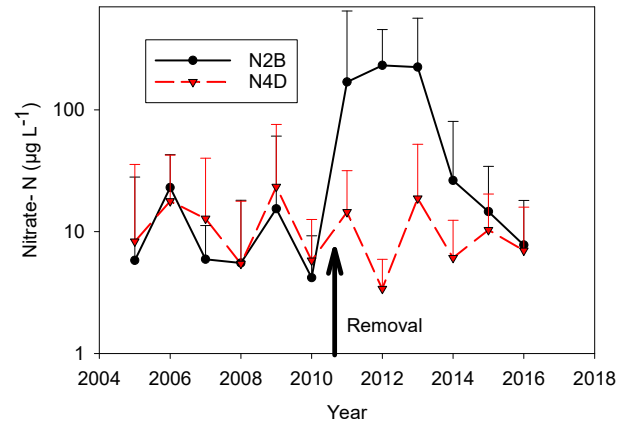


Figure 4. Record of nitrate conc. (note log scale)



Citations and Selected References

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- Riley, A. J., and W. K. Dodds. 2012. The expansion of woody riparian vegetation, and subsequent stream restoration, influences the metabolism of prairie streams. *Freshwater Biology* **57**:1138-1150.
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- Veach, A. M., W. K. Dodds, and A. Jumpponen. 2015. Woody plant encroachment, and its removal, impact bacterial and fungal communities across stream and terrestrial habitats in a tallgrass prairie ecosystem. *FEMS microbiology ecology* **91**:fiv109.
- Wilcox, B. P., M. K. Owens, R. W. Knight, and R. K. Lyons. 2005. Do woody plants affect streamflow on semiarid karst rangelands? *Ecological Applications* **15**:127-136.

Fire Reversal Experiment

Investigators: John M. Briggs, John M. Blair, Scott L. Collins, Jesse Nippert, Jeff Taylor and Zak Ratajczak

Long-term fire treatments were ‘reversed’ in 2001: two watersheds previously burned every 20 years were switched to an annual fire frequency (Fig 1A), and two watersheds burned annually were switched to a (planned) 20-year fire interval (Fig 1B). Annual fire in long-term unburned areas quickly resulted in increased cover and biomass of grasses in many plots (Fig 1C). However, some plots have shown very slow recovery rates (Fig 1B) and while woody plant expansion has ceased, 16 years of prescribed annual fires has not removed established woody vegetation (Fig 2). Switching from infrequent fire to annual burns (Fig 1B) has elicited slower responses. We attribute these time-lags to initially slow rates of growth by juvenile woody plants and the importance of grass meristems, which decrease the rate of grass loss (Spasojevic et al. 2010, Ratajczak et al. 2017a,b, Briggs et al. *In Prep*).

We are continuing to use these experiments to understand the reversibility of changes in plant communities and ecosystem functions, looking at long-term states, time-lags, and how they vary over space. Data from this experiment have also been used to assess so-called “early warning signs” that locations are coming close to community thresholds (Ratajczak et al. 2017a). In 2011, a portion of the reversal watersheds were affected by a mid-drought wildfire, which are predicted to become more frequent with climate change. We are using this “natural experiment” to determine the resistance and resilience to combinations of novel disturbance and climate extremes (*In revision*).

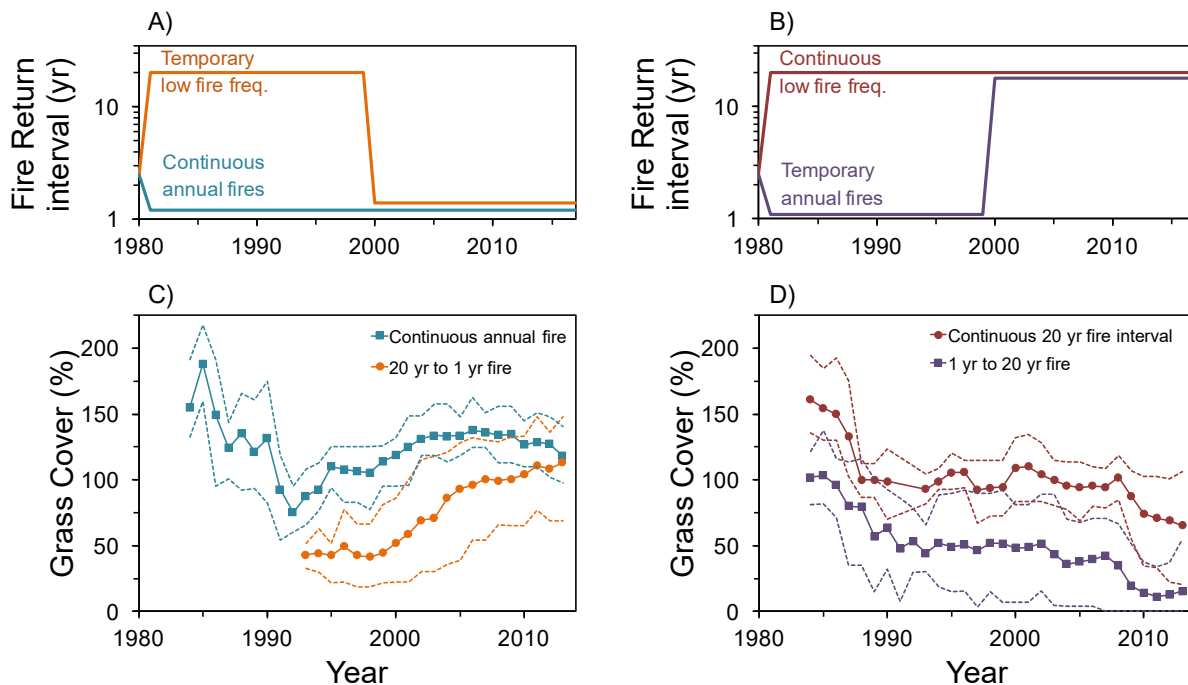


Fig. 1. (A) and (B) are patterns of fire interval change in the reversal experiments (orange and purple lines) relative to long-term fire treatments initiated at the beginning of the Konza LTER (teal and red lines). (C) and (D) show changes in grass cover, with markers and solid lines denoting average cover each year and dashed lines denoting the 5th and 95th percentiles of plots, which shows how responses vary over space. (Figures modified from Ratajczak et al. 2017a,b). All data are from lowland plots.

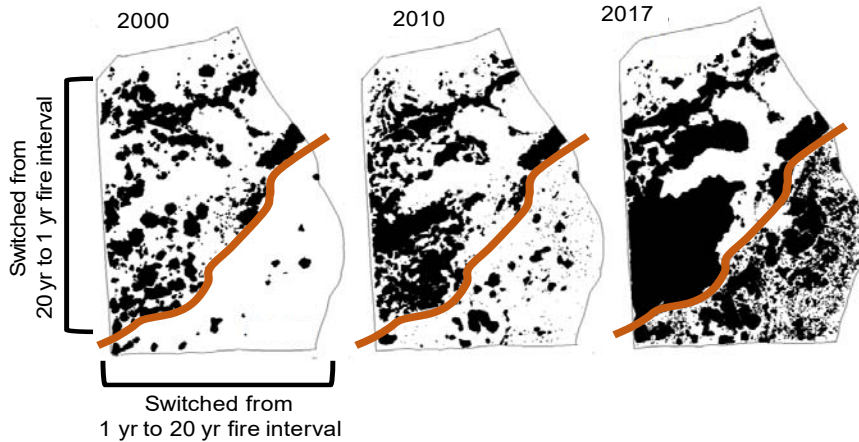


Fig. 2. Cover of all shrub species from 2000 (1 year before the treatments were reversed) to 2017 on one set of the fire reversal watersheds. The orange line separates the two reversal watersheds and black shading denotes shrub canopies. Shrub height is not shown, but freq. fire reduces shrub height. Trees are not shown but show a similar pattern. After 16 years of

annual fire, the watershed formerly under a 20-yr fire interval has lost only one woody species (*Juniperus virginiana*). Seven new tree species have been recorded watershed R1 to 20 (Briggs et al *In Prep*).

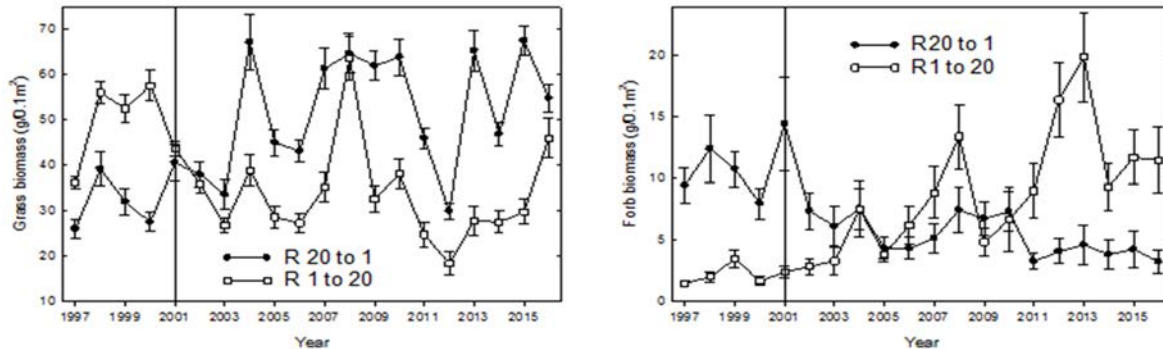


Fig. 3. Grass biomass (left panel) and forb biomass (right) from 1997 to 2016 in lowland soils sites. The vertical line designates the switch in fire frequency. Annual fire in long-term unburned areas quickly results in increased cover and biomass of grasses while suppression of fire in the annual burned watersheds resulted in increased forb biomass. From 1997-2000, total (data not shown) and grass biomass were significantly higher on R1 to 20 when compared to R20 to 1, and forb biomass was significantly higher on R20 to 1 then R1 to 20. From 2001-2016, total and grass biomass were significantly higher on R20 to 1 when compared to R1 to 20 and forb biomass was significantly higher on R1 to 20 then R20 to 1.

KNZ Long-term data sets:

CSM05--Seasonal summary of numbers of small mammals on the six LTER traplines in prairie habitats on which fire regime has been reversed at Konza Prairie.

NSC01--Chemistry and Physical Characteristics of Soils from Konza LTER Watersheds with different fire and grazing treatments.

PAB05--Aboveground Net Primary Productivity of Tallgrass Prairie Based on Accumulated Plant Biomass on the LTER Fire Reversal Experiment Watersheds.

PRE02--Reproductive Effort of Big Bluestem, Indiangrass and Little Bluestem on Selected Konza Prairie LTER Watersheds.

PVC02--Plant Species Composition on Selected Watersheds at Konza Prairie.

PWV01--Cover of Woody Vegetation at Konza Prairie.

Literature Cited

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Woody Shrub Encroachment Leads to Alternative Stable States

Investigators: J. Blair, J. Briggs, N. Brunsell, J. Nippert, Z. Ratajczak, K. O’Keefe*, R. O’Connor#, B. Hoch[‡] *former grad students; # current grad students; ‡ REU student

During LTER V and LTER VI, the drivers and consequences of shrub encroachment in tallgrass prairie were identified. Reduced fire frequency permits rapid shrub expansion, especially in deep-soil lowland sites (Briggs et al. 2005). Shrub expansion alters carbon dynamics (Knapp et al. 2008) and reduces biodiversity (Ratajczak et al. 2012). Current research focuses on identifying the ecological mechanisms that underpin shrub encroachment and its interactions with fire, climate, and other global change pressures.

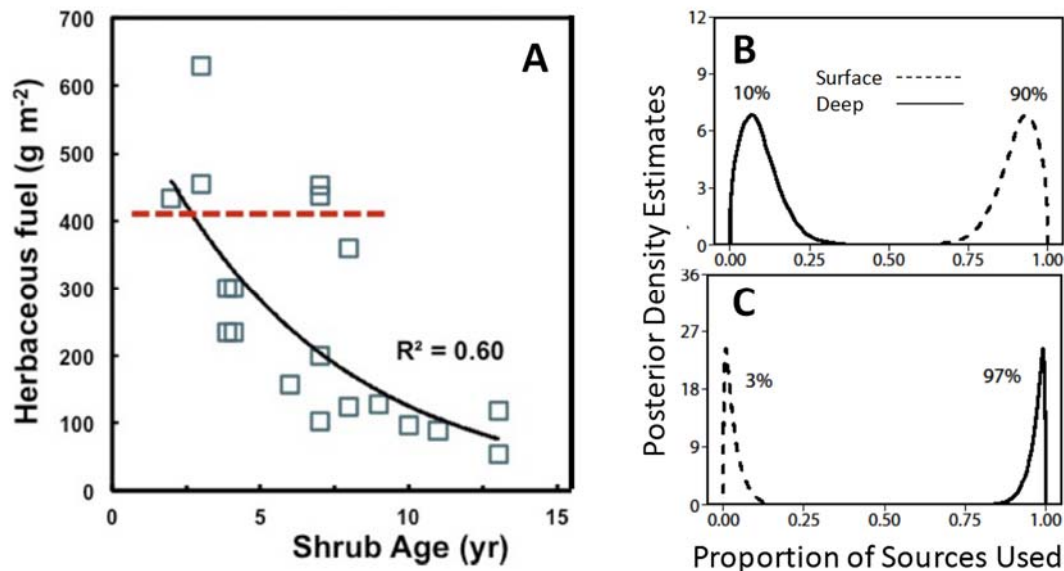


Fig. 1A: As shrub age and size increases, herbaceous fuel declines, reducing fire effectiveness. The red line indicates average fuel in open grassland. B/C: Stable isotopic analyses illustrate niche partitioning, as clonal shrubs (B) avoid competition with grasses (C) by using water from deeper in the soil profile (Ratajczak et al. 2011; O’Keefe and Nippert 2017).

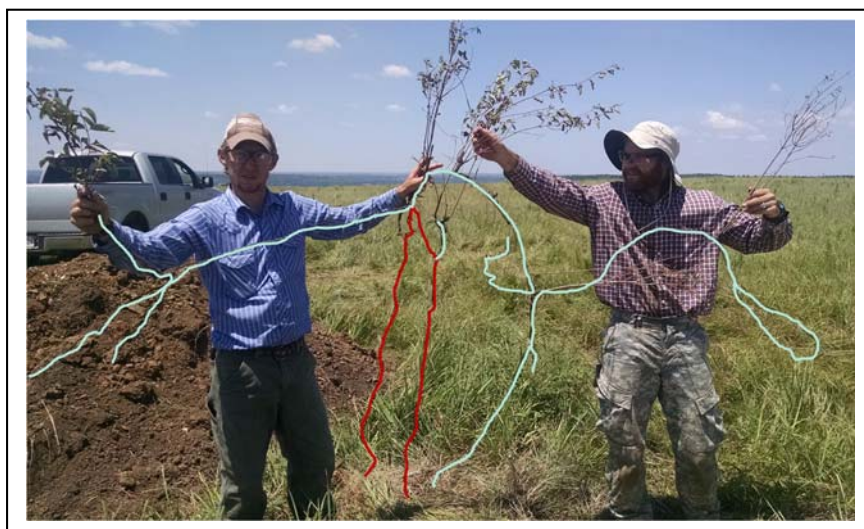


Fig. 2: Rough-leaf dogwood allocates >90% of root biomass to lateral roots (blue shading) that link aboveground ramets. Water is accessed > 1m deep by only a few deep roots (red shading) then supplied to all ramets via lateral roots. Only 1-5% of all root production occurs in the top 30 cm where grass root density is the highest. PhD students O’Connor and Bachle shown here.

Reduced fire effectiveness and decreased competition with grasses for water in shallow soil layers promote the development of positive feedbacks. These positive feedbacks result in hysteresis, where climate extremes and returning frequent fire does not reverse shrub expansion (Ratajczak et al. 2014).

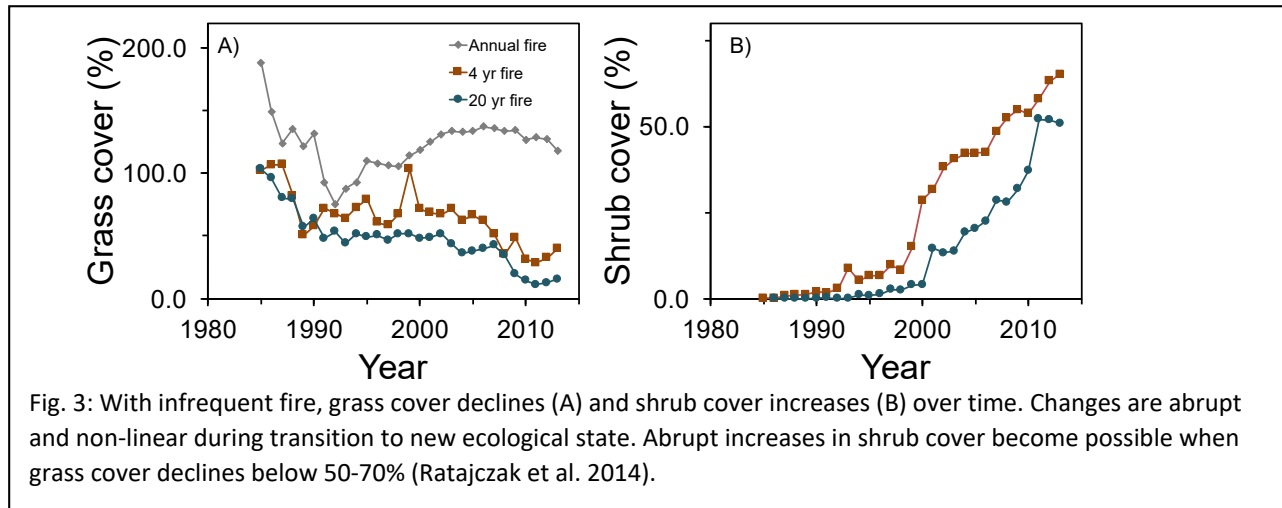


Fig. 3: With infrequent fire, grass cover declines (A) and shrub cover increases (B) over time. Changes are abrupt and non-linear during transition to new ecological state. Abrupt increases in shrub cover become possible when grass cover declines below 50-70% (Ratajczak et al. 2014).

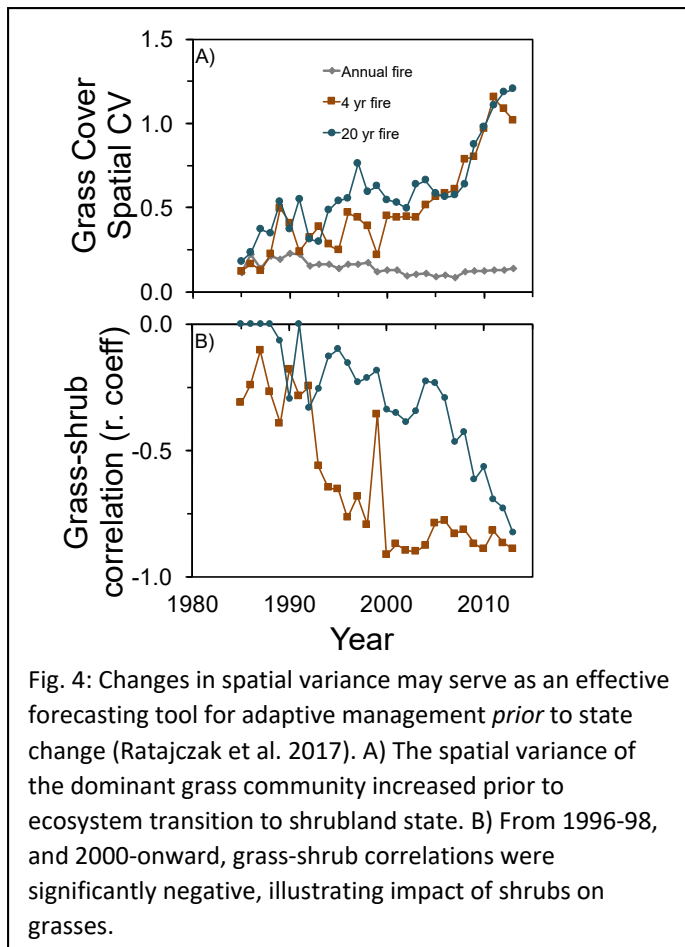


Fig. 4: Changes in spatial variance may serve as an effective forecasting tool for adaptive management *prior* to state change (Ratajczak et al. 2017). A) The spatial variance of the dominant grass community increased prior to ecosystem transition to shrubland state. B) From 1996-98, and 2000-onward, grass-shrub correlations were significantly negative, illustrating impact of shrubs on grasses.

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KNZ LTER Datasets used: PVC02

Browsing and Fire Effects on *Cornus drummondii*

Investigators: Rory O'Connor*, Jeff Taylor, Mira Ensley-Fields†, Jesse Nippert

*current graduate student, †REU Student

Historically, North American tallgrass prairie had a suite of large herbivores that not only grazed (i.e. bison) but also browsed (i.e. elk, pronghorn). Elk once maintained similar herd sizes as bison but were completely extirpated by the late 1800's (Shaw 1996), releasing woody plants from browsing pressure. Concurrent decreases in fire frequency and intensity have contributed to woody expansion. Two groups of woody species contribute to expansion: non-resprouting species killed with fire; and resprouting species that cannot be killed with fire (Knapp et al. 2008, Ratajczak et al. 2014). With the release from browsing pressure and fire, resprouting woody species require additional active management strategies. In this study we investigate community, stem density and physiological effects of continuous simulated browsing and prescribed fire on *Cornus drummondii*, a resprouting woody species. These results help us to understand how the interaction of multiple drivers (fire and browsing) impact woody expansion in resprouting species.

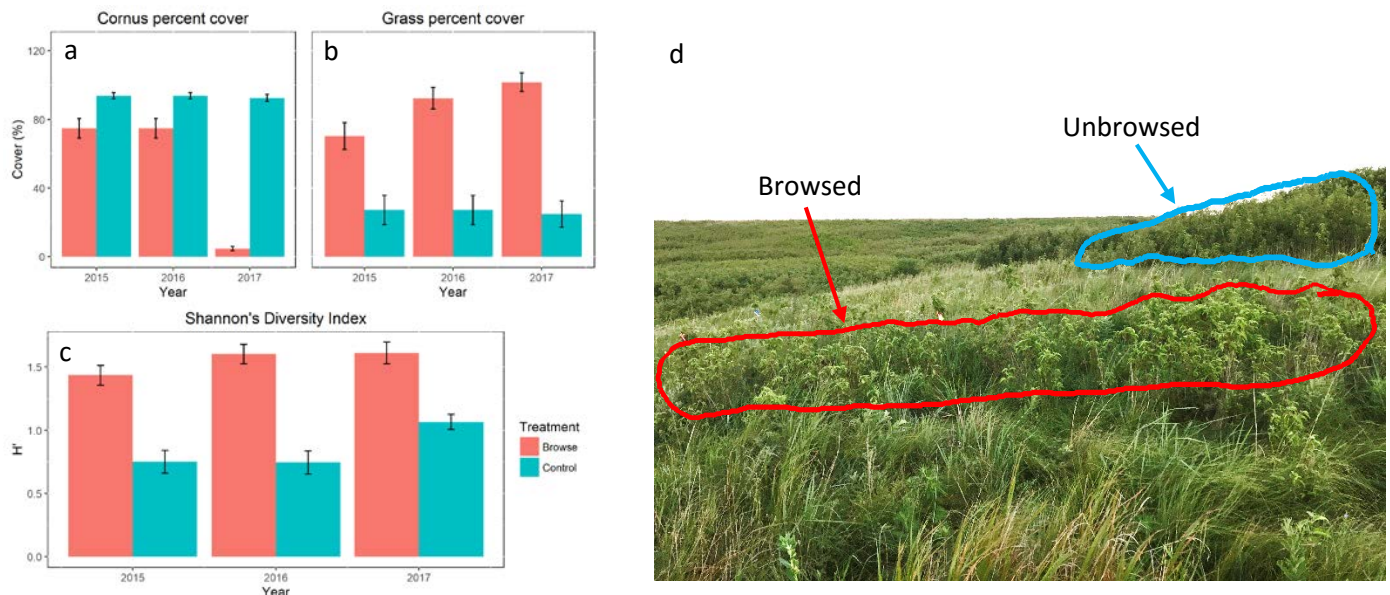


Figure 1. **(a)** Browsing reduced *Cornus drummondii* cover while allowing **(b)** grass cover to increase substantially each year. **(a & b)** Increases in grass cover led to a fine-fuel buildup and in 2017 watershed 4B was burned causing a 70% decrease in *Cornus drummondii* cover while increasing grass to 100% cover. **(c)** The increase in grass cover also allowed for other herbaceous species to re-establish allowing for a slow increase in species diversity within the *Cornus drummondii* shrub island. **(d)** Browsed islands are shorter in stature which allows for the increases in light for herbaceous plant growth.

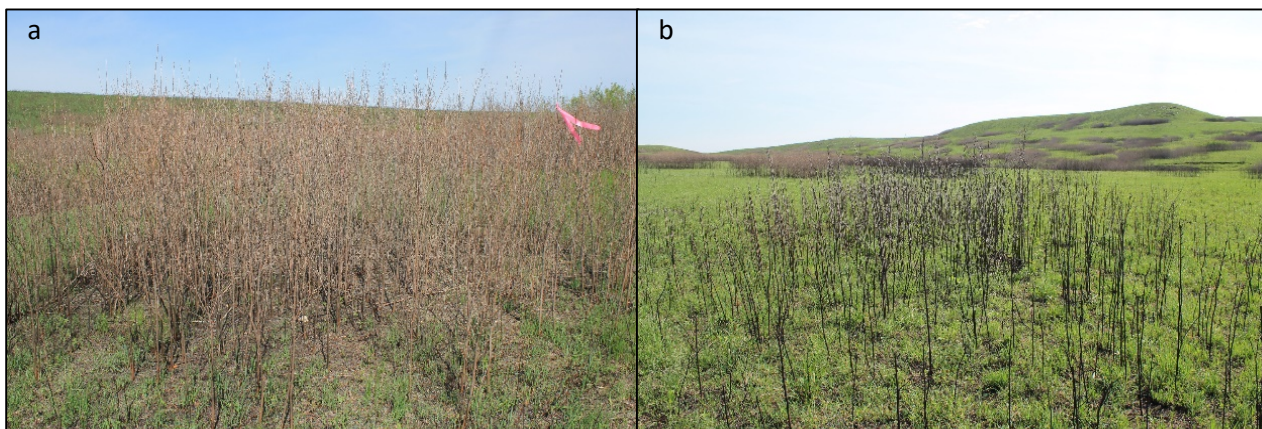


Figure 2. Two *Cornus drummondii* shrub islands of similar size. **(a)** A browsing control shrub island that had fire burn through the understory but not kill the ramets. **(b)** is a browsed shrub island that had 100% fire top kill of all ramets. Photo taken in May 2017, one month after the prescribed fire.

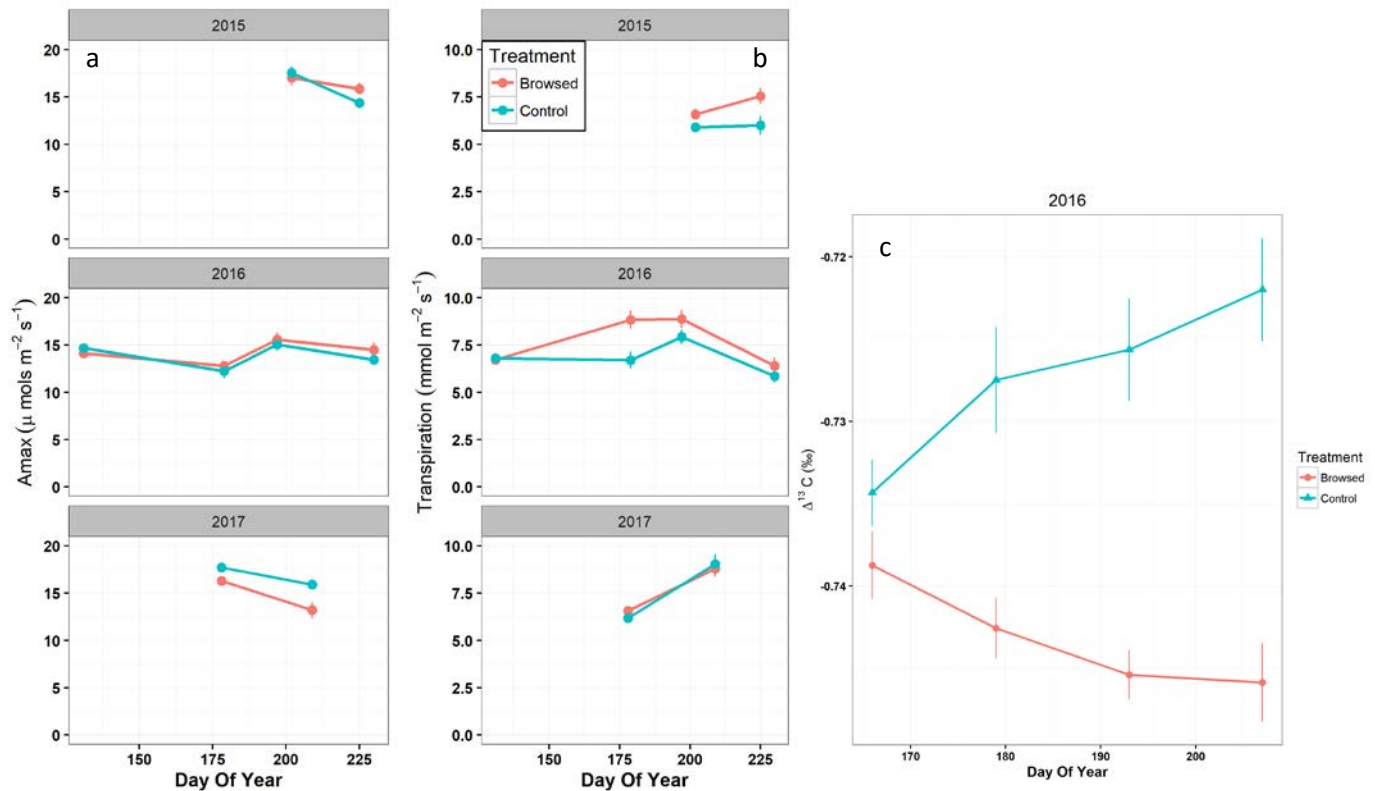


Figure 3. (a) For the first 2 years (2015 and 2016) photosynthetic rates (A_{max}) of browsed *Cornus drummondii* shrub islands saw no changes in rates compared to the control, unbrowsed, shrub islands. In 2017 after the prescribed fire and with continued browsing, photosynthetic rates decreased for the browse treatment compared to the control. (b) Transpiration rates were higher for the browsed shrub compared to the control shrubs until 2017 when transpiration rates were similar. (c) In 2016, $\Delta^{13}\text{C}$ or the integrated water use efficiency of *Cornus drummondii* showed that over the growing season browsed shrubs kept their stomata open wider allowing for increased rates of transpiration compared to the unbrowsed shrubs.

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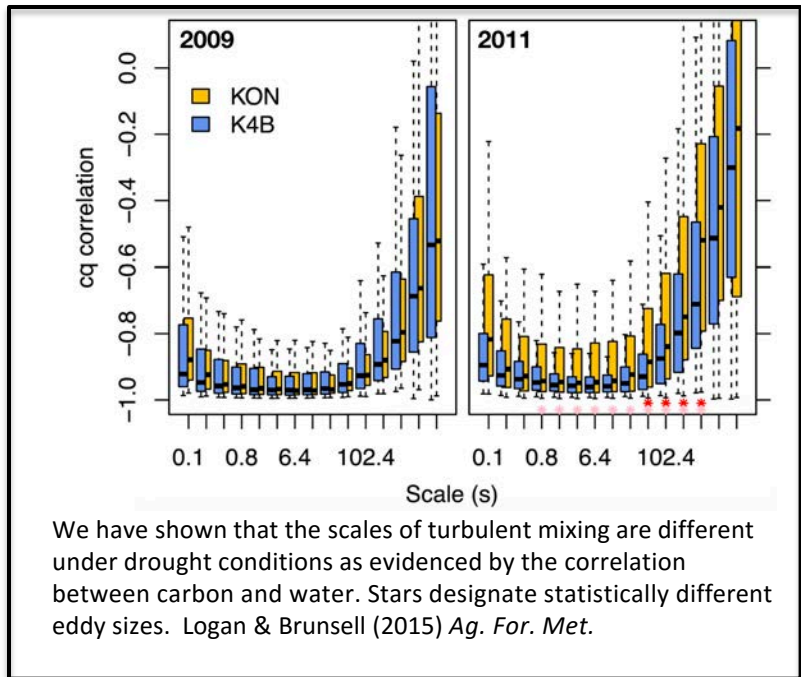
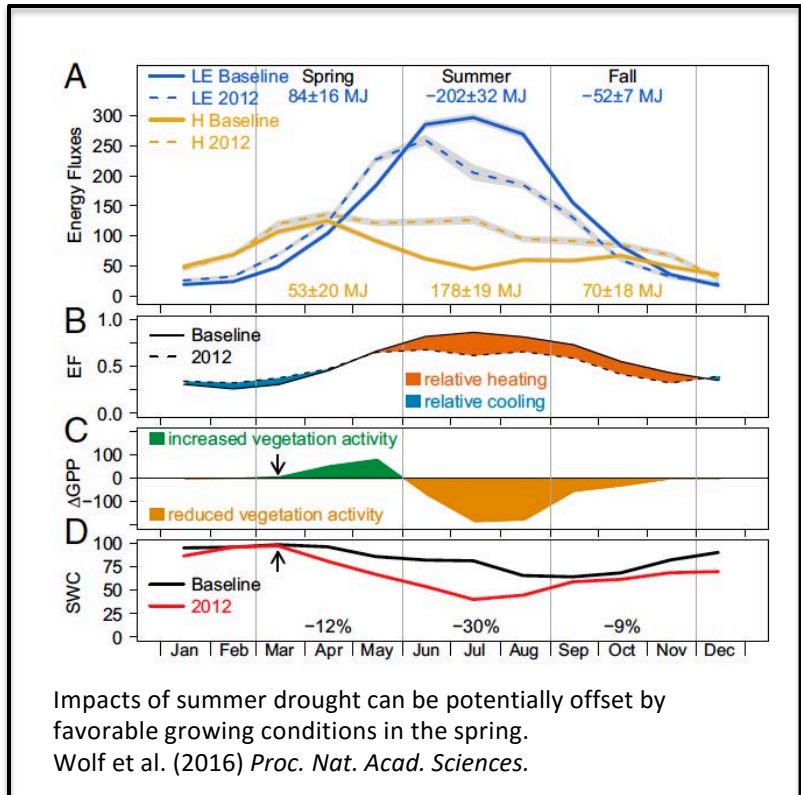
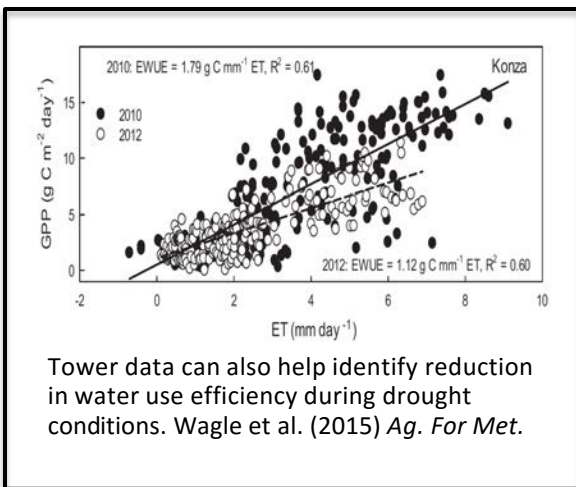
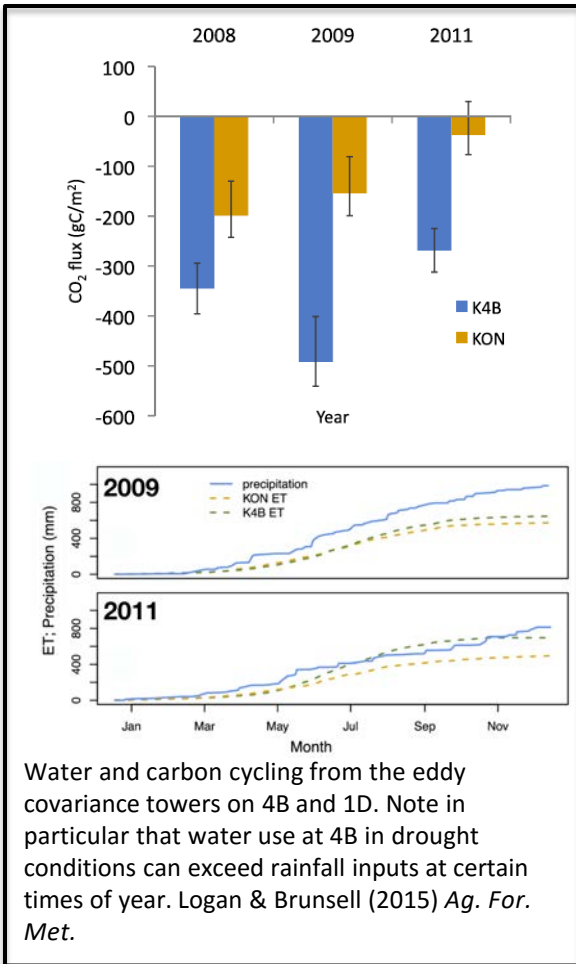
LTER Data: FWE01

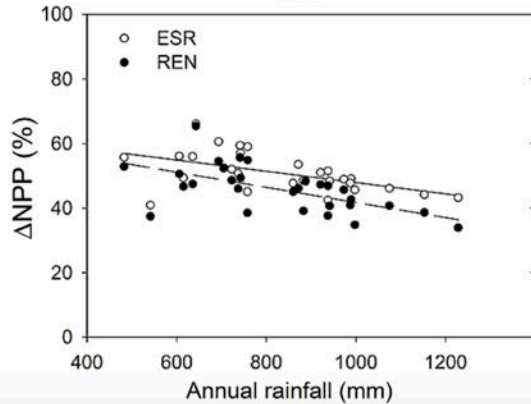
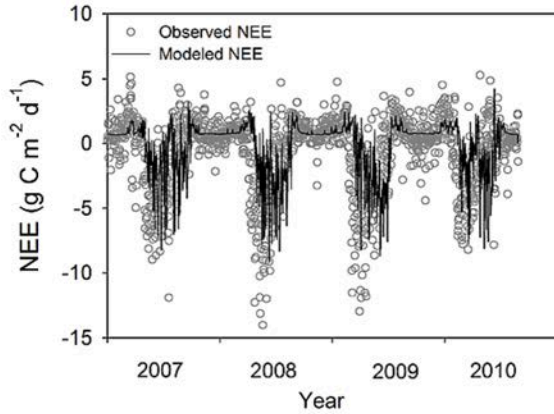
Using Eddy Covariance to Assess Water and Carbon Cycling

Investigators: N. A. Brunsell, K. E. Logan#, G. de Oliveira*, M. D. Petrie^, J. Nippert

Current Graduate Student, * Current Post-doc, ^ Former Graduate Student

Ameriflux sites on watersheds 1D and 4B have been used to examine the processes controlling water and carbon cycling at Konza. We have focused on ascertaining the biophysical drivers of land-atmosphere exchanges at site-specific scales as well as synthesis studies across the United States. Following the 2011 and 2012 droughts, a particular emphasis has been on the role of drought in grasslands. Additional studies have examined the role of land surface models and remote sensing data for model validation studies and extrapolation of the results to a broader spatial extent.





TECO model fit to 1D tower results (top) and simulations related to precipitation event size reduction (ESR) and reduction of number of events (REN). Shi et al. (2014) *Biogeosciences*

Selected Publications

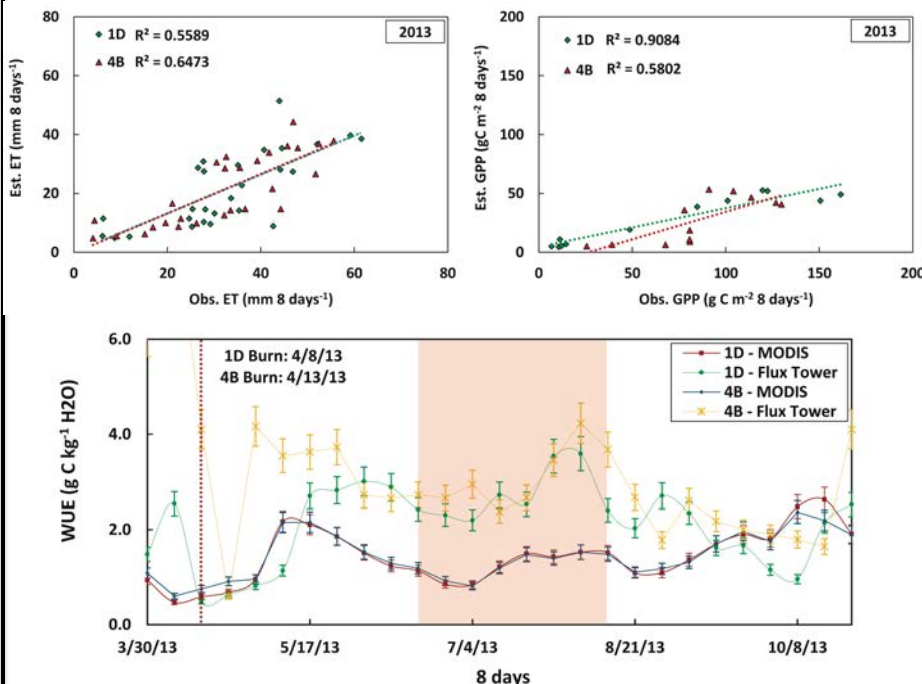
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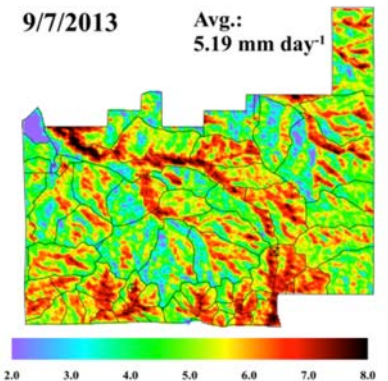
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Wolf, S., T. F. Keenan, J. B. Fisher, D. D. Baldocchi, A. R. Desai, A. D. Richardson, R. L. Scott, B. E. Law, M. E. Litvak and N. A. Brunzell, W. Peters, I. T. van der Lan-Luijckx. 2016. Warm spring reduced carbon cycle impact of the 2012 US summer drought. *Proceedings of the National Academy of Sciences* doi:10.1073/pnas.1519620113.



Comparison of MODIS and tower ET, GPP for 2013, as well as comparison of tower and MODIS Water Use Efficiency through time.



Spatially distributed ET derived from Landsat data using the METRIC model.

Phosphorus Addition Plots (P-Plots)

Investigators: Meghan Avolio, Sally Koerner, Kimberly La Pierre, Kevin Wilcox, Melinda Smith, Scott Collins

Rationale

- Increased nutrient inputs is one of many global change factors predicted to affect the composition and ecosystem function of plant communities.
- In general, nitrogen (N) deposition decreases diversity and increases productivity.
- The effects of phosphorus (P) addition, however, have received less attention, and the interactive effect of both nutrients is likely to exacerbate diversity loss over time.

Methods

- Pretreatment data was collected in 2002.
- Starting in 2003, N and P are added in a fully factorial design.
- There are 8 treatments: **N1P0** (0 g m⁻² N, 0 g m⁻² P); **N1P1** (0 g m⁻² N, 2.5 g m⁻² P); **N1P2** (0 g m⁻² N, 5 g m⁻² P); **N1P3** (0 g m⁻² N, 10 g m⁻² P); **N2P0** (10 g m⁻² N, 0 g m⁻² P); **N2P1** (10 g m⁻² N, 2.5 g m⁻² P); **N2P2** (10 g m⁻² N, 5 g m⁻² P); **N2P3** (10 g m⁻² N, 10 g m⁻² P)
- Species composition is measured twice yearly, and aboveground net primary productivity (ANPP) is measured at the end of each growing season.

Overall Question and Results

Do phosphorus and nitrogen interact to affect tallgrass prairie community composition and resultant ecosystem function?

- N and P additions reduce plant richness (2015 data: N1P0: 12.3 species ± 0.8 (mean ± S.E.); N1P1: 10.5 ± 0.8; N1P2: 13.2 ± 0.7; N1P3: 11.5 ± 0.5; N2P0: 9.7 ± 1.0; N2P1: 9.0 ± 0.7; N2P2: 9.0 ± 0.7; N2P3: 7.3 ± 0.9).
- Phosphorus alone has little effect on plant community composition, as does N alone. However, together, C₄ grasses lose their dominance and non N-fixing forbs and annual forbs become highly abundant. This shift started to occur in 2006, after three years of nutrient additions (Fig. 1; Avolio *et al.* 2014).
- N and P additions not only cause community composition to change, but the species composition of replicates within a treatment become more variable (Fig. 2; Koerner *et al.* 2016).
- As a result of the changed community composition, productivity is more variable from year to year (Fig. 3; Avolio *et al.* 2014) and is no longer tightly driven by annual precipitation (Fig. 4; Koerner *et al.* 2016). Overall, productivity is less stable and more difficult to predict.

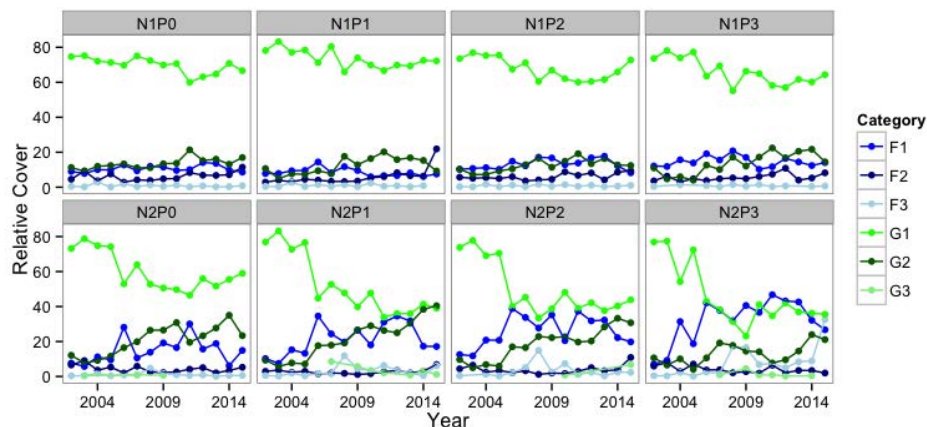


Fig. 1. Relative cover of plant functional types across N and P treatments. F1 – perennial, non N-fixing forbs; F2 – perennial N-fixing forbs; F3 annual forbs; G1 – perennial C₄ grasses; G2 – perennial C₃ grasses; G3 – annual grasses.

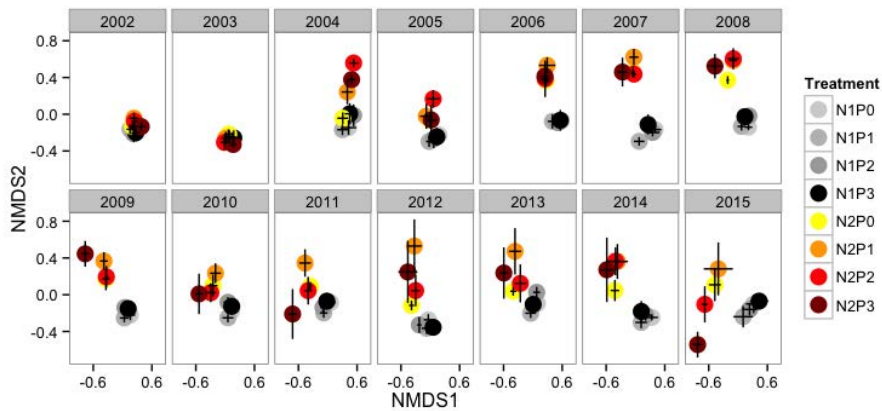


Fig. 2. NMDS of community composition. At the beginning of the experiment (2002-2003) all treatments have similar composition (are near one another in NMDS space, and replicates are similar to one-another (small error bars). P alone has little effect on the community (grayscale colors always cluster). However, N alone, and N and P together cause the community to diverge from the controls (light gray). Additionally, N and P together result in large community composition variability among replicates (large error bars).

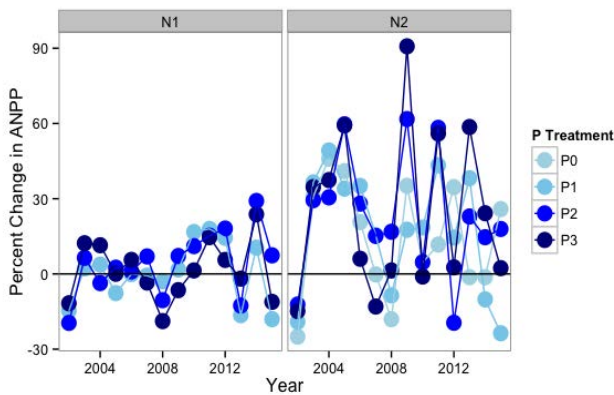


Fig. 3. Change in ANPP relative to the controls. With P alone there is little change in productivity (black line at zero is no change from controls). Initially (2003-2005) the N alone and N + P additions result in greater productivity. However, starting in 2006, productivity becomes more variable from year to year, which is a result of the biennial fires.

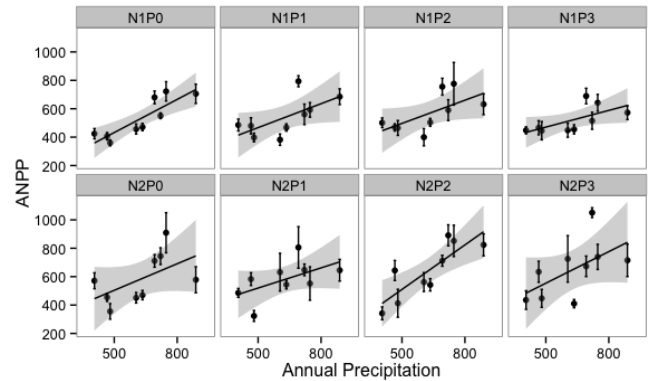


Fig. 4. In natural prairie (N1P0) productivity is related to growing season precipitation. N and P additions decouple this relationship, with productivity being more variable among replicates (larger error bars) and is not well predicted by growing season precipitation.

Publications:

- Avolio, M. L., & Koerner, S. E. (*In preparation*). Eutrophication induced community changes reduce resistance and resilience of tallgrass prairie to drought.
- Avolio, M. L., Koerner, S. E., La Pierre, K. J., Wilcox, K. R., Wilson, G. W., Smith, M. D., & Collins, S. L. 2014. Changes in plant community composition, not diversity, during a decade of nitrogen and phosphorus additions drive above-ground productivity in tallgrass prairie. *Journal of Ecology*, 102, 1649-1660.
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The Nutrient Network (NutNet)

Investigators: Kimberly La Pierre, John Blair, Melinda Smith

Rationale:

Theory predicts top-down and bottom-up forces may interact in complex ways to influence grassland systems. NutNet was established to collect data from a broad range of sites in a consistent manner to allow direct comparisons of environment-productivity-diversity relationships.

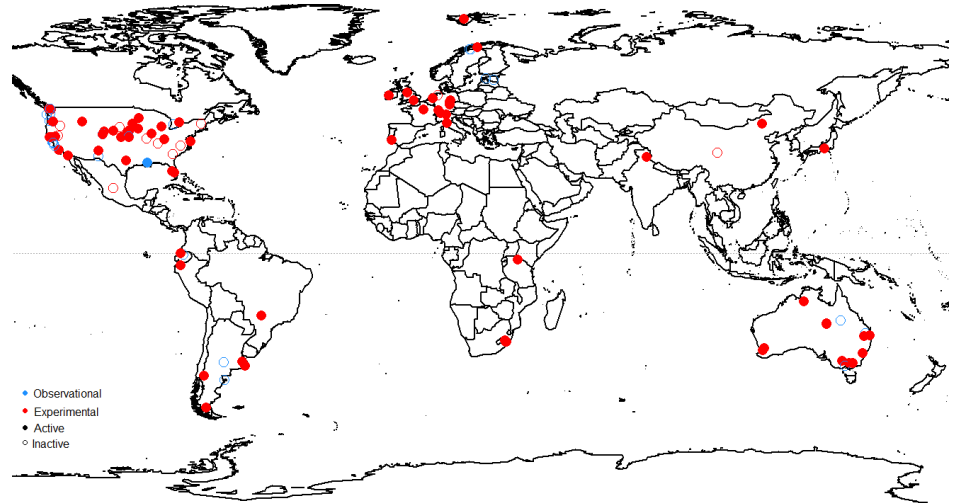


Fig. 1. Map of the 108 NutNet sites around the world.

Focal Questions:

- (1) How general is our current understanding of productivity-diversity relationships?
- (2) To what extent are plant production and community composition co-limited by multiple nutrients in herbaceous-dominated communities?
- (3) Under what conditions do herbivores and/or fertilization control plant biomass and community composition and how do these forces interact?

Network-Level Results:

- (1) Observational data across NutNet sites shows that productivity is best predicted by an integrated model incorporating site-level climatic variability, shading, edaphic factors, and species richness (Adler *et al.* 2011; Grace *et al.*, 2016)
- (2) Productivity in grasslands worldwide is co-limited by multiple nutrients. Diversity is reduced when niche dimensionality declines. (Fay *et al.*, 2015; Harpole *et al.*, 2016)
- (3) Herbivores affect diversity at grassland sites where they impact light availability (Borer *et al.*, 2014).

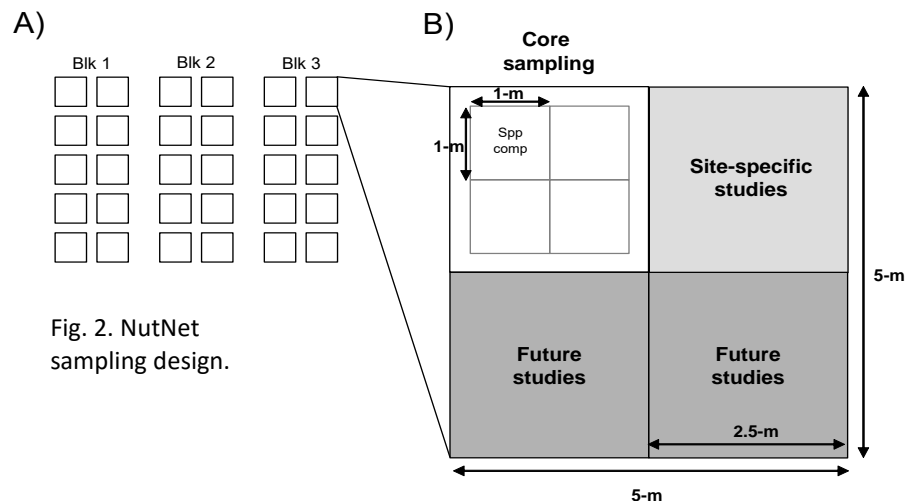


Fig. 2. NutNet sampling design.

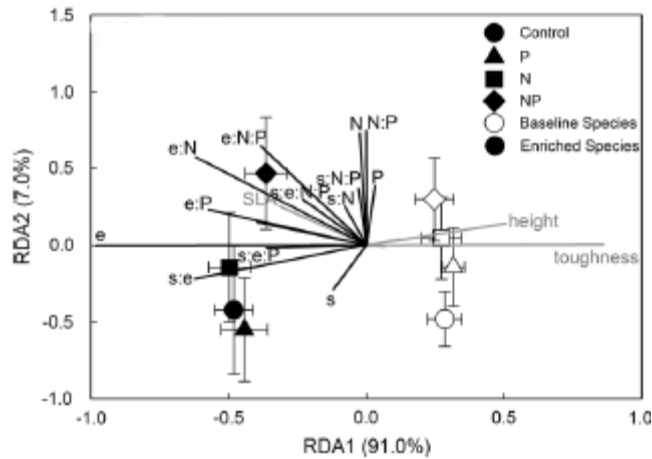


Fig. 3. Effects of nutrient additions on traits of the dominant species within the NutNet plots.

Regional and Site-Specific Research at Konza:

- (1) *Plant Community and Productivity Responses:* At Konza, as well as in the shortgrass steppe ecosystem, productivity is co-limited by precipitation and nutrient availability, while in mixed-grass prairie nutrient availability determines productivity exclusive of the effects of precipitation. (La Pierre *et al.*, 2016)
- (2) *Plant Traits and Plasticity:* Plant species that dominate under altered nutrient conditions tend to have higher SLA, a proxy of growth rate, and lower leaf toughness and height (Fig. 3). These results are consistent across both the NutNet and pplots experiments. (La Pierre and Smith, 2015)

- (3) *Invertebrate Community Responses:* Nitrogen additions have a significant indirect effect on leaf chewing herbivores through alterations in productivity, which feed up to impact parasitoid abundances (Fig. 4). However, because of tradeoffs in plant tissue quality and quantity, the feeding rate of leaf chewing invertebrate herbivores does not vary with nutrient additions. (La Pierre and Smith, 2016)

Ongoing NutNet Research at Konza:

- nitrogen cycling: litter decomposition, N-mineralization, leaf stoichiometry
- functional trait assessment
- N-fixation by legumes

NutNet 2.0 – where are we going?

- (1) How do effects of nutrient additions vary through time? How do these effects compare to other Konza nutrient addition experiments? What is the impact of precipitation or burning in driving these temporal trajectories?
- (2) Can the plant community recover if nutrient addition treatments cease? If so, what is the trajectory of return?

Selected Publications (23 total):

Adler *et al.* 2011. Productivity is a poor predictor of plant species richness. *Science* 333:1750-1753.
 Borer *et al.* 2014. Herbivores and nutrients control grassland plant diversity via light limitation. *Nature* 508(7497):517-520.
 Fay *et al.* 2015. Grassland productivity limited by multiple nutrients. *Nature Plants*. 1(7):15080.
 Grace *et al.* 2016. Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature*. 529(7586):390-393.
 Harpole *et al.* 2016. Addition of multiple limiting resources reduces grassland diversity. *Nature*. 537:93-96.
 La Pierre *et al.* 2016. Drivers of Variation in Aboveground Net Primary Productivity and Plant Community Composition Differ Across a Broad Precipitation Gradient. *Ecosystems*. 19(3):521-533.
 La Pierre and Smith. 2015. Functional trait expression of grassland species shift with short- and long-term nutrient additions. *Plant Ecology*. 216:307-318.
 La Pierre and Smith. 2016. Soil nutrient additions increase invertebrate herbivore abundances, but not herbivory, across three grassland systems. *Oecologia*. 180(2):485-497.

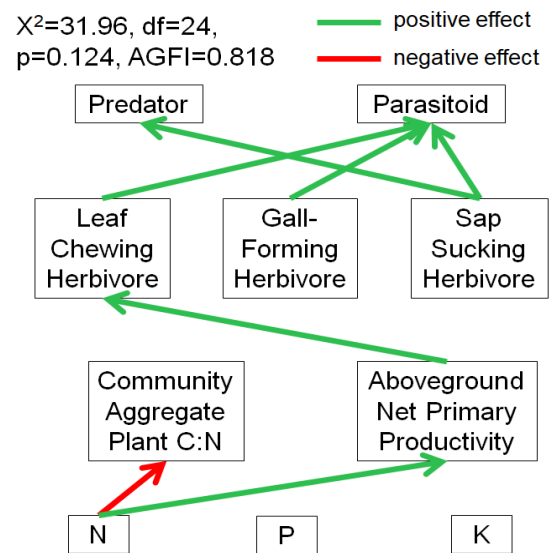


Fig. 4. Effects of nutrient additions on grassland arthropod communities.

Vertebrate and Invertebrate Removal Plots

Investigators: Kimberly La Pierre, Anthony Joern, Melinda Smith

Rationale:

The effects of herbivores and their interactions with nutrient availability on primary production and plant community composition in grassland systems is expected to vary with herbivore type. Since 2009, we've examined the interactive effects of invertebrate and small vertebrate herbivores and nutrient availability on grassland plant community composition and aboveground biomass.

Focal Questions:

- (1) What are the independent and interactive effects of invertebrate and small vertebrate herbivores on grassland community composition?
- (2) How does increased soil nutrient availability impact grassland community responses to herbivore removals?
- (3) Do changes in the plant community with herbivore removals and/or nutrient additions impact ecosystem function?

Results:

- (1) While small vertebrate herbivores have had no significant effect on the plant community here, invertebrate herbivores suppress forb abundance in favor of the dominant grasses (Fig. 1). However, these alternate communities are not stable, with dominant species shifting annually, seemingly in response to the two-year burn regime in this watershed.
- (2) Nutrient additions also support forb production, which in combination with invertebrate removals leads to a variety of altered community states driven by priority effects (Fig. 1).

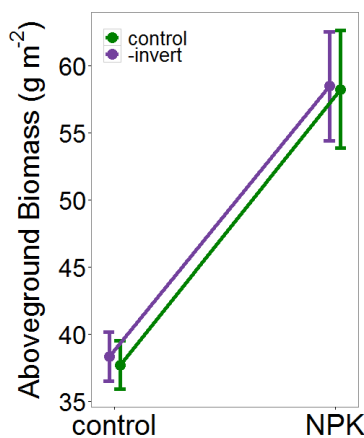


Fig. 2. Total aboveground biomass is not impacted by invertebrate herbivore removals, despite a large shift in community composition.

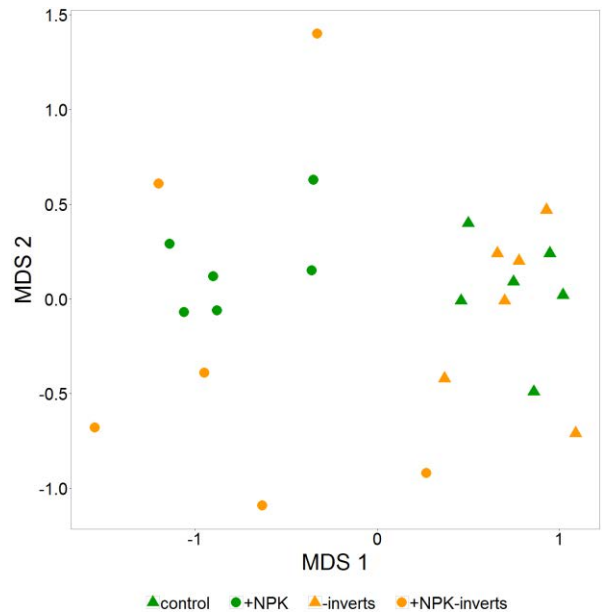


Fig. 1. NMDS plot illustrating a shift towards a forb dominated community with nutrient additions, further exacerbated by the removal of invertebrate herbivores.

- (3) A tradeoff in grass and forb production in communities altered by nutrient addition and invertebrate herbivore removals results in no net change in total aboveground biomass (Fig. 2).

Where are we going from here?

- (1) How does altered nutrient availability and invertebrate herbivore presence affect plant community trajectories through time? Is an alternate stable state reached?
- (2) How do herbivores of various size classes affect plant community composition throughout Konza, and do these effects vary with burn regime?

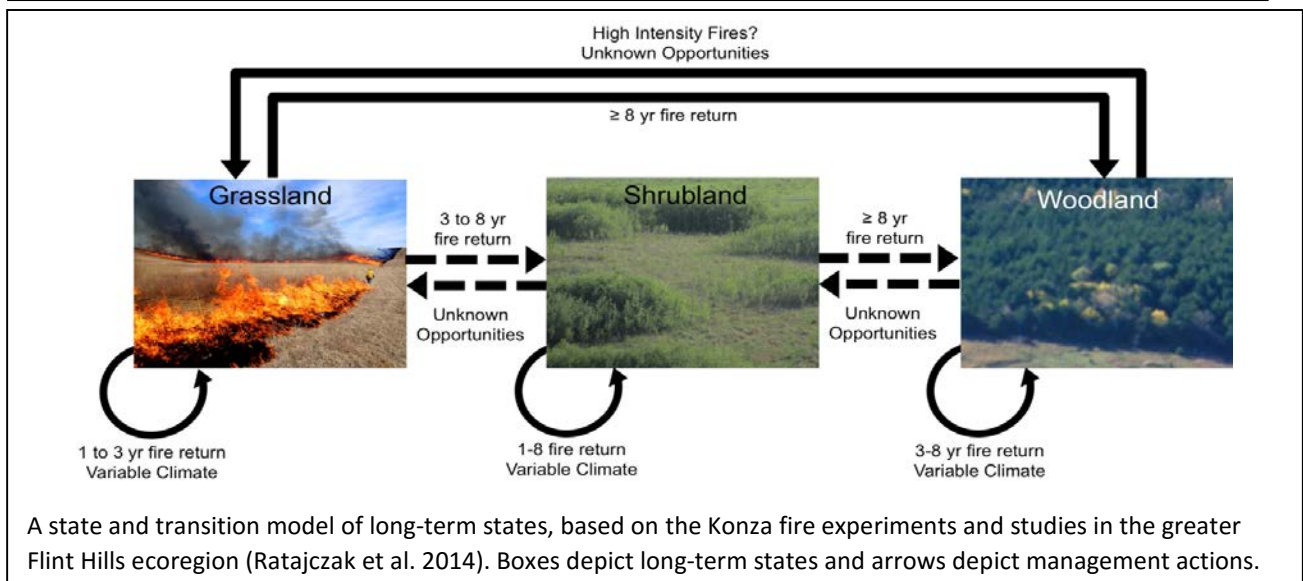
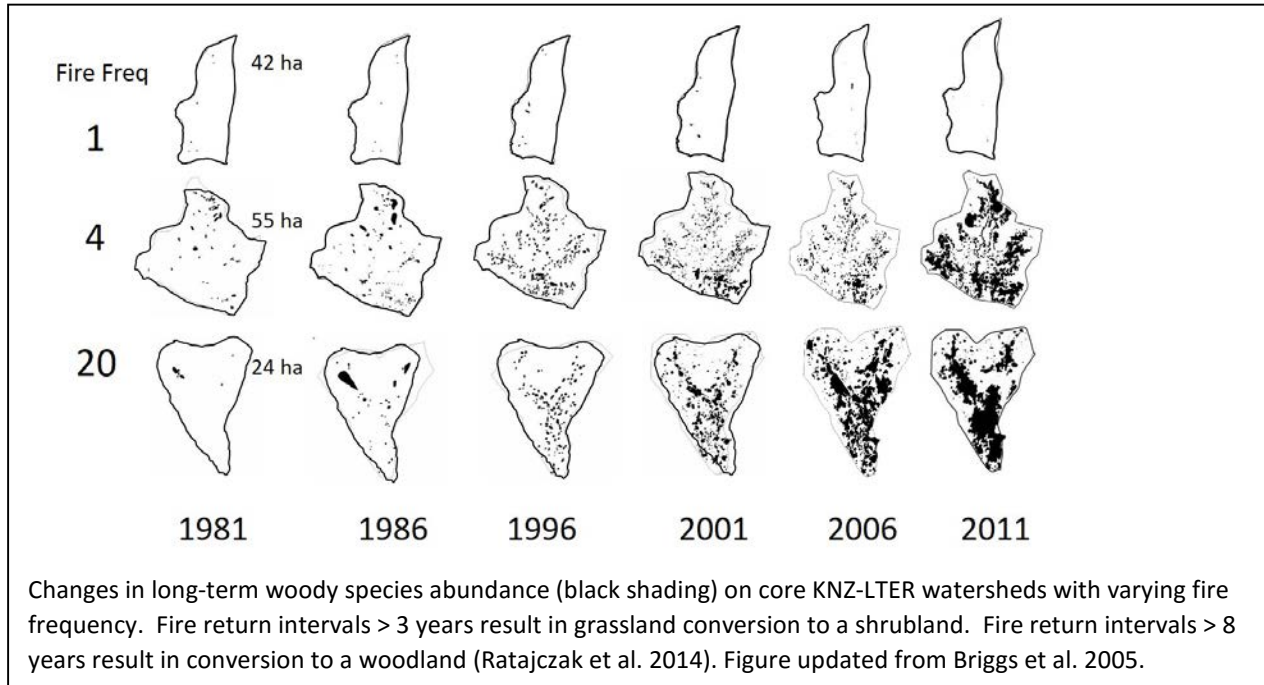
Publications:

La Pierre KJ, Joern A, Smith MD. 2015. Invertebrate, not small vertebrate, herbivory interacts with nutrient availability to impact tallgrass prairie community composition and forb biomass. *Oikos*. 124:842-850.

KNZ Dataset: VIR01

Effects of Long-Term Fire Suppression on Land Use / Land Cover Change at KPBS

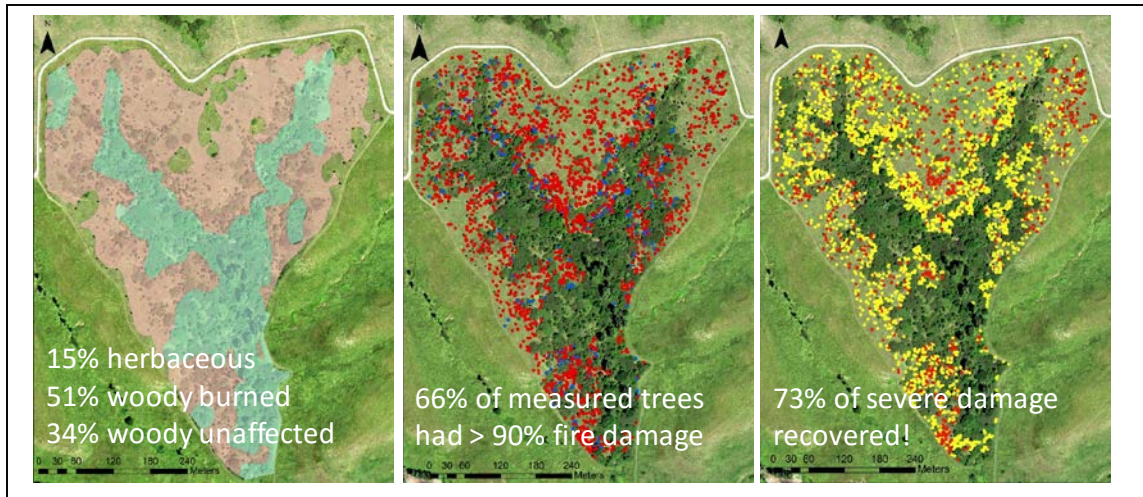
Investigators: J. Blair, J. Briggs, J. Nippert, Z. Ratajczak*, K. O’Keefe*, R. O’Connor#, A. Muench[‡]; L. Telleria[‡] *former grad students; # current grad students; ‡ REU student



Briggs JM, Knapp AK, Blair JM, et al. 2005. An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland. *BioScience* 55:243 -254.

Ratajczak Z, Nippert JB, Briggs JM, Blair JM. 2014. Fire dynamics distinguish grasslands, shrublands, and woodlands as alternative attractors in the Central Great Plains of North America. *Journal of Ecology* 102:1374 -1385.

KNZ Long-Term Datasets: PVCO2, PWV01



Once woody plants are established in grasslands (i.e. reach a large size and canopy density), the impacts of fire are minimal. During the summer, 2017, REU student Lizeth Telleria (Cal St Poly – Pomona) measured fire impacts in watershed 20B following nearly 30 years without fire. Fire impacts were species-specific, with interactions by topographic position and height class. While 66% of 20B was impacted by fire after burn, 73% of woody species recovered (non-lethal, resprouting, or new clonal stems).



Watershed 20B following the spring burn.

Conversion of grassland to shrubland or woodland alters ecosystem structure & function. In particular, plant species richness declines and growth is shifted from belowground to aboveground.

Attribute	C ₄ grassland	<i>Cornus</i> islands	<i>Juniperus</i> woodland
Dominant growth form	Graminoid	Shrubs	Tree
Biomass allocation	> Belowground	Equivalent	> Aboveground
Annual aboveground NPP	400-800 g/m	1000-1300 g/m	725-1044 g/m
Standing aboveground biomass	400-1200 g/m	4201 ± 835 g/m	14860 ± 3123 g/m
Leaf phenology	Deciduous	Deciduous	Evergreen
Root system	Fibrous, shallow	Mostly lateral, few deep	Tap root, deep
Sensitivity to drought	Sensitive	Persist using deep water	Drought tolerant
Response to fire	Positive	Size-dependent	Negative
Species richness (10 m ²)	High (21.4 + 1.1)	Intermediate (6.0 + 1.0)	Low (1.2 + 0.3)

Annually Burned, Ungrazed Grasslands – Sentinels for Climate Change

Investigators: John M. Blair (KSU), John M. Briggs (KSU), Scott L. Collins (UNM), Alan K. Knapp (CSU), Jesse B. Nippert (KSU), Melinda D. Smith (CSU), Kevin R. Wilcox (USDA-ARS)

KNZ LTER Data: PAB01, PAB03, PAB04

Background and Rationale:

- KNZ has a number of “core watersheds” that have been well-characterized and have had continuous core LTER data collected for >30 years. The 001D watershed is one of these and has been annually burned in the spring since 1978.
- Annual fire (with no large grazers) in tallgrass prairie results in a grassland that is highly productive, strongly dominated by C4 grasses with stable plant communities (no woody plant or exotic species invasions), strongly limited by climate (water availability) and N, and perhaps best approximates historic tallgrass prairie structure and function.
- The long-term record of inter-annual variability in ANPP in the 001D watershed as well as other annually burned sites on Konza have become extremely valuable for assessing climate-ecosystem functional interactions. These data sets serve as sentinels for detecting changes in abiotic drivers of ecosystem function as well as platforms for both short- and long-term experiments designed to elucidate mechanisms.

Key Findings:

- No statistically significant directional temporal trends in primary climatic variables likely to drive ANPP have been detected; although there are trends for increased temperatures and annual precipitation. Similarly, there are no significant trends in ANPP in 001D.
- As expected, lowlands in 001D (deeper soils and water subsidies from uplands) are consistently more productive, but more of the interannual variability in ANPP is explained by annual precipitation in uplands (Fig. 1).

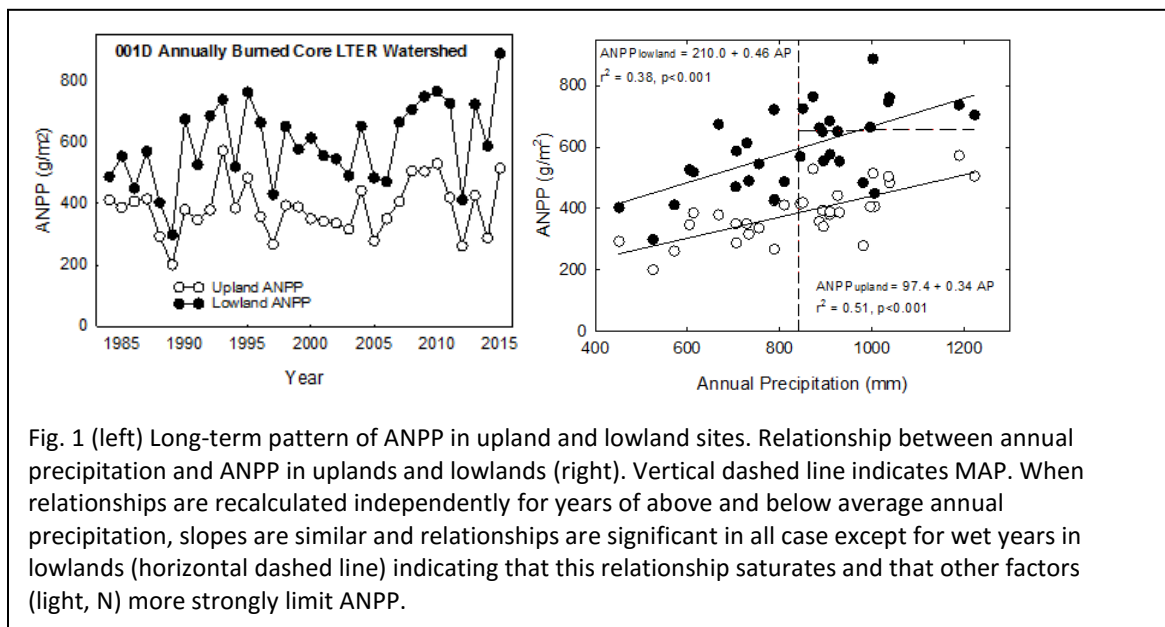
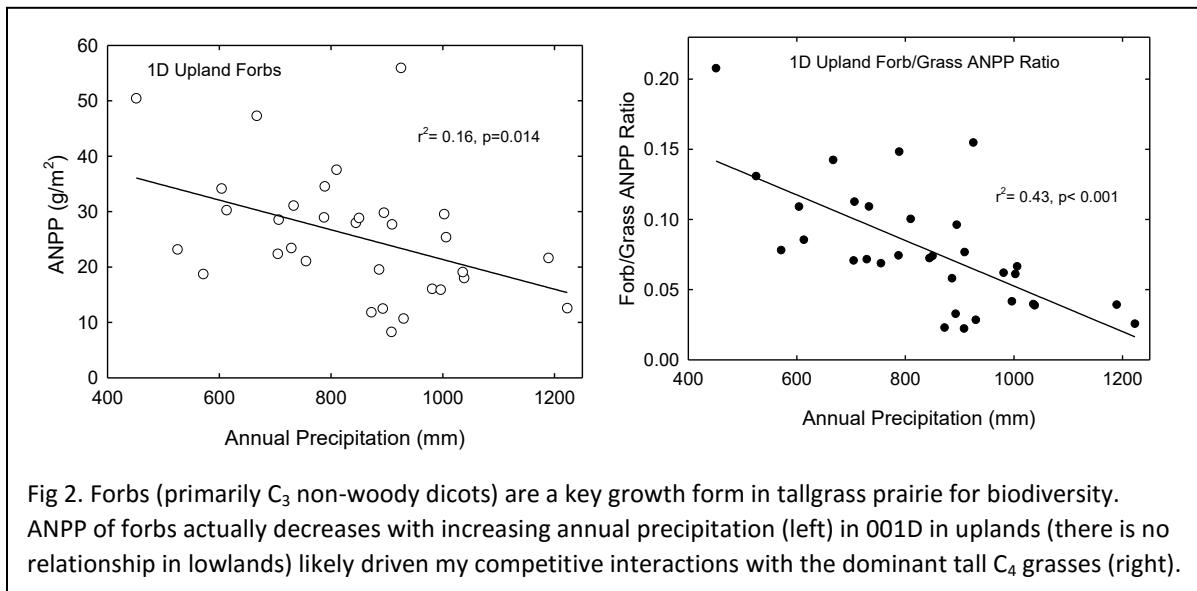
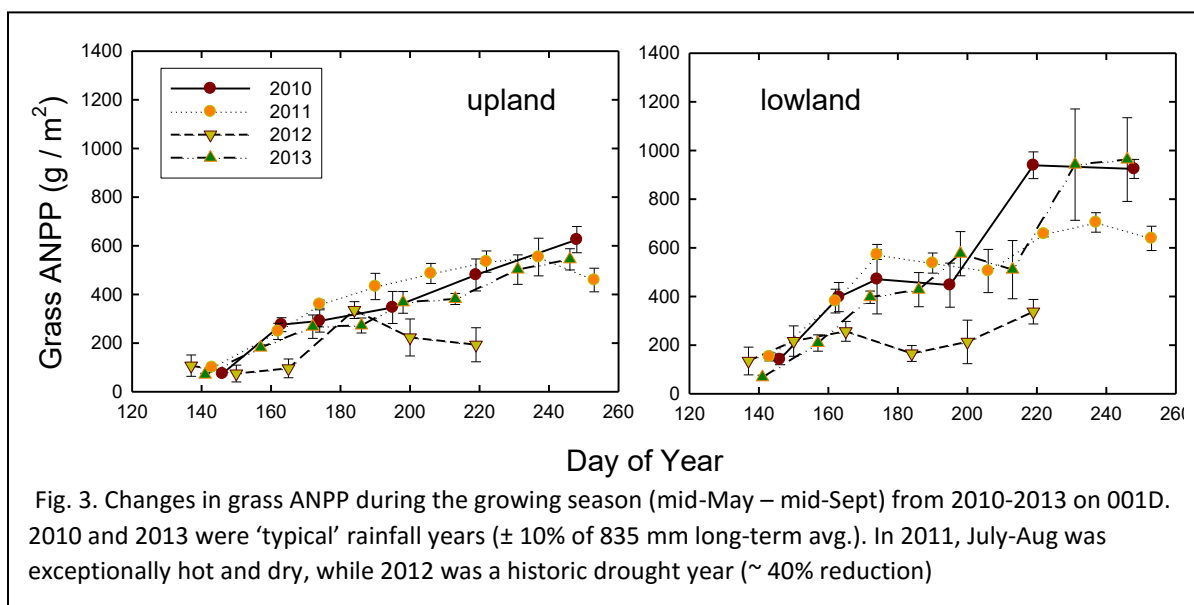


Fig. 1 (left) Long-term pattern of ANPP in upland and lowland sites. Relationship between annual precipitation and ANPP in uplands and lowlands (right). Vertical dashed line indicates MAP. When relationships are recalculated independently for years of above and below average annual precipitation, slopes are similar and relationships are significant in all case except for wet years in lowlands (horizontal dashed line) indicating that this relationship saturates and that other factors (light, N) more strongly limit ANPP.

- Annually burned grassland is strongly dominated by C4 tall grasses in both uplands and lowlands. The dominant role they play in this grassland is illustrated by their impact on forb ANPP (Fig. 2)



- From 2010-2013 bi-weekly measurements of ANPP, species height, and leaf area index, were coupled with continuous microclimate measurements (soil moisture, temperature (air, soil, leaf), VPD, wind speed/direction) on watershed 1D, 1B, 4A, 4F. **KNZ Dataset: AMCO1**
- Grass ANPP in lowlands has faster rates of increase than lowlands, early in the growing season. Between DOY 200-220, ANPP in lowlands nearly doubles from flowering stem production during years with average or above-average rainfall (2010, 2013) (Fig. 3).
- During an extreme drought (2012), grass ANPP was very low (~ 200 g/m²). No flowering stems were produced. ANPP was similar among topographic positions in 2012, despite available soil moisture at 1m soil depth in the lowlands. This result reinforces previous KNZ results illustrating the low functional reliance by grasses on deep soil moisture.



Beyond Konza – The Extreme Drought in Grasslands Experiment (EDGE)

- Extreme drought has long been recognized as a key driver of long-term grassland structure and function and severe regional scale droughts (like the dust-bowl of the 1930's) are expected to increase with climate change, impacting multiple grassland types concurrently.
- The goal of the EDGE study is to assess how different grassland types, from desert grassland in NM to shortgrass steppe in CO, mixed grass prairies in WY and KS and tallgrass prairie (Konza) will respond to extreme drought (4 years of a 66% reduction in growing season rainfall, 45-50% reduction in MAP) imposed with identical infrastructure (Fig. 4) in each grassland.



Fig. 4. Passive precipitation reduction shelters at Konza Prairie in an annually burned watershed near 001D.

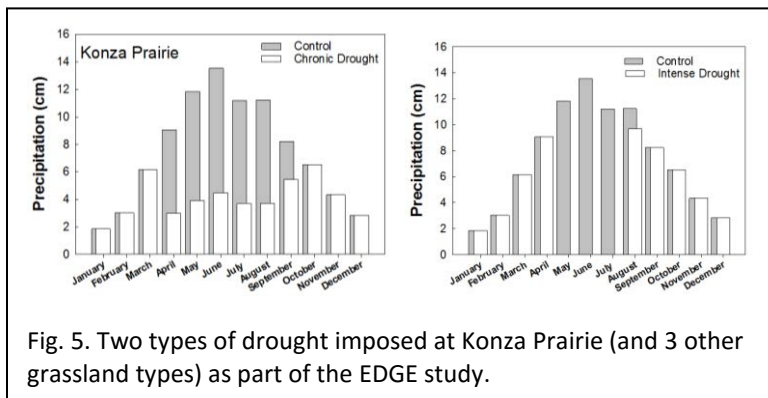


Fig. 5. Two types of drought imposed at Konza Prairie (and 3 other grassland types) as part of the EDGE study.

- At some of these grassland sites, two types of drought have been imposed – a reduction in all rainfall events (chronic drought) for the entire growing season vs. a shorter period of complete rain exclusion (intense drought, Fig. 5).
- Results indicate that the “type” of drought can have dramatic impacts on how these grasslands respond extreme precipitation reductions.

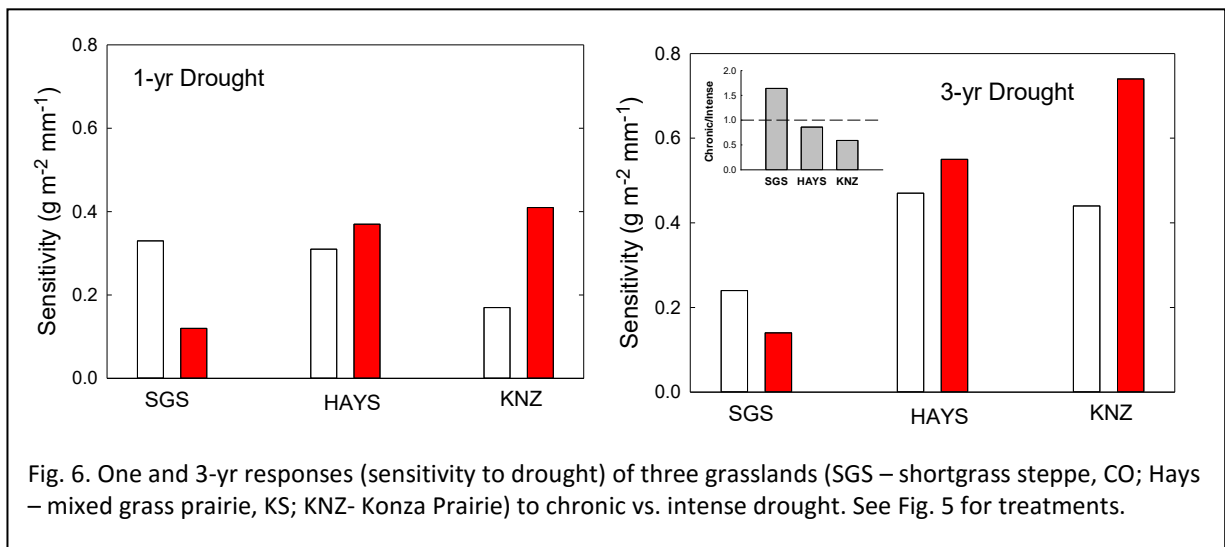


Fig. 6. One and 3-yr responses (sensitivity to drought) of three grasslands (SGS – shortgrass steppe, CO; Hays – mixed grass prairie, KS; KNZ- Konza Prairie) to chronic vs. intense drought. See Fig. 5 for treatments.

Linking Experiments and Monitoring

- The long-term ANPP record from 001D and other sites on Konza have been combined with a number of shorter-term experiments and studies to both develop and test theory (Smith 2011, Knapp *et al.* 2017, Fig. 7), assess ecosystem sensitivity to climate change (Yu *et al.* 2015, Wilcox *et al.* 2015, 2016) and provide context for interpreting results from climate change experiments (Hoover *et al.* 2014).

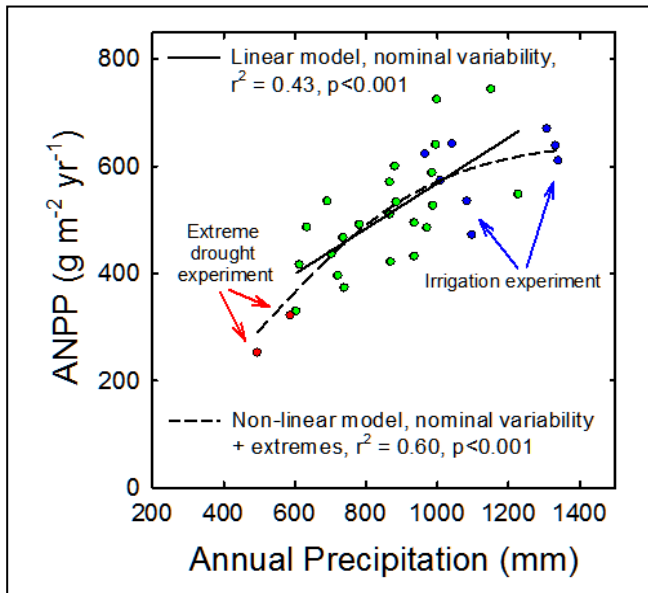


Fig. 7. Smith (2011), based in part on data from Konza and other LTER sites (Smith *et al.* 2015) proposed that ecosystem responses to climate extremes would not be predictable based on functional relationships based on nominal conditions. In support of this, Knapp *et al.* (2017) combined data from two experiments on Konza with long-term monitoring data to show that the linear ANPP-precipitation model that characterized most ecosystems under nominal conditions becomes non-linear as the frequency of climate extremes increases. This alteration in a foundational functional relationship has important implications for models that currently employ linear models to describe how NPP is affected by precipitation.

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Ghost Fire

Investigators: Sally Koerner, Meghan Avolio, Kimberly La Pierre, Melinda Smith, Kevin Wilcox, Lydia Zeglin, Matthew Clark*, Dave Hoover *graduate student

Rationale/Questions: Frequent burning, a common management practice in many grasslands worldwide, alters plant community composition, decreases richness, and increases plant production via increasing light availability (fire removes old plant litter and clears the canopy) and decreasing nitrogen (N) availability (organic N is volatilized in fire). The strength of these mechanisms likely differs between short and long-term time scales, as plant community composition or belowground factors change through time, which can feed back to impact availability of light and N. The Ghost Fire project aims to identify the mechanisms underlying community and ecosystem differences between historic annually burned grassland and 20-year burned (hereafter called unburned) grassland by explicitly evaluating the direct and interactive influences of each mechanism through experimental manipulation of N availability and litter cover, independent of an actual fire disturbance (a "ghost fire"). This experiment asks: 1) What are the independent and interactive effects of litter and N availability on the prairie community and ecosystem? 2) How quickly does each factor affect transitions between burned and unburned prairie states?

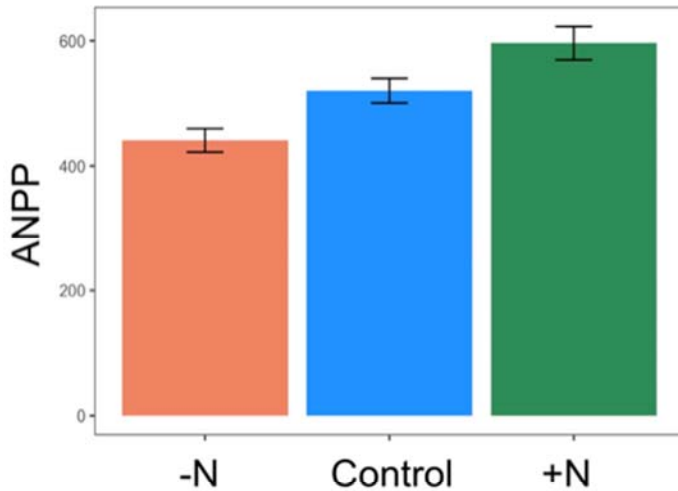
Experimental Design: We impose litter cover and N availability conditions found in unburned grassland onto annually burned grassland, and vice versa. To understand plant responses, belowground feedbacks mediating responses, and implications for higher trophic levels, Ghost Fire measures below- and above-ground plant community and ecosystem dynamics, soil microbial and mycorrhizal processes and structure, and insect community composition and biomass. Litter cover is manipulated by adding litter to half of the burned plots and removing litter from half of the unburned plots (Fig. 1). Soil N availability is increased by adding urea-N and decreased by adding labile carbon (C), which stimulates microbial growth and immobilization of N, reducing plant N availability.



Figure 1. Experimental design. Above: Photos of the litter treatment in Spring. Below: Schematic of theoretical soil C:N levels created by our treatment. Control plots are clear, N addition are red, and carbon addition are green.



Results: Pretreatment data was collected in 2014 and response variables will be collected through KNZ LTER VII for up to 10 years total.



After the first 2 treatment years, Annual Net Primary Production (ANPP) was significantly affected by N availability but not litter cover or fire history (Fig. 2): ANPP responded positively/negatively to increased/decreased N, respectively. This indicates that while direct N availability affects grassland ecosystem processes, this mechanism alone, at least in the short term, does not explain the effects of regular burning on ANPP.

Figure 2. Effect of N treatments on Annual Net Primary Production (ANPP; g/m²). Year, litter treatment and burn history were not significant.

Plant species richness was significantly affected by burn history and N and litter treatments (Fig. 3): historically unburned plots had higher richness, but after 2 years, lack of litter and lower N availability caused higher richness in both unburned and burned prairie. Thus the direct and immediate effects of altered light and N availability do not replicate the effects of long-term fire cessation on plant species richness.

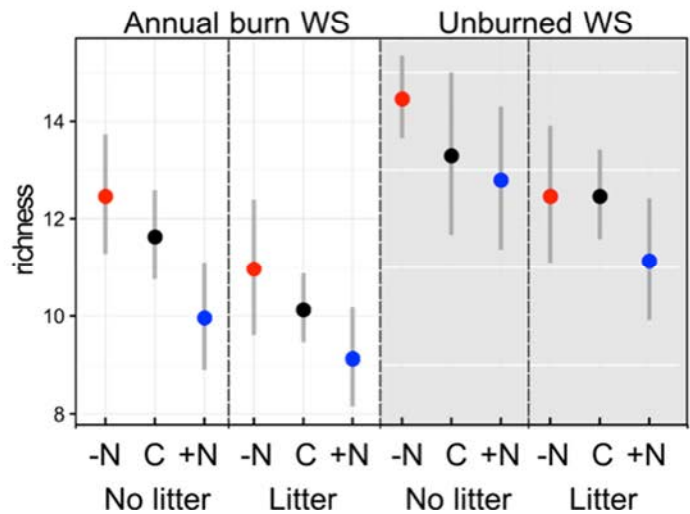


Figure 3. Effect of N and litter treatments on plant richness per 1m². Year was not significant.

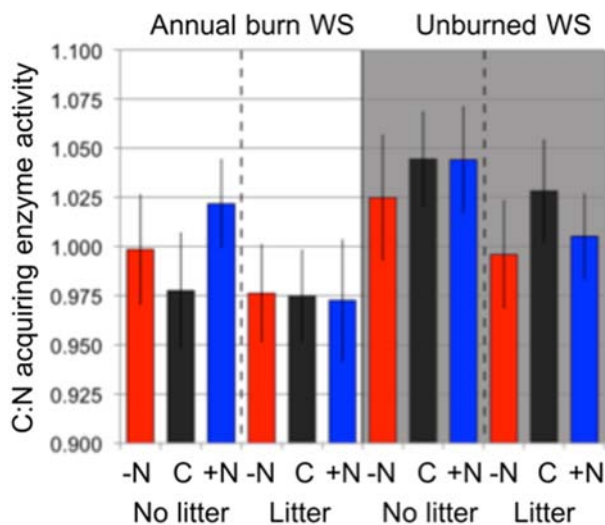


Figure 4. C:N acquiring soil enzyme activity, 1yr of treatments. Lower values reflect soil microbial N limitation. Only burn history was significant.

After 1 year, treatments did not affect the legacy of soil microbial N limitation (Fig. 4): enzymatic N demand relative to C demand in annually burned soils remained higher than in unburned soils, suggesting that soil N availability feedbacks will develop over longer timescales.

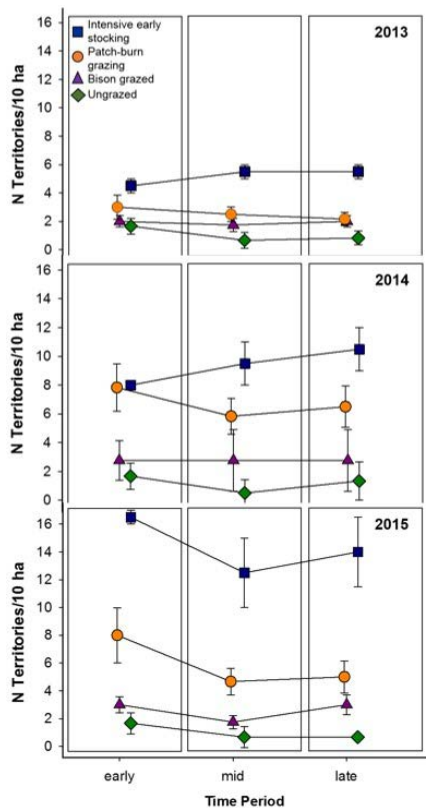
Together, early Ghost Fire results suggest that factors supporting differences in annually burned and unburned prairie take more than 2 years to establish. As many prairie plants are perennial, we expect species turnover through time will reveal the dynamic nature of fire regime impacts, which this long-term experiment will be uniquely able to capture.

Behavioral Plasticity of Grassland Birds: Mobility Mediates Within- and Between Year Environmental Heterogeneity

Investigators: A. Boyle, E. Williams*, S. Winnicki#, Yisel Márquez[‡], Darrien Savage[‡], M. Gustafson[§]

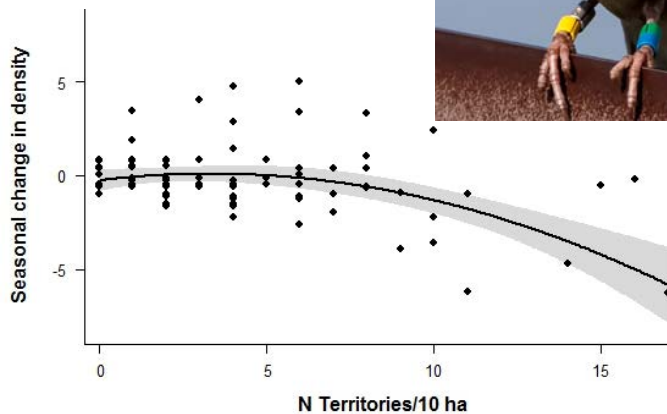
*former grad students; # current grad students; [‡] REU student; [§] K-State undergraduate

Grassland-dependent birds exhibit large, unexplained fluctuations in local abundance (Dornak et al. 2013). Analyses of Konza bird community data have demonstrated species-specific responses to spatial heterogeneity in vegetation structure resulting from different fire and grazing regimes (Powell 2006). However, neither the mechanisms underlying spatial patterns, nor the causes of temporal variability are well understood. Our studies of individually color-banded Grasshopper Sparrows (*Ammodramus savannarum*) encompass 16 Konza watersheds (+ 2 off-site) representing replicated cattle, bison, and ungrazed areas, burned on 1, 2, or 3-yr (patch-burn) intervals. We have documented the patterns of breeding dispersal within and among years (Williams and Boyle, in press), tested hypotheses to explain causes of dispersal and local distribution (Williams 2016), and linked reproductive biology and adult condition to temporal variation in weather.

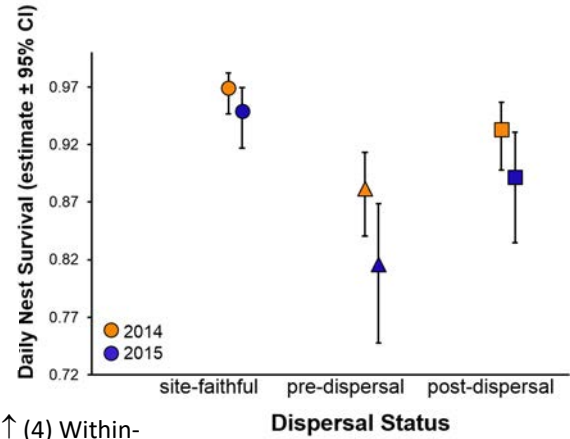
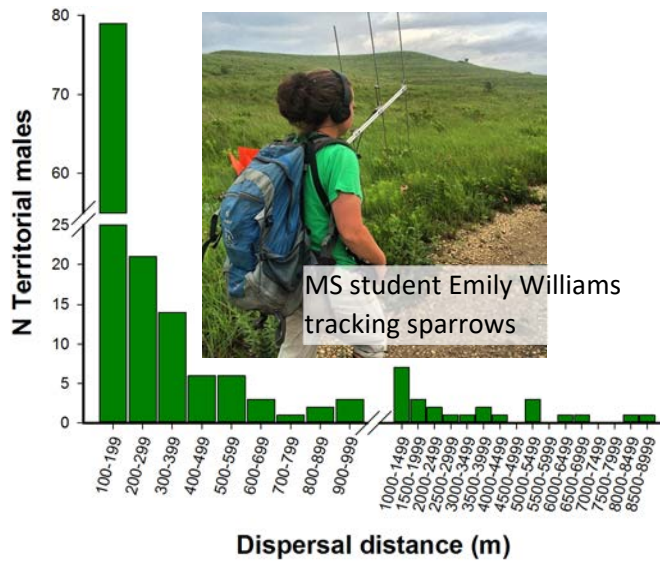


← (1) Densities higher in cattle-grazed than bison- and ungrazed watersheds, temporal changes differ by year. High densities not associated with higher food availability or mean nest success (Williams 2016).

↓ (2) Changes in density not driven by conspecific attraction

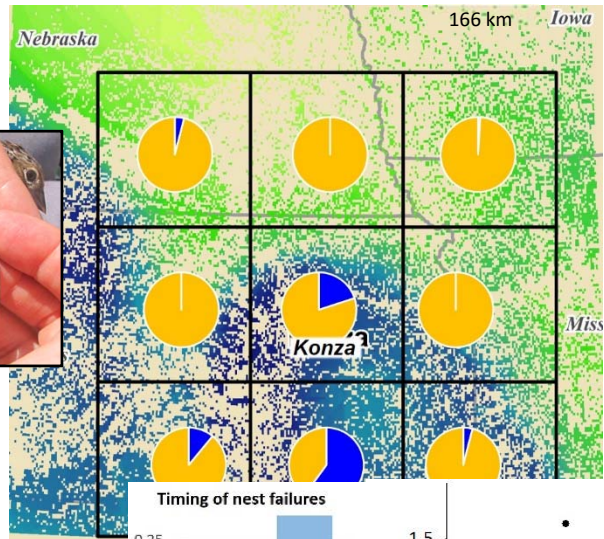


↓ (3) Changes in density result from within-season dispersal between breeding attempts. Between 33% (based on observations of marked birds defending ≥ 2 different territories sequentially) and 52% (based on turn-over of territory holders within plots) of males made such movements each year. Half the dispersers moved >4 territory widths; 4% dispersed >5 km.



↑ (4) Within-season dispersal decisions shaped by prior experience, and moving increases success of 2nd nest. Birds did not preferentially settle post-dispersal in high-food areas.

→ (5) Between years, 16-22% of previously-marked males return to Konza. Birds frequently skipped years, but then return to initial territories 2 yr later. Isotopic evidence suggests that long-distance dispersal is common; 80% of new arrivals in 2015 matched feather isotopic signatures of birds molt locations >80 km away.



(6) Birds track shifting locations of preferred nesting vegetation structure and composition despite phenological changes.

(7) Climate variability affects sparrows. Severe storms doubles chances of nest failure. Adult body composition affected by storms and periods of high heat and humidity.

→

KNZ LTER Datasets: CBS02, CBS03

Dornak, L. L., N. Barve, and A. T. Peterson. 2013. Spatial scaling of prevalence and population variation in three grassland sparrows. *Condor* 115:186-197. doi:10.1525/cond.2013.120055.

Powell, A. F. L. A. 2006. Effects of prescribed burns and bison (*Bos bison*) grazing on breeding bird abundances in tallgrass prairie. *Auk* 123:183-197.

Powell, A. F. L. A. 2008. Responses of breeding birds in tallgrass prairie to fire and cattle grazing. *Journal of Field Ornithology* 79:41-52.

Williams, E. J. 2016. Grasshopper Sparrows on the move: patterns and causes of within-season breeding dispersal in a declining grassland songbird. Kansas State University, Manhattan, KS.

Williams, E. J., and W. A. Boyle. *in press*. Patterns and correlates of within-season breeding dispersal: a common strategy in a declining grassland songbird. *The Auk: Ornithological Advances*.

Dynamic Responses to Patch-Burn-Grazing Treatments

Investigators: Anthony Joern, K.C. Olson, John Briggs, Brett Sandercock, Bill Jensen, Alice Boyle, Walter Dodds, Jeff Taylor, Amanda Kuhl, *Andrew Ricketts, *Bram Verheijen, *Danelle Larson, #Sarah Winnicki, #Kelsey Girvin

*former grad student, #current grad student, #former undergraduate student

Questions

- (1) How does cattle grazing in annually burned pastures affect vegetation structure and heterogeneity compared to patch burn treatments?
- (2) How do representative consumers respond to patch-burn treatments?
- (3) Does increased heterogeneity beget increased diversity?

Basic Setup

- Patch Burned watersheds burned every 3 years; cattle have access to entire area [North – Shane WS in 2011 and South - C-units in 2010) manipulations]
- Reference – annual burn with grazing, and (b) 1- and 4- year burn with no grazing
- Seasonal grazing with cow-calf herd @ 8 acres/ cow-calf unit



Fig. 1. Patch-burn grazing at end of growing season. Note higher grazing activity in foreground, which was most recently burned.

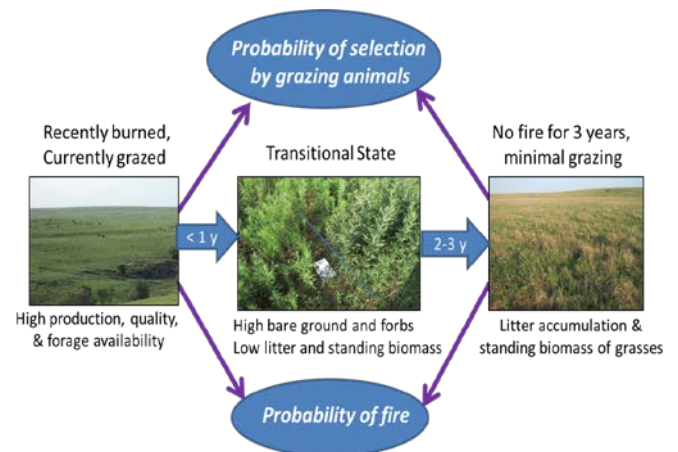


Fig. 2: Motivation for study, modified from (Weir et al. 2007)

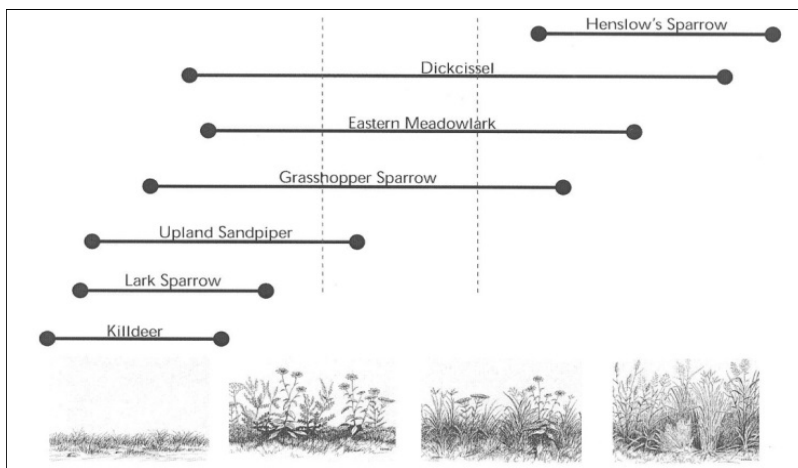


Fig. 3: Varying habitat structure for KNZ bird species

Burning sections of the landscape in a patch-burn dynamic creates a mosaic of vegetation structure. This habitat heterogeneity facilitates use by a more diverse array of grassland birds (Fig. 3) (Verheijen 2017).

Avian Responses (B. Verheijen, B. Sandercock, B. Jensen, A. Boyle, S. Winnicki)

- Observe higher densities and species diversity in patch burn treatments (data not shown)
- No demographic differences were seen in representative species (Fig. 4)

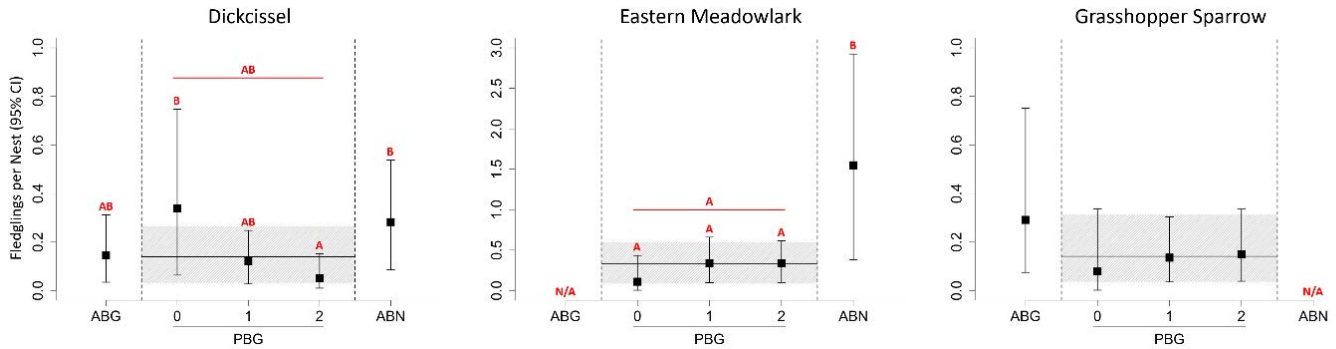


Fig. 4: Fledglings per nest for 3 grassland bird species in response to time since fire.

Vegetation Height (John Briggs, Jeff Taylor)

- Cattle selectively use recently burned watersheds in most years (Fig. 5)
- During the 2012 drought, the overall use of watersheds was more uniform
- Cattle distributions shift among years

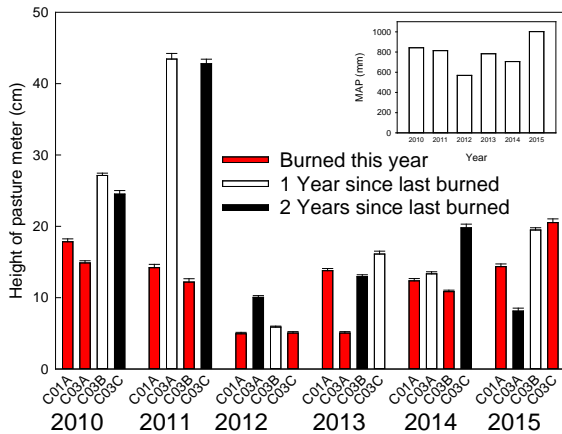


Fig. 5: Height of disk pasture meter (proxy for standing biomass) by watershed*time.

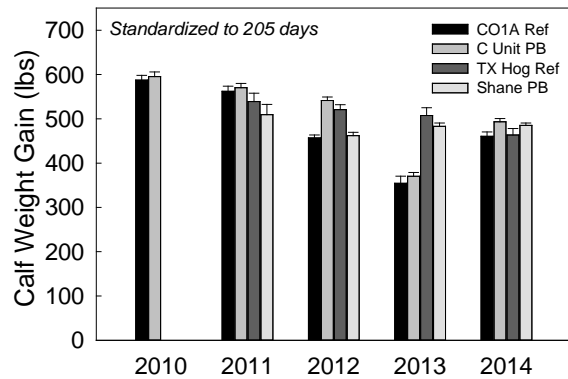


Fig. 6: Changes in calf weight gain over time are similar among varying fire treatments compared.

Cattle Performance and Resource Use (K.C. Olson)

- Little effect of patch burn treatments on calf weight vs. annually- burned controls (Fig. 6)
- Body condition of heifers did not differ (data not shown)
- During the 2012 drought, the use of the unburned areas initiated a buffering effect; during this year, the cattle had food available that was not typically used in other years
- Patch-burn grazing regime provides an indirect rancher benefit, as it's easier to find the cows

Small Mammals (Andrew Ricketts & Brett Sandercock)

- Diversity was significantly higher in patch-burn grazing and the positive control vs. the negative control, increasing somewhat with increased time since burn (Fig. 7, 8).
- Canonical correspondence analysis revealed that the fire-grazing interaction was a major driver of small mammal communities (Fig. 9)

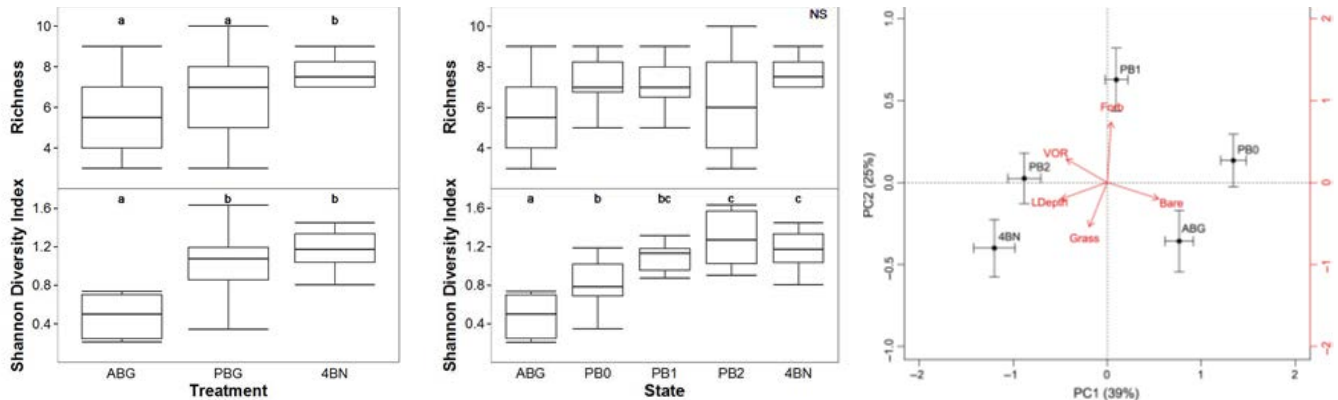


Fig. 7-9: Results from the 2016 dissertation by Andrew Ricketts; Ricketts & Sandercock 2016. Fig. 7 and 8 illustrate changes in diversity and richness to varying patch-burn treatments, while Fig. 9 illustrates drivers of small mammal species composition.

Grasshoppers (Antony Joern, Jeff Taylor)

- With grazing, species richness declines with 3-y burn rotation (Fig. 10, 11)
- No grazing, longer burn interval leads to increased species richness in year of burn (Fig. 12)
- Ungrazed reference sites have similar number of species (Fig. 12)
- Densities highest in annually burned, grazed treatments (C1A, C1SB)

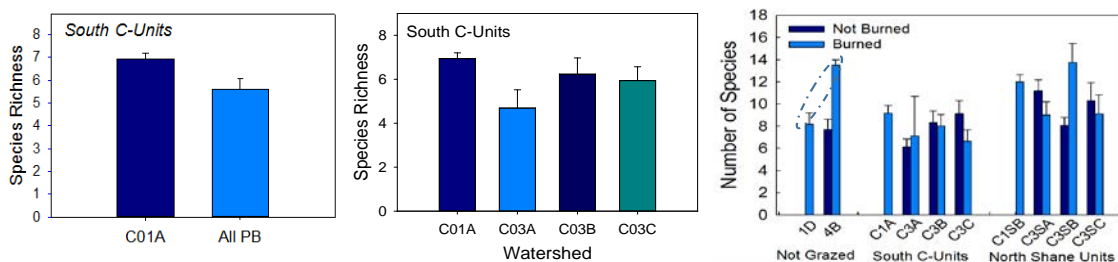


Fig. 10-12: Changes in grasshopper species richness driven by burn frequency and grazing

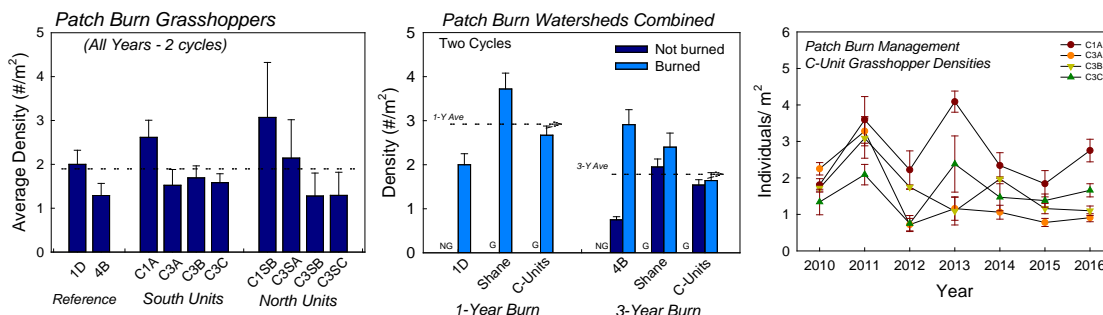


Fig. 13-15: Average grasshopper density shows a strong year of burning effect, if burned every 2 or more years.

Literature Cited

- Ricketts AM. 2016. Of mice and coyotes: Mammalian Responses to Rangeland Management Practices in Tallgrass Prairie. PhD Dissertation, Kansas State University.
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- Weir, J.R., S.D. Fuhlendorf, D.M. Engle, T.G. Bidwell, D. Chad Cummings, D. Elmore. 2007. Patch Burning: Integrating Fire and Grazing to Promote Heterogeneity. E-998. Oklahoma Cooperative Extension Service, Oklahoma State University, Stillwater, Okla. 28 p.

KNZ Data Sets for Patch Burn Studies

- PBG01--Plant species composition in the Patch-Burn Grazing experiment at Konza Prairie
- PBG02--Aboveground primary productivity within permanent and rotating grazing exclosures in the Patch-Burn Grazing experiment at Konza Prairie
- PBG03--Disk pasture meter measurements to estimate plant standing biomass in the Patch-Burn Grazing experiment at Konza Prairie
- PBG04--Reproductive effort of Big Bluestem, Indiangrass and Little Bluestem in the Patch-Burn Grazing experiment at Konza Prairie
- PBG05--Response of bird abundance to the Patch-Burn Grazing experiment at Konza Prairie
- PBG06--Cattle grazing and cattle performance in the Patch-Burn Grazing experiment at Konza Prairie
- PBG07--Grasshopper species abundances in the Patch-Burn Grazing experiment at Konza Prairie
- PBG08--Grasshopper density survey in the Patch-Burn Grazing experiment at Konza Prairie
- PBG10--Soil physical and chemical characteristics in the Patch-Burn Grazing experiment at Konza Prairie
- PBG11--Stream Water Chemistry for the King's Creek drainage basin in the Patch-Burn Grazing experiment at Konza Prairie

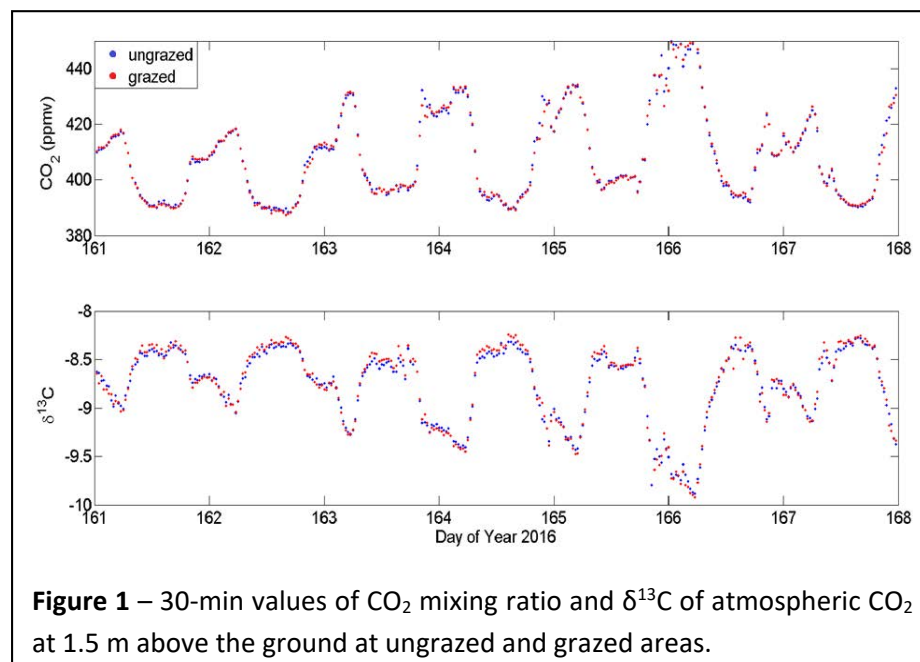
Applying *in situ* High Frequency Measurements of Stable Isotopes (^{12}C and ^{13}C) of CO_2 to Study the Effect of Grazing and Fire on the Carbon Cycle

Investigators: E. Santos, J. Nippert, K. Stropes*, M. dos Santos#

*former grad student; # current grad student

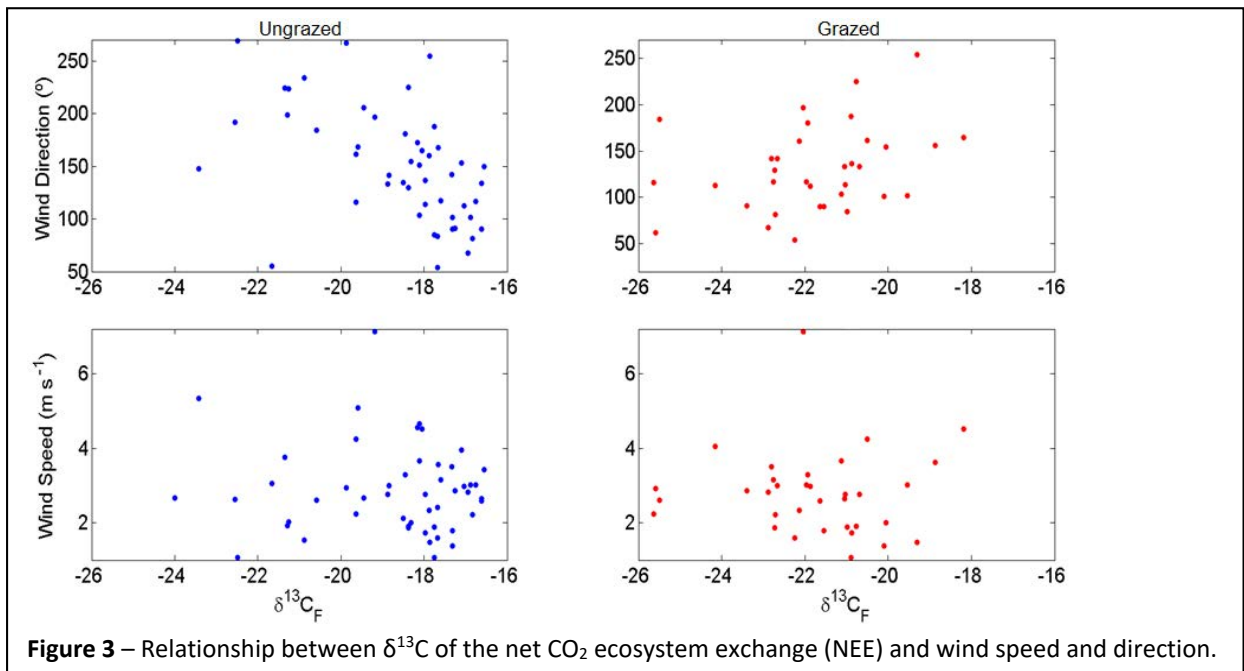
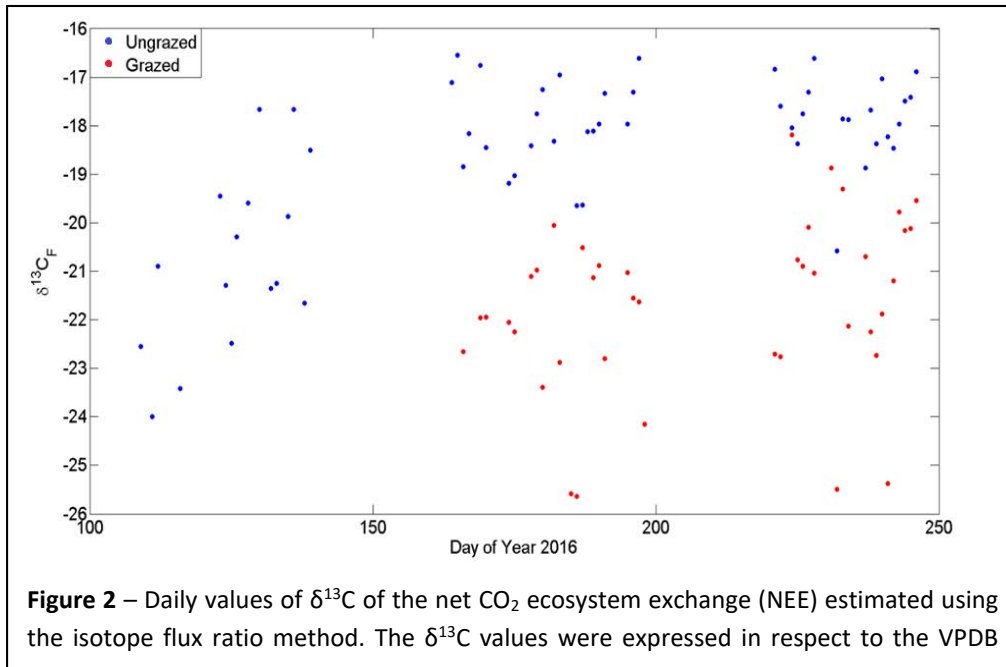
The central goal of this study is to use a *combination of in-situ isotope measurements with micrometeorological methods to improve our understanding of the effect of fire, grazing and climate variability on carbon and water cycles in grasslands*. These isotope measurements, several support variables measured at the site, and a nearby NEON tower are being used to address several research questions related to the carbon cycle at the ecosystem scale, including:

- Is local advection important for the isotopic and CO_2 flux measurements?
- How do environmental drivers (temperature, soil moisture, air humidity, precipitation, etc.) control the temporal dynamics of $\delta^{13}\text{C}$ of NEE in grazed and ungrazed areas?
- How do fire and grazing affect C_3 and C_4 plant contribution to the net ecosystem CO_2 exchange in scales ranging from hours to years?
- Could the isotopic data be used for partitioning plant and soil contributions to the Net CO_2 Ecosystem exchange?
- What are the biotic and abiotic variables affecting the $\delta^{13}\text{C}$ of ecosystem respiration? Could this information be used to improve current models to estimate carbon exchange at the ecosystem level?



Values of $\delta^{13}\text{C}$ of atmospheric CO_2 showed a clear diel pattern with less negative values during the daytime and more negative values during the nighttime (Figure 1). This diel pattern is an effect of the plant canopy discrimination against the heavier isotopologue ($^{13}\text{CO}_2$) and changes in the atmospheric boundary layer (Griffis et al. 2007). Furthermore, small differences in $\delta^{13}\text{C}$ of atmospheric CO_2 between grazed and ungrazed areas was observed.

The effect of C₃ and C₄ dominance was noticeable for the δ¹³C of NEE, which was often more negative for the grazed compared to the ungrazed areas (Fig. 2). Higher δ¹³C in the ungrazed area indicates a larger contribution of C₃ plants to the net CO₂ ecosystem exchange at C3A than at K2A.



Griffis, T.J., Zhang, J., Baker, J.M., Kljun, N. and Billmark, K., 2007. Determining carbon isotope signatures from micrometeorological measurements: implications for studying biosphere-atmosphere exchange processes. *Boundary-Layer Meteorology*, 123(2): 295-316.

Stropes, K. 2017. Investigating the exchange of CO₂ in a tallgrass prairie ecosystem using stable isotopes and micrometeorological methods. MS Thesis. Kansas State University.

Stream Ecosystem Processes

Investigators: Walter Dodds, Matt Whiles, Keith Gido, Lydia Zeglin, James Guinnip*, Sophie Higgs*
**current graduate student*

KNZ Data sets used: ASD02, ASD04, ASD05, ASD06 and USGS Kings Creek gaging station for discharge; ASW01 stream suspended sediments, and NWC01 stream nutrients

Rationale:

There are more publications from Kings Creek on wholly protected grassland streams than from any other we know of. This site was part of the Lotic Intersite Nitrogen Experiments (LINX collaborators 2015) and the SCALER NSF Macrosystems project, and our research team actively participates in LTER synthesis and data sharing efforts. The stream is also an important baseline for regional water quality comparisons (e.g., Dodds and Oakes 2006, Larson et. al. 2013).

Streams are highly dynamic in this climate, where potential and actual evapotranspiration are, on average, about equal. Thus, we operate under the overall framework that prairie streams are non-equilibrium systems punctuated with different limiting factors and disturbances. This working concept extends to all of our stream research topics, from biogeochemistry to fishes, and it is addressed here with respect to stream ecosystem processes

Basic Questions:

- (1) What are the consequences of directional influences of climate, riparian canopy expansion, and nitrogen deposition in a grassland watershed? We refer to the 2-page document on woody expansion for discussion and results on causes of long-term discharge decreases. The long-term data show large shifts in forms of stream nitrogen that may correspond to shifts in atmospheric loading, and a progressive decrease in discharge in many of the watersheds.
- (2) What controls stream metabolism in the King's Creek stream network? In systems that experience flood and drought, there are rapid biological responses to those disturbances and we are how these responses scale to the integrated Kings Creek network level. We rely on the long-term data from the 4 discharge monitoring stations to create a whole-network model of stream flow and extrapolate gas flux from existing experiments.
- (3) What controls long-term trends in carbon export? We conduct long-term sampling of dissolved organic carbon across 9 collection stations in Kings Creek. We also have participated in sampling efforts to identify the sources and processing of organic carbon in stream sediments and water.

Representative Results to Date:

There are directional changes in long-term records of discharge, nitrogen concentrations and atmospheric deposition. Our data show a dramatic increase and then leveling off of ammonium concentrations in stream waters but the only nitrate trend is a decrease in the lowermost segment. The increase of ammonium could be caused by a shift in atmospheric N deposition away from nitrate to ammonium or a consequence of increased riparian cover fundamentally altering biogeochemical pathways. The downstream decrease in nitrate may be due to restoration of cropland and better nutrient management near headquarters. In addition, we are documenting (1) whole watershed metabolism patterns following disturbance (Fig. 1), (2) spatial heterogeneity of metabolism (Fig. 2), and (3) patterns and controls of dissolved organic carbon across the landscape (Fig. 3). Downstream declines in DOC concentration reflect the importance of in-stream processing and integrated metabolism on the C retentive status of Kings Creek.

Figure 1. Time series of whole stream metabolism (4 of 8 sites) following a modest flood (3 year return interval). We used the long-term record of Konza discharge to create a model of discharge as a function of watershed area above the point of interest. As we could not monitor discharge directly at all these sites, so this allowed us to estimate discharge for each day after the flood and use diurnal oxygen signals to estimate metabolism (manuscript in preparation).

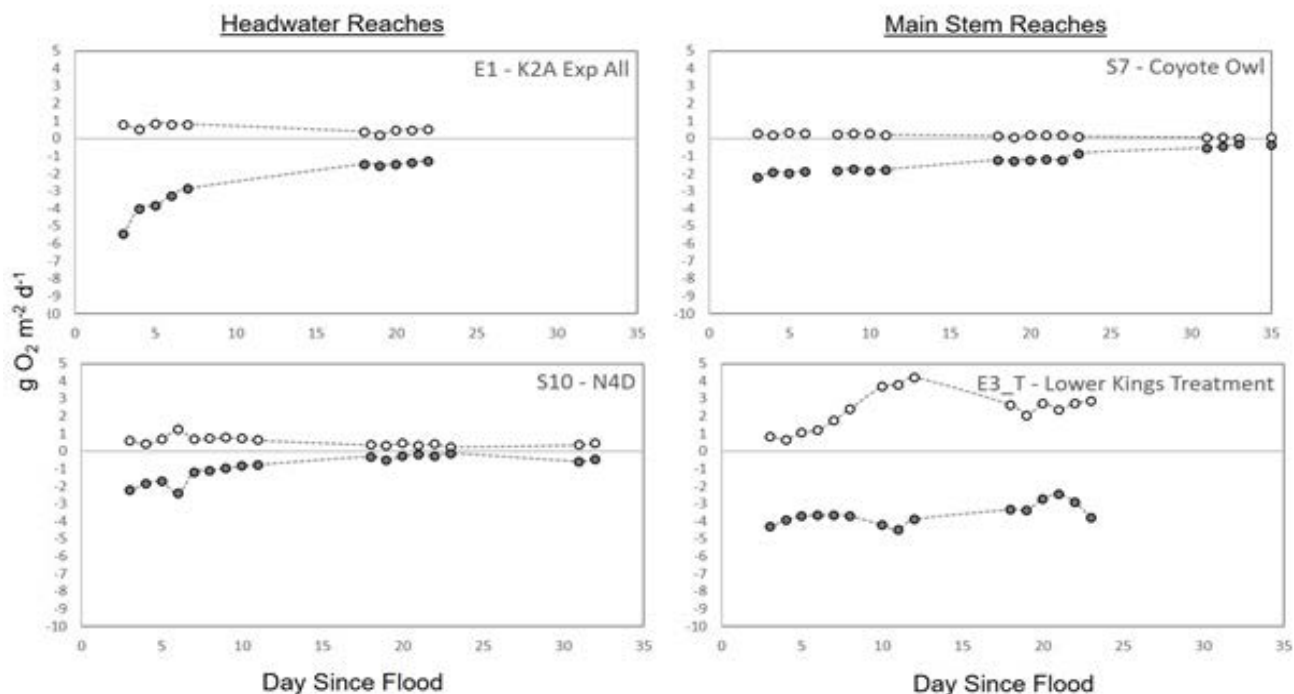


Figure 2. Spatial variability in stream metabolism illustrate by data from one pool (Siders et al. 2015)

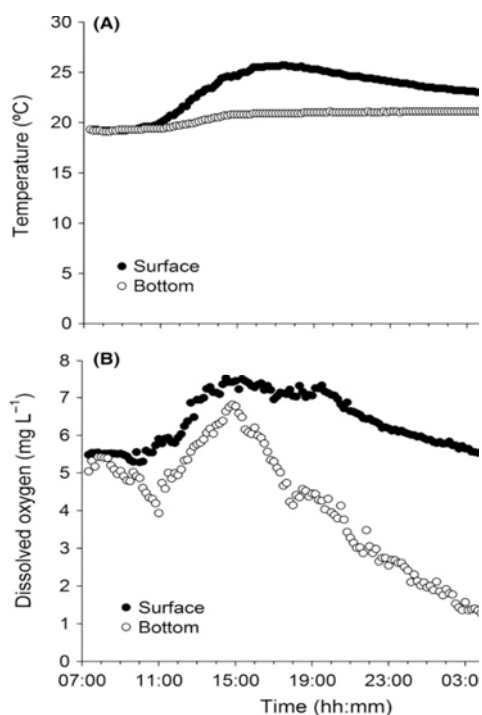
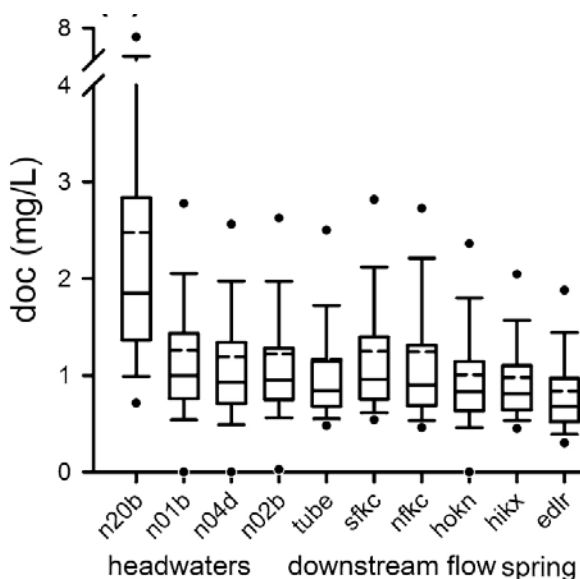


Figure 3. Spatial distribution of dissolved organic carbon from long-term records (Rüegg, et. al. 2015)



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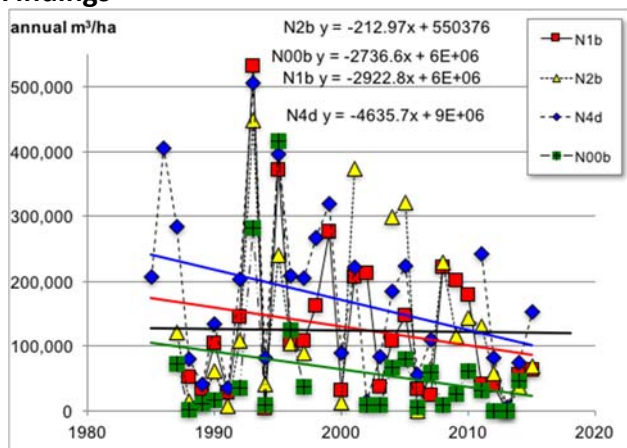
Hydrology and Hydrogeology at Konza Prairie LTER Site

Investigators: Gwendolyn L. Macpherson^a, Pamela L. Sullivan^b, Walter K. Dodds^c, *Brock Norwood^a (M.S. candidate), *Emily Barry^a (M.S. candidate), *Ellis Spangler^a (REU student), *Chantelle Davis^a (B.S. research)
^a University of Kansas, Dept. of Geology, ^b University of Kansas, Dept. of Geography, ^c KSU, Division of Biology

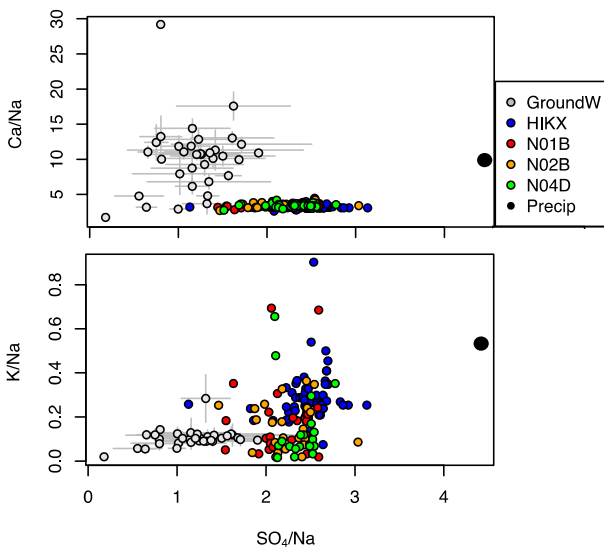
Installations and data sets:

- 4 V-shaped flumes in headwater streams (N1b, N2b, N4d, N20b)
- 35 wells in limestone *Upstream Bedrock Aquifers* (UBAs), N4d watershed
- 14 wells in *Downstream Alluvial Aquifers* (DAAs)
- Data sets: AGW01, 02, 03 (groundwater elevation, chemistry, temperature); ASD02, 04, 05, 06 (stream discharge); ASS01, ASW01 (stream water quality); AWT01, 02 (stream temperature)

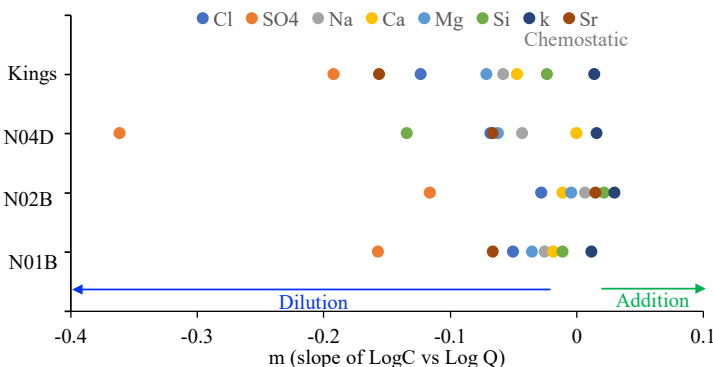
Findings



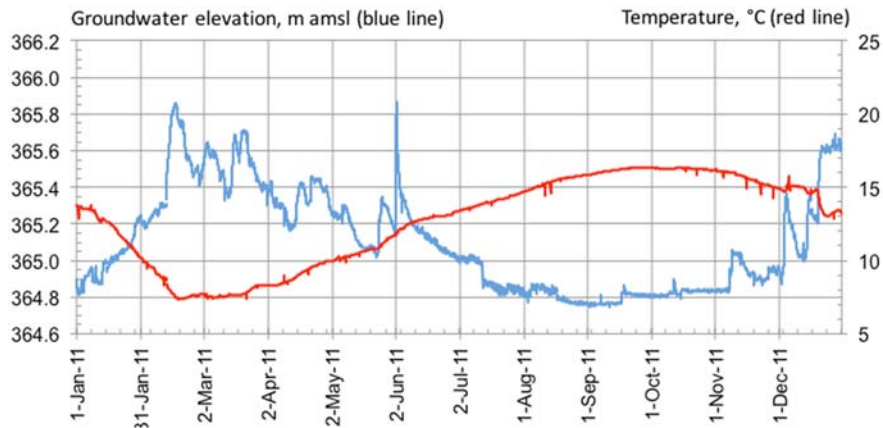
Groundwater discharge to streams maintains baseflow and is the sustaining source of water and nutrients for aquatic biota. Stream discharge is decreasing in KNZ streams (unpublished), whether plotted as total discharge (not shown) or normalized per hectare. N4D has decreased at the fastest rate; N2B shows much less decrease, possibly because the watershed orientation is different (SW to NE) from the others (SE to NW or S to N). Watershed with the most woody vegetation (N20B), also has the lowest per-hectare discharge although it is the smallest of the four.



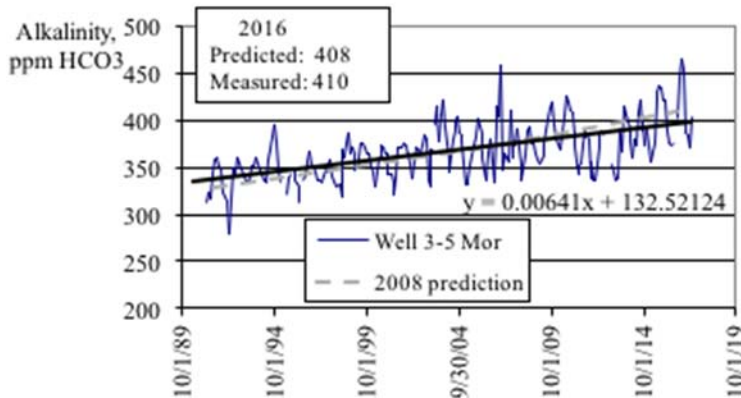
Mixing models comparing stream water (colorful) solutes normalized to Na to the composition of groundwater (GroundW) and precipitation (black filled circle). Results suggest interflow (horizontal, saturated flow through the vadose zone) has a large influence on stream water chemistry. Together these sources of water determine nutrient available to aquatic biota; and amounts of nutrients and non-nutrient export from watersheds as stream-water discharge.



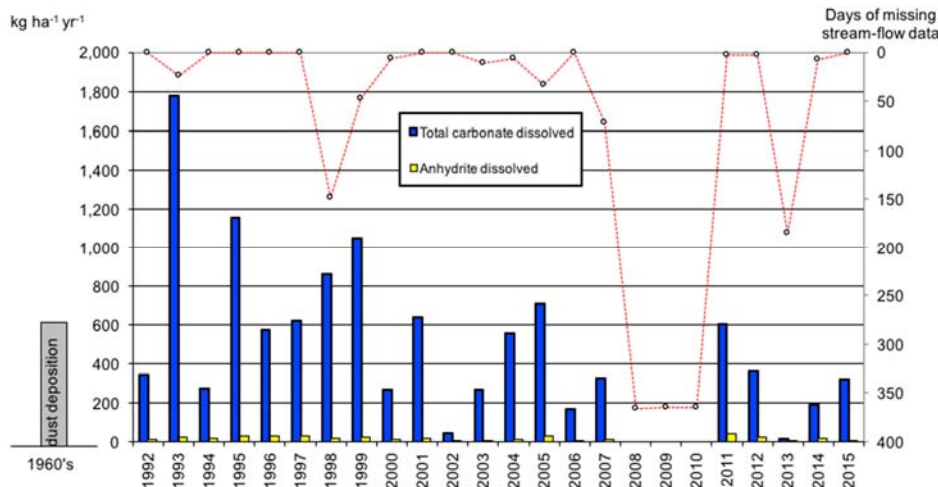
Stream chemistry is influenced by groundwater and soil water. The slope of the concentration discharge behaviour (C-Q) for solutes across headwater catchments (N01B, N02B, N04D) and Kings Creek—the downstream site that integrates these and other headwater catchments—suggest hydraulic connectivity differs spatially. Stream water exhibits dilution behaviour ($m < 0$), chemostatic behaviour ($m \approx 0$), and addition behaviour ($m > 0$).



UBAs receive the most recharge during times of modest amounts of meteoric precipitation and inactive vegetation (late Fall through early Spring); precipitation response times (water level rise and temperature change) are on the order of 4-5 hours (Brookfield et al., 2017).



Increasing alkalinity in well 3-5 Mor is indicative of increasing groundwater pCO_2 (log partial pressure of CO_2 in equilibrium with water). Trend line in Macpherson et al. (2008) predicts 2016 average annual alkalinity of 408 ppm; measured average alkalinity in 2016 was 410 ppm. Rate of pCO_2 increase is ~ 180 ppmv yr^{-1} ; groundwater is a sink for soil CO_2 . In 2016, pCO_2 in illustrated well was -1.60 ($>25,200$ ppmv CO_2).



Calculated weathering rates, corrected for meteoric precipitation, use stream chemistry and discharge to quantify mass of solids removed from watershed N4d. Over 24 years, these ranged from 45 to 1,777 kg ha⁻¹ yr⁻¹, suggesting all limestone should have dissolved in 1-2 million yrs. Thus, limestone is not the primary phase that is dissolving. Instead, it is possibly dust. Dust deposition rates (1960's) were ~ 600 kg ha⁻¹ yr⁻¹.

References

Brookfield, A., Macpherson, G. L., Covington, M. 2017. Effects of changing meteoric precipitation patterns on groundwater temperature in karst environments. *Groundwater*, 55(2): pp 227-236; DOI 10.1111/gwat.12456.

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Macpherson, G. L., Roberts, J. A., Blair, J. M., Townsend, M. A., Fowle, D. A., & Beisner, K. R. 2008. Increasing shallow groundwater CO_2 and limestone weathering, Konza Prairie, USA. *Geochimica et Cosmochimica Acta*, 72(23), 5581-5599. doi:10.1016/j.gca.2008.09.004.

Fish Community Dynamics in an Intermittent Prairie Stream

Investigators: Keith Gido, Sky Hedden, Lindsey Bruckerhoff*, Bryan Frenette*, Casey Pennock*, Garrett Hopper* *graduate students

Rationale: Kings Creek is composed of perennial reaches connected by intermittent (that periodically cease to flow) and ephemeral (that dry completely) reaches. Fish metacommunity dynamics and the ability of fishes to recover from drought and other disturbances have not been well studied in these highly stochastic, non-equilibrium prairie streams. However, dispersal is predicted to be a main driver of community structure because movement across intermittent and ephemeral reaches is constrained. Kings Creek can be classified as a “mid-reach drying” stream with an ephemeral middle reach separating perennial downstream fish populations from perennial headwater spring populations (Figure 1). Long-term KNZ LTER data (**CFC011**)

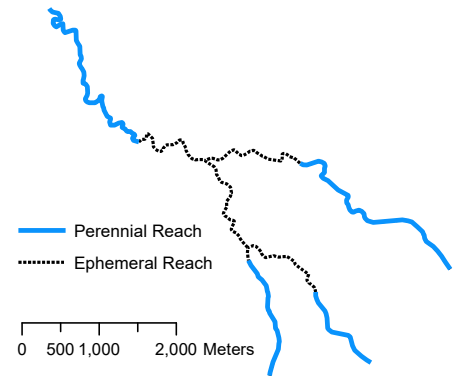


Figure 1. Map of Kings Creek showing perennially flowing (blue) and ephemeral reaches (dashed)

from these perennial habitats has quantified the stability of fish populations. The downstream perennial reach has maintained a stable fish community, where the rank abundance of the three most abundant species has remained constant over the 20 years of monitoring (Figure 2 top panel). In contrast, the fish community in headwater spring habitats is less stable. At our headwater site in the N4D watershed central stoneroller abundance has markedly declined (Figure 2 middle panel) and in the N1B watershed we have seen a decline and disappearance of all species (Figure 2 lower panel). It is possible that reduced connectivity with the downstream and more stable populations has caused the observed declines in fish populations in these headwater sites.

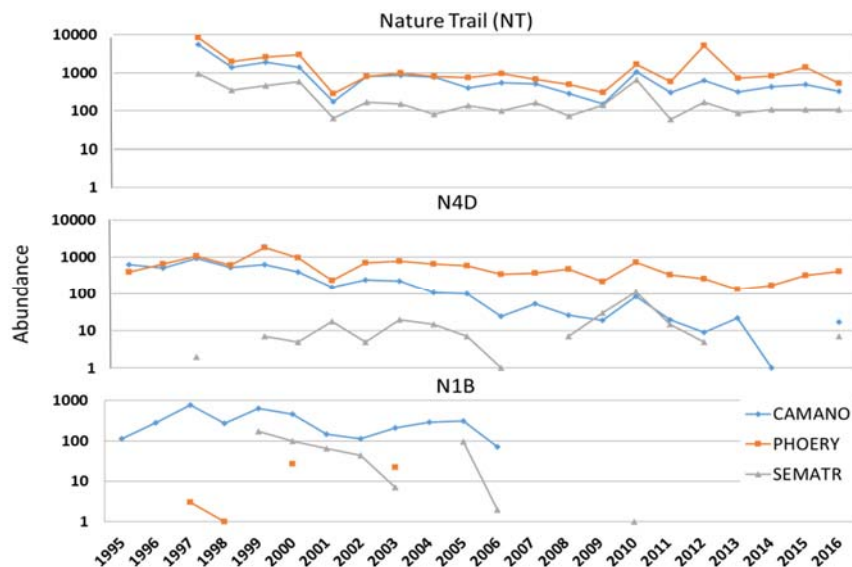


Figure 2. Long-term trends in abundance of the three dominant fish species sampled in perennally flowing stream reaches in Kings Creek. Declines in abundance and occurrence at two headwater sites (lower two panels) might be due to severed connection with the downstream perennial reach caused by a poorly constructed road crossing.

Basic questions: 1) What proportion of fish from perennial reaches move into the ephemeral middle reach of Kings Creek? 2) Are there differences in movement tendencies of the three common fish species? and 3) Does a poorly constructed road crossing inhibit movement through the ephemeral reach (Fig. 3)?



Figure 3. Road crossing on Kings Creek ephemeral reach.

Representative results to date: Beginning in Fall 2015, we initiated a tagging experiment to quantify the dispersal among fish metacommunities in Kings Creek. Fish captured at three LTER fish community sampling sites (N4D, K2A and Nature Trail) were implanted with passive integrated transponder (PIT) tags in November 2015 and 2016. Remote antennas that detected PIT tags were placed in the ephemeral reach of Kings Creek following spring rains (April and May) that restored flow to those habitats in spring. A substantial percent (up to 16%) of the fish populations in the downstream perennial reach moved into the ephemeral reach (Figure 4). Only a few fish were detected moving downstream into the ephemeral reach from headwater populations and no fish were detected moving upstream through the road crossing.

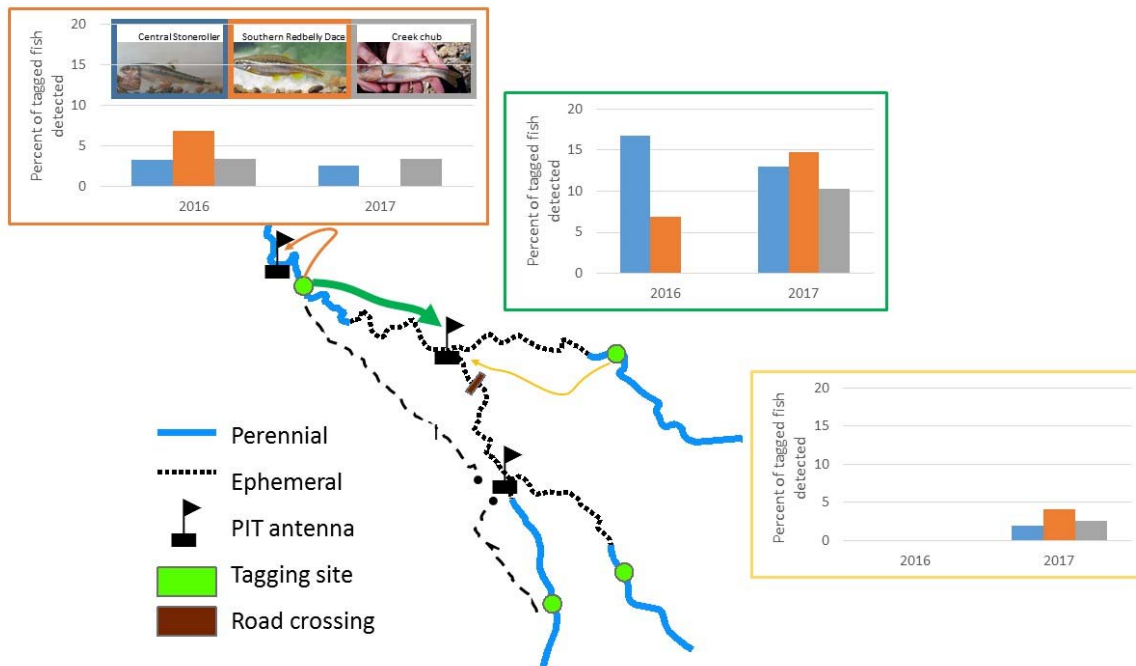


Figure 4. Percent of PIT tagged fish detected at three antenna locations in Kings Creek. Color of box around graph coincides with color of arrow representing movement; a dashed line represents no detected movement between sites and antennas. The majority of movement was from the downstream perennial site into the ephemeral stream reach downstream of the road crossing and no fish moved upstream of the road crossing.

Selected references:

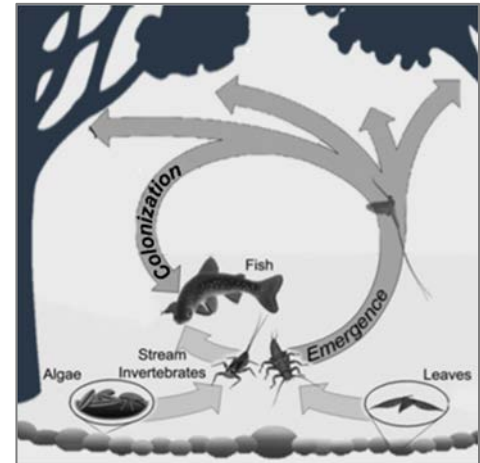
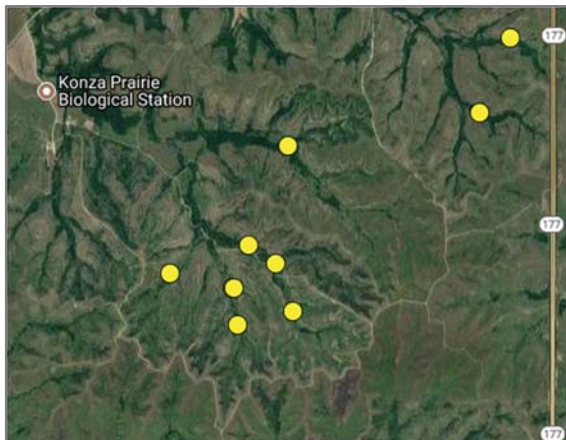
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- Franssen, N.R., K. B. Gido, T. R. Strakosh, K. N. Bertrand, C. M. Franssen, C. P. Paukert, K. L. Pitts, C. S. Guy, J. A. Tripe, S. J. Shrank. 2006. Effects of floods on fish assemblages in an intermittent prairie stream. *Freshwater Biology* 51: 2072–2086.
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- Whitney, J.E., K.B. Gido, E.C. Martin and K.J. Hase. 2016. The first to go and the last to leave: colonization and extinction dynamics of common and rare fishes in intermittent prairie streams. 61:1321–1334. *Freshwater Biology*.

Influence of Fishes on Macroinvertebrate Communities in Permanent Water Refugia

Investigators: Sophia Bonjour*, Matt Whiles, Keith Gido, Walter Dodds *grad student

Rationale:

Hydrology is a major structuring force of invertebrate communities in prairie streams, with permanent reaches serving as refugia during hydrologic disturbances. Invertebrate densities decrease dramatically in response to hydrologic extremes, making perennial reaches critical for recolonization. Fishes can also become concentrated in permanent pools and may influence invertebrate communities present in these systems, and thus recolonization dynamics. Fish predation may also influence connections (subsidies) between stream and riparian habitats via emerging adult aquatic insects.



Objectives:

- (1) Examine the effects of fish presence on invertebrate community structure and algal abundance in perennial refugia.
- (2) Assess the effects of fish on invertebrates at different life stages, particularly emerging adult insects.
- (3) Isolate the effects of fish density on invertebrate and algal colonization in mesocosms.

Selected results-to-date:

Field study: We examined benthic and emergent invertebrate communities at permanent water sites across KPBS watersheds with natural variation in densities of fishes.

- Fish biomass was inversely correlated with predatory invertebrate and collector-gatherer invertebrate biomass, but not total invertebrate biomass.
- Total fish biomass did not affect total emergence biomass, but an increase in benthic feeding darter biomass was correlated with a decrease in midge emergence.
- An interaction between predatory fish biomass and date in linear models indicated fish may delay insect emergence (Figure 2).

Take away: Like hydrologic disturbance, fishes are an important factor in shaping prairie stream communities. In particular, they can alter insect community structure, body size, and timing of adult emergence in refugia that are critical for recolonization after hydrologic disturbance.

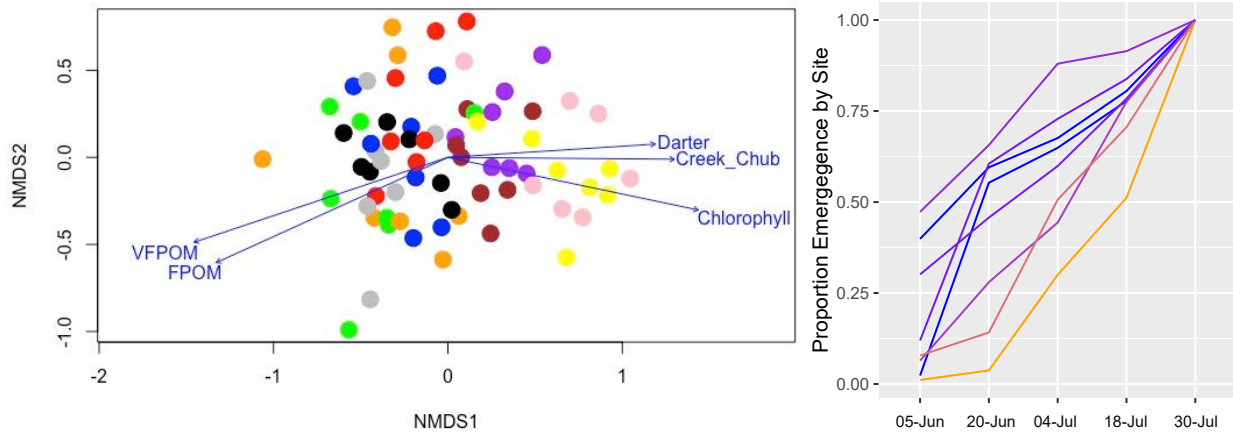
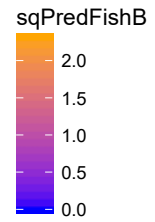


Figure 2 (above) Invertebrate were sampled at 10 sites (colors are samples from a site during 7 dates). Community shifts were driven by darter and creek chub abundance, chlorophyll, and organic matter.

Figure 3 (right) Sites with higher predatory fish biomass had a greater percentage of emergence later during summer sampling season than sites with lower predatory fish.



Colonization experiment: During summer 2015, twenty small mesocosms (1.8m²) were stocked at three densities of fish (zero, low, high) and allowed to colonize for 5 weeks.

- Abundances of invertebrate colonists were higher in fishless pools than in pools with low or high densities of fish ($p < 0.001$).
- High fish densities reduced predatory insect biomass, but increased collector-gatherer biomass (Figure 4, below).
- No difference was observed in algal biomass among treatments.

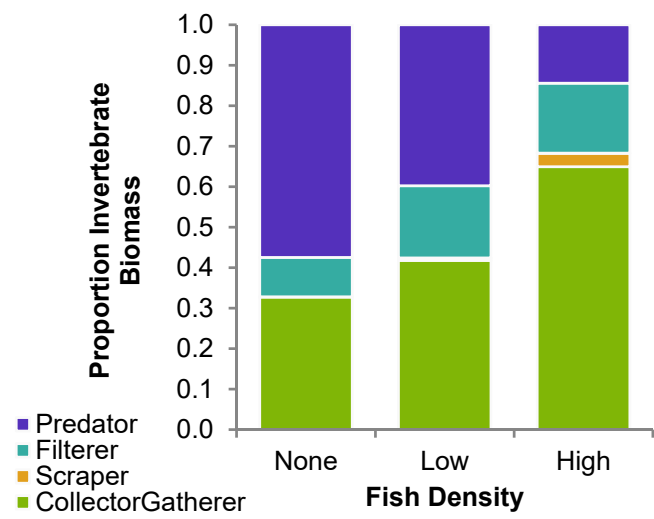


Figure 4 Invertebrate communities shifted from predominantly predatory to collector-gatherer taxa with increased fish density, mirroring the inverse relationship between fish and predatory insect biomass observed in the field study.

Selected KNZ Publications:

Bertrand, K.N., et al. 2013. Influence of macroconsumers, stream position, and nutrient gradients on invertebrate assemblage development following flooding in intermittent prairie streams. *Hydrobiologia* 714:169–182.

Franssen, N.R., et al. 2006. Effects of floods on fish assemblages in an intermittent prairie stream. *Freshwater Biology* 51: 2072–2086.

Murdock, J. N., et al. 2010. Consumers alter the recovery trajectory of stream ecosystem structure and function following drought. *Ecology* 91: 1048-1062.

Whiting, D. P., et al. 2011. Patterns of macroinvertebrate production, trophic structure, and energy flow along a tallgrass prairie stream continuum. *Limnology and Oceanography* 56:887-898.

The Belowground Plot Experiment

Investigators: John Blair, Mac Callahan, Christine Carson*, Michael Carson*, Priscilla Moley#, Rosemary Ramundo, Charles Rice, Tim Todd, Gail Wilson, Lydia Zeglin
 *former graduate students, #current graduate students

Background and Rationale

Soil biogeochemical processes and communities are influenced by, and exert feedbacks on, aboveground plant and consumer responses to fire, grazing and drought. The Belowground Plot Experiment (BGP, Fig. 1) was established in 1986 to assess relationships between above- and belowground processes, and the independent and interactive effects of fire (annually burned (**B**) or unburned (**UB**) treatments), aboveground biomass removal (annually mowed or unmowed until 2004), and chronic nutrient additions (no fertilizer control (**C**), **N** only, **P** only, or **N+P**). A suite of above- and below-ground responses has been documented, including: plant species composition, aboveground plant productivity (ANPP), root and rhizome biomass and nutrients, root growth dynamics, litter decomposition, soil C and N pools and fluxes, soil and soil solution chemistry, soil microbial communities, mycorrhizae, and soil invertebrates.

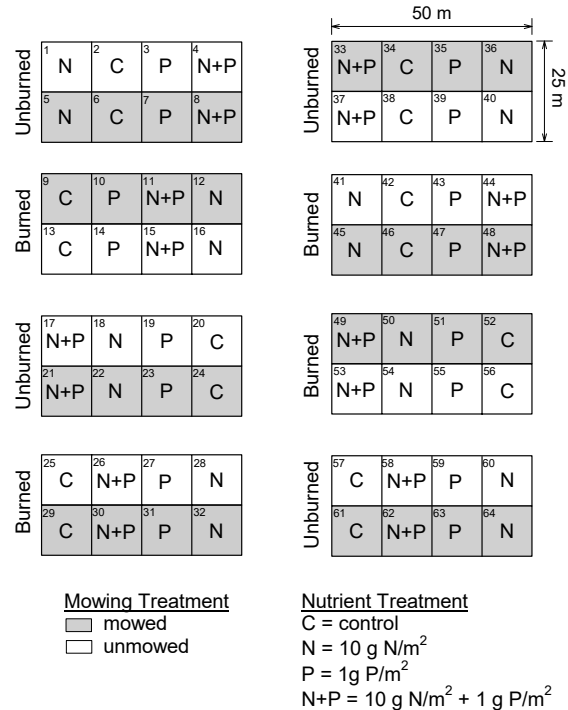


Fig. 1. Experimental design & plot map.

Long-term data reveal strong interactions between fire and N enrichment in both above- and belowground responses. After an initial lag, total ANPP increased up to 3-fold with long-term N enrichment in annually burned plots, with warm-season grasses driving the increase. Without fire, forbs and woody plants now dominate the plant

community and N enrichment does not have a strong or consistent effect on ANPP (Collins et al. 1998, Fig. 2). Ecosystem responses are linked to microbial feedbacks: In burned prairie, soil microbial N immobilization is high, helping to maintain the N-limited status of ANPP (Dell et al. 2005). Root colonization by arbuscular mycorrhizal (AM) fungi is higher with N addition, due to increased P limitation, and in turn AM activity enhances aggregation and C stabilization in fertilized soils (Wilson et al. 2009). Also, both

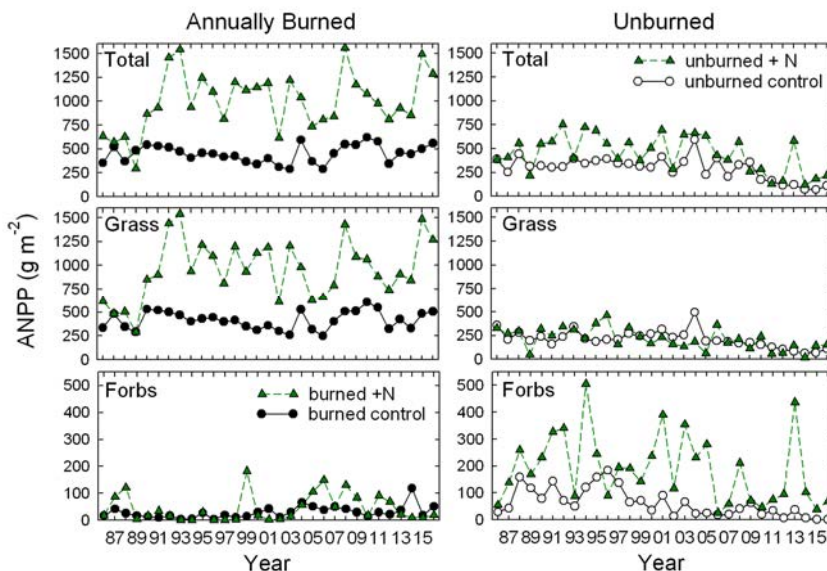


Fig. 2. Aboveground responses to fire and N addition treatments.

plant and soil invertebrate communities show direct and interactive responses to management and +N treatments, with trait-based shifts suggesting feedbacks on ecosystem processes: e.g., losses of N-fixing plants (Cleland et al. 2006) and increases in bacterivorous soil nematodes (Todd et al. 2006, Jones et al. 2006) in N-fertilized, unburned plots. These interactive responses suggest that fire mediates responses to N enrichment. In light of these long-term changes in ecosystem structure and function, the LTER VII goal for the BGP experiment is to cease fertilization treatments, and evaluate the resilience of the ecosystem in annually burned and unburned conditions.

Soil Nutrient Feedbacks: Predictions and Results

We hypothesize that the resilience of above- and belowground parameters, or time to recovery to reference (unfertilized) conditions after cessation of N fertilization depends on decreases in soil available N. So, factors that promote N loss should also promote resilience. These factors include volatilization of plant litter N via burning, and higher nitrification, leaching and denitrification in the absence of fire, such that fire history

mediates rates and mechanisms of recovery. Resilience may also be mediated by feedbacks resulting from functionally important community changes caused by chronic N enrichment and/or lack of fire. For example, if the shift from grass to woody vegetation, or shifts in microbial communities (Coolon et al. 2013) affects N retention or loss pathways, resilience and recovery will be affected accordingly.

Prior to ceasing fertilization in 2017, we conducted an intensive sampling campaign to document 30-year impacts on soil biogeochemistry and above- and belowground communities, including C and N inputs and losses, and soil biota (bacteria, fungi, nematodes, arthropods). Results suggest that different feedbacks mediate resilience under contrasting fire history: (a) Lower microbial biomass (Carson & Blair 2013) coupled with altered bacterial community structure, particularly in unburned soils (Fig. 3), suggests that lower N immobilization and promotion of N loss through nitrification and leaching or denitrification, will enhance recovery in unburned plots, while volatilization of N will drive recovery in annually burned plots. However, (b) in woody-encroached unburned plots, soil fungal communities have not become "forest-like" nor lost SOM-degradation capacity (Carson & Zeglin 2017) as observed in chronically fertilized forest soils, so altered soil biogeochemical feedbacks due to woody encroachment per se are not expected. Now, first-year plant and microbial resilience to cessation of N addition is being measured: Microbial recovery is expected to be faster, and as microbial feedbacks affect plant N availability, plant recovery will follow.

KNZ Datasets Used: BGPVC, BNS01, OMB01, PBB01

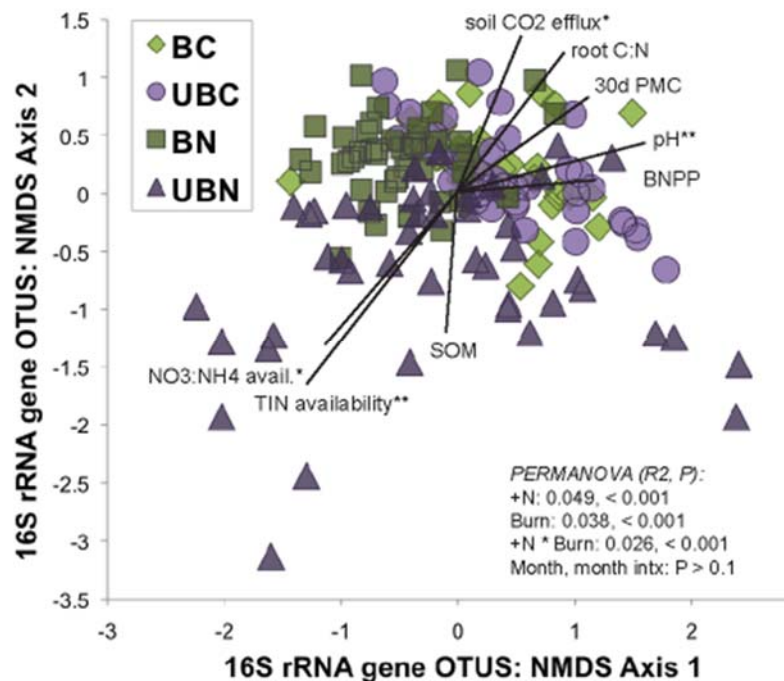


Fig. 3. Soil microbial community structure at BGP, collected monthly in 2015. Lines: correlations ($P < 0.1$, * $P < 0.05$, ** $P < 0.01$). Other factors e.g. water content, ANPP: $P > 0.1$.

Selected KNZ Publications:

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- Jones, K.L., T.C. Todd, J.L. Wall-Beam, J.D. Coolon, J.M. Blair and M.A. Herman. 2006. Molecular approach for assessing responses of microbial-feeding nematodes to burning and chronic nitrogen enrichment in a native grassland. *Molecular Ecology* 15:2601-2609
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- Smith, M.D., K. La Pierre, S.L. Collins, A.K. Knapp, K.L. Gross, J.E. Barrett, S.D. Frey, L. Gough, R.J. Miller, J.T. Morris, L.E. Rustad, and J. Yarie. 2015. Global environmental change and the nature of aboveground net primary productivity responses: insights from long-term experiments. *Oecologia* 177:935-947
- Todd, T.C., T.O. Powers, and P.G. Mullin. 2006. Sentinel nematodes of land-use change and restoration in tallgrass prairie. *Journal of Nematology* 38:20-27.
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Belowground Plots: Restoration Following Invasive Grass

Investigators: Gail Wilson, Eric Duell*, Luci Wilson*, Karen Hickman, Anna O’Hare**, Jim Bever
 *graduate students, ** undergraduate REU student

Background and baseline data: Invasion of grasslands by non-native species results in a state change and represents a strong biotic filter that can limit recovery of native prairie species (Reed et al. 2005). Our baseline data, assessed in an invaded KNZ site adjacent to these Belowground Plots, indicates invasion by a non-native C₄ grass (*Bothriochloa bladhii*) alters soil microbial communities (particularly arbuscular mycorrhizal fungi [AMF]: Fig. 1) and plant-soil feedbacks in ways that limit recovery of prairie composition and function. Disruption of soil biota decreases soil aggregate stability, thereby reducing soil carbon. Following *B. bladhii* eradication (glyphosate applications), native seedling survivorship was greater with ‘live’ native soil inoculum (Fig. 2).

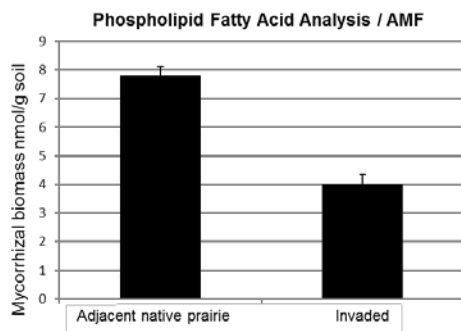
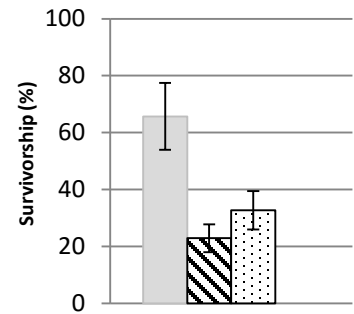


Figure 1: Soil AMF biomass is reduced following invasion by *Bothriochloa bladhii*

Figure 2: Seedling survivorship was greater following inoculation with native prairie soil (grey bars), compared to inoculation with autoclaved soil (hashed), or no soil (stippled)



Inoculation with native ‘live’ soil also suppressed re-invasion by the non-native. At the end of the growing season, plots receiving no soil inoculum averaged 63-70% cover by the invasive species, while plots receiving ‘live’ native soil inoculum, averaged 38% cover by *B. bladhii*.

Role of plant-soil feedbacks in restoring invaded grasslands: An experimental evaluation of mechanisms promoting restoration to the native prairie state following invasion by *B. bladhii* is in progress on a subset of the Belowground Plots. Release from light limitation in annually mowed plots initially enhanced plant diversity¹, however mowing treatments ultimately facilitated invasion of *B. bladhii* (70-95% cover by the invasive in mowed plots). During Spring 2016, we established eight replicate 2m x 2m plots with 70-95% invasive grass cover (n=12) and in corresponding non-invaded plots (n=12). In each replicate plot, prior to eradication (baseline data), we assessed AM fungal communities by quantifying extra- and intra-radical hyphal abundance using phospholipid and neutral lipid fatty acid (PLFA/NLFA) analyses and rDNA sequences from field-collected roots and rhizosphere soil. We also quantified plant species composition, soil aggregate stability, and soil nutrient availability.

Our baseline data indicate invasion by *B. bladhii* reduced AMF biomass (supporting data [Fig. 1] from adjacent site), and significantly reduced water-stable aggregate stability (native soils contained 81% macroaggregates, while macroaggregates of soils from invaded plots were reduced to 74%). Furthermore, using environmental sequencing targeting the large subunit of the ribosomal RNA gene to characterize the composition of the AM fungal community, AMF community composition from invaded plots was distinct from those of corresponding native sites (Fig. 3).

During Spring 2016, we eradicated (or reduced the abundance of) *B. bladhii* through solarization by securing UV-resistant polyethylene sheets across each plot for one growing

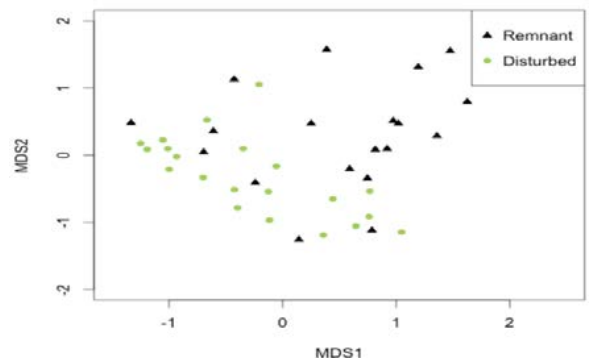


Fig. 3: Differences in MDS scores of AM fungal communities from invaded vs. native sites.

season (Fig. 4). Following solarization, pre-inoculated native nurse plants (*Andropogon gerardii*, *Pascopyrum smithii*, *Asclepias syriaca*, *Ratibida columnifera*, and *Lespedeza capitata*) were transplanted into each 2mx2m plot in Spring 2017. Nurse plants were pre-inoculated with one of the following mycorrhizal fungal treatments: 1) Whole 'live' soil freshly collected from KNZ, 2) AMF spores isolated from KNZ soil [KNZ spores], 3) Inoculum selected from KNZ soil that had been previously selected as highly beneficial to native tallgrass plant species [selected spores], and 4) Non-inoculated sterile control. We will test if inoculated nurse plants allow native AMF to colonize adjacent non-inoculated plants. After transplanting, we have quantified (monthly) nurse plant survivorship and size. At the end of each growing season, we will determine plant species composition, AMF composition, soil aggregate stability, SOC, and soil nutrient availability. We will test the spread of AMF from inoculated nurse plants; assessing AMF community composition through PLFA/NLFA and rRNA analyses.

Eight weeks following transplant, survivorship of *R. columnifera* and *L. capitata* was greater with 'live' KNZ soil or selected KNZ inoculum, compared to plants inoculated either with KNZ spores or not inoculated (Fig. 5).



Fig. 4: Eradication of *B. bladhii* through solarization.

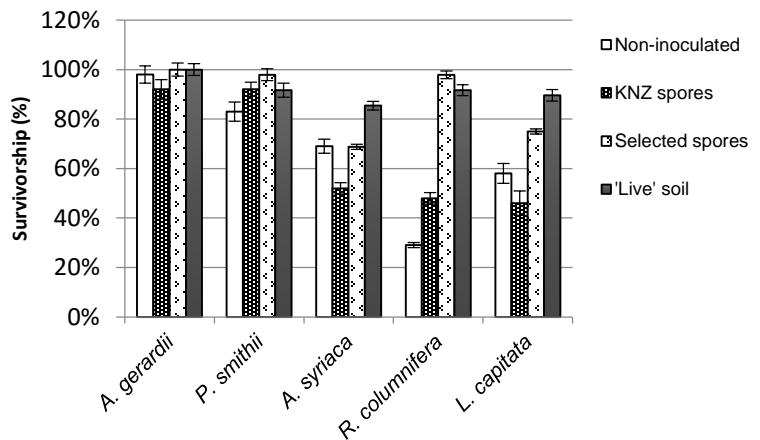


Fig. 5: Nurse plant survivorship 8 weeks following transplant.

Selected publications/Theses: (*graduate students, ** undergraduate REU student)

- Duell, E.B.*, G.W.T. Wilson, and K.R. Hickman. 2016. Above- and belowground responses of native and invasive prairie grasses to future climate scenarios. *Botany. Special Edition: Mycorrhiza and Climate Change*. 94:471-479.
- Duell, Eric B.* 2015. Elevated temperature and drought favor invasive grasses over native species. MS Thesis. Oklahoma State University.
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- Zaiger, K*. May 2016. Environmental extremes drive plant and soil community dynamics of native and disturbed grasslands. MS Thesis. Oklahoma State University.

ChANGE: Chronic Addition of Nitrogen Gradient Experiment

Investigators: Melinda Smith, Sally Koerner, Meghan Avolio, Kim La Pierre, Lydia Zeglin, Alan Knapp, Nate Lemoine, Madison Rode* * = *REU student*

Rationale:

Chronic nutrient additions can lead to drastic shifts in the plant community through time, both within tallgrass prairie and in other grassland ecosystems worldwide. Nutrient addition experiments have answered many questions about patterns of diversity loss and community shifts; however, the level of nutrients which must be added to cause community shifts is unknown. To date, all nitrogen (N) addition experiments at Konza have added 10 g m^{-2} (e.g., NutNet Plots; Phosphorus (P) Plots; Belowground Plots), yet current rates of N deposition are one-tenth of that level. Even predicted rates of future N deposition in grasslands are not expected to exceed 5 g m^{-2} by the year 2050 and will likely be around 2 g m^{-2} for most of the US. This mismatch begs the question will 10 g m^{-2} affect grasslands the same way as 2 or 5 g m^{-2} ? There are two main goals for this long-term experiment: (1) to identify the nutrient threshold needed to drive plant community change with nutrient additions, and (2) to determine what factors underlie those threshold responses (build up of nutrients, mycorrhizal loss, invertebrate herbivory).

Konza ChANGE is part of a multi-site experiment spanning grasslands on two different continents: North America – tallgrass prairie (KNZ) and shortgrass steppe (SGS), and China – three sites in Inner Mongolia. By including multiple grasslands, we expand our ability to make generalizations about how grasslands are affected by N additions, and whether thresholds, if they exist, vary with precipitation, natural nutrient availability, and species identity/composition.

Research Questions:

- (1) Do ecosystems have N tolerance thresholds above which community composition will change, and does that differ between grassland types (i.e. mesic and xeric grasslands)?
- (2) Does adding a large amount of nutrients in one season result in an equivalent community change as adding a small amount over multiple years? (For example does 5 g m^{-2} for 6 years create the same community change as 30 g m^{-2} for 1 year or 15 g m^{-2} for 2 years?)
- (3) Will predicted levels of N deposition (2.5 g m^{-2} or 5 g m^{-2}) elicit a community change?
- (4) Are there different thresholds for different plant functional types? For example, does a small amount of nutrients cause a decrease in N-fixing forb composition, while a larger amount of nutrients are necessary to reduce the abundance of the dominant C_4 grasses? At what point does the community change state from a perennial grassland to the predicted annual forb community? Is it a gradual linear change or an abrupt transition?
- (5) Is decreased light availability, due to increased ANPP, the primary determinant leading to community shifts (similar to species loss), or do other factors determine when nutrients impact communities, such as interactions with invertebrate herbivory or loss of mycorrhizal symbionts.

Experimental Design:

Forty-eight $5 \times 5 \text{ m}$ plots were established in June 2013 in R1B in 6 blocks, with 8 plots per block (Fig. 1). Each plot is divided into 4, $2.5 \times 2.5 \text{ m}$ subplots. One subplot is used for core experiment measurements (species composition, ANPP, soil N availability, light availability, soil CO_2 flux and other measurements). The remaining 3 subplots are set aside for future studies by the project PIs (e.g., insect herbivory monitoring and manipulations), as well as other Konza investigators. In 2013 pretreatment species composition and ANPP data were collected. In 2014 the nitrogen manipulations began. Each plot within a block receives a different nitrogen addition treatment: 0, 2.5, 5, 7.5, 10, 15, 20, or 30 g m^{-2} as slow time-release Urea. Plant community composition is measured in early and late growing season by

estimating the aerial cover to the nearest 1% in a permanent 1 x 1 m plot located within the core subplot of each 5 x 5 m plot. Productivity is measured by clipping all aboveground biomass within two 20 x 50 cm quadrats in the core subplot of each 5x5m plot at the end of each growing season.

Project Status:

Given the long-term nature of the questions we are addressing, data collection and analysis is ongoing. To date, we have observed a threshold response of aboveground net primary production (ANPP), with minimal response to the 2.5 g m⁻² treatment and increased productivity with N addition levels above 5 g m⁻² (Fig. 2). Analysis of plant community responses are in progress. In 2016, a secondary experiment was conducted to determine whether insect herbivores are subject to N-P co-limitation in tallgrass prairie. Results suggest that P-limitation of insects might be as strong as N-limitation (Rode et al. *in press*). This fall all data collected to date will be analyzed to assess short-term responses to the N addition gradient. The plan is to continue the experiment for at least 10 years to assess long-term plant community and ecosystem responses.

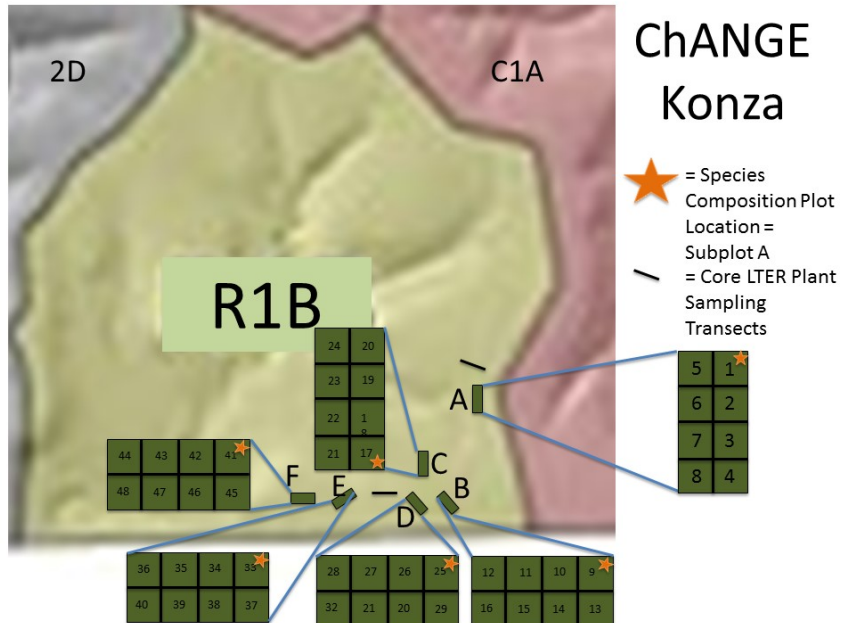


Figure 1. Location and layout of the Konza ChANGE experiment.

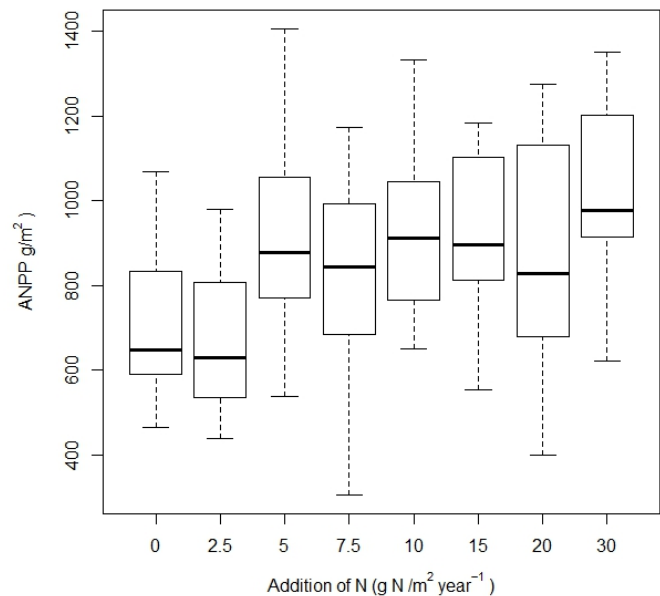


Figure 2. Aboveground net primary productivity (ANPP) response to the gradient of nitrogen addition treatments.

Publications to Date:

Rode M, Lemoine NP, Smith MD. 2017. Prospective evidence for independent nitrogen and phosphorus limitation of grasshopper (*Chorthippus curtipennis*) growth in a tallgrass prairie. PLoS ONE 12(5): e0177754. <https://doi.org/10.1371/journal.pone.0177754>

The Irrigation Transect Experiment: Long-Term Removal of Water Limitation in Annually Burned Grassland

Investigators: John Blair (KSU), John Briggs (KSU), Caitlin Broderick* (KSU), Cheyenne Butler** (KSU), Tiffany Carter* (KSU), Scott Collins (UNM), Alan Knapp (CSU), Trisha Moore (KSU), Matt Price** (KSU), Charles Rice (KSU), Melinda Smith (CSU), Jeff Taylor (KSU), Leena Vilonen* (CSU), Kevin Wilcox# (USDA) *current graduate student; #former graduate student, **undergraduate

Rationale:

- Growing season water limitations as well as intra- and interannual precipitation variability are important characteristics of all grassland ecosystems. Irrigation, scheduled to reduce water limitations to primary production and reduce precipitation variability, allows us to assess the importance of these factors for tallgrass prairie structure and function.
- Century model predictions indicate that long-term annual fire in mesic grasslands should lead to reductions in soil N and C storage, and greater soil N limitations to plant growth. Maximizing primary production each year by eliminating water deficits should maximize plant growth and amplify the effect of annual fire on soil C and N pools, allowing us to test this model prediction.
- Many aspects of climate change can be viewed as chronic changes in resource availability. This experiment provides support for development and testing of new theory – The Hierarchical Response Framework (HRF, Fig. 1; Smith et al. 2009) – linking the mechanisms and the types of responses that ecosystems may exhibit with chronic changes in resources.

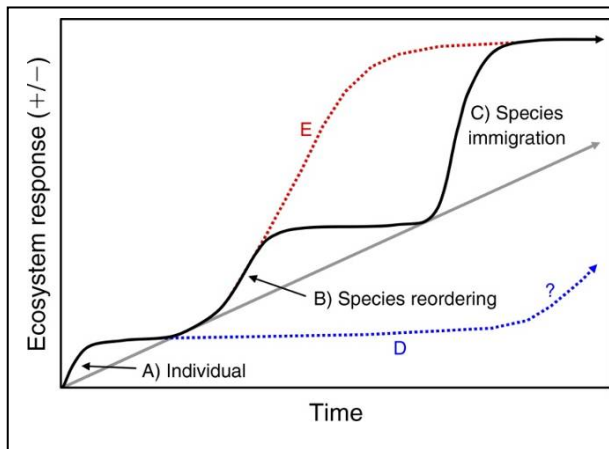


Fig. 1. The hierarchical-response framework (HRF) postulates a hierarchy of mechanisms underlying non-linear ecological change (black line) in response to chronic resource alterations. Initially small ecosystem responses are driven by (A) individual-level (physiological/metabolic, mortality) responses. 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 promote 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.

Initial Questions:

- How often and by how much does water limit key ecosystem processes in mesic grasslands?
- Is there evidence for non-linear change in ecosystem function as predicted by the HRF?
- Can productivity be maintained under an annual fire regime with production maximized each year by irrigation?
- Will plant species composition shift to a more diverse grassland (increased C₃ forbs) as water stress is reduced or will diversity decrease as productivity increases?

Key Results to Date:

Despite decreased BNPP and root:shoot ratios, model predictions of decreased soil C and N storage, increased N limitation and reduced ANPP were not supported (Wilcox et al. 2016a.).

ANPP responses to supplemental water in the 1st decade were modest and consistent with MAP-ANPP relationships for KNZ and for Central US grasslands. However, ANPP responses in the 2nd decade were much greater than expected based on historical or broader regional relationships (Fig. 2; Knapp et al. 2012). This lagged response corresponded with species reordering and increased cover of *Panicum virgatum* (Fig. 3; Collins et al. 2012, Wilcox et al. 2016b).

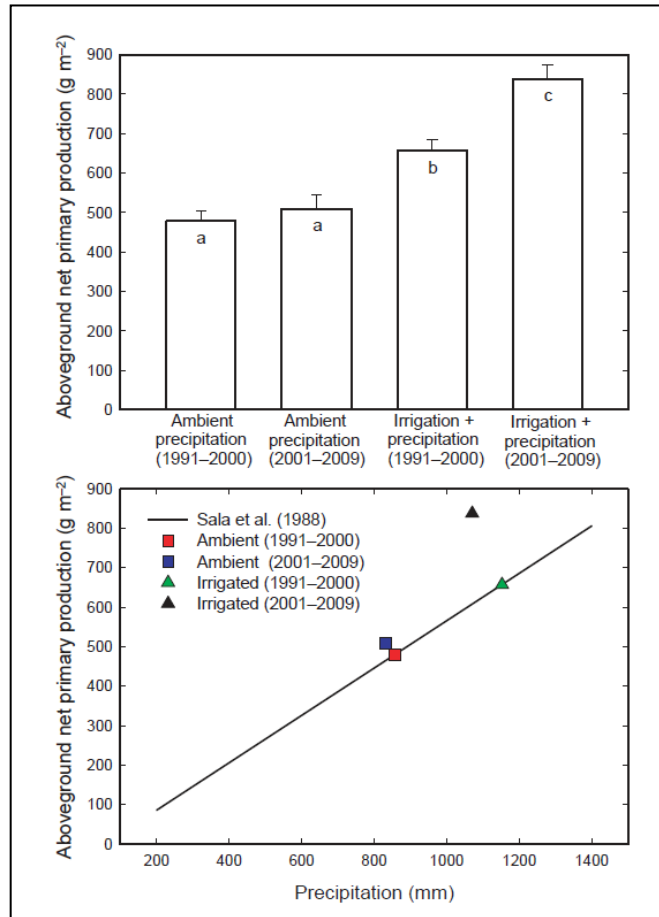


Fig. 2. Top: Mean annual ANPP in the control and irrigated lowland plots of the irrigation transect. Data are shown for two time periods; the first 10 years of the experiment when *A. gerardii* was the dominant species in both control and irrigated transects, and the next 9 years when *Panicum virgatum* replaced *Andropogon gerardii* as the dominant C4 grass in the irrigated transects (see Fig. 3 below). Different letters in each bar indicate significant differences ($P < 0.05$) among treatments and periods

Bottom: Relationship between mean annual precipitation (MAP) and ANPP for the Central US grassland region (solid line, $r^2 = 0.90$) based on Sala et al. (1988). Plotted on top of this regional relationship are points representing mean ANPP and MAP for the same treatments and time periods shown in the top panel. Note the dramatic deviation in the general MAP-ANPP relationship for the time period when *P. virgatum* replaced *A. gerardii* as the dominant C4 grass (black triangle).

From Knapp et al. 2012

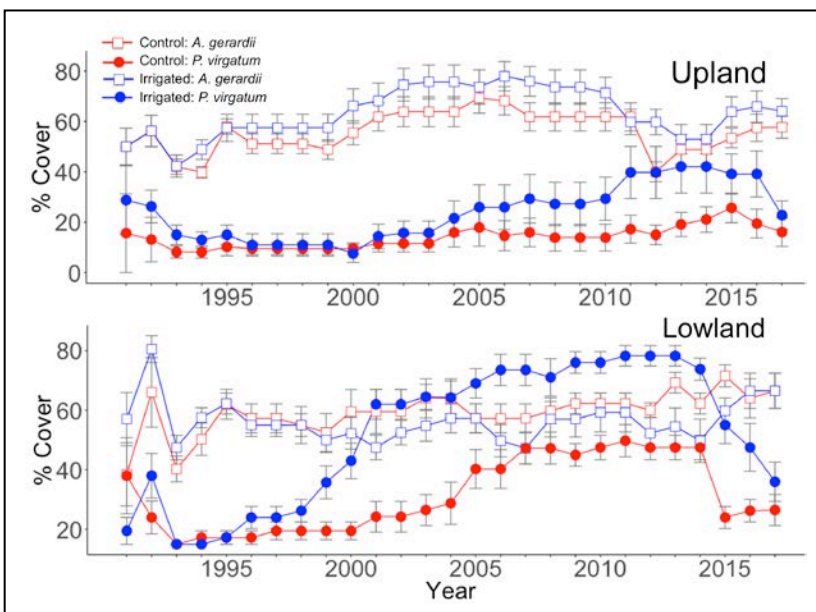


Fig. 3. Changes in the abundance (percent cover) of dominant grasses in upland (top) and lowland (bottom) control (red) and irrigated (blue) plots. Irrigation had limited effects on overall species richness, but there was a strong response to irrigation within the dominant functional type (perennial C4 grasses). After ~10 yrs of irrigation, *Panicum virgatum* increased in cover and became the dominant species in irrigated lowlands, whereas cover of *Andropogon gerardii* remained relatively constant. Upland responses were less pronounced and delayed relative to lowlands.

Updated from Collins et al. 2012

Next Steps:

Building on 25 years of documented community and ecosystem responses to altered water availability, we have modified the treatment structure of this experiment by “switching” treatments on subset of historically irrigated and control plots. This new treatment structure (Fig. 4) allows us to ask new questions about the legacy effects of 25 yrs of supplemental water and assess how past conditions affect the sensitivity of tallgrass prairie to climate variability and drought. Maintaining a subset of plots under the original treatments will allow us to continue assessing longer-term responses to a chronic change in water availability (Wilcox et al. 2017, Caplan et al. in prep).

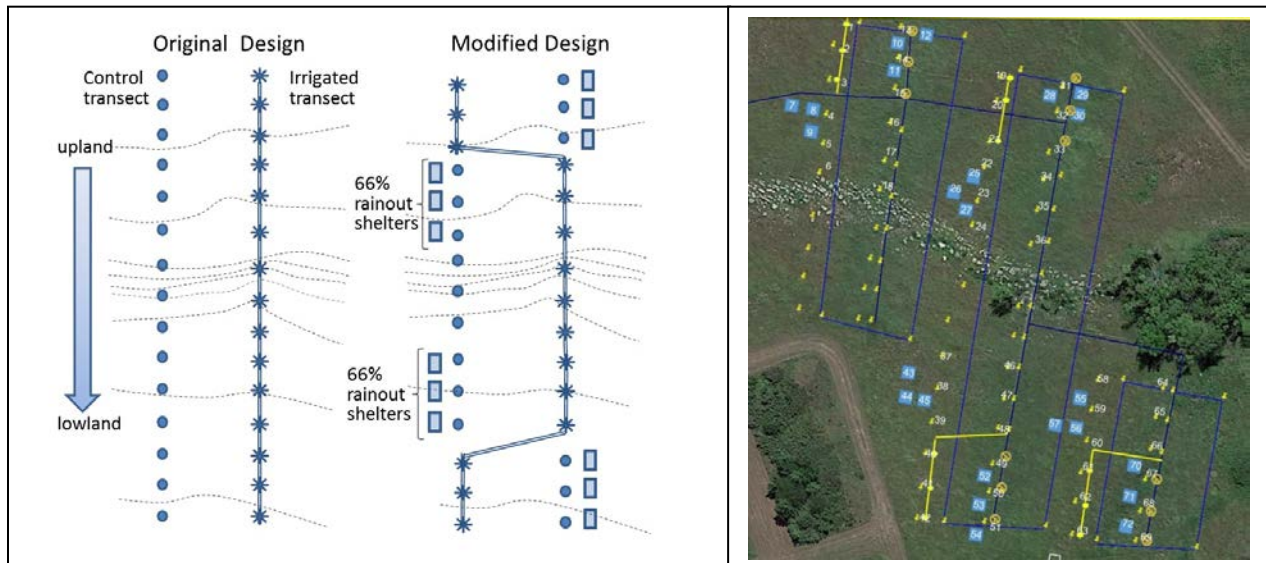


Fig. 4. Left: Schematic representation of original and modified experimental design of the KNZ Irrigation Transect Study, showing treatment designations on one of two replicate transect pairs. Each transect is ca. 140 m long with 15 irrigated and 15 control sampling locations each. Irrigated plots receive sufficient water to minimize growing season water stress, while control plots receive ambient precipitation. Passive rainout shelters reduce growing season rainfall by 66%. Right: Aerial view of irrigated and control transects with locations of rainout shelters (blue squares) and sampling plots for modified experimental design.

Treatments:

Irrigation Treatment	Reversal treatment	Drought treatment
Control	Control	Control
	Irrigated	Drought
Irrigated	Irrigated	
	Control	Control
		Drought

New Questions:

- What is the continued response to chronic alleviation of water stress in long-term treatments?
- What is the nature and pace of recovery of ecosystem structure and function following cessation of long-term alleviation of water limitation?
- How does the legacy of past climatic conditions affect sensitivity to future climatic variability?
- Does the legacy of long-term alleviation of water limitation affect tallgrass prairie ecosystem sensitivity and resilience to drought?

Data sets: WAT011, WAT012, WAT013, WAT014, WAT015, WAT016

Selected Publications

- Caplan, J.S., D. Giménez, D.R. Hirmas, N.A. Brunsell, J.M. Blair, and A.K. Knapp. Increased precipitation can induce decadal-scale shifts in soil hydraulic properties. *In preparation*.
- Collins, S.L., S.E. Koerner, J.A. Plaut, J.G. Okie, D. Brese, L.B. Calabrese, A. Carvajal, R.J. Evanse, and E. Nonaka. 2012. Stability of tallgrass prairie during a 19-year increase in growing season precipitation. *Functional Ecology* 26:1450-1459.
- Knapp, A.K., J.M. Briggs, and M.D. Smith. 2012. Community stability does not preclude ecosystem sensitivity to chronic resource alteration. *Functional Ecology* 26:1231 -1233.
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The Climate Extremes Experiment (CEE)

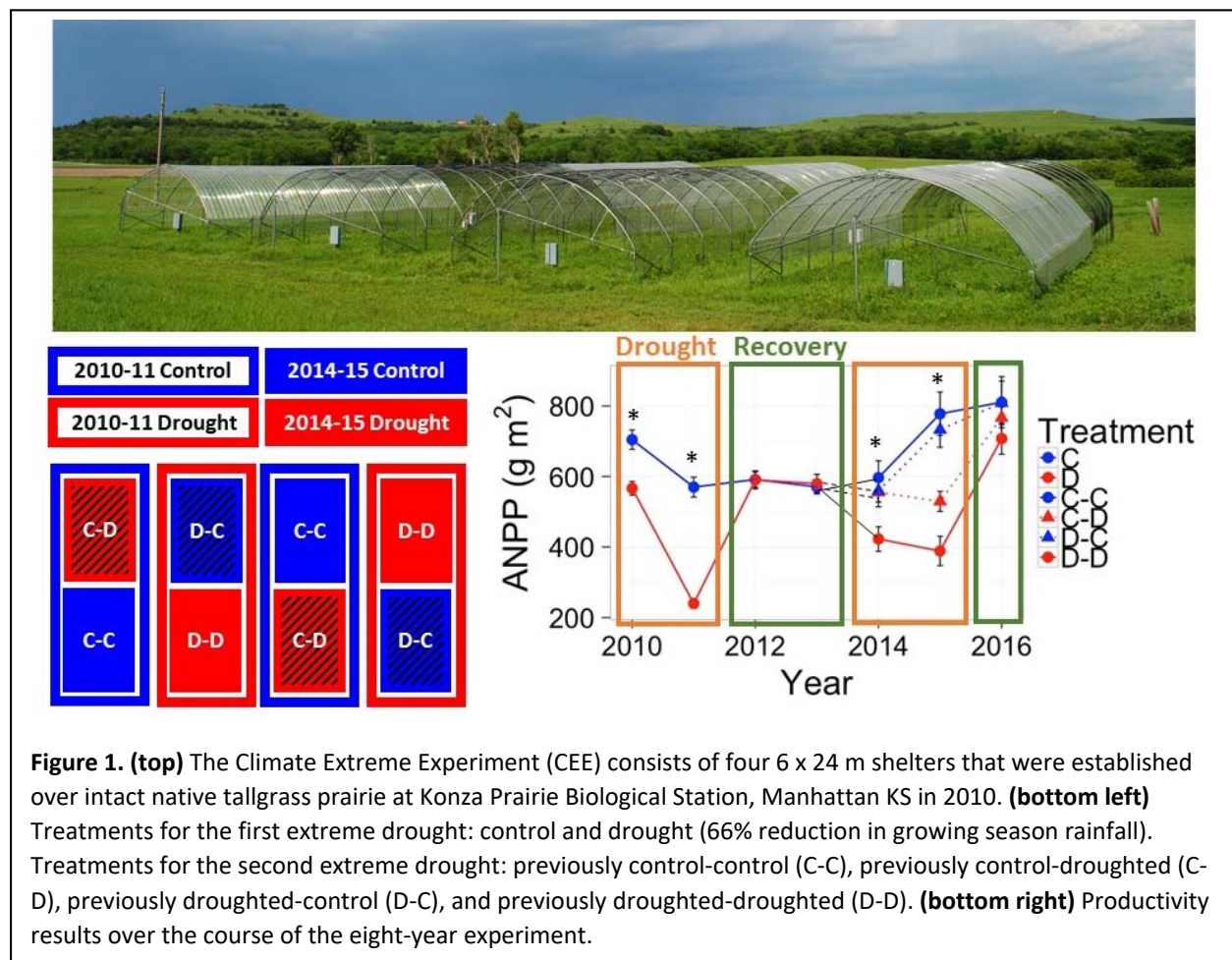
Assessing Ecosystem Resistance and Resilience to Repeated Climate Extremes

Investigators: Melinda D. Smith, Alan K. Knapp, Ava Hoffman*, David L. Hoover⁺, Meghan L. Avolio, Andrew Felton*, Ingrid Slette*, and Kevin R. Wilcox

*current graduate students, ⁺former graduate student/current investigator

Rationale:

Climate extremes, such as drought, are increasing in frequency and intensity, and the ecological consequences of these extreme events can be substantial and widespread. Yet, little is known about the factors that determine recovery (or resilience) of ecosystem function post-drought. Such knowledge is particularly important because post-drought recovery periods can be protracted depending on drought legacy effects (e.g., loss of key plant populations, altered community structure and/or biogeochemical processes). These drought legacies may alter ecosystem function for many years post-drought and may impact future sensitivity (both resistance and resilience) to climate extremes. With forecasts of more frequent drought, there is an imperative to understand whether and how post-drought legacies will affect ecosystem response to future drought events. To address this knowledge gap, we experimentally imposed two extreme growing season droughts over an eight-year period; each two years in duration followed by a two-year recovery period, in annually burned tallgrass prairie (Fig. 1).



Selected Results-to-Date:

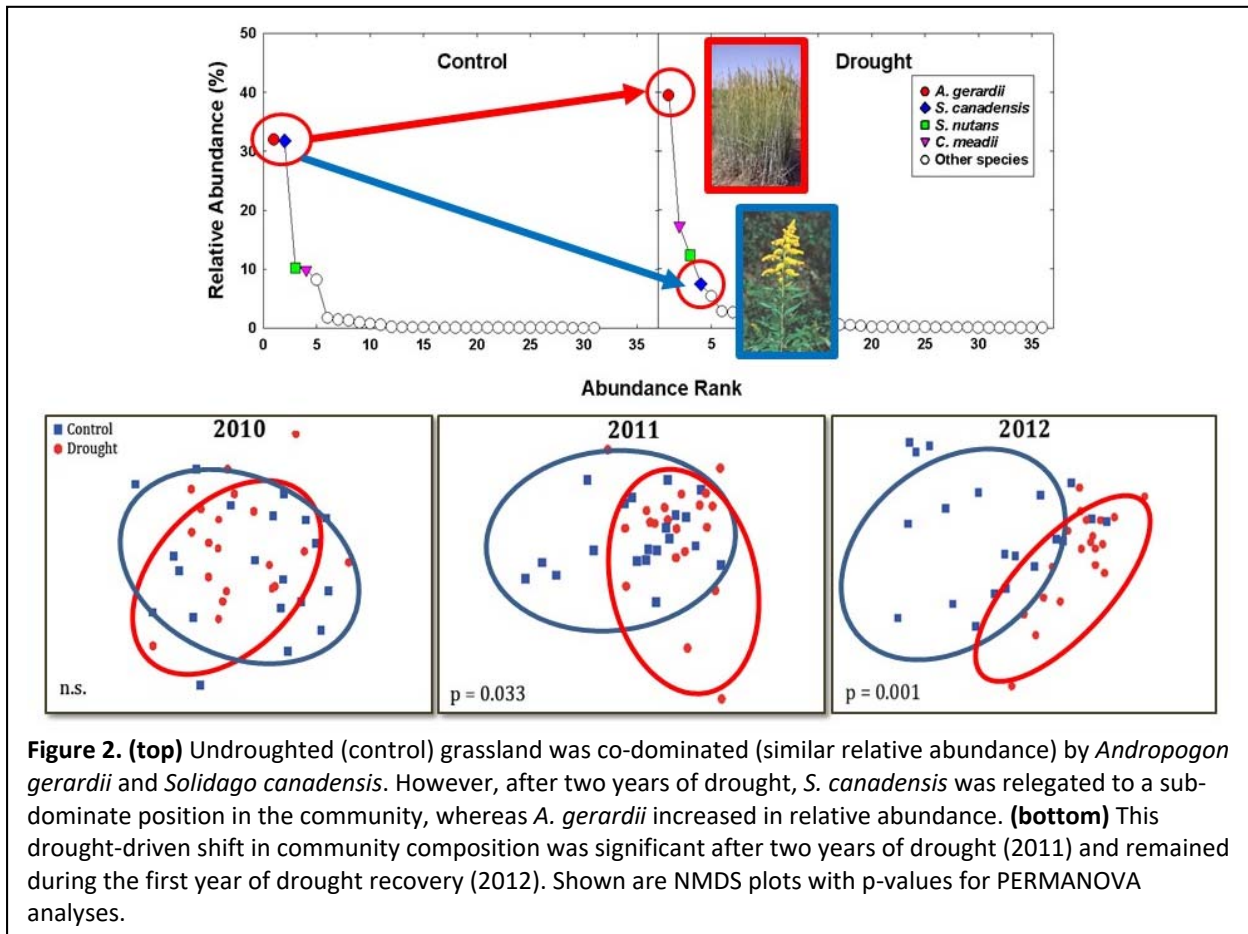


Figure 2. (top) Undroughted (control) grassland was co-dominated (similar relative abundance) by *Andropogon gerardii* and *Solidago canadensis*. However, after two years of drought, *S. canadensis* was relegated to a subordinate position in the community, whereas *A. gerardii* increased in relative abundance. **(bottom)** This drought-driven shift in community composition was significant after two years of drought (2011) and remained during the first year of drought recovery (2012). Shown are NMDS plots with p-values for PERMANOVA analyses.

We found that aboveground net primary productivity (ANPP) declined dramatically with the first two-year extreme drought (Fig. 1) and was accompanied by a large shift in plant species composition, driven the loss of C₃ forbs (primarily *Solidago canadensis*) and increase in C₄ grasses (primarily *Andropogon gerardii*; Fig. 2). This drought legacy – shift in plant composition - persisted two years post-drought (Fig. 3). Yet, despite this legacy, ANPP recovered fully (Figs. 1 & 3). We expected that previously-droughted grassland would be less sensitive to a second extreme, two-year drought of similar magnitude due to the shift in plant composition. However, contrary to this expectation, previously droughted grassland (PD-D) experienced a greater loss in ANPP than grassland that had not experienced a second drought (C-C, PD-C) or experienced drought for the first time (C-D; Fig. 1). Furthermore, previously droughted grassland (PD-D) did not fully recover after the second drought (Fig. 1). Potential mechanisms that may have contributed to this increased sensitivity are a significant reduction in root biomass production (Fig. 4), as well as greater water stress of *A. gerardii* in the PD-D plots (data not shown). Thus, legacies of drought – a shift in plant community composition and reduced root production – appeared to decrease ecosystem resilience to a future extreme drought event.

Next Steps:

The year two of the second round of recovery is now ending and final data is being collected. The plan is to analyze data and write a manuscript synthesizing results from the 8-years of the experiment.

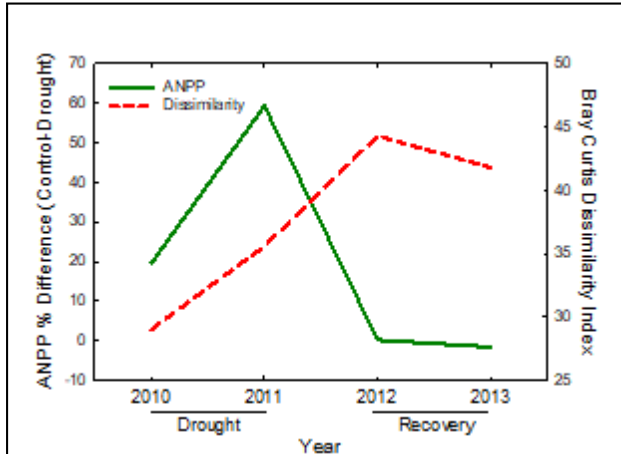


Figure 3. The shift in plant community composition that occurred during the first extreme drought event persisted two-years post-drought (measured here as Bray-Curtis dissimilarity between droughted and control plots). Yet, despite this shift in composition, aboveground net primary productivity fully recovered.

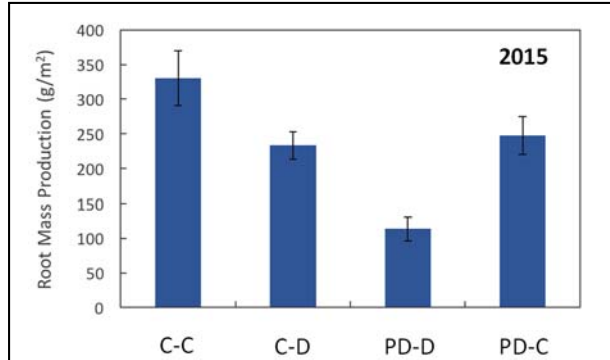


Figure 4. Significant reduction in root mass production in previously droughted plots (PD-D) after two years of a second drought.

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- Smith, M.D. 2011 (a). The ecological role of climate extremes: current understanding and future prospects. *Journal of Ecology* 99:651-655.
- Smith, M.D. 2011 (b). An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. *Journal of Ecology* 99:656-663.

Rainfall Manipulation Plots (RaMPs) Legacy Experiment

Investigators: Meghan Avolio (Johns Hopkins), John Blair (KSU), Scott Collins (UNM), Philip Fay (USDA), Andrew Felton* (CSU), Sydney Jones* (UNM), Alan Knapp (CSU), Sally Koerner (UNC-Greensboro), Jesse Nippert (KSU), Ingrid Slette* (CSU), Melinda Smith (CSU) - *graduate student

Background:

- Grassland ecosystems are characterized by high variability in precipitation, inter- and intra-annually. Intra-annual rainfall regimes have two important, interrelated elements: **rain event quantity**, and the **length of inter-rainfall dry periods**.
- Global climate models predict, and current data suggest, that rainfall event size is increasing (more severe storms) and that droughts will intensify with climate change (Knapp *et al.* 2002, 2008).
- The RaMPs experiment (began in 1998) was designed to increase rain event size and lengthen intervening dry periods without changing overall growing season rainfall quantity.
- The experiment has two main treatments: 1) ambient rainfall timing and 2) altered rainfall timing - a 50% increase in the length of the interval between rainfall events and an accompanying increase in rainfall event size.

Summary of 15 years of RaMPs results:

- RaMPs treatments led to a dramatic shift in rainfall patterns with no change in total amount (Fig. 1).
- The altered precipitation treatment led to significant increase in variability in soil moisture, with drier shallow soil layers and wetter deep soils (Fig. 2).
- Altering soil moisture in this way led to modest decreases in ANPP (11% average over 15 yrs, Fig. 3), revealed a strong relationship between soil moisture CV and ANPP (Fig. 4, Fay *et al.* 2011) and led to decreased soil CO₂ flux (Harper *et al.* 2005). Plant community responses were relatively minor with deeper rooted forbs increasing slightly with altered rainfall patterns (Jones *et al.* 2016). Avolio & Smith (2013) also detected significant shifts in the genotypic composition (and phenotypic traits) of the dominant grass, *A. gerardii*.

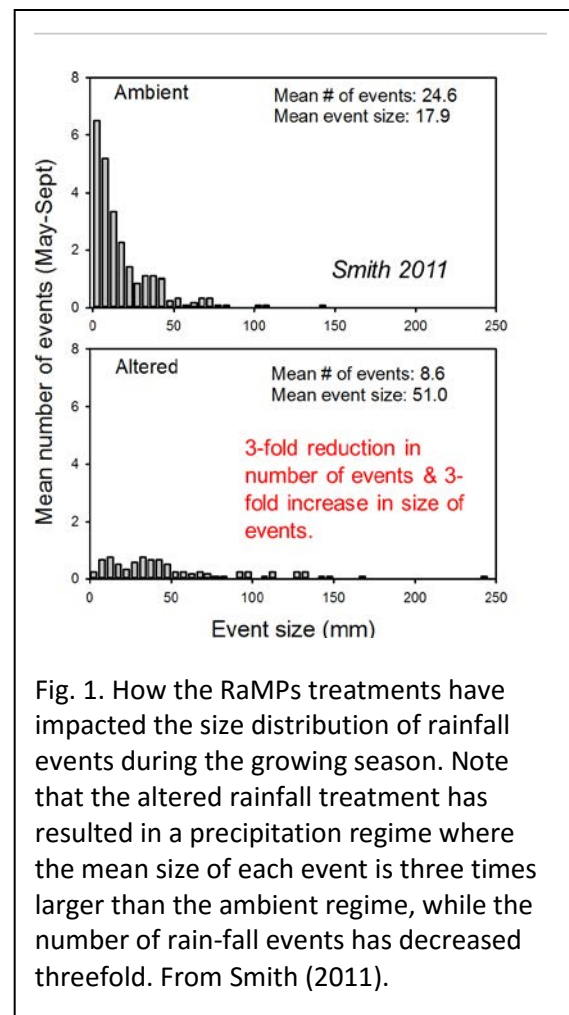
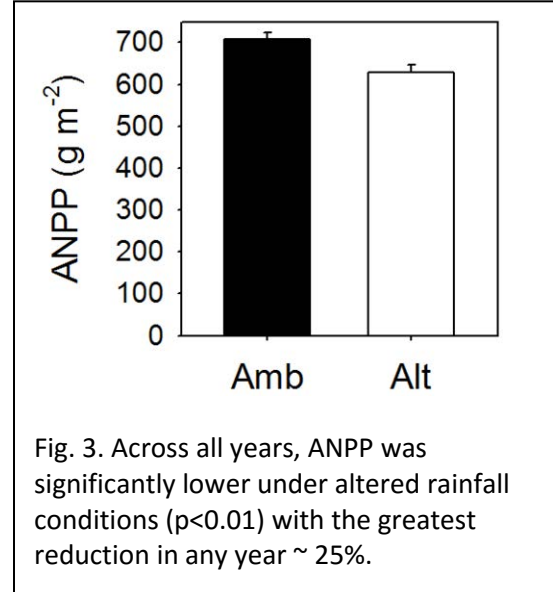
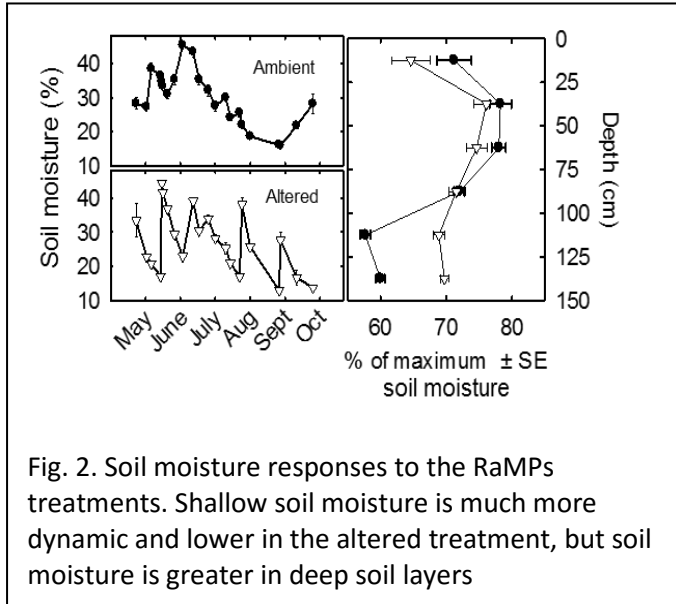


Fig. 1. How the RaMPs treatments have impacted the size distribution of rainfall events during the growing season. Note that the altered rainfall treatment has resulted in a precipitation regime where the mean size of each event is three times larger than the ambient regime, while the number of rain-fall events has decreased threefold. From Smith (2011).

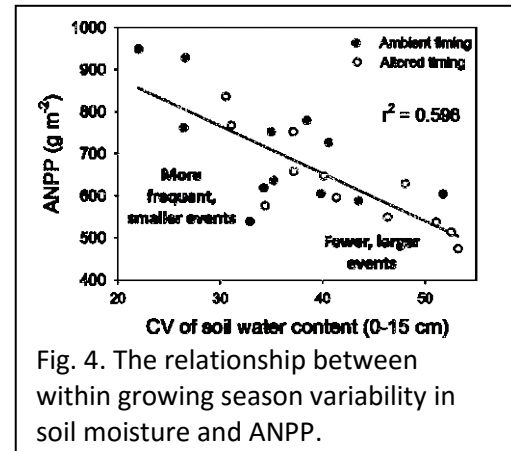


The Legacy Hypothesis:

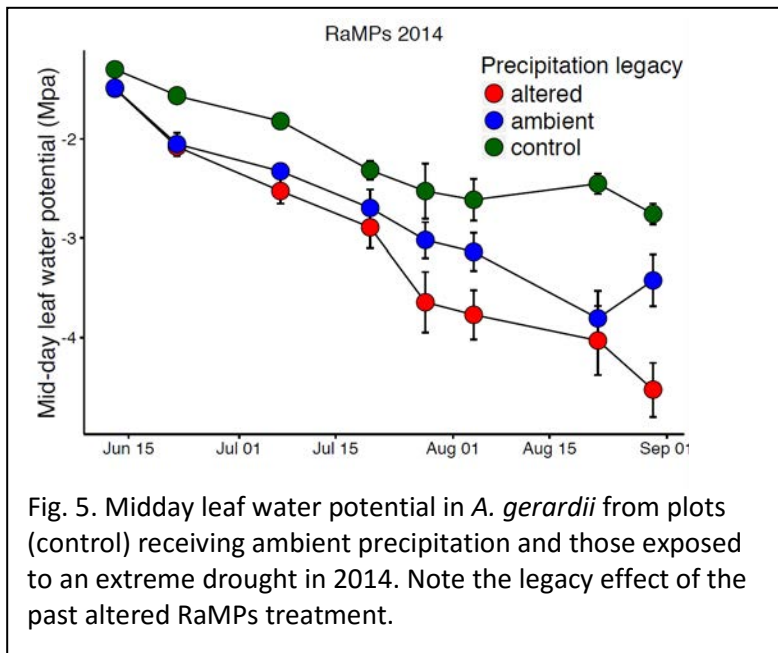
- After 15 years of altered precipitation regimes, we tested the hypothesis that the cumulative ecological effects of this chronic climate change (i.e., the legacy effects of the RaMPs experiment) would affect the resistance and/or resilience of this mesic grassland to a 2-yr period of extreme drought. Specifically, because the altered treatment resulted in drier shallow soil layers, greater water stress in the dominant grasses (Knapp *et al.* 2002) and shifts in their phenotypes expected to increase drought tolerance, we predicted that plots that had experienced 15 years of altered rainfall regimes would be more resistant to an extreme drought than the ambient plots.
- In 2014, we imposed a 2-yr extreme drought in all plots (66% reduction in growing season rainfall) to test this hypothesis.

Initial results:

- There was no legacy effect of the past treatments on ANPP responses to drought. Overall, 2-yr of extreme drought reduced ANPP by $>50\%$ (Fig. 4).
- In contrast to ANPP, drought reduced BNPP (0-30 cm) significantly more in plots previously exposed to an altered precipitation regime vs. ambient plots (Fig. 4).
- Consistent with this greater effect of drought on roots from previously altered plots, *A. gerardii* had reduced midday water potentials in previously altered vs. ambient plots.
- This reduction in BNPP did not affect recovery of aboveground after the drought was alleviated in 2016, but based on results from the adjacent CEE experiment, reduced BNPP may represent a hidden legacy that may impact ecosystem responses to future droughts.

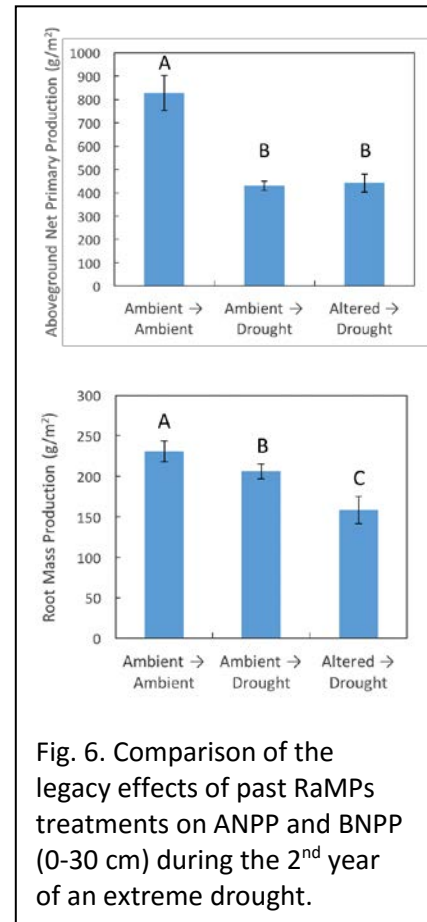


KNZ Data Used: RMP01



Key Publications:

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Testing the Influence of Deterministic and Stochastic Processes on Community Assembly and Belowground Ecosystem Recovery

Investigators: Sara Baer, John Blair, Scott Collins, George Manning*, Sarah Black*, Patrick Harris*, Juliette Fitzgibbon#, Drew Scott*, Steven Rozensweig†. *graduate student; #undergraduate; †REU

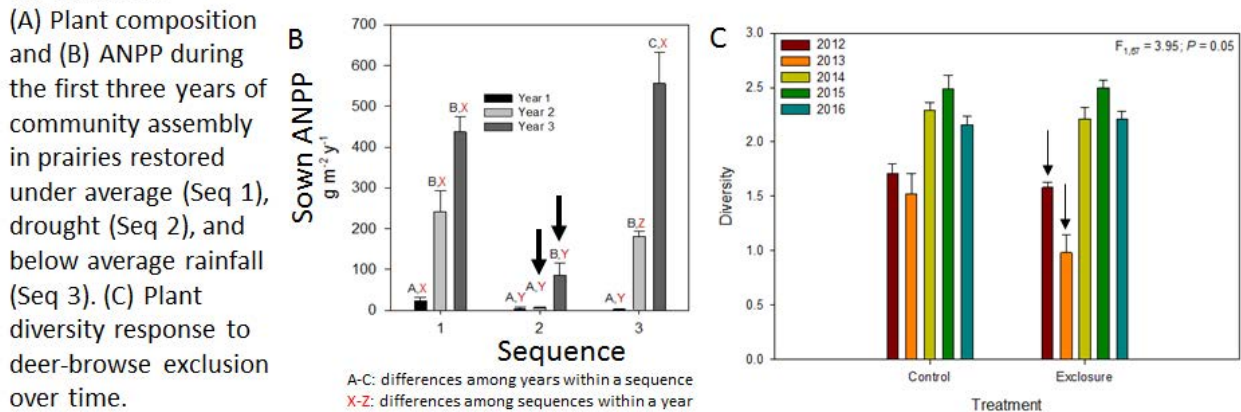
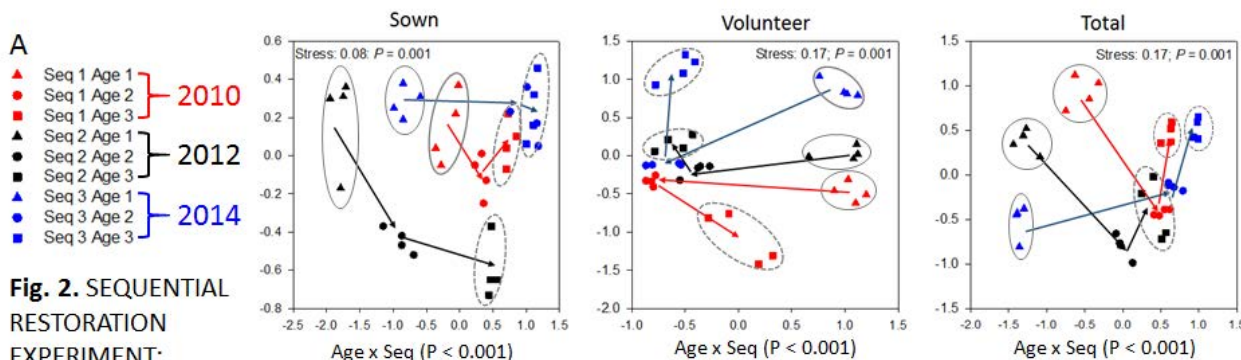
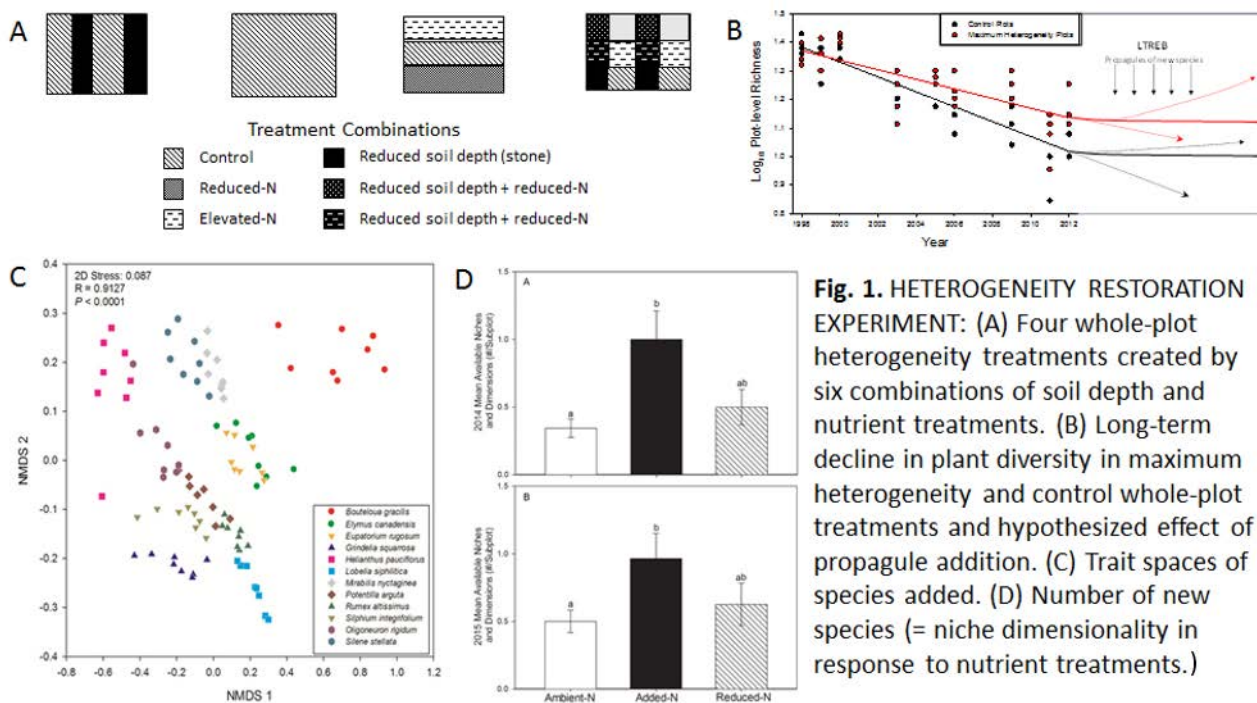
Background: Restoration studies at KNZ have applied ecological theory to reveal the role abiotic and biotic factors influencing the structure of communities and ecosystem functioning in prairie recovering from long-term agricultural disturbance (Baer et al. 2003, 2004, 2005; Baer & Blair 2008, Klopff et al. 2013, Baer et al. 2016). Two ongoing restoration experiments examine the role of deterministic (e.g., soil nutrient availability and heterogeneity) and stochastic processes (e.g., dispersal and interannual variability in climate) on community development and consequences for ecosystem functioning.

One hypothesized deterministic influence on plant community development is the ‘environmental heterogeneity-diversity relationship’ (Ricklefs 1977), which predicts that greater resource heterogeneity promotes species coexistence. We have been studying the effects of manipulated soil nutrients and depth on diversity and productivity for 20 years in the “heterogeneity restoration experiment”. Initially strong community and productivity responses to soil nutrient availability, transitions in dominant species over time, a continuous decline in species diversity across contrasting heterogeneity treatments, and an overall weak effect of soil heterogeneity on diversity demonstrate the value of long-term research in revealing transient roles of some manipulations (e.g., reduced N availability), unpredictable effects of nutrient enrichment over the long term, and interactive effects of soil heterogeneity and dispersal on species richness (Baer et al. 2016). With supplemental funding (NSF-LTREB Program), we are investigating whether spatial and temporal variation in soil and vegetation promotes niche availability and dimensionality, indexed by trait spaces of newly recruited species, to stabilize or increase plant diversity (Fig. 1).

Less is known about the role of stochastic processes on restoration, including interannual variation in abiotic factors (i.e., climate), and the influence of higher trophic levels (i.e., herbivores) on trajectories of plant community and ecosystem recovery. We began to address this knowledge gap in LTER VI by sequentially restoring prairie in an agricultural field and relying on interannual variability in climate to examine the role of stochastic processes on community assembly and ecosystem functioning. We are quantifying the effect of aboveground herbivory on plant communities using deer exclosures in one sequence, and more recently, insecticide treatments in two other sequences.

Questions, Approach, and Results:

- 1) Does soil heterogeneity create more niches for new species to exploit, and subsequently, the role of heterogeneity (deterministic process) on species coexistence dependent on dispersal (stochastic process)? To address this, we have been adding 18 new species with unique trait spaces to prairie restored under varying soil heterogeneity conditions. Trait spaces were analyzed using a suite of morphological and physiological characteristics in NMDS followed by analysis of similarity (Fig. 1C). We use the number of new species recreated to assess niche dimensionality under different treatments (Fig. 1D).
- 2) How do interannual variation in climate and higher trophic levels influence the trajectory of community and ecosystem recovery? To address this, we are continuing to sequentially restore prairie in an agricultural field containing similar soil and land-use history, and using the same species and seeding rates. Species composition and ANPP are quantified each year from 16 subplots each (4/plot) in each sequence to evaluate convergence or divergence in community structure (Fig. 2A) and functioning (Fig. 2B). Sequence 2 also contains a deer browse exclusion treatment, where species composition has been measured since 2012 to assess the effect of herbivory on community development (Fig. 2C).



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Datasets: HRE01, SPR01, PRP01

Notes:

