

LONG-TERM EFFECTS OF CLIMATE CHANGE ON GRASSLAND SOIL SYSTEMS: A
RECIPROCAL TRANSPLANT APPROACH

by

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Abstract

Climate change predictions for the Great Plains region of North America include increased temperatures, changes to annual precipitation, and reduced growing season precipitation, which will likely alter grassland soil systems. To date, few studies have examined belowground community responses to predicted climate change scenarios, with fewer assessing long-term changes. My research focused on the impacts of long-term changes in precipitation and associated soil water content on belowground grassland systems (belowground plant biomass, soil carbon (C) and nitrogen (N) pools, microbial biomass C and N, and invertebrate communities) using recently collected samples from a long-term (16-yr) reciprocal core transplant between Konza Prairie Biological Station (MAP = 850 mm) and Kansas State Agricultural Research Center at Hays (MAP = 580 mm), with the Hays site having a long-term average annual precipitation amount that is ~30% less than the Konza site. Results from the experiment indicate that either increases or decreases in annual precipitation can have profound effects on belowground grassland systems. Belowground plant biomass, microbial biomass, and potential C mineralization rates were greater at the wetter Konza site regardless of soil origin. Total C stored in soils incubated at Konza was significantly greater as well, likely due to greater root inputs. The effects of precipitation were most apparent in the surface soil layers (0-20 cm), while soil origin impacted soil properties to a greater extent with increasing depth. This contrasted with results for the soil mesofauna, where total microarthropods responded negatively and nematodes responded positively to increased annual precipitation. Results of this study indicate important changes in soil C and N pools, belowground plant biomass, and soil mesofauna within grassland systems subject to changing precipitation regimes, and suggest more

mesic prairie systems are more sensitive to changes in soil water availability than those in more arid grassland systems.

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Chapter 1 - Introduction

Increases in atmospheric concentrations of carbon dioxide (CO₂) and other greenhouse gases have altered the global physical and chemical environment, and contributed to well-documented increases in global surface temperatures (IPCC 2001, 2007a). At the current rate of atmospheric accumulation, CO₂ is expected to double by the end of the century causing increases of 1.1-6.4°C in global surface temperatures (Hansen et al. 2006; IPCC 2007a). As a consequence of increasing temperatures, alterations in atmospheric circulation and hydrological processes will modify mean annual precipitation and temporal variability of precipitation (Crane and Hewitson 1998; Karl and Knight 1998; Easterling et al. 2000; Andrews and Forester 2010). In fact, evidence suggests that changes in precipitation have already begun to occur (Karl and Trenberth 2003; Allan and Soden 2008). Global circulation models are still unclear about the direction and magnitude of precipitation changes in some regions; however, deficits in soil water availability will occur despite precipitation changes due to increased latent heat fluxes (Jackson et al. 2001; Mellander et al. 2004). Therefore, various ecosystem-level processes dependant on soil water availability will be altered as a result of climate change (Mosier 1998; Harper et al. 2005; Knapp et al. 2008).

In light of potential climate change scenarios, studies investigating long-term ecological responses to changes in precipitation regimes are becoming increasingly important. Terrestrial ecosystems, such as grasslands, agricultural lands, and forests, provide various goods (food production, medicinal plants, etc.) and services (carbon storage, nutrient regeneration, water purification, etc.). Although humans can circumvent various environmental pressures on small scales, natural systems are responsible for a majority of these benefits. Changes in phenologies,

ranges, community composition, and species interactions will further alter ecosystem functioning. Studies have suggested various species have already begun to be impacted (Hardy 2003; IPCC 2007b). Studies of past climatic shifts have revealed various alterations in ecosystem processes and ranges on global and local scales (Weaver 1954; Weaver and Albertson 1956), some which are observed presently. Although some ecological responses to past climatic shifts have been well-studied (e.g. species range shifts), current climate predictions are unprecedented and may cause novel changes in ecosystem functions and community compositions.

Grassland ecosystems account for 24% of the world's vegetation cover (Sims and Risser 2000), and their structure and function makes them one of the most vulnerable to global climate change of any terrestrial ecosystem (Sala et al. 2000; IPCC 2007b). Changes in soil water availability, such as those likely to result from climate changes, have been linked to changes in plant community composition (Weaver and Albertson 1944), primary productivity (Briggs and Knapp 1995), nutrient dynamics (Mikha et al. 2005), and decomposition rates (Epstein et al. 2002). As a result, grassland systems worldwide will likely undergo various alterations in both soil processes and plant community dynamics as a function of climate change.

Grassland ecosystems of the Central Plains region of the United States would be directly impacted by changes in climate, particularly aspects of climate that affect water availability and water limitation. In this region, the distribution and composition of grassland species is largely dependant on local and regional temperatures and the strong east-west precipitation gradient characteristic of the region (Risser et al. 1981). Plant species composition shifts from short-grass to tallgrass prairies (Kuchler 1974), and aboveground primary productivity increases with higher mean annual precipitation (Sala et al. 1988). In addition to aboveground responses, climatic

shifts would likely alter belowground dynamics, as well. As studies have shown positive relationships between increased soil water availability and belowground primary productivity, microbial biomass, and soil organic carbon concentrations, reduced amounts of soil water available would likely negatively impact these grassland properties. Cascading effects from changes in belowground resource availability, as well as direct changes in the soil environment will likely impact soil fauna, including microarthropod and nematode composition and densities.

The potential impacts of climate change on these soil systems are still relatively unknown. Therefore, the major questions addressed in this thesis are: 1) How will grassland soils and soil biota respond to a simulated climate change (i.e., transplantation from a more mesic climate to a more arid climate and from a more arid climate to a more mesic climate)? 2) What ecological responses will be most sensitive to these precipitation changes? 3) Will a reciprocal change in rainfall patterns have comparable effects on soils adapted to wetter or drier conditions? To address these questions, an experiment was conducted utilizing reciprocal core transplants between a more mesic site, Konza Prairie Biological Station (Konza), and a more arid site, Kansas State University Agricultural Research Center at Hays (Hays). These sites vary primarily in mean annual precipitation, Konza Prairie receiving ~850 mm of rainfall per year and Hays receiving ~580 mm of rainfall (almost 30% less). Specific locations with comparable surface soils and vegetation were chosen at each site to reduce confounding factors and facilitate comparisons of the effects of altered precipitation. This experiment is novel in the fact that it is one of the only experiments to analyze the longer-term (16 years) effects of altered precipitation on grassland soil systems. In the first chapter, I report on the responses of selected plant and soil properties, including belowground plant and microbial biomass and carbon (C) and nitrogen (N) content and soil C and N pools, in response to long-term transplantation of intact soil-plant cores

to wetter or drier climates. This yielded information on the changes in belowground biomass and selected C and N pools under altered precipitation regimes. In the second chapter, I assessed the responses of soil mesofauna, including microarthropods and nematodes, to long-term transplantation, yielding information on the long-term changes in soil fauna and their depth distribution in response to climatic changes.

BIBLIOGRAPHY

- Albertson FW, Weaver JE (1944) Nature and degree of recovery of grassland from the great drought of 1933 to 1940. *Ecological Monographs*, **14**,393-479.
- Allan RP, Soden BJ (2008) Atmospheric warming and the amplification of precipitation extremes. *Science*, **321**,1481-1484.
- Andrews T, Forster PM (2010) The transient response of global-mean precipitation to increasing carbon dioxide levels. *Environmental Research Letters*, **5**, 205-212.
- Briggs JM, Knapp AK (1995) Interannual variability in primary production in tallgrass prairie – climate, soil – moisture, topographic position, and fire as determinants of aboveground biomass. *American Journal of Botany*, **82**, 1024-1030.
- Crane RG, Hewitson BC (1998) Doubled CO₂ precipitation changes for the Susquehanna Basin: down-scaling from the genesis general circulation model. *International Journal of Climatology*, **18**, 65-76.
- Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO (2000) Climate extremes: Observations, modeling, and impacts. *Science*, **289**, 2068-2074.
- Epstein HE, Burke IC, Lauenroth WK (2002) Regional patterns of decomposition and primary production rates in the US Great Plains. *Ecology*, **83**, 320-327.
- Hansen J, Sato M, Ruedy R, Lo K, Lea DW, Medina-Elizade M (2006) Global temperature change. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 14288-14293.
- Hardy JT (2003) *Climate Change: Causes, Effects, and Solutions*. John Wiley and Sons Ltd, West Sussex, England.
- Harper CW, Blair JM, Fay PA, Knapp AK, Carlisle JD (2005) Increased rainfall variability and reduced rainfall amount decreases soil CO₂ flux in a grassland ecosystem. *Global Change Biology*, **11**, 322-334.
- Intergovernmental Panel on Climate Change (IPCC) (2001), Summary for policymakers, in *Climate Change 2001: The Scientific Basis. Contribution of the Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press, New York.

- Intergovernmental Panel on Climate Change (IPCC) (2007a), Summary for policymakers, in *Climate Change 2007: The Scientific Basis. Contribution of the Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press, New York.
- Intergovernmental Panel on Climate Change (IPCC) (2007b), Summary for policymakers, in *Climate Change 2001: Impacts, Adaptation, and Vulnerability. Contribution of the Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press, New York.
- Jackson RB, Carpenter SR, Dahm CN, McKnight DM, Naiman RJ, Postel SL, Running SW (2001) Water in a changing world. *Ecological Applications*, **11**, 1027-1045.
- Karl TR, Knight RW (1998) Secular trends of precipitation amount, frequency, and intensity in the United States. *Bulletin of the American Meteorological Society*, **79**, 231-241.
- Karl TR, Trenberth KE (2003) Modern global climate change. *Science*, **302**, 1719-1723.
- Knapp AK, Beier C, Briske DD, Classen AT, Luo Y, Reichstein M, Smith MD, Smith SD, Bell JE, Fay PA, Heisler JL, Leavitt SW, Sherry R, Smith B, Weng ES (2008) Consequences of more extreme precipitation regimes for terrestrial ecosystems. *Bioscience*, **58**, 811-821.
- Kuchler AW (1974) New vegetation map of Kansas. *Ecology*, **55**, 586-604.
- Mellander PE, Bishop K, Lundmark T (2004) The influence of soil temperature on transpiration: a plot scale manipulation in a young Scots pine stand. *Forest Ecology and Management*, **195**, 15-28.
- Mikha MM, Rice CW, and Milliken GA (2005) Carbon and nitrogen mineralization as affected by wetting and drying cycles. *Soil Biology and Biochemistry*, **37**, 339-347.
- Mosier AR (1998) Soil processes and global change. *Biology and Fertility of Soils*, **27**, 221-229.
- O'Lear HA, Blair JM (1999) Responses of soil microarthropods to changes in soil water availability in tallgrass prairie. *Biology and Fertility of Soils*, **29**, 207-217.
- Risser PG, Birney CE, Blocker HD, May S.W, Parton WJ, Wiens JA (1981). *The True Prairie Ecosystem. US/IBP Synthesis Series 16*. Hutchinson Ross Publishing Company, Stroudsburg, PA.

- Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Biodiversity - global biodiversity scenarios for the year 2100. *Science*, **287**, 1770-1774.
- Sala OE, Parton WJ, Joyce LA, Lauenroth WK (1988) Primary production of the central grassland region of the United States. *Ecology*, **69**, 40-45.
- Sims PL, and Risser PG (2000) Grasslands in Barbour MG and Billings WD (Eds) *North American Terrestrial Vegetation, Second Edition*. Cambridge University Press, New York, USA.
- Weaver, JE (1954). *North American Prairie*. Johnson Publish Company, Lincoln, NE.
- Weaver, JE and Albertson FW (1956). *Grasslands of the Great Plains, Their Nature and Use*. Johnson Publishing Company, Lincoln, NE.

Chapter 2 - Subsurface Plant and Soil Responses to Changes in Soil Water Availability in a Grassland System

ABSTRACT

Studies in a range of grasslands types have shown relationships between soil water availability and ecosystem structure (e.g. community composition) and function (e.g. primary productivity, nutrients dynamics, and decomposition). Climate predictions based on global circulation models (GCMs) suggest increased temperatures and altered precipitation regimes with an overall reduction in soil water availability in many grasslands. To assess the impacts of altered soil water availability on grassland soil systems, a reciprocal core transplant experiment was initiated in 1993 between a relatively mesic grassland site (Konza Prairie, mean annual precipitation = 850 mm) and a more arid grassland site (Hays, mean annual precipitation = 580 mm). After 16-years, in May 2009, 10 large, intact plant-soil cores at each site (5 “native” and 5 “transplanted”) were harvested and sectioned into five depth increments (0-10, 10-20, 20-30, 30-40, and 40-60 cm). Each core section was analyzed for selected biological, physical and chemical properties (belowground plant biomass, soil carbon (C) and nitrogen (N), and potential C and N mineralization rates). We assessed the influence of incubation location and soil origin on these properties both for whole cores (0-60 cm) and by depth increment. In general, transplanting cores from the mesic site to a more arid climate had greater effects than transplanting cores from the arid site to the more mesic environment. Transplantation of Konza soils to the more arid Hays site led to reductions in belowground plant biomass (~20%) and microbial biomass (~20%), resulting in reduced soil carbon storage (~5%). Hays cores transplanted to the more mesic Konza site experienced modest increases in some properties (plant biomass = ~7.4%; microbial biomass = ~9.2%; SOC = ~4%); however, these altered

properties not statistically different from comparable values for “non-transplanted” Hays cores. Analysis by depth revealed that a majority of significant responses to transplantation occurred in the top 20 cm. Results of this study highlight the importance of changes in precipitation regimes on belowground grassland systems, and suggests a reduction in the ability for grasslands to sequester C under reduced annual precipitation.

INTRODUCTION

Water availability is generally accepted to be an influential abiotic driver of ecological processes in many terrestrial ecosystems (Le Houerou et al. 1988; Churkina and Running 1998). Various physical and chemical components of terrestrial ecosystems are often limited by water availability (Stark and Firestone 1995; Harper et al. 2005). Therefore, alterations to water cycle components (i.e., precipitation and latent heat fluxes) will likely incur ecological responses in terrestrial ecosystems. As a consequence of increased atmospheric greenhouse gases, global circulation models (GCMs) predict changes in global surface temperatures and precipitation regimes (Karl and Knight 1998; Hansen et al. 2006; IPCC 2007a). Evidence exists that shifts in mean annual temperature (Cox 2000; IPCC 2007a) and precipitation (Karl and Knight 1998; Gabrecht and Rossel 2002) have already begun to occur. As a result of recent climatic shifts, changes in plant and animal ranges have already become evident with species shifting toward the poles, toward higher elevations, or becoming extinct (IPCC 2007b; Kelley and Gouldin 2008). While some effects of recent climate change have been observed, further changes to the global climate are expected and the magnitude of ecological impacts remains unclear.

Changes in mean annual precipitation are likely to have strong and rapid ecosystem-level effects in grassland ecosystems (Austin et al. 2002), especially in the Central Plains region of the United States. The grassland systems of this region consist of short-grass, mixed-grass, and tallgrass prairies (Samson and Knopf 1994). The distribution and composition of these grasslands are largely dependent on climate patterns and a strong east-west precipitation gradient characteristic of the region (Risser et al. 1981). With increasing annual precipitation to the east, the community composition shifts from a short-grass to mixed-grass to tallgrass prairies (Weaver 1954; Kuchler 1974), with corresponding increases in primary productivity (Sala et al. 1988;

Knapp and Smith 2001). Similar patterns of precipitation, community composition (Pyankov et al. 2000), and productivity (Shankar et al. 1993) occur in other grassland systems. Specific climate change models for this region have predicted increasing mean annual temperatures and variable changes in annual precipitation ranging from modest increases or decreases with less frequent, more intense rainfall events (Karl and Trenberth 2003; IPCC 2007a). Predictions also include decreased growing season precipitation for the Great Plains region (Karl et al. 1991). As a result, these climatic alterations will strongly influence growing season soil water availability by increasing latent heat fluxes faster than precipitation inputs can recharge the soil (Jackson et al. 2001). Studies have begun to investigate ecological responses to climate changes in these grasslands, including potential changes in primary productivity, plant community composition, and soil respiration (Knapp et al. 2002; Fay et al. 2003; Harper et al. 2005; Sherry et al. 2008).

The potential impacts of these predicted climate changes on belowground dynamics in grassland systems are largely unknown. In these systems, plants have proportionally higher belowground than aboveground biomass (Simms et al. 1978; Rice et al. 1998; Milchunas et al. 2005), with greater root-to-shoot ratios in more arid grasslands (Schulze et al. 1996) relative to more mesic grasslands (Knapp and Seastedt 1986). Higher quality of belowground plant biomass (e.g., lower C:N ratio) has been reported in more arid grasslands, as well (Schlesinger 1997). Climate-driven differences in belowground plant quality and quantity have direct (i.e., carbon inputs) and indirect (i.e., aggregation) effects on soil organic matter (Kelly et al. 1996). Rhizodeposition, root decomposition, and sloughing of root cap cells are the primary sources of soil organic matter (Rasse et al. 2005), especially in frequently burned prairies where surface litter inputs are reduced. The composition, abundance, and activity of microbial populations within the soil are dependent on plant inputs and water availability (Hinsinger et al. 2005), and in

turn, influence organic matter processing and nutrient cycling (Rice et al. 1998). With temperate grasslands sequestering ~12% of the world's soil organic matter (Schlesinger 1997), changes in water availability in these grassland ecosystems could lead to drastic changes in biogeochemical cycling, with local, regional, and global consequences.

Since climate change represents a chronic, not transient, alteration in global climates, the need for research investigating key ecological responses to long-term changes is becoming increasingly important. This study was designed to assess longer-term (16-year) ecological responses to altered precipitation regimes, using a simple reciprocal transplant of intact plant-soil cores to simulate an increase or decrease in soil water availability. The major questions addressed in this study are: 1) How will grassland soils respond to transplantation from a more mesic climate to a more arid climate and from a more arid climate to a more mesic climate? 2) What ecological responses will be most sensitive to these precipitation changes? 3) Will a reciprocal change in rainfall patterns have comparable effects on soils adapted to wetter or drier conditions? We hypothesized that the movement of soil from a more arid site to a more mesic site would result in increased belowground plant and microbial biomass and increased storage of carbon (C) and nitrogen (N) within the soil. We hypothesized that the movement of soil from a more mesic site to a more arid site would show a proportional opposite effect.

METHODS

Description of Study Sites

The reciprocal transplant study was conducted between Konza Prairie Biological Station (Konza) and Kansas State University Agricultural Center at Hays (Hays), as part of an experiment funded by the Department of Energy/National Institute for Global Environmental Change (DOE/NIGEC) to investigate how vegetation, soil organisms, and soil processes of

grassland systems respond to altered soil moisture regimes. Konza is a 3487-ha area of native tallgrass prairie in the Flint Hills of northeastern Kansas (39°05'N and 96°35'W), located approximately 13 km south of Manhattan, KS. Konza is owned by The Nature Conservancy and Kansas State University and operated as a field research station by the Kansas State University Division of Biology as a Long-Term Ecological Research site. Native grassland vegetation is dominated by *Andropogon gerardii* (big bluestem), *Sorghastrum nutans* (Indian grass), *Panicum virgatum* (switchgrass), and *A. scoparius* (little bluestem), which is typical for a mesic tallgrass system. Average annual precipitation is 835 mm, with high interannual variability (Figure 2.1). The Hays site is a native grassland owned by Kansas State University and located 240 miles west of Konza (39°05'N and 96°35'W). The vegetation is primarily mixed-grass species, including *Bouteloua curtipendula* (side-oats gramma), *B. gracillis* (blue gramma), *Buchloe dactyloides* (buffalo grass), and *Agropyron smithii* (western wheat grass); however, *A. gerardii* and *P. virgatum* were common and well represented at the specific site chosen for this study. Average annual precipitation for this location is roughly 580 mm (30% less than the Konza site), with high interannual variability. The regional scale difference in climate allowed us to address the effects of altered soil water availability on belowground plant biomass and tissue chemistry and soil properties. Although differences in fire management occurred during the 16-year study period, with the Konza site being burned annually and the Hays site being burned sporadically (1993, 1994, 1995, 2000, 2003, and 2007), both sites were ungrazed and there were no other differences in management. The Konza site was on a deep, nearly level (0–1% slope) Reading silt loam formed from alluvial sediments. Reading soils are fine, mixed mesic Typic Argiustolls with a silt loam A horizon (approximately 28 cm deep) overlaying light to heavy silty clay loam B1 and B2t horizons. The Hays site was located on a deep, nearly level (0–1% slope) Harney silt

loam formed in calcareous, medium textured loess. The A₁ and A₃ horizons were silt loams and light silty clay loams, respectively, overlaying light to heavy silty clay loam B horizons. Therefore, soils are texturally similar in the top 30 cm; however, below 30cm, notable increases in clay content were observed in Konza soils that were not present in Hays soils.

Experimental Design

The reciprocal transplant experiment was initiated in 1993. Seventy large (25 cm diameter × 70 cm depth) plant-soil cores, encased in intact, open-ended polyvinylchloride cylinders (PVC) were extracted from both the more mesic Konza site and the more arid Hays grassland site, using hydraulic coring equipment (Swallow et al. 1987). Using a paired randomized block design, half of the cores extracted were placed back into their respective holes, while the other half were reciprocally transplanted between sites. This resulted in 70 plant-soil cores at each site (35 “transplanted” and 35 “native”). In 1994-1996, a subset of cores was destructively sampled twice per year to assess short-term effects of transplantation (O’lear and Blair 1999; Todd et al. 1999). An additional subset of soil cores remained incubating at each site to assess the longer-term effects of the transplantation, which is the focus of this study. These long-term plant-soil cores (5 “native” and 5 “transplanted” at each site) were harvested in May of 2009. Each core was separated into 0-10, 10-20, 20-30, 30-40, and 40-60 cm depth increments. All plant-soil cores at each depth increment were processed and selected physical-chemical and biological responses were assessed. Analysis of “native” cores from both sites allowed for comparison of belowground plant biomass and tissue chemistry and soil properties between grassland soils formed under different precipitation regimes. Comparison of “native” cores to both sets of “transplanted” cores was used to assess differences in soils as a result of incubation location, and differences between soil type at each location (i.e., the effects of soil origin).

Belowground Plant Biomass and Tissue Chemistry

Belowground plant biomass and root tissue C and N concentrations were quantified at each core depth through a combination of hand-sorting and wet sieving of soil, followed by chemical analysis of plant tissues. In the laboratory, I separated the soil by hand, removed large roots, and dried the roots for 1 week at 60°C. The remaining soil was immediately stored at 4°C, until more time-sensitive analyses of soil properties were completed. The remaining soil was then washed over a 2-mm sieve to retrieve fine roots. I did not attempt to distinguish between live and dead roots; all wet sieved roots were dried for one week at 60°C. Both hand-sorted and wet-sieved roots were then combined, weighed, ground, and redried at 60°C. Carbon and N concentrations were determined by dry combustion coupled with gas chromatography on a Thermo Finnigan Flash EA1112 autoanalyzer.

Carbon and Nitrogen Pools and Mineralization

Soil C and N pools and potential mineralization rates reflect both long-term accumulation and storage of C and N, and potentially available organic C and N pool within the soil. During the initial processing of the plant-soil cores, a subsample (~500g) of soil was taken from each depth increment in each core. In the laboratory, I homogenized the soil through a 4-mm sieve. Gravimetric soil water content was determined for each increment from a 20 g field-moist subsample that was weighed, dried at 60°C, and reweighed. Once gravimetric soil water content was determined, the soil was ground into fine powder to determine percent C and N on a Thermo Finnigan Flash EA1112 autoanalyzer (Thermo Finnigan, Rodano, Milan, Italy).

Extractable inorganic N was determined from a field-moist sample of homogenized soil taken from each core section. Approximately 11 g of soil (~10 g dry weight) was extracted with 2 M KCL shaken on an orbital shaker at 200 rpm for 1 hour. Solutions were filtered through 0.4-

mm polycarbonate membranes and stored at 4°C until analysis. Concentrations of ammonium (NH₄-N) and nitrate (NO₃-N) were determined on an OI Analytical Flow Solution IV autoanalyzer (formerly Alpkem; College Station, Texas, USA) using cadmium reduction/sulfanilamide diazotization for nitrate and an indophenol blue method for ammonium.

Soil microbial biomass was determined using the chloroform fumigation-incubation procedure (Jenkinson and Powlson 1976). Field-moist samples (~20 g) were brought to 28% gravimetric water content (~60% water-filled pore space) and allowed to pre-incubate in 125-ml Erlenmeyer flasks for 5 days at 25°C. Afterwards, half of the samples were fumigated with ethanol-free chloroform for 24 hours. After fumigation, chloroform was removed by repeated evacuation of the dissector. All flasks were resealed and incubated for 10 days at 25°C. After this final incubation period, a subsample (0.5 mL) of headspace gas from each flask was analyzed on a gas chromatograph. Following CO₂ measurements, all samples were analyzed for inorganic N (see procedure above). Microbial biomass C and N were calculated by the difference between fumigated and unfumigated samples, using a correction factor of 0.4 and 0.6, respectively (Voroney and Paul 1984). In addition, potential C and N mineralization were calculated from the unfumigated microbial biomass samples, based on 10-day potentially mineralizable C incubations and 15-day potentially mineralizable N incubations (Robertson et al. 1999).

Statistical Analysis

Analysis of variance was performed using SAS PROC MIXED (SAS Institute) to assess differences in belowground plant biomass and tissue C and N content, total C and N in soil, microbial biomass C and N, and potential mineralization rates among treatments. To determine the effect of transplantation on whole core (0-60 cm) dynamics of selected C and N pools, a 2-

way ANOVA was used with soil origin and incubation location as independent variables. A 3-way ANOVA was performed on all variables using soil origin, incubation location, and depth as independent variables to identify potential effects of soil origin and location by depth for all variables. The SAS SLICE featured was used to determine at which depth the main effects of location and origin, or their interactions, were observed. In the case of a significant 3-way interaction (origin \times location \times depth), pair-wise comparisons of all combinations of soil origin and location were done at the specified depth. Results were considered statistically significant at $p < 0.05$, unless otherwise specified. Data are reported as treatment means \pm one SE.

RESULTS

Precipitation

The mean annual precipitation at Konza Prairie (964 mm) was significantly greater than Hays (635 mm) during the study period (1993-2009) (Figure 2.1). Over the course of the study Konza received ~37% greater annual precipitation on average than Hays, which was greater than the long-term 30% difference. Although the average percentage difference during the study was above the long-term average, precipitation amounts were not consistently higher at Konza relative to Hays. Differences in precipitation between sites were below the long-term average for several years (1993, 2000, 2001, 2003, and 2007), and in two years (1995 and 1996) Konza received less annual rainfall than Hays (Figure 2.1).

Belowground Plant Biomass

Total belowground plant biomass (0-60 cm) was significantly affected by location, soil origin, and their interaction (Figure 2.2). The location \times origin interaction was due to the greater responsiveness of cores originating from Konza (the more mesic site) when transplanted to Hays

(the more arid site). This transplantation resulted in a 20% decrease in total belowground plant biomass. In contrast, the transplantation of cores originating from Hay to Konza did not result in a significant increase in total belowground plant biomass.

To further analyze belowground plant biomass responses, rhizomes and roots were analyzed separately. Rhizome biomass, representing ~25% of total belowground plant biomass (0-60 cm), was affected by a location \times origin interaction, and was more responsive to the transplantation of Konza cores to the more arid Hays site (35% reduction), relative to the transplantation of Hays cores to Konza (non-significant increase of 6%) (Figure 2.3). Further analysis of root biomass was performed using a three-way ANOVA, adding depth as an additional variable. Analysis over all treatments by depth revealed significant effects of location, location \times origin interaction, depth, location \times depth interaction, and a location \times origin \times depth interaction (Figure 2.3). The main effect of depth was due to decreasing root biomass with increasing depth. Significant three-way interactions were due to treatment effects on root biomass at the 0-10 and 10-20 cm depth increments. At these depths, decreases of 23% (0-10 cm) and 18% (10-20 cm) were experienced by Konza cores transplanted to Hays, while small, non-significant increases in root biomass occurred in the Hays cores transplanted to Konza. The main effect of location was significant at these depths as well, with cores incubated at Konza supporting 16% higher root biomass than cores incubated at Hays. Therefore, decreasing annual precipitation for Konza cores (transplanting Konza cores to Hays) resulted in greater responses in root biomass, relative to increasing annual precipitation for Hays cores, with the differences apparent in both rhizomes and roots in the upper 20 cm of the soil.

Carbon concentrations in rhizome biomass were not affected by location or soil origin (Figure 2.4), and concentrations remained at ~42%. Carbon concentrations in root biomass were

not affected by location but were affected by soil origin, with differences apparent at 30-40 and 40-60 depth increments. At these depths, cores originating from Konza had significantly lower root C concentrations relative to cores originating from Hays. The average C concentration in root biomass across all treatments was ~37%. As a result of the lack of responsiveness of root C concentrations to precipitation change and small differences due to soil origin, the amount of C sequestered in root biomass was primarily a function of root biomass (Figure 2.5). Therefore, increases and decreases in root biomass drove proportional changes in belowground storage of plant C.

Nitrogen concentrations within rhizome and root biomass across soil origin showed similar responses to precipitation, with significantly higher N concentrations in cores incubated at the drier Hays site relative to cores incubated at Konza. Rhizome N concentrations were greatest in Konza cores transplanted to Hays, which almost doubled in concentration compared to native Konza soil cores. More detailed analysis of root N concentrations revealed no significant location \times depth interaction overall; however, the differentiation between locations appears to be the greatest at the 0-10 cm and 10-20 cm depth increments. As a result, change in belowground plant N storage was a function of increased N concentrations at Hays and increased belowground biomass at Konza. Rhizome N storage was greater at Hays relative to Konza, regardless of soil origin. Nitrogen storage within rhizomes increased ~39% in Konza cores transplanted to Hays, and decreased by 28% in Hays cores transplanted to Konza. A location \times depth interaction in root biomass indicated that roots in the top 10 cm of the soil had significantly greater storage of N at Hays relative to Konza. The change in storage of plant N between cores transplanted in both directions was restricted to the surface soil layer (0-10 cm),

with cores incubated at Hays containing significantly greater total belowground plant N compared to cores incubated at Konza.

The combination of relatively small changes in root and rhizome tissue C concentrations and more substantial changes in N concentrations resulted in altered belowground biomass quality (i.e., C:N ratio) among treatments at all soil depths. Since plant C concentrations were not altered by treatment effects in either rhizomes or roots, trends in belowground plant quality were driven primarily by changes in N concentrations. Belowground plant biomass quality averaged across soil origin and depth was significantly poorer in cores incubated at Konza relative to Hays (Figure 2.4). The significance of the depth term revealed plant biomass quality was not consistent with increasing depth, with C:N ratios being highest at 20-30 and 30-40 cm, intermediate at 0-10 and 40-60 cm, and the lowest at 10-20 cm.

Soil Carbon and Nitrogen Pools and Mineralization

Soil C and N concentrations were not significantly affected by either incubation location or soil origin, averaged across the total soil core. Despite a lack of general treatment effects on C concentration, total soil C storage was significantly affected by both location and soil origin (Figure 2.7). Total C stored in soils incubated at Konza was greater than soils incubated at Hays, regardless of soil origin, while soils originating from Konza contained more C than soils originating from Hays. No location \times depth or origin \times depth effect was detected. No effects of location or soil origin were found in total N storage; however, an origin \times depth interaction indicated that cores originating from Konza stored greater amounts of total soil N at the 40-60 cm depth increment relative to Hays cores. At this depth, Konza cores stored ~18% more soil N than Hays cores (Figure 2.7). The relative lack of treatment effects on soil C and N concentrations led to no responses in the soil C:N ratio (Figure 2.6).

Both microbial biomass carbon (MBC) concentrations and storage were similarly effected by transplantation to the alternate site. ANOVA of MBC across origin and location revealed that cores incubated at Konza supported a greater MBC than cores incubated at Hays (Figure 2.8, 2.9). Transplanting Konza cores to Hays resulted in a significant 27% reduction in MBC, with a majority of the differentiation between sites occurring at 0-10, 10-20, and 40-60 cm depth increments. Within these depth increments, Konza cores transplanted to Hays experienced a significant reduction in MBC (Figure 2.8, 2.9). Total microbial biomass N (MBN) was unaffected by either the main effects of incubation location or soil origin; however, a significant location \times depth interaction occurred, with the differences in location being apparent at the 0-10 cm depth increment. At these depths microbial biomass N storage was greater within cores incubated at Konza relative to Hays (Figure 2.8, 2.9). Microbial biomass C:N ratio was also not affected by treatments (Figure 2.8), but a significant location \times depth interaction was found, and indicated that the effect of location was significant at the 20-30 cm depth.

Analysis of potentially mineralizable C, assessed from a 10-day aerobic incubations, revealed significant main effects of location and origin. Potentially mineralizable C was found to be greater in soils incubated at Konza relative to Hays, regardless of origin; however, no significant location \times depth interaction occurred. Soil cores originating from Konza had greater overall potentially mineralizable C, but no origin \times depth interaction was discovered. Potentially mineralizable N was not affected by location or origin alone; however, a significant origin \times depth interaction occurred. At 0-10 and 10-20 cm depth increments, soils originating from Konza had more potentially mineralizable N than soils originating from Hays.

DISCUSSION

Grasslands are dynamic ecosystems likely to respond to short-term changes in precipitation; however, the longer-term responses are perhaps more important and critical for assessing potential changes in grassland ecosystem functioning under altered future climates. In grasslands, greater plant biomass is allocated belowground relative to aboveground, and belowground plant productivity is an important metric of ecosystem processes (Sala et al. 1998). Our results indicated that belowground plant biomass in grasslands was positively related to precipitation during the incubation period. Regardless of soil origin, we found greater standing stocks of belowground plant biomass in soils incubated in the more mesic Konza climate. A notable decrease in plant root biomass of 28% was observed when Konza soil cores were transplanted to Hays, while a non-significant increase of 12% was observed when Hays soils were transplanted to Konza. These results were only partially consistent with our initial hypotheses, in that transplanting cores to a drier site resulted in a significant loss of root biomass. However, the responses of cores moved from an arid to a more mesic climate was not proportional; there was a trend for increasing root biomass, but it was not significant. A majority of the difference in root biomass was found at the 0-10 cm and 10-20 cm depths within the soil, where a substantial (80%) proportion of belowground plant biomass was recovered. Declines in plant biomass at these depths in Konza soil cores incubated at Hays were likely the result of prolonged deficits in soil moisture, which were not experienced at Konza. Studies have shown that periods of droughts can have prolonged effects on root activity (Wraith et al. 1995), with recovery of root activity taking days or weeks after more favorable conditions occur (Casper and Jackson 1997; Wraith and Wright 1998). As a result, water uptake is lessened, having cascading effects on leaf-level photosynthesis (Hu et al. 2010; Taylor et al. 2010) and ultimately reducing plant productivity (Rice et al. 1998). Therefore, we suggest periods of water deficits experienced

at Hays led to lower plant water status, hindering C gain, and resulting in lower belowground plant biomass. Similar responses to decreases in precipitation have been observed within the region for both aboveground biomass (Knapp 1985; Fay et al 2003) and belowground biomass (Schenk and Jackson 2002; Hays and Seastedt 1987).

The three-way interaction for belowground plant biomass indicates differential responses to precipitation among plants in soil cores originating from different locations and at different depths. In general, plants originating from Konza were more responsive to transplantation relative to plants from Hays, and this location effect was driven by responses in the upper soil profile, while soil origin affected root biomass in the lower depths. Increased clay content in Konza soils at lower depths limited root biomass slightly, compared to cores originating from Hays, and may have restricted root activity and water uptake primarily to the upper soil layers where water availability is less stable, likely affecting productivity, as explained previously. This phenomenon was not experienced in Hays soils. Plants in soil originating at Hays apparently were not able to capitalize on the additional water received when transplanted to Konza, suggesting that nitrogen became the limiting factor in biomass production.

While precipitation did not influence rhizome or root C concentrations or storage, it greatly influenced rhizome and root N concentrations. Greater N concentrations were found in plants incubated at the more arid Hays site, regardless of soil origin. The differences were apparent in top 30 cm of the soil. The dynamics between plant water status and plant N concentration in grassland systems are dependent upon each other, as these systems are typically co-limited by both resources (Vinton and Burke 1995). Across this region, water limitation is greater in the western, more arid region, while N is generally more limiting in the eastern, more mesic region (McCulley et al. 2009). Therefore, it was expected that N concentrations would be

higher in cores originating from, and incubated at, Hays. Alternatively, the reduction of N content with increasing precipitation could be due to the response of N retranslocation that occurs during periods of drought (Heckathorn et al. 1996). Since Hays was more likely to have greater periods of drought, N levels within roots would be expected to be higher at this location. Hecklethorn and DeLucia (1994) noted significant differences in N content comparing pre- and post-droughts samples, where drought greatly reduced N content in aboveground biomass and increased N in rhizomes and roots. Studies across this precipitation gradient have shown similar results in response to precipitation, with greater N concentrations in drier areas (McCulley et al. 2009). Changes in N storage within root systems are the net result of changes in root biomass and N concentrations. In the present study, N storage within plant root tissues was significantly greater at Hays relative to Konza due to higher root N concentration in cores incubated at Hays, which overwhelmed differences in biomass. Alterations in N concentrations led to changes in plant quality (i.e., C:N ratios). With no apparent changes in C concentrations, increased N content led to higher plant tissue quality (lower C:N ratio) in cores incubated at Hays relative to Konza. Other studies have confirmed this trend using comparative studies between grassland sites (McCulley et al. 2009) and experimental manipulations (Fay et al. 2003).

Microbial biomass is the physiologically active component of soil organic matter (Schlesinger et al. 1997). Studies in terrestrial ecosystems have identified soil water availability as an important factor regulating MBC and MBN. Our results showed that transplanting Konza soil cores to Hays reduced MBC by 27%, and transplanting Hays soil cores to Konza increased MBC by 12%. Differences due to location were apparent in top 0-20 cm of the soil, and were greatest in Konza soils. Similar dynamics were experienced with microbial biomass N. Limitations on microbial biomass accumulation have been well-studied, including factors such as

nutrient limitation and plant quality inputs, and these limitations are also affected by soil moisture availability. Microbial biomass is strongly correlated with high organic matter inputs and available soil organic matter, as they are the primary energy sources for heterotrophic soil microorganisms. Many studies have shown that soil C inputs can significantly impact soil MBC (Bardgett 1999; Brant et al. 2006). Thus, the addition of readily decomposable C can result in rapid increases in microbial biomass. Microbial biomass also is limited by the availability of N (Hongmei et al. 2010). Additions of NH_4 and NO_3 have been shown to increase microbial biomass. Gallardo and Schlesinger (1994) found that addition of both organic and inorganic forms of N into the soil increased MBN. As the availability of nutrients is directly related to soil moisture, it is likely that increased soil moisture enhances microbial biomass. Direct effects of water on soil microbial populations are generally related to the balance between water and oxygen within the soil. Linn and Duran (1984) found that microbial biomass was typically highest when soil water- filled pore space was between 50-60%. Therefore, microbial biomass is dependent on various limitations, which are typically satisfied under more water balanced soil conditions.

Potential soil C mineralization rates were affected by changes in precipitation regimes, and followed dynamics similar to those of MBC. Potentially mineralizable C was significantly greater in soils incubated at Konza relative to Hays. These results are consistent with those of other studies within the region. Other studies also indicate that mineralized C and N rates may be reduced by increased wetting and drying cycles, which were likely experienced to a greater extent at Hays. Mikha et al. (2005) found that increased drying and wetting cycles caused an initial flush of mineralized C. However, it lasted for only 8h and did not compensate for the loss in microbial activity. I found that the effects of precipitation were the most evident in the surface

soil (0-20 cm), which is where cores at Hays likely experienced the greatest wetting and drying cycles. The surface soil layers have been identified as critical for ecosystem-level processes, like C mineralization (Briggs and Knapp 1995; Austin et al. 2004). The lack of response in potentially mineralizable C at lower soil depths, where water content is more stable, may also be related to reduced C inputs at those depths from plant biomass. Changes in potentially mineralizable C could be a function of microbial biomass, where greater microbial biomass would infer greater mineralization rates.

Changes in the above soil core properties and characteristics can influence the total amount of C and N stored with these grassland soils. The accumulation of C and N within the soil is dependent upon inputs and outputs of these elements within the soil environment. Epstein et al. (2002) indicated that the amount of soil organic matter and its associated nutrient characteristics are dependent on net primary productivity and decomposition rates. My results indicated that soil C accumulation was positively correlated with increases in annual precipitation, but soil N remained relatively unaffected. Greater soil C storage was found in cores incubated at Konza relative to Hays, with a majority of this differentiation occurring in the top 20 cm, and although not significant, N storage was greater at 0-10 cm depths on Konza. The accumulation of C within the system was likely the result of increased plant inputs, quality of plant inputs, and the activity of the microbes (Swift 1977). Studies have shown that greater quantities of plant input and lower quality plant inputs can promote C accumulation within the soil (Kelley et al. 1996). As the balance between inputs and outputs govern C accumulation, we suggest that greater inputs outweighed the losses due to C mineralization. In addition, although decomposition does lead to C losses, increased processing of soil organic matter will result in some increased deposits of more recalcitrant C structures (e.g., humus) (Six et al. 2002; Allison

et al. 2008). The lack of response in N storage may be due to the high potential for retention of N with grassland systems. Nitrogen storage within plants is conserved through translocation of N during senescence, which may be enhanced by drought (Hecklathorn et al. 1996). Nitrogen mineralized during decomposition of residues is either immobilized by microbes within the soil or rapidly incorporated back into plant biomass. Therefore, as a result of N limitation in grasslands, these systems tightly conserve N (McCulley 2009).

CONCLUSION

This study provided new information of the potential effects of climate change and altered precipitation on grassland soil systems. We found that soil water availability, as influenced by increased annual precipitation, had the largest affect in the surface soils relative to the deeper soils, as a majority of observed responses occurred at depths of 0-20 cm. Positive correlations were observed between precipitation and belowground plant biomass, microbial biomass C, and total soil C. We found that plant N content increased with reduced precipitation, consistent with grassland co-limitation by water and N. Furthermore, we found greater plant N storage at the more arid Hays site, driven by proportionally greater increases in root N concentrations relative to decreases in root biomass at the drier Hays site. These changes in soil properties and nutrient dynamics were more evident in cores originating from at Konza relative to cores originating at Hays. The differential response provides an indication that more mesic grasslands are more susceptible to drought conditions than arid grasslands are to more mesic conditions. Therefore, a decrease in soil water availability in more mesic Konza site will likely result in altered ecosystem processes in these grasslands, while an increase in water availability at the more arid Hays site will likely remain unaltered.

BIBLIOGRAPHY

- Allison SD, Teseder KK (2008) Warming and drying suppress microbial activity and carbon cycling in boreal forest soils. *Global Change Biology*, **14**, 2898-2909.
- Austin AT (2002) Differential effects of precipitation on production and decomposition along a rainfall gradient in Hawaii. *Ecology*, **83**, 328-338.
- Austin AT, Yahdjian L, Stark JM, Belnap J, Norton U, Porporato A, Ravetta D, Schaeffer SM, (2004) Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia* **141**, 221–235.
- Bardgett RD, Lovell DL, Hobbs PJ (1999) Seasonal changes in soil microbial communities along a fertility gradient of temperate grasslands. *Soil Biology and Biochemistry* **31**, 1021–30.
- Brant JB, Sulzman EW, Myrold DD (2006) Microbial community utilization of added C substrates in response to long-term C input manipulation. *Soil Biology and Biochemistry* **38**, 2219–32.
- Briggs JM, Knapp AK (1995) Interannual variability in primary production in tallgrass prairie – climate, soil – moisture, topographic position, and fire as determinants of aboveground biomass. *American Journal of Botany*, **82**, 1024-1030.
- Casper BB, Jackson RB (1997) Plant competition underground. *Annual Review of Ecology and Systematics*, **28**, 545–570.
- Churkina G, Running SW (1998) Contrasting climatic controls on the estimated productivity of global terrestrial biomes. *Ecosystems*, **1**, 206-215.
- Cox PM, Betts RA, Jones CD, Spall SA, Totterdell IJ (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature*, **408**, 184-187.
- Epstein HE, Burke IC, Lauenroth WK (2002) Regional patterns of decomposition and primary production rates in the US Great Plains. *Ecology*, **83**, 320-327.
- Fay PA, Carlisle JD, Knapp AK, Blair JM, Collins SL (2003) Productivity responses to altered rainfall patterns in a C-4-dominated grassland. *Oecologia*, **137**, 245-251.
- Gallardo A, Schlesinger WH (1994) Factors limiting microbial biomass in the mineral soil and forest floor of a warm-temperate forest. *Soil Biology and Biochemistry*, **26**, 1409-1415,
- Garbrecht JD, Rossel FE (2002) Decade-scale precipitation increase in Great Plains at end of 20th century. *Journal of Hydrologic Engineering*, **7**, 64-75.

- Hays, D C, Seastedt T R (1987) Root dynamics of tallgrass prairie in wet and dry years. *Canadian Journal of Botany*, **65**, 787-791.
- Hansen J, Sato M, Ruedy R, Lo K, Lea DW, Medina-Elizade M (2006) Global temperature change. *Proceedings of the National Academy of Sciences of the United States of America*, **103**,:14288-14293.
- Harper CW, Blair JM, Fay PA, Knapp AK, Carlisle JD (2005) Increased rainfall variability and reduced rainfall amount decreases soil CO₂ flux in a grassland ecosystem. *Global Change Biology*, **11**, 322-334.
- Heckathorn SA, DeLucia EH (1996) Retranslocation of shoot nitrogen to rhizomes and roots in prairie grasses may limit loss of N to grazing and fire during drought. *Functional Ecology*, **10**, 396-400.
- Heckathorn, SA, DeLucia EH (1994) Drought-induced nitrogen retranslocation in perennial C₄ grass of tallgrass prairie. *Ecology*, **75**, 1877-1886.
- Hinsinger P, Gobran GR, Gregory PJ, Wenzel WW (2005) Rhizosphere geometry and heterogeneity arising from root-mediated physical and chemical processes. *New Phytologist*, **168**, 293-303.
- Hongmei J, Osbert JS, Jianfeng L (2010) Changes in soil microbial biomass and community structure with addition of contrasting types of plant litter in a semiarid grassland ecosystem. *Journal of Plant Ecology*, **10**, 1-9.
- Hu L, Wang Z, Huang B (2010) Diffusion limitations and metabolic factors associated with inhibition and recovery of photosynthesis from drought stress in a perennial grass species. *Plant Physiology*. **139**, 93-106.
- Intergovernmental Panel on Climate Change (IPCC) (2007a), Summary for policymakers, in *Climate Change 2007: The Scientific Basis. Contribution of the Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press, New York.
- Intergovernmental Panel on Climate Change (IPCC) (2007b), Summary for policymakers, in *Climate Change 2001: Impacts, Adaptation, and Vulnerability. Contribution of the Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press, New York.

- Jackson RB, Carpenter SR, Dahm CN, McKnight DM, Naiman RJ, Postel SL, Running SW (2001) Water in a changing world. *Ecological Applications*, **11**, 1027-1045.
- Jenkinson DS, Powelson DS (1976) The effects of biocidal treatments on metabolism in soil. *Soil Biology and Biochemistry*, **8**, 209-213.
- Karl TR, Heim RR, Quayle RG (1991) The greenhouse effect in central North America: If not now, when? *Science*, **251**, 1058-1061.
- Karl TR, Knight RW (1998) Secular trends of precipitation amount, frequency, and intensity in the United States. *Bulletin of the American Meteorological Society*, **79**, 231-241.
- Karl TR, Trenberth KE (2003) Modern global climate change. *Science*, **302**, 1719-1723.
- Kelly AE, Goulden ML (2008) Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 11823-11826.
- Kelly RH, Burke IC, Lauenroth WK (1996) Soil organic matter and nutrient availability responses to reduced plant inputs in shortgrass steppe. *Ecology*, **77**, 2516-2527.
- Knapp AK, Fay PA, Blair JM, Collins SL, Smith MD, Carlisle JD, Harper CW, Danner BT, Lett MS, McCarron JK (2002) Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science*, **298**, 2202-2205.
- Knapp, AK (1985) Effect of fire and drought on the ecophysiology of *Andropogon gerardii* and *Panicum virgatum* in a tallgrass prairie. *Ecology*, **66**, 1309-1320.
- Knapp AK, Seastedt TR (1986) Detritus accumulation limits productivity of tallgrass prairie. *Bioscience*, **36** 662-668.
- Knapp AK, Smith MD (2001) Variation among biomes in temporal dynamics of aboveground primary production. *Science*, **291**, 481-484.
- Kuchler AW (1974) New vegetation map of Kansas. *Ecology*, **55**, 586-604.
- Le Houerou HN, Bingham RL, Skerbek W (1988) Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. *Journal of Arid Environments*, **15**,:1-18.
- Linn DM, Doran JW (1984) Aerobic and anaerobic microbial populations in no-till and plowed soils. *Soil Science Society of America Journal*, **48**, 794-799.

- McCulley RL, Burke IC, Lauenroth WK (2009) Conservation of nitrogen increases with precipitation across a major grassland gradient in the Central Great Plains of North America. *Oecologia*, **159**, 571-581.
- Mikha MM, Rice CW, Milliken GA (2005) Carbon and nitrogen mineralization as affected by drying and wetting cycles. *Soil Biology and Biochemistry*, **37**, 339-347.
- Milchunas DG, Mosier AR, Morgan JA, LeCain DR, King JY, Nelson JA (2005) Root production and tissue quality in a shortgrass steppe exposed to elevated CO₂: Using a new ingrowth method. *Plant and Soil*, **268**, 111-122.
- O'Lear HA, Blair JM (1999) Responses of soil microarthropods to changes in soil water availability in tallgrass prairie. *Biology and Fertility of Soils*, **29**, 207-217.
- Pyankov VI, Gunin PD, Tsoog S, Black CC (2000) C-4 plants in the vegetation of Mongolia: their natural occurrence and geographical distribution in relation to climate. *Oecologia*, **123**, 15-31.
- Rasse DP, Rumpel C, Dignac MF (2005) Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. *Plant and Soil*, **269**, 341-356.
- Rice CW, Todd TC, Blair JM, Seastedt TR, Ramundo RA, Wilson GWT (1998) Belowground biology and process in Knapp AK, Briggs JM, Harnett DC, Collins SL (Eds) *Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie*. Oxford University Press. New York, USA.
- Risser PG, Birney CE, Blocker HD, May S.W, Parton WJ, Wiens JA (1981). *The True Prairie Ecosystem. US/IBP Synthesis Series 16*. Hutchinson Ross Publishing Company, Stroudsburg, PA.
- Robertson GP, Wedin D, Groffman PM, Blair JM, Holland E, Nadelhoffer KJ, Harris D (1999) Soil carbon and nitrogen availability: nitrogen mineralization, nitrification, soil respiration potentials in 258-271 in G. P. Robertson, C. S. Bledsoe, D. C. Coleman, and P. Sollins (Eds) *Standard Soil Methods for Long Term Ecological Research*. Oxford University Press, New York, USA.
- Sala OE, Parton WJ, Joyce LA, Lauenroth WK (1988) Primary production of the Central Grassland region of the United States. *Ecology*, **69**, 40-45.
- Samson F, Knopf F (1994) Prairie conservation in North America. *Bioscience*, **44**, 418-421.

- Schenk, HJ, Jackson, RB (2002) Rooting depths, lateral spreads, and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology*, **90**, 480-494.
- Schlesinger WH (1997) *Biogeochemistry: an Analysis of Global Change, Second Edition*. Academic Press, California, USA.
- Schulze ED, Mooney HA, Sala OE, Jobbagy E, Buchmann N, Bauer G, Canadell J, Jackson RB, Loreti J, Oesterheld M, Ehleringer JR (1996b) Rooting depth, water availability, and vegetation cover along an aridity gradient in Patagonia. *Oecologia*, **108**, 503-511.
- Shankar U, Pandey HN, Tripathi RS (1993) Phytomass dynamics and primary productivity in humid grasslands along altitudinal and rainfall gradients. *Acta Oecologica-International Journal of Ecology*, **14**, 197-209.
- Sherry RA, Weng ES, Arnone JA, Johnson DW, Schimel DS, Verburg PS, Wallace LL, Luo YQ (2008) Lagged effects of experimental warming and doubled precipitation on annual and seasonal aboveground biomass production in a tallgrass prairie. *Global Change Biology*, **14**, 2923-2936.
- Sims PL, Singh JS, Lauenroth WK (1978) Structure and function of ten western North American grasslands: abiotic and vegetational characteristics. *Journal of Ecology*, **66**, 251-259.
- Six J, Conant RT, Paul EA, Paustian K (2002) Stabilization of soil organic matter: Implications for C-saturation of soils. *Plant and Soil*, **241**, 155-176.
- Stark JM, Firestone MK (1995) Mechanisms for soil moisture effects on activity of nitrifying bacteria. *Applied and Environmental Microbiology*, **61**, 218-221.
- Swallow CW, Kissel DE, Owensby CE (1987) Soil coring machine for microplots and large soil cores. *Agronomy Journal*, **79**, 756-758.
- Taylor SH, Ripley BS, Woodward FL, Osborne CP (2010) Drought limitation of photosynthesis differs between C₃ and C₄ grass species in a comparative experiment. *Plant, Cell and Environment*, **34**, 65-75.
- Todd TC, Blair JM, Miliken GA (1999) Effects of altered soil-water availability on a tallgrass prairie nematode community. *Applied Soil Ecology*, **13**, 45-55.
- Wraith JM, Wright CK (1998) Soil water and root growth. *Horticultural Science*, **33**, 951-959
- Wraith JM, Baker JM, Blake TK (1995) Water uptake resumption following soil drought: a comparison among four barley genotypes. *Journal of Experimental Botany*, **46**, 873-880.

- Weaver, J.E. 1954. *North American Prairie*. Johnson Publish Company, Lincoln, NE.
- Vinton MA, Burke IC (1995) Interactions between individual plant species and soil nutrient status in short grass steppe. *Ecology*, **76**, 1116-1133.
- Voroney RP, Paul EA (1984) Determination of K_c and K_n in situ for calibration of the chloroform fumigation-incubation method. *Soil Biology and Biogeochemistry*, **16**, 9-14.

FIGURES

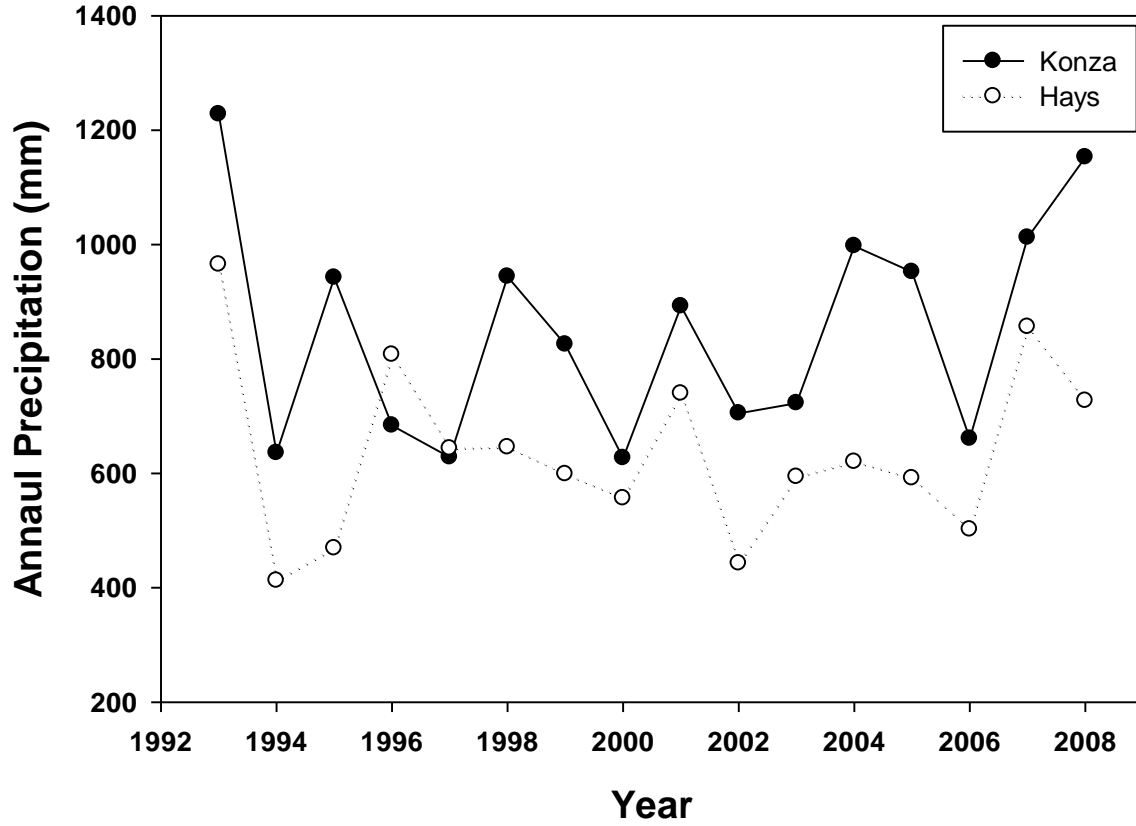


Figure 2.1 Annual precipitation (1993-2009) at Konza Prairie Biological Station (solid line) and Kansas State University Agricultural Research Center at Hays (dotted line).

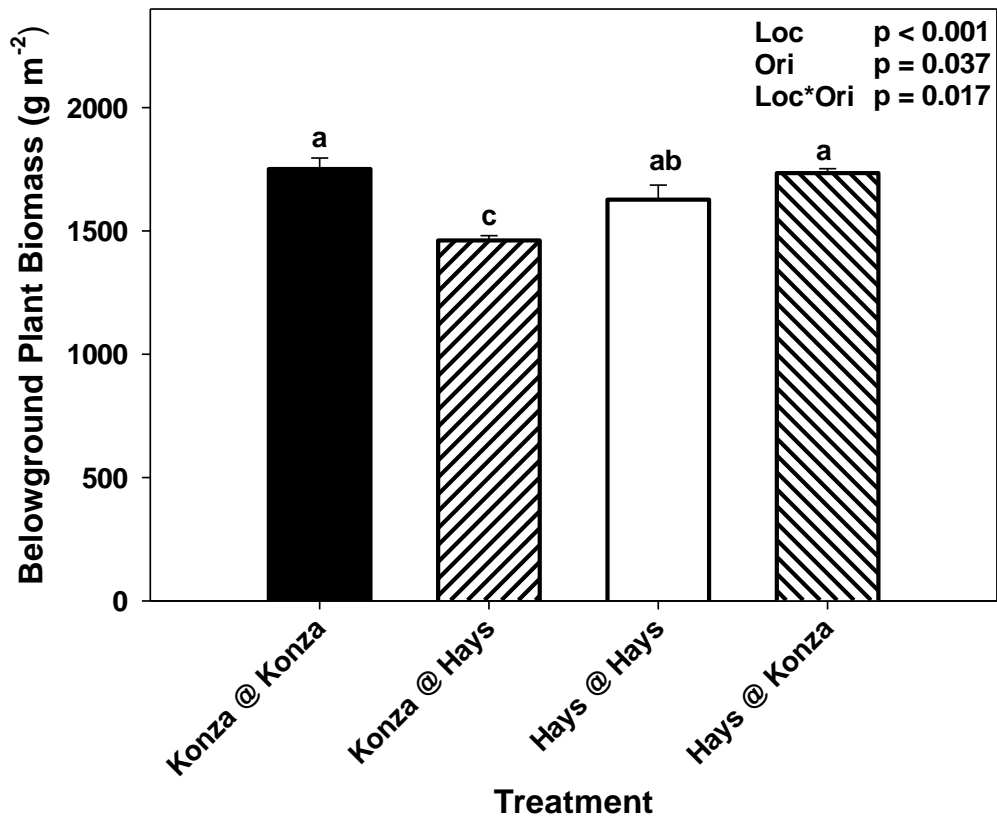


Figure 2.2 Average belowground plant biomass (0-60 cm) from four combinations of soil core origin and incubation location. Error bars are ± 1 SE. Lower-case letters indicate pair-wise significant differences at $p = 0.05$.

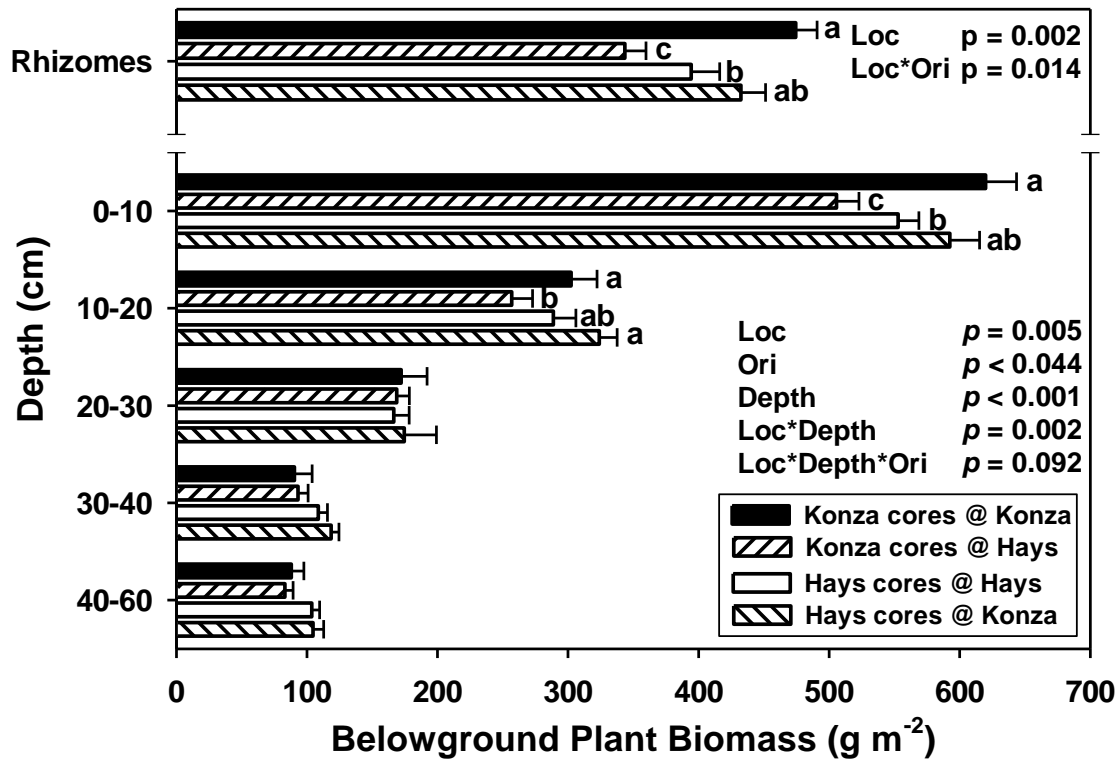


Figure 2.3 Average belowground plant biomass from four combinations of soil core origin and incubation location by depth. Error bars are ± 1 SE. Lower-case letters indicate pairwise significant differences at $p < 0.05$, at the specified depth.

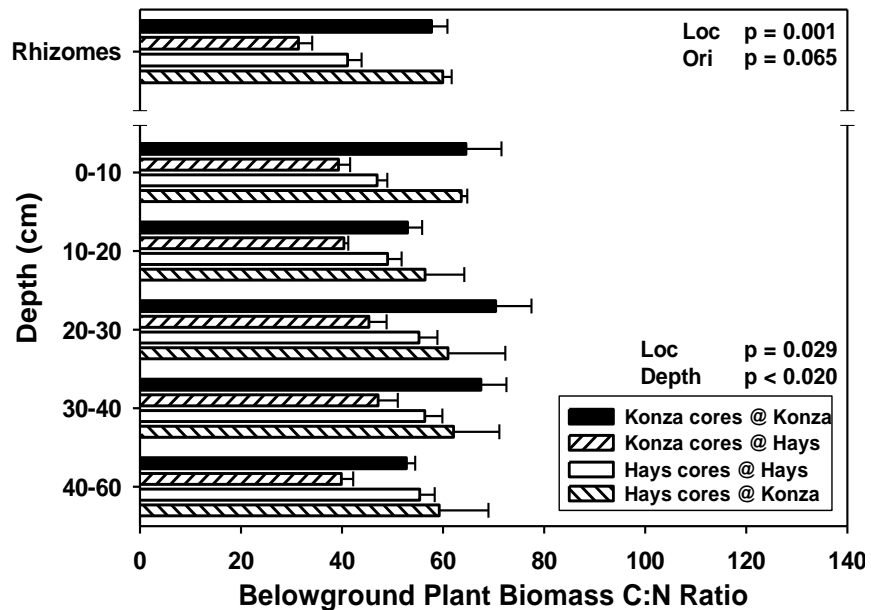
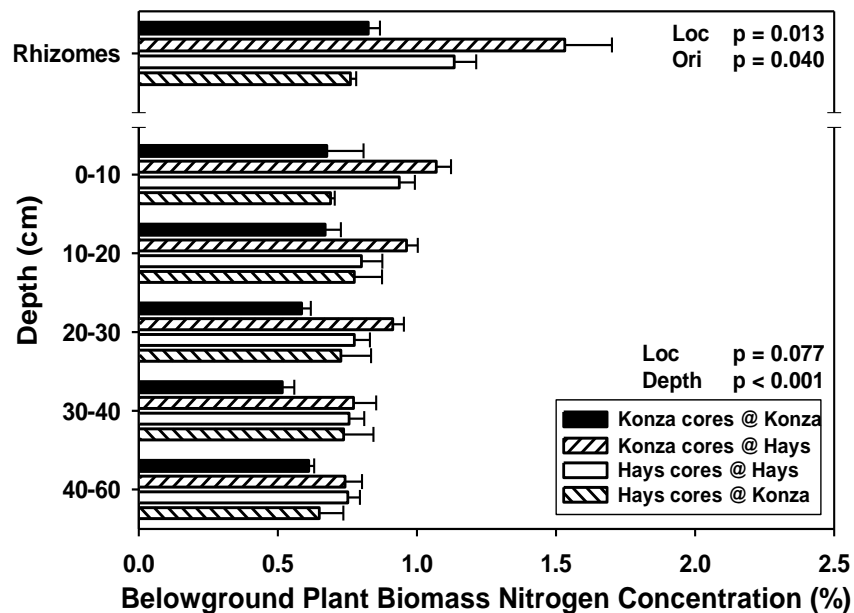
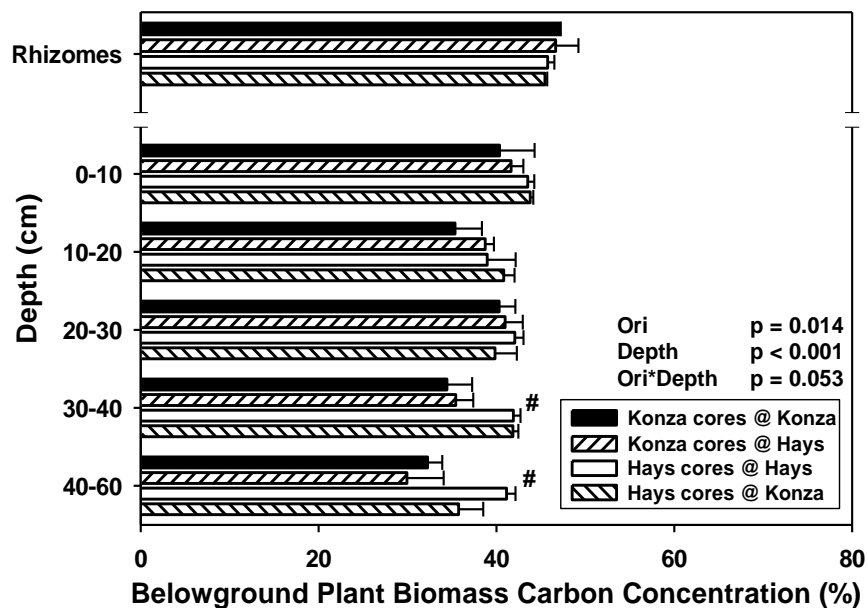


Figure 2.4 Belowground plant biomass carbon concentration (top left), nitrogen concentration (top right), and C:N ratio (bottom left) from four combinations of soil core origin and incubation location by depth. Error bars are ± 1 SE. A number symbol (#) indicates significant ($p < 0.05$) origin effects, at the specified depth.

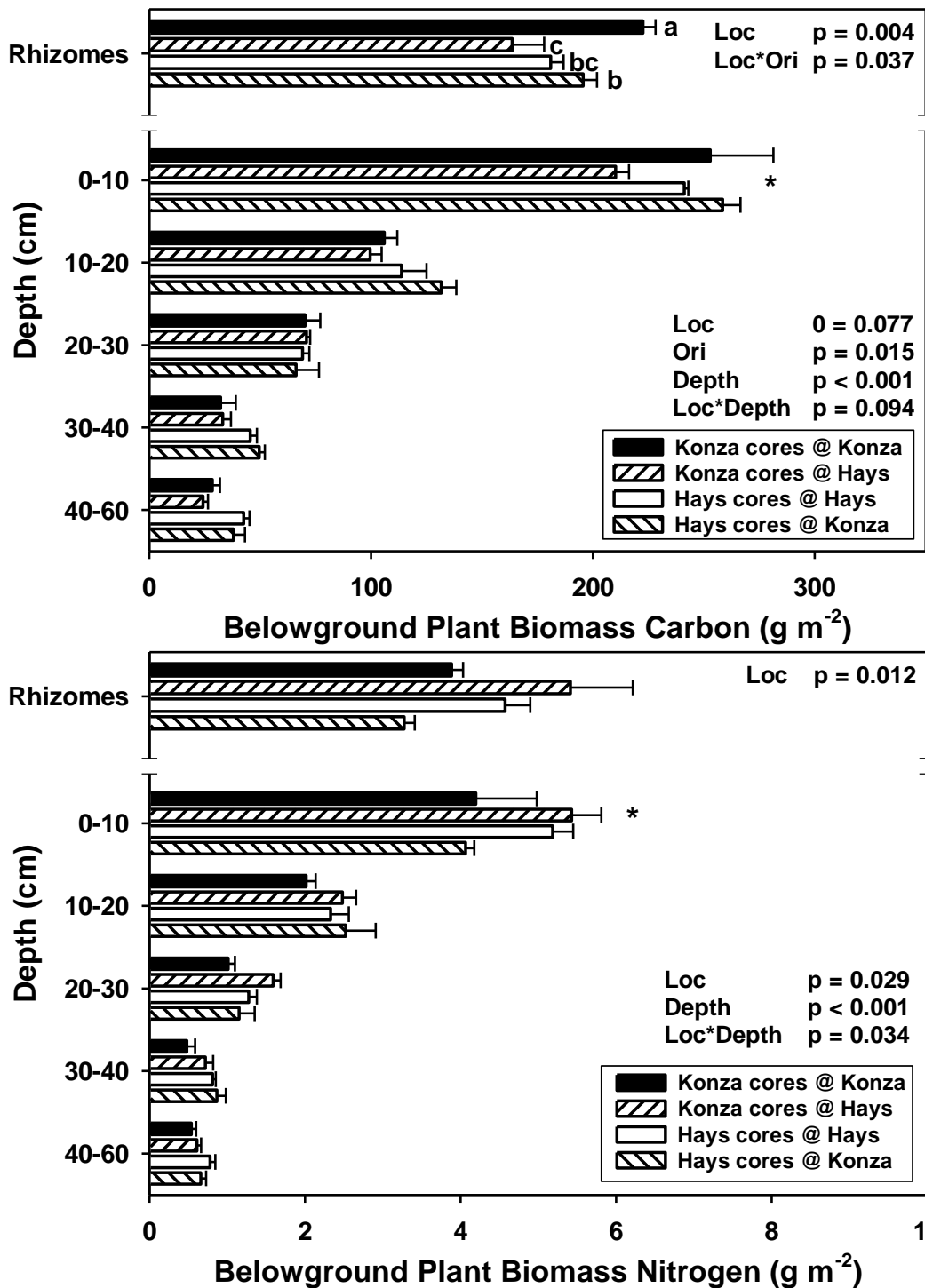


Figure 2.5 Average belowground plant biomass storage of carbon (top) and nitrogen (bottom) from four combinations of soil core origin and incubation location by depth. Error bars are ± 1 SE. Lower-case letters indicate pair-wise significant differences at $p < 0.05$, at the specified depth. An asterisks (*) indicates significant ($p < 0.05$) location effects, at the specified depth.

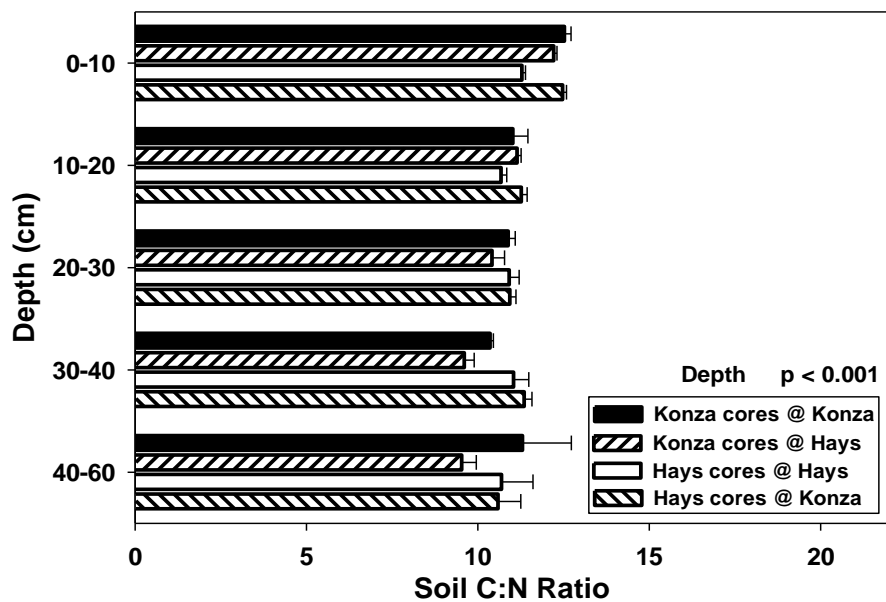
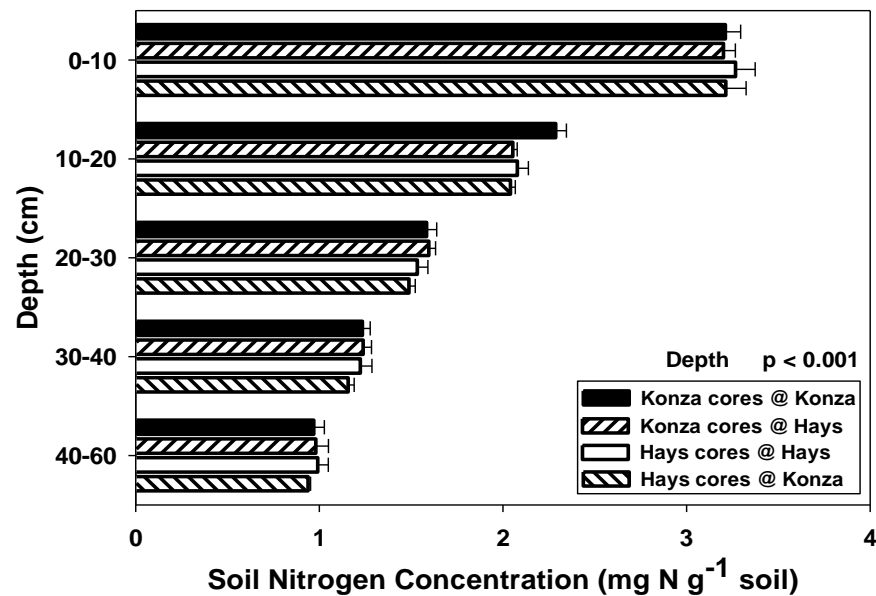
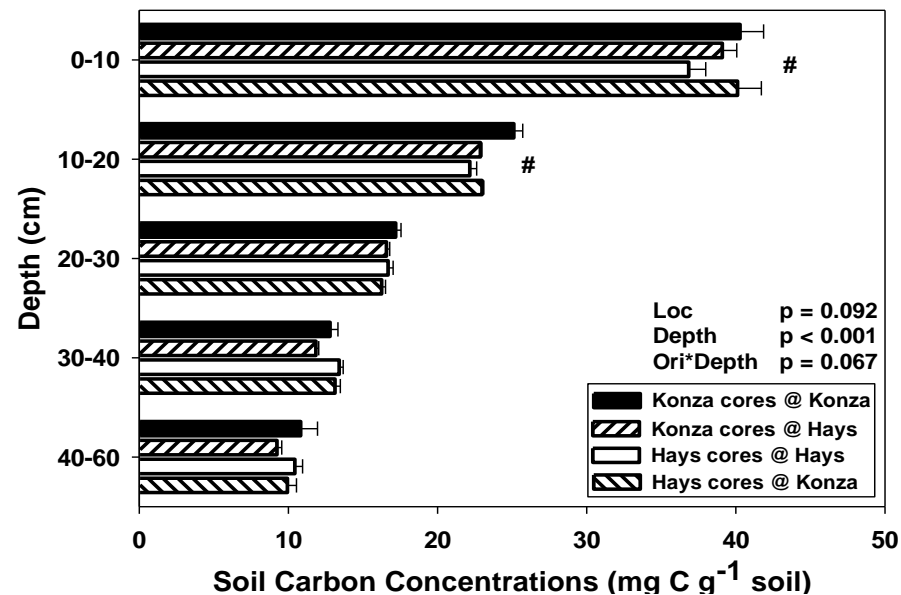


Figure 2.6 Total soil carbon concentration (top left), nitrogen concentration (top right), and C:N ratio (bottom left) from combinations of soil core origin and incubation location by depth. Error bars are ± 1 SE. A number symbol (#) indicates significant ($p < 0.05$) origin effects, at the specified depth.

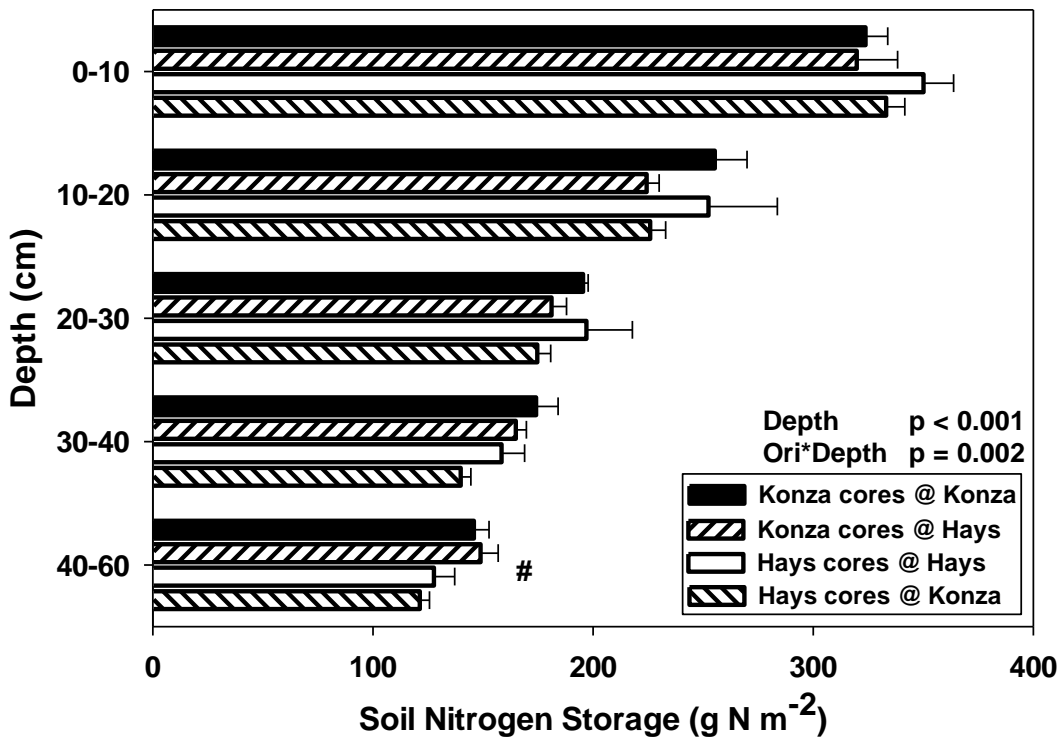
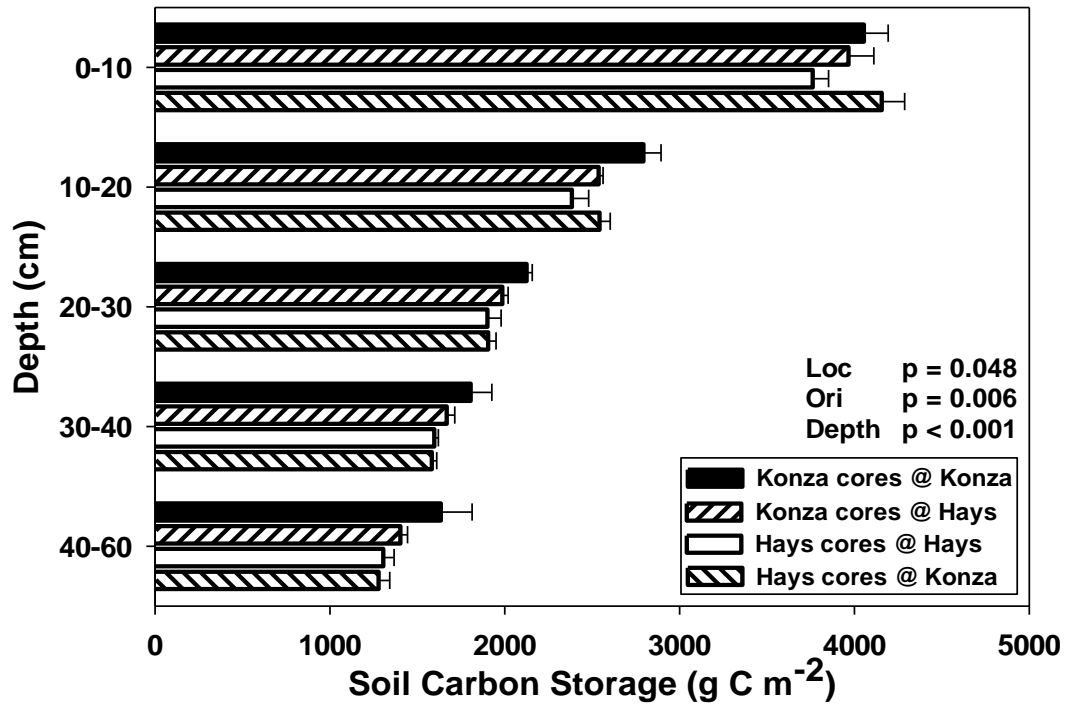


Figure 2.7 Total carbon storage (top) and nitrogen storage (bottom) from four combinations of soil core origin and incubation location by depth. Error bars are ± 1 SE. A number symbol (#) indicates significant ($p < 0.05$) origin effects, at the specified depth.

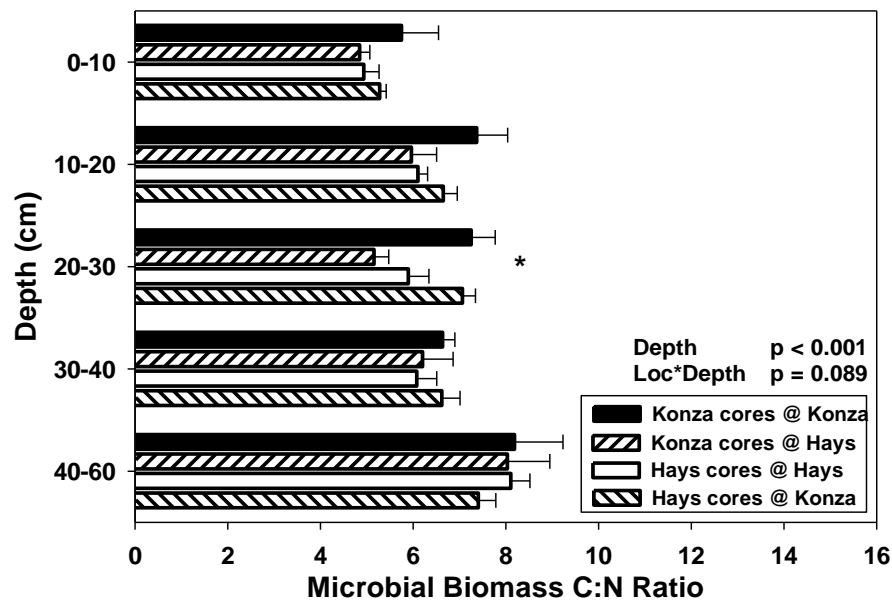
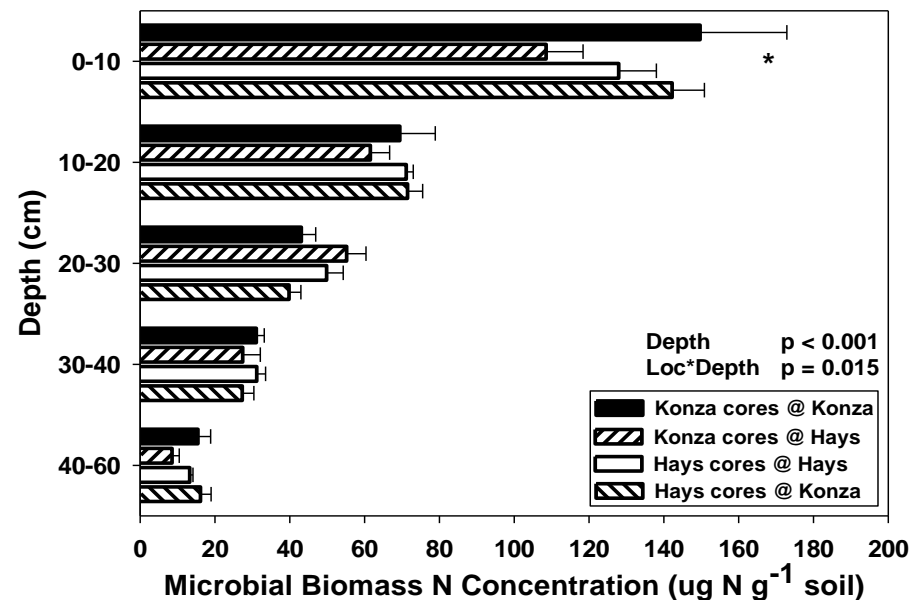
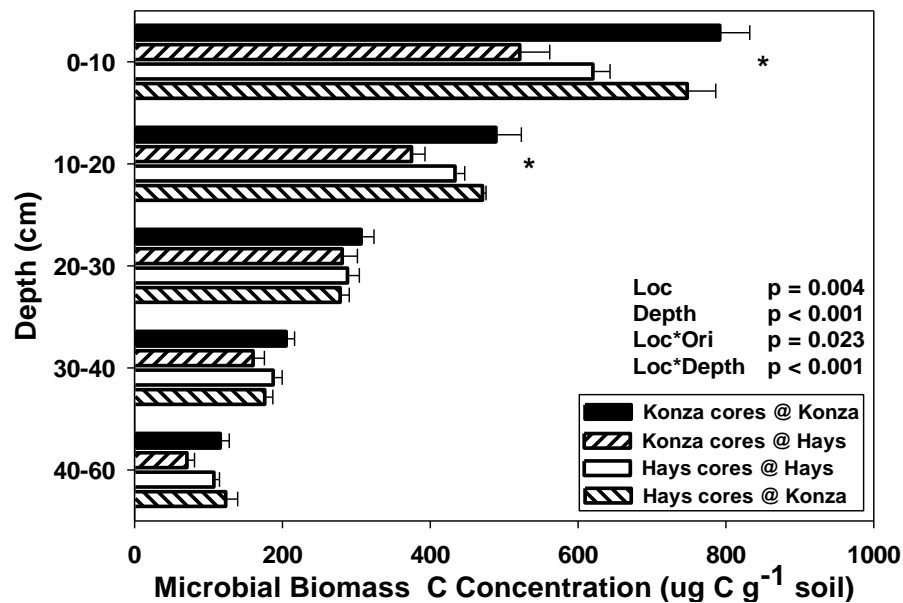


Figure 2.8 Total microbial biomass carbon concentration (top left), nitrogen concentration (top right), and C:N ratio (bottom left) from four combinations of soil core origin and incubation location by depth. Error bars are ± 1 SE. An asterisks (*) indicates significant ($p < 0.05$) location effects, at the specified depth.

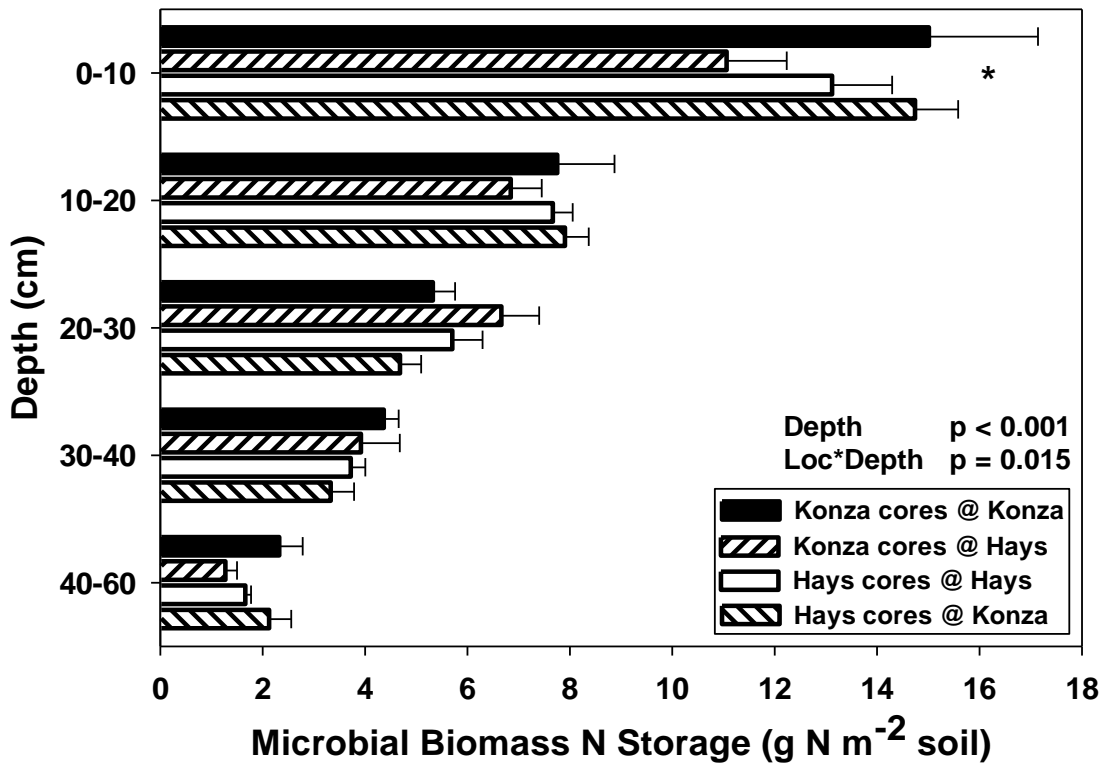
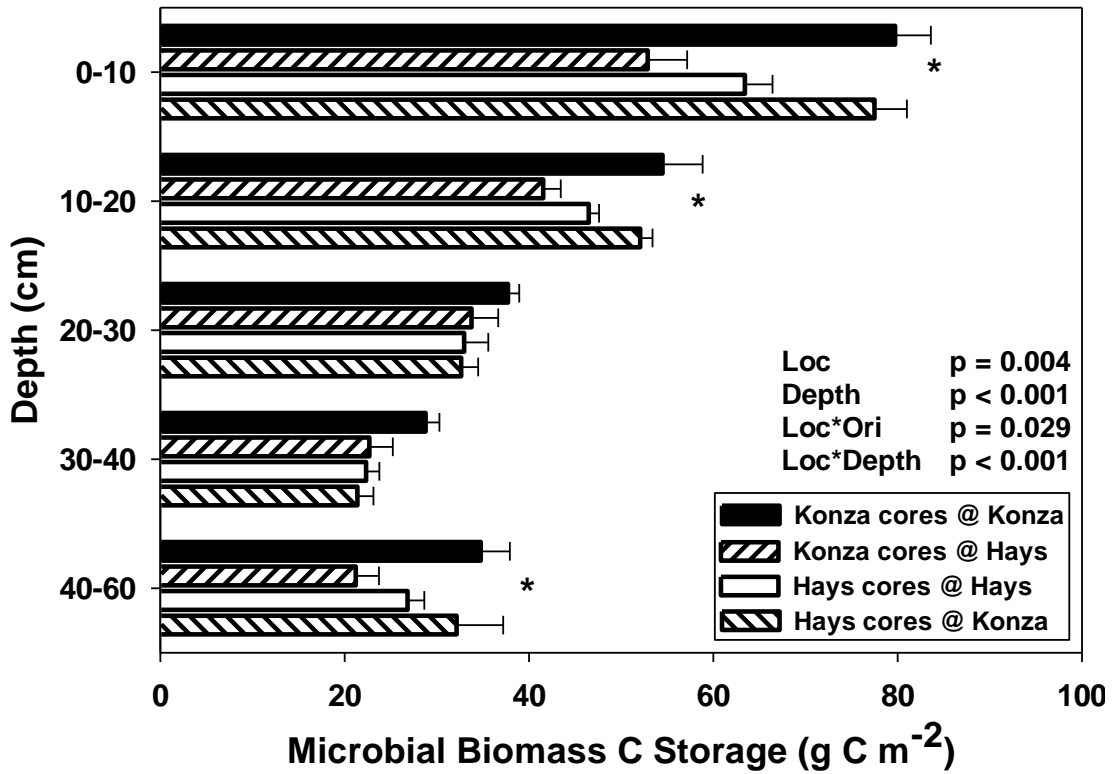


Figure 2.9 Average microbial biomass C (top) and N (bottom) storage from four combinations of soil core origin and incubation location by depth. Error bars are ± 1 SE. An asterisks (*) indicates significant ($p < 0.05$) location effects, at the specified depth.

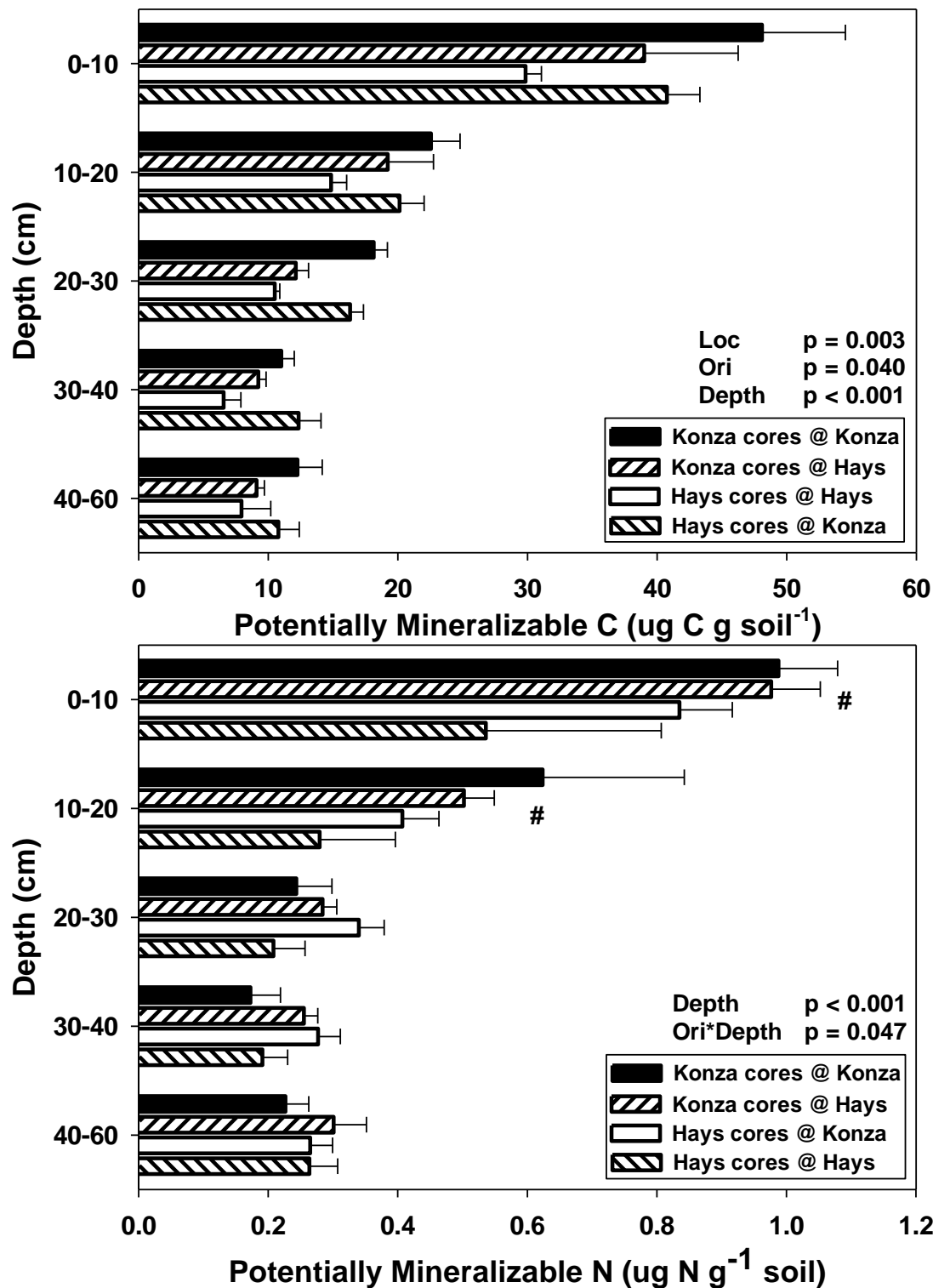


Figure 2.10 Average mineralizable C (top) and N (bottom) assessed from aerobic incubations from four combinations of soil core origin and incubation location by depth. Error bars are ± 1 SE. A number symbol (#) indicates significant ($p < 0.05$) origin effects, at the specified depth.

Chapter 3 - Soil Microarthropod and Nematodes Responses to Changes in Soil Water Availability in a Grassland System

ABSTRACT

Soil water availability is generally considered to be one of the most influential abiotic drivers of soil invertebrate communities, especially in water-limited systems such as grasslands. Global climate change predictions suggest that grasslands in the Great Plains region of North America will undergo changes in precipitation regimes, which will alter soil water availability. This study was designed to assess the impact of altered soil water availability on soil microarthropod and nematode composition and abundance. To quantify their responses, a reciprocal core transplant experiment was initiated in 1993 between a more mesic grassland site (Konza Prairie, mean annual precipitation = 850 mm) and a more arid grassland site (Hays, mean annual precipitation = 580 mm). In May 2009, large, intact plant-soil cores at each site were harvested (5 “native” and 5 “transplanted” cores at each site) and sectioned into five depth increments (0-10, 10-20, 20-30, 30-40, and 40-60 cm). Each core depth increment was subsampled for both microarthropods and nematodes. We assessed the influence of incubation location and soil origin on soil biota for both whole cores and individual depth increments. Microarthropods, primarily Acari, responded to changes in soil water availability, with greater densities under drier conditions, regardless of soil origin. Responses of the three main groups of microarthropods (prostigmatid, mesostigmatid, and oribatid mites) were not consistent. Prostigmatid mites were more abundant under drier conditions, while oribatid and mesostigmatid mites were more abundant under wetter conditions. Nematode densities were drastically affected by changes in soil water availability but only in cores originating from Konza. Herbivorous nematodes were the most abundant group, and analysis of the families Criconeematidae and

Telotylenchidae revealed greater densities in cores incubated at Konza relative to core incubated at Hays. The inconsistency in response to soil water availability among different soil fauna taxa suggests complex relationships between soil water availability and mesofaunal communities.

INTRODUCTION

Annual precipitation and water limitation are key environmental factors influencing grassland ecosystems (Sala et al. 1988; Burke et al. 1997; Zhou et al. 2009). In the Great Plains region of North America, soil water availability varies across a strong east-west precipitation gradient characteristic of the region (Weaver 1954; Risser et al. 1981). Studies along this, and other gradients, have linked water availability to primary productivity (Briggs and Knapp 1995; Knapp and Smith 2001), plant community composition (Albertson and Weaver 1944), nutrient cycling (McCulley et al. 2005), and decomposition rates (Epstein et al. 2002; Austin 2002). As a result, changes in precipitation will likely incur responses in ecological processes at a range of scales, from population dynamics to ecosystem processes. Recent global circulation models (GCMs) have indicated this region will undergo a variety of climatic shifts, including increases in mean annual temperature (Manabe and Wethererald 1975; Hansen et al. 2006; IPCC 2007) and potential changes in annual precipitation (Crane and Hewitson 1998; Easterling et al. 2000; Andrews and Forester 2010), with an overall reduction in soil water availability (Jackson et al. 2001). Climatic shifts have altered water availability in the past causing ecosystem-level responses (Weaver 1954; Weaver and Albertson 1944); however, the effects of unprecedented contemporary alterations in global climatic patterns are unknown.

While many global climate change experiments have examined various ecosystem and plant community responses, few have examined the responses of soil fauna. Grassland soil fauna are an important component soil food webs (Ingham et al. 1986), and soil food webs link aboveground and belowground systems and are responsible for a variety of ecosystem processes (Wardle 2002; Sackett et al. 2010), such as decomposition (Smith and Bradford 2003) and nutrient cycling (Ingham et al. 1986). Soil fauna have a wide range of feeding strategies, body

sizes, and movement capabilities (Lavelle 1997), which can directly or indirectly affect rates of many soil processes. Soil microorganisms are responsible for more than 90% of decomposition and nutrient cycling (Fitter 2005; Lavelle 2002), while larger soil fauna indirectly affect the rates of microbial decomposition and nutrient cycling by comminution (Seastedt 1984), selective grazing (Hanlon and Anderson 1980), fecal production, and survival within larger organisms. Soil fauna are sensitive to environmental conditions in the soil. While a few studies have focused on responses of grassland soil fauna to short-term changes in climate (O'Lear et al. 1999; Todd et al. 1999); no known study has assessed the longer-term impacts of an experimentally altered climate. As a result of changing climatic patterns it is likely that the abundance, distribution, and functioning of the soil fauna within grassland systems will be altered.

Microarthropods are a major component of soil fauna in grassland systems and can influence multiple aspects of soil structure and function. They are numerically abundant (Leetham and Milchunas 1985; O'lear and Blair 1999) and relatively ubiquitous within the soil, existing in air-filled pore spaces (Coleman et al. 2004). Microarthropods encompass a wide range of feeding behaviors (Moore et al. 1988; Ingham et al. 1989). Community composition, abundances, and biomass of microarthropods have been studied in many terrestrial ecosystems (Kinnear and Tongway 2004), as have the ecological effects of their activities. Studies have investigated interactions with other soil biota, primarily plant roots and microbial communities (Bardgett et al. 1993), and selective feeding on these organisms has been shown to cause changes in soil processes. Microarthropods have been shown to directly alter soil processes, including decomposition rates and nutrient cycling, through comminution, fecal production, and dissemination of propagules (Seastedt et al. 1984). As many soil properties and characteristics

are influenced to some extent by the activity of microarthropods, a basic understanding of their responses to altered precipitation patterns is important.

Nematodes, like microarthropods, have a wide range of feeding behaviors, and interact with other soil biota in multiple trophic pathways (Ransom 1998; De Ruiter et al. 2002). They influence ecosystem processes directly as herbivores, parasites, or both (Yeates et al. 1993; Todd 1996; Ingham and Detling 1990) and indirectly as consumers of parasitic or beneficial soil microbes (Hunt et al. 1987). Many studies on feeding behaviors have been conducted and are well-documented in agroecosystems (Freckman and Caswell 1985; Freckman and Ettema 1993; Yeates and Bongers 1999). As a result, it is clear they directly and indirectly alter various soil processes. As nematodes are abundant and reproduce quickly, studies have used their abundances and trophic structures as indicators of soil fertility (Yeates 2003; Shao 2008). Based on nematode functions within the soil, an understanding of their susceptibility to altered precipitation patterns is vital to accurately predict potential changes in grassland soils to altered precipitation patterns

The abundances and activities of microarthropods (Seastedt et al. 1984) and nematodes (Todd 1994) have been documented in grasslands; however few studies have focused on depth distribution within the soil (but see O'lear and Blair 1999; Todd et al. 1999) and no known studies have addressed the longer-term impacts of climate change. Since global climate change represents a permanent alteration to grassland soil systems, such studies are becoming increasingly important. The objective of this study was to assess long-term responses of microarthropod and nematode communities to alternate climate conditions. Using a simple reciprocal core transplant to simulate increased and decreased annual precipitation and associated changes in soil water availability, we were able to assess the potential impacts of

climate change on grassland soil fauna. This experiment was focused specifically on microarthropod and nematode community responses, including abundance, trophic structure, and vertical depth distribution.

METHODS

Description of Study Sites

This study was a part of a larger experiment funded by the Department of Energy/National Institute for Global Environmental Change (DOE/NIGEC) to investigate how vegetation, soil organisms, and soil processes of grassland systems respond to altered soil moisture regimes. This reciprocal transplant study was conducted between Konza Prairie Biological Station (Konza) and Kansas State University Agricultural Center at Hays (Hays). These research sites are located across a strong east-west precipitation gradient in the Great Plains region of North America. Konza, a representative mesic grassland site, is a 3,487 ha area of native tallgrass prairie in northeastern Kansas (39°05'N and 96°35'W), located approximately 13 km south of Manhattan, KS. Hays, a representative semi-arid grassland site, is located at an agriculture station 240 km west of Konza Prairie. The dominant vegetation of Konza consisted primarily of *Andropogon gerardii* (big bluestem), *Sorghastrum nutans* (Indian grass), *Panicum virgatum* (switchgrass), and *A. scoparius* (little bluestem), which is typical for a mesic tallgrass system. Dominant vegetation at Hays included *Bouteloua curtipendula* (side-oats gramma), *Bouteloua gracillis* (blue gramma), *Buchloe dactyloides* (buffalo grass), and *Agropyron smithii* (western wheat grass); however, *A. gerardii* and *P. virgatum* were well represented at the specific site chosen for this study.

The long-term mean annual precipitation at Konza is 850 mm and at Hays is 580 mm (approximately 30% less). Air and soil temperatures are similar at both locations. Reciprocal

transplants of intact plant-soil cores between two sites in close geography proximity with altered amounts of precipitation allowed us to address the effects of altered soil water availability on soil microarthropod and nematode abundances and their vertical distributions within the soil. Although differences in fire management occurred during the 16-year study period, with the Konza site being burned annually and the Hays site being burned sporadically (1993, 1994, 1995, 2000, 2003, and 2007), both sites were ungrazed and there were no other differences in management. The Konza site was on a deep, nearly level (0–1% slope) Reading silt loam formed from alluvial sediments. Reading soils are fine, mixed mesic Typic Argiustolls with a silt loam A horizon (approximately 28 cm deep) overlaying light to heavy silty clay loam B1 and B2t horizons. The Hays site was located on a deep, nearly level (0–1% slope) Harney silt loam formed in calcareous, medium textured loess. The A₁ and A₃ horizons were silt loams and light silty clay loams, respectively, overlaying light to heavy silty clay loam B horizons. Therefore, soils are texturally similar in the top 30 cm; however, below 30cm, notable increases in clay content were observed in Konza soils that were not present in Hays soils.

Experimental Design

The reciprocal transplant experiment was initiated in 1993. Seventy large (25 cm diameter × 70 cm depth) intact plant-soil cores, encased in open-ended polyvinylchloride cylinders (PVC) were extracted from both the more mesic Konza site and the more arid Hays grassland site, using hydraulic coring equipment (Swallow et al. 1987). As stated previously, cores were extracted from both sites in an area dominated by *A. gerardii* to reduce variability due to plant community differences between locations. Half of the extracted plant-soil cores were placed into their original holes, while the remaining cores were transplanted to the alternate site. This resulted in 70 plant-soil cores at each site (35 “transplanted” and 35 “native”). In 1994-

1996, a subset of cores was destructively sampled twice per year to assess short-term effects of transplantation (O'lear and Blair 1999; Todd et al. 1999). An additional subset of soil cores remained incubating at each site to assess the longer-term effects of the transplantation, which is the focus of this study. These long-term plant-soil cores were harvested in May of 2009 and sectioned into 0-10, 10-20, 20-30, 30-40, and 40-60 cm depth increments. Along with various physical/chemical responses (Chapter 2, this thesis), these cores were used to assess the potential impacts of altered soil water availability on microarthropod and nematode abundances, community composition, and vertical distribution.

Microarthropod Extraction

To assess impacts of soil water availability on microarthropod abundances, community composition, and vertical distribution, 5-cm diameter × 5-cm deep soil cores were extracted from the upper surface of each depth increment. Microarthropods were extracted from each core over a 1-week period using modified Tullgren type, high-gradient extractors (Crossley and Blair 1991). The organisms recovered were stored in glass vials containing 90% ethanol until identification. Microarthropods were identified to taxonomic order in general, and to suborder for Acari. These broad identification categories were used to assess abundances, community composition, and vertical distribution of soil microarthropods. Since subsamples of microarthropods were extracted from the upper 5-cm only of each depth increment, an averaging method was used to estimate microarthropod abundances in the lower portions of each increment and in whole soil cores. To estimate microarthropod abundances at 5-10, 15-20, 25-30, and 35-40 cm, averages from subsamples above and below each increment were used to interpolate abundances in the intervening depths, and these values were added to extracted subsamples to estimate entire plant-soil core (0-45 cm) microarthropod abundance.

Nematode Extraction

To assess impacts of soil water availability on nematode abundances, community composition, and vertical distribution, nematodes were extracted from field-moist (~100 g dry weight equivalent), mixed soil subsamples using a standard centrifugal flotation technique (Jenkins 1964). Nematodes were identified to family level and assigned to feeding guilds based on Yeates et al. (1993). A complete list of the dominant nematode taxa of the Konza Prairie Biological Station and their trophic groupings can be found in Ransom et al. (1998).

Statistical Analysis

Analysis of variance (ANOVA) was performed using SAS PROC MIXED (SAS Institute) to assess differences in microarthropod and nematode densities among treatments (soil origin and soil incubation location). To determine the effect of transplantation on whole core dynamics of microarthropods (0-45 cm) and nematodes (0-60), a 2-way ANOVA was used with soil origin and incubation location as independent variables. A 3-way ANOVA was performed using soil origin, incubation location, and depth as independent variables to identify at which depths significance occurred. The SAS SLICE featured was used to determine at which depth treatment the main effects of location and origin were observed. In the case of a 3-way interaction, pair-wise comparisons were used to compare all treatments separately. A logarithmic transformation ($x+1$) was used to normalize density data prior to statistical analyses (Berthet and Gerard 1965). Results were considered statistically significant at $p < 0.05$, unless otherwise specified. Data are reported as treatment means \pm one SE.

RESULTS

Precipitation

During the course of this study (1993-2009), mean annual precipitation at both locations varied greatly (Figure 3.1). Mean annual precipitation at Konza ranged from 627 mm to 1228, while precipitation at Hays ranged from 412 mm to 965. Overall, annual precipitation at Konza was significantly ($p = 0.012$) greater than at Hays. The average difference between locations on a yearly basis was ~37%, which was greater than the long-term average. Although higher than average, precipitation at Konza was not consistently greater than Hays. Many years, including 1993, 2000, 2001, 2003, and 2007, had less than the long-term average difference in precipitation between sites, and in some years (1995 and 1996), Hays received greater annual rainfall than Konza.

Microarthropods

Estimates of total microarthropod densities to a depth of 45 cm ranged from 173,060 to 418,144 individuals per m². Analysis of the effects of location (where the cores were incubated during the experiment) and origin (where the soil cores originated) on total microarthropod densities indicated a significant ($p \leq 0.05$) location effect but no effects of origin and no location \times origin interaction (Figure 3.2). Greater densities were recovered from cores incubated at the more arid Hays site relative to the more mesic Konza site, regardless of soil origin. The lack of an interaction indicated that both Konza and Hays cores responded to location similarly, with both Konza and Hays cores having lower densities at the wetter site, and higher densities at the drier site.

A more detailed analysis of microarthropod densities utilizing depth as an additional factor was performed to examine the effects of depth on recovered microarthropod abundances

and possible interactive effects of depth with location and origin. Analysis of microarthropod densities revealed significant effects of location, depth, and a three-way interaction among all three factors, with marginal ($0.5 < p \leq 0.1$) effects of origin and an origin \times depth interaction. Microarthropod densities were greater in soils incubated at the more arid Hays location at the 10-15 cm, 20-25 cm, and 40-45 cm depths. The three-way interaction revealed differences in magnitude of response at each soil depth. At depth 30-35 cm, transplanting Konza cores to the drier Hays site significantly increased microarthropod densities, while there was no significant effect of transplanting Hays cores to Konza. At 40-45 cm, Hays cores were more responsive and there was a significant decrease when Hays cores were transplanted to Konza (Figure 3.3).

A majority of the microarthropods recovered were members of the Order Acari (mites). Soil mites comprised 78%-93% of total microarthropod densities across depth increments. Since soil mites represented such a large majority of microarthropods, analysis of total Acari responses were similar to those of total microarthropods (Figure 3.4). The most abundant Acari suborders (Prostigmata, Oribatida, and Mesostigmata) were all responsive to location, origin, and depth effects. Prostigmatid mites were affected by location, origin, depth, and a two-way origin \times depth interaction. Greater prostigmatid densities were found in cores incubated at Hays relative to Konza, with similar responses to location regardless of core origin. The significant origin \times depth interaction showed Hay soils supported greater densities of prostigmatid mites at 0-5 and 30-35 cm depths relative to Konza cores. Oribatid and mesostigmatid mite densities were affected by location, with greater densities found in cores incubated at Konza (Figure 3.5). While both oribatid and mesostigmatid mite densities were higher at Konza, differences in responses occurred with depth. Oribatid mites had higher densities at 40-45 cm in cores

incubated at Konza relative to Hays, while mesostigmatid mites were significantly higher at both 30-35 and 40-45 cm depths in cores incubated at Konza (Figure 3.5).

Nematodes

Estimates of total nematode densities to a depth of 60 cm ranged from 401,429 to 4,526,742 individuals per m². Analysis of location and origin effects indicated total nematode densities were influenced by location, origin, and their interaction (Figure 3.6). The significance of the location \times origin interaction term revealed that cores originating from Konza were more responsive to transplantation than were soils originating from Hays. The transplantation of Konza cores to Hays resulted in a 70% decrease in total nematode densities, while cores originating from Hays were statistically similar regardless of incubation location.

Further analysis of nematode densities was conducted as a function of location, origin, and depth to reveal interactions among depth with the other factors. Results of this analysis showed that origin, depth, and an origin \times depth interaction were the significant factors influencing total nematode densities. Origin effects were the most significant factor in determining nematode densities, with greater densities recovered from Hays soil cores. This trend was driven by the interactive effect of origin \times depth, with origin having a significant effect at 30-40 and 40-60 cm depth increments (Figure 3.7). At the lower depths, Konza soils displayed a drastic decrease in nematode abundance, while abundances in Hays soils were more consistent across depths. This trend appeared to be explained by the large textural differences between Konza soils and Hays soils at lower soil depths. Konza soils had a marked increase in clay content below \sim 30 cm that was not observed in Hays soils. A three-way ANOVA was performed on nematode data excluding the 30-40 and 40-60 cm depths to remove the effect of these lower depths (with higher clay content in Konza cores) on nematode densities (Figure 3.7).

With these depths removed, there was no significant effect of origin nor an origin \times depth interaction. Therefore, differences in nematode densities based on origin were the result of the lower depths analyzed.

To better understand nematode responses to the treatments, analyses were performed on specific functional groups. Herbivorous nematode densities were the only taxa responsive to treatments in whole core analysis, and were affected by origin and a location \times origin interaction. Effects of location were only apparent in soils originating from Konza, where transplantation of Konza soils to Hays resulted in a 76% decrease (76%) in herbivore densities. Herbivore, fungivore, and microbivore nematodes all exhibited three-way interactions ($p < 0.1$) among incubation location, soil origin, and soil depth, with differences being variable and dependent on taxa. Herbivorous nematode densities at lower soil depths (30-40 and 40-60 cm) were more responsive in Konza cores, Konza cores transplanted to Hays experiencing significant decreases in densities, while herbivorous nematodes densities in Hays cores did not change significantly when transplanted to Konza (Figure 3.8). Fungivorous nematodes showed similar dynamics, with transplantation of Konza cores to Hays significantly decreasing densities at 40-60 cm. In contrast, three-way interactions of bacterivorous nematodes were not restricted solely to the lower soil depths, with interactions occurring at 10-20, 20-30, and 40-60 cm depths, with soil cores originating from Konza being more responsive to transplantation at 10-20 and 20-30 cm depths and soil cores originating from Hays being more responsive to transplantation at 40-60 cm depths (Figure 3.8).

The herbivorous taxa were the most abundant and arguably the most responsive to the effects of transplantation. We identified two families (out of nine) that responded to transplantation. Analysis of location and origin effects on total core (0-60 cm) abundances of the

two families yielded only origin as a significant factor influencing densities; however, analysis by depth revealed significant location \times depth, and location \times origin \times depth interactions. Nematodes in the family Telotylenchidae were significantly altered by transplantation at 0-10 cm and 40-60 cm. Transplanting Hays cores to Konza resulted in significantly ($p = 0.006$) increased densities at 0-10 cm, while significant ($p = 0.098$) decreases occurred at 40-60 cm. Nematodes in the family Criconematidae had greatest densities in soils incubating at Konza relative to Hays, regardless of soil origin, and the differentiation was driven by densities in the 20-30 cm depth increment ($p = 0.003$).

DISCUSSION

Climate change represents a chronic, not transient, alteration in global hydrologic cycles requiring long-term studies to assess possible impacts. The longevity of this experiment allowed for comparisons to be made concerning the potential effects of global climate change on soil microarthropod and nematode abundances and composition. There is increasing evidence that climate changes can affect soil mesofauna and the functions they provide (Hagvar and Klanderud 2009; Lindroth 2010;). Our results indicate that changes in long-term mean annual precipitation amounts and associated soil water availability, a potential consequence of climate change, can alter the abundance and community dynamics of soil microarthropods and nematodes. Results from our experiment indicate that microarthropods and nematodes are responsive to experimentally altered soil water content to varying degrees among the different subgroups studied.

We found soil microarthropods to be responsive to changes in mean annual precipitation; however the direction of this response was unexpected. Transplanting soil cores originating from Hays to the more mesic Konza site significantly decreased microarthropod densities, while

the transplantation of Konza soils to the drier conditions at Hays led to a significant increase in densities. We anticipated greater abundances of microarthropods would be found at the more mesic Konza site, due to the increased availability of food sources (i.e., plant residues, microbial biomass) (Yeates et al. 1993; Vreeken-Buijs et al. 1998). Studies in other ecosystems have reported that greater soil water availability typically results in greater microarthropod abundance (Lindberg et al. 2002; Taylor et al. 2004). In contrast, O'lear and Blair (1999) found that in a tallgrass prairie the abundance of Acari decreased due to irrigation. The negative response to higher soil water content could be a function of many underlying factors, including competition with other organisms, survival ability, and reproductive rates; however, these mechanisms were not assessed in the present study.

The trends in microarthropod densities were primarily driven by the soil mite fauna, which constituted between 78% and 93% of the extracted microarthropods densities. Several grassland studies have observed similar percentages of soil mite fauna in total microarthropod densities (O'Lear and Blair 1999; Osler et al. 2008). The response of soil mite fauna to precipitation was the primary driver of the total microarthropod response, with greater abundances occurring at the more arid Hays site. Although the abundances of total mites was greater at the more arid grassland site, the response was not consistent among the three most abundant soil mite suborders. Prostigmatid mites were consistently the most abundant of extracted soil mites, constituting 61-81% of the total soil mites, a percentage consistent with other grassland studies (Leetham et al. 1981; Leetham and Milchunsa 1985). Prostigmatid mites showed an overall preference for the drier environment at Hays relative to Konza, regardless of soil origin. Leetham and Michunas (1985) found that in prairie soils, two peaks in mites densities occurred through the soil profile, associated with root biomass and stability of soil

water deeper within the soil. This separation could involve migrations within the soil profile (Whitford et al. 1981), where frequent water cycles experienced in the surface soils may force mites to assemble deeper within the soil profile. Kethley (1990) suggested that some phytophagous and mycophagous prostigmatid mites, having short life cycles, may be able quickly respond to wet periods allowing for feeding on root and fungal.

Both oribatid and mesostigmatid mites were found to be significantly greater at the more mesic site relative to the more arid site, regardless of soil origin. This was a trend we assumed would be indicative of total Acari populations. This is consistent with studies in temperate forest ecosystems, showing that oribatids are very sensitive to climatic alterations (i.e., drier, warmer conditions) associated with forest canopy removal (Seastedt and Crossley 1981; Blair and Crossley 1988). Studies have indicated that oribatid mites are generally the most abundant of the soil mite fauna in more mesic habitats (Wood 1966; Coleman et al. 2004). In grasslands, there is a strong possibility that increased plant residues within more mesic grassland sites may contribute to higher oribatid populations. Mesostigmatid mites are primarily predaceous; therefore, we suggest their reaction to soil moisture content is a function of increased prey densities in the presence of increased plant biomass and soil organic matter. Also, evidence exists suggesting that mesostigmatid mites, particularly the Gamasina, show little microhabitat preferences (Coja and Bruckner 2003). The differences in the response to experimental treatments suggest complex interactions between soil water content and other factors, which was beyond the scope of this experiment.

Studies on total microarthropod assemblages typically focus on the surface soil layers (0-20 cm). Results from our experiment indicate that while a majority of microarthropod densities do reside in upper soil layers (0-20 cm), a large quantity of microarthropods occurred at greater

depths. I found that roughly 75% of the microarthropods in our study were located in the 10-15 cm and 20-25 cm soil depths. Very few studies have investigated the vertical depth distribution of microarthropods in grassland soils. O'Lear and Blair (1999) found a statistical majority of microarthropods located at depths of 20-25 cm. Some studies have even suggested that mites with smaller bodies are able to move throughout the soil profile better than those with larger bodies (Holt 1981). In addition, Whitford et al. (1981) found that soil mite fauna have diurnal migrations throughout the soil column. Therefore, the vertical distribution of soil mites with our experiment indicates that soil microarthropod assemblages are potentially a function of both biotic and abiotic factors, and that greater sampling of soils at lower depths may provide valuable information on microarthropod densities in grassland soil systems.

Our results on nematode densities indicate that total nematode densities are positively related to mean annual precipitation; however, these trends occurred only in cores originating from Konza. The transplantation of Konza cores to Hays significantly decreased nematode densities by 70%, while only small, insignificant increases were observed in transplanted Hays cores. We anticipated greater abundances of nematodes would be found at the more mesic Konza site, but were surprised in the lack of response in nematodes from Hays. There is conflicting literature concerning the effect of soil moisture on the density of nematodes, with results ranging from increases (Steinberger and Sarig 1993; Todd et al. 1999), to no response (Papatheodorou et al. 2004), to decreases (Bonkonyi et al. 2007) to increasing soil moisture levels. These differences in observations may be due to differences in habitat preference by members in the same functional groups. Sohlenius (1985) demonstrated that there are different optimum soil moisture values for different taxa in the same functional groups. This, therefore,

allows mixed nematode communities to maintain high densities over a wide range of environments.

The herbivorous taxa were the most abundant and arguably the most responsive to transplantation. Transplanting cores originating from Konza to Hays resulted in a 66% decrease in plant-feeding nematodes. The magnitude of this response was unexpected. Many studies have been conducted across various ecosystems and have shown different responses in plant-feeding nematodes and soil water availability (Smolik and Dodd 1983; Bakonyi et al 2000). Grasslands, in particular support large, herbivore-dominated nematode populations in the soil, and herbivorous nematodes are major controllers of plant production in these ecosystems (Smolik 1974; Lauenroth and Milchunas 1991). Therefore, the presence of plant-feeding nematodes could be a function of either direct or indirect effects of greater precipitation. In our study, we found two families of nematodes were the most responsive to transplantation. The largest response to altered precipitation patterns was found within the nematode Family Criconematididae, where we recorded significant reductions in nematodes when transplanting Konza cores to Hays ($p = 0.0249$). Criconematid nematodes have been found in a variety of ecosystems (Peneva et al. 2000; Liscova et al. 2004; Todd et al. 2006) and have been reported to feed upon multiple plant species. Nematodes in the family Telotylenchidae were also responsive to transplantation. In this case, Telotylenchidae were only responsive in cores originating at Konza. The greatest response was observed in the upper soil layers, and was likely due to reduced root biomass in Konza cores transplanted to Hays (See Chapter 2 of this thesis). Therefore, in the present study, we found responses of plant-feeding nematodes were positively correlated with increase precipitation.

The remaining trophic groups were less abundant and exhibited very few significant responses to changes in soil moisture. Fungivore and microbivore densities have shown inconsistencies with respect to increased soil water availability, ranging from negative (Solenius 1985), to positive (Ekschmitt and Griffiths 1998) responses. In our study, we found fungivorous nematodes were not responsive to the effects of location, suggesting that mean annual precipitation has little influence on their abundance in grassland systems. Bacterial-feeding nematodes showed few responses to transplantation, as well. Studies have indicated that greater densities of bacterial-feeding nematodes typically are higher in areas with greater soil water availability due to increased microbial biomass and microbial N (Todd 2006). In the present study, we found bacterivorous nematodes did respond to changes in precipitation regime; however, these responses were greatest in Konza soils at 10-20 and 20-30 cm. Solenus (1985) found a positive correlation between soil water availability and bacterivorous nematodes. This contrasts with Gomez et al. (2003) findings that increased soil water availability in agricultural grasslands hindered bacterivorous nematode densities, noting some of this nematode community responded differently.

The vertical distribution of nematodes at Konza and Hays were similar to those reported for tallgrass and mixed-grass prairies, with most nematodes being concentrated in the upper 20 cm of the soil profile (Risser et al. 1981; Smolik and Lewis 1982). The exception was the herbivorous taxa which appeared to have a large population deeper within the soil in cores originating from Hays. Also, it is important that a majority of the significant interactions and main effects occurred at depths below 30 cm. This emphasizes the importance of sampling lower soil depths.

CONCLUSION

This study provided new information of the potential effects of climate change and altered precipitation on soil microarthropod and nematode densities and community structure. We found that climate change had a large effect on microarthropod densities at 10-20, 20-30, and 30-40 cm depths. At these depths, microarthropod densities were significantly greater at Hays relative to Konza. Soil mites (Acari) accounted for a majority of the total microarthropod densities, and largely drove the responses to transplantation of soil cores. However, different suborders of mites varied in their responses. Greater densities of prostigmatid mites were found at Hays, while oribatid and mesostigmatid mite densities were greater at Konza. Soil nematodes showed no consistent response to altered climates; however, Konza soil cores transplanted to Hays did experience drastic reductions in soil nematode densities. Furthermore, nematodes were the most responsive to soil core origin, where high clay content in Konza soils hindered nematode densities. Nematode trophic groups did not exhibit consistent responses, but nematodes in the Families Telotylenchidae and Criconematidae did appear to sustain higher densities at Konza. Therefore, changes in soil water availability, a consequence of climate change, will alter belowground soil invertebrate communities, distributions, and densities.

BIBLIOGRAPHY

- Albertson FW, Weaver JE (1944) Nature and degree of recovery of grassland from the great drought of 1933 to 1940. *Ecological Monographs*, **14**, 393-479.
- Andrews T, Forster PM (2010) The transient response of global-mean precipitation to increasing carbon dioxide levels. *Environmental Research Letters*, **5**, 205-212.
- Austin, AT (2002) Differential effects of precipitation on production and decomposition along a rainfall gradient in Hawaii. *Ecology*, **83**, 328-338.
- Bardgett RD, Hobbs PJ, and Frostegae AE (1996) Changes in fungal:bacterial biomass ratios following reductions in the intensity of management on an upland grassland. *Biology and Fertility of Soils*, **22**, 261-264.
- Berthet P, Gerard G (1965) A statistical study of micro-distribution of Oribatei (Acari). Part 1. The distribution pattern. *Oikos*, **16**, 214-227.
- Blair JM, Crossley DA Jr (1988) Litter decomposition, nutrient dynamics and litter microarthropods in a southern Appalachian hardwood forest eight years following clearcutting. *Journal of Applied Ecology*, **25**, 683-698
- Briggs JM, Knapp AK (1995) Interannual variability in primary production in tallgrass prairie – climate, soil – moisture, topographic position, and fire as determinants of aboveground biomass. *American Journal of Botany*, **82**, 1024-1030.
- Burke IC, Lauenroth WK, Parton WJ (1997) Regional and temporal variation in net primary production and nitrogen mineralization in grasslands. *Ecology*, **78**, 1330-1340.
- Coja T, Bruckner A (2003) Soil microhabitat diversity of a temperate Norway spruce (*Picea abies*) forest does not influence the community composition of gamasid mites (Gamasida, Acari). *European Journal of Soil Biology*, **39**, 79–84.
- Coleman DC, Crossley DA, Hendrix PF (2004) *Fundamentals of Soil Ecology*. Elsevier Academic Press, Burlington, MA.
- Crane RG, Hewitson BC (1998) Doubled CO₂ precipitation changes for the Susquehanna Basin: down-scaling from the genesis general circulation model. *International Journal of Climatology*, **18**, 65-76.
- Crossley DA Jr, Blair JM (1991) A high efficiency, 'low technology' Tullgren-type extractor for soil microarthropods. *Agriculture, Ecosystems and Environment*, **34**, 182-187.

- De Ruiter PC, Griffiths B, Moore JC (2002) Biodiversity and stability in soil ecosystems: patterns, processes and the effects of disturbance in Loreau M, Naeem S, Inchausti P (Eds) *Biodiversity and Ecosystem Functioning – Synthesis and Perspectives*. Oxford University Press, Oxford, UK.
- Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO (2000) Climate extremes: Observations, modeling, and impacts. *Science*, **289**, 2068-2074.
- Ekschmitt K, Griffiths BS (1998) Soil biodiversity and its implications for ecosystem functioning in a heterogeneous and variable environment. *Applied Soil Ecology*, **10**, 201-215.
- Epstein HE, Burke IC, Lauenroth WK (2002) Regional patterns of decomposition and primary production rates in the US Great Plains. *Ecology*, **83**, 320-327.
- Fitter, AH (2005) Darkness visible: reflections on underground ecology. *Journal of Ecology*, **93**, 231-243.
- Freckman DW, Caswell EP (1985) The ecology of nematodes in agroecosystems. *Annual Review of Phytopathology*, **23**, 275-296.
- Freckman DW, Ettema CH (1993) Assessing nematode communities in agroecosystems of varying human intervention. *Agriculture, Ecosystems, and Environment*, **45**, 239-261.
- Hågvar S, Klanderud K (2009) Effect of simulated environmental change on alpine soil arthropods. *Global Change Biology*, **15**, 2972-2980.
- Hanlon A, Anderson JM (1980) The influence of microarthropod feeding activities on microflora in decomposing oak leaver. *Soil Biology and Biochemistry*, **12**, 255-261.
- Hansen J, Sato M, Ruedy R, Lo K, Lea DW, Medina-Elizade M (2006) Global temperature change. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 14288-14293.
- Holt, JA (1981). The vertical distribution of cryptostigmatic mites, soil organic matter and macroporosity in three North Queensland Rainforest Soils. *Pedobiologia*, **22**, 202-209.
- Hunt HW, Coleman DC, Ingham ER, Elliott ET, Moore JC, Rose SL, Reid CPP, and Morley CR (1987) The detrital foodweb in a shortgrass prairie. *Biology and Fertility of Soils*, **3**, 57-68.

- Ingham ER, Trofymow JA, Ames RN, Hunt HW, Morely CR, Moore JC, Coleman DC (1986) Trophic interactions and nitrogen cycling in a semi-arid grassland soil: I. Seasonal dynamics of the natural populations, their interactions and effects on nitrogen cycling. *Journal of Applied Ecology*, **23**, 597-614.
- Ingham ER, Trofymow JA, Ames RN, Hunt HW, Morely CR, Moore JC, Coleman DC, (1986). Trophic interactions and nitrogen cycling in a semi-arid grassland soil: II. System responses to removal of different groups of soil microbes or fauna. *Journal of Applied Ecology*, **23**, 5-630.
- Ingham ER, Coleman DC, Moore JC (1989) An analysis of foodweb structure and function in a shortgrass prairie, a mountain meadow, and a lodgepole pine forest. *Biology and Fertility of Soils*, **8**, 29–37.
- Ingham, RE and Detling JK (1990) Effects of root-feeding nematodes on aboveground net primary production in a North American grassland. *Plant and Soil*, **121**, 279-281.
- Intergovernmental Panel on Climate Change (IPCC) (2007a), Summary for policymakers, in *Climate Change 2007: The Scientific Basis. Contribution of the Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press, New York.
- Jackson RB, Carpenter SR, Dahm CN, McKnight DM, Naiman RJ, Postel SL, Running SW (2001) Water in a changing world. *Ecological Applications*, **11**, 1027-1045.
- Jenkins WR (1964) A rapid centrifugal-flotation technique for separating nematodes from soil. *Plant Disease Reporter*, **48**, 692.
- Kethley J (1990) Acarina: Prostigmata (Actinedida) in Dindal W (Eds) *Soil Biology Guide*. Wiley & Sons, New York, USA.
- Kinnear, A, Tongway D (2004) Grazing impacts on soil mites of semi-arid chenopod shrublands in Western Australia. *Journal of Arid Environments*, **56**, 63-82.
- Knapp AK, Smith MD (2001) Variation among biomes in temporal dynamics of aboveground primary production. *Science*, **291**, 481-484.
- Lauenroth WK, Milchunas DG, (1991) Short-grass steppe in Coupan RT (Ed.) *Ecosystems of the World 8A. Natural Grasslands*.
- Lavelle, P (1997) Faunal activities and soil processes: adaptive strategies that determine ecosystem function. *Advances in Ecological Research*, **27**, 93-132.

- Lavelle P (2002) Functional domains in soils. *Ecological Research*, **17**, 441-450.
- Leatham JW, Milchunas DG (1985) The composition and distribution of soil microarthropods in the shortgrass steppe in relation to soil water, root biomass, and grazing by cattle. *Pedobiologia*, **28**, 311-325.
- Lindberg N, Bengtsson JB, Persson T (2002) Effects of experimental irrigation and drought on the composition and diversity of soil fauna in a coniferous stand. *Journal of Applied Ecology*, **39**, 924-936.
- Lindroth RL (2010) Impacts of elevated atmospheric CO₂ and O₃ on forests: phytochemistry, trophic interactions, and ecosystem dynamics. *Journal of Chemical Ecology*, **36**, 2-21.
- Liskova M, Vovlas N, Sasanelli N (2004) Criconematidae (Nematoda) in the Slovak Republic. *Helminthologia*, **41**, 161-170.
- Manabe S, Wetherald RT (1975) Effects of doubling CO₂ concentrations on climate of a general circulation model. *Journal of the Atmospheric Sciences*, **32**, 3-15.
- McCulley RL, Burke IC, Nelson JA, Lauenroth WK, Knapp AK, Kelly EF (2005) Regional patterns in carbon cycling across the Great Plains of North America. *Ecosystems*, **8**, 106-121.
- Moore JC, Walter DE, Hunt HW (1988) Arthropod regulation of micro- and mesobiota in below-ground detrital food webs. *Annual Review of Entomology*, **33**, 419-439.
- O'Lear HA, Blair JM (1999) Responses of soil microarthropods to changes in soil water availability in tallgrass prairie. *Biology and Fertility of Soils*, **29**, 207-217.
- Osler GHR, Harrison L, Kanashiro DK, and Clapperton MJ (2008) Soil microarthropod assemblages under different arable crop rotations in Alberta, Canada. *Applied Soil Ecology*, **38**, 71-78.
- Papatheodorou EM, Argyropoulou MD, Stamou GP (2004) The effects of large- and small-scale differences in soil temperature and moisture on bacterial functional diversity and the community of bacterivorous nematodes. *Applied Soil Ecology*, **25**, 37-49.
- Peneva V, Neilson R, Boag B, Brown DJF (2000) Criconematidae (Tylenchida) from forest nurseries in Bulgaria. *Khelmitogiya*, **24**, 37-51.
- Ransom MD, Rice CW, Todd TC, Wehmueller WA (1998) Soils and soil biota. In: Knapp AK, Briggs JM, Hartnett DC, Collins SL (Eds.), *Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie*. Oxford University Press, Oxford, NY.

- Risser PG, Birney CE, Blocker HD, May S.W, Parton WJ, Wiens JA (1981). *The True Prairie Ecosystem. US/IBP Synthesis Series 16*. Hutchinson Ross Publishing Company, Stroudsburg, PA.
- Sackett T, Classen AT, and Sanders NJ (2010) Linking soil food web structure to above- and below-ground ecosystem processes: a meta-analysis. *Oikos*, **199**, 1984-1922.
- Sala OE, Parton WJ, Joyce LA, Lauenroth WK (1988) Primary production of the Central Grassland region of the United States. *Ecology*, **69**, 40-45.
- Seastedt TR (1984) Microarthropods of burned and unburned tallgrass prairie. *Journal of the Kansas Entomological Society*, **57**, 468-476.
- Shao YW, Zhang J, Zhou L, Xia H, Shu W, Ferris H, Fu S (2008) Nematodes as indicators of soil recovery in tailings of a lead/zinc mine. *Soil Biology and Biochemistry* **40**,:2040–2046.
- Smith VC, Bradford MA (2003) Do non-additive effects on decomposition in litter-mix experiments result from differences in resource quality between litters? *Oikos* **102**, 235–243.
- Smolik JD, Dodd JL (1983) Effect of water and nitrogen and grazing on nematodes in a shortgrass prairie. *Journal of Range Management*, **36**, 744–748.
- Sohlenius B (1985) Influence of climatic conditions on nematode coexistence: a laboratory experiment with a coniferous forest soil. *Oikos*, **44**, 430-438
- Smolik JD (1974) Nematode studies at the Cottonwood site. *US/IBP Grassland Biome Technical Report 251*, Colorado State University, Fort Collins.
- Smolik JD, and JK Lewis. (1982) Effect of range condition on density and biomass of nematodes in a mixed prairie ecosystem. *Journal of Range Management*, **35**, 657-663.
- Steinberger Y, Sarig S (1993) Response by soil nematode populations in the soil microbial biomass to a rain episode in the hot, dry Negev desert. *Biology and Fertility of Soils*, **16**, 188-192.
- Swallow CW, Kissel DE, Owensby CE (1987) Soil coring machine for microplots and large soil cores. *Agronomy Journal*, **79**, 756-758.
- Taylor AR, Pflug A, Schroeter D, Wolters V (2004) Colonization of spruce litter: response of different decomposer communities to experimental alterations in moisture availability. *Global Change Biology*, **10**, 1313-1324.

- Todd TC, Blair JM, Miliken GA (1999) Effects of altered soil-water availability on a tallgrass prairie nematode community. *Applied Soil Ecology*, **13**, 45-55.
- Todd TC, Powers TO, Mullin PG (2006) Sentinel nematodes of land-use change and restoration in tallgrass prairie. *Journal of Nematology*, **38**, 20-27.
- Vreeken-Buijs MJ, Hassink J, and Brussaard L (1998.) Relationships of soil microarthropods biomass with organic matter and pore size distribution in soils under different land use. *Soil Biology and Biochemistry*, **30**, 97-106.
- Wardle DA (2002) Communities and Ecosystems: Linking the Aboveground and Belowground Components. Monographs in Population Biology, 31, Princeton University Press. New Jersey.
- Weaver JE (1954) *North American Prairie*. Johnson Publish Company, Lincoln, NE.
- Whitford WG, Freckman DW, Elkins NZ, Parker LW, Parmalee R, Phillips J, Tucker S (1981) Diurnal migration and responses to stimulated rainfall in desert soil microarthropods and nematodes. *Soil Biology and Biochemistry*, **13**, 417-425.
- Wood TG (1966) The fauna of grasslands soil with special reference to Acari and Collembola. *Proceedings of the New Zealand Ecological Society*, **13**, 79-85.
- Yeates GW, Bongers T (1999) Nematode diversity in agroecosystems. *Agriculture, Ecosystems, and Environment*, **74**, 113-135.
- Yeates GW, Bongers T, de Goede RGM, Freckman DW, Georgieva SS (1993) Feeding habits in soil nematode families and genera – an outline for soil ecologists. *Journal of Nematology*, **25**, 315-331.
- Yeates GW (2003) Nematodes as soil indicators: functional and biodiversity aspects. *Biology and Fertility of Soils*, **37**, 199-210.
- Zhou X, Talley M, Luo Y (2009) Biomass, litter, and soil respiration along a precipitation gradient in southern Great Plains, USA. *Ecosystems* , **12**, 1369-1380.

FIGURES AND TABLES

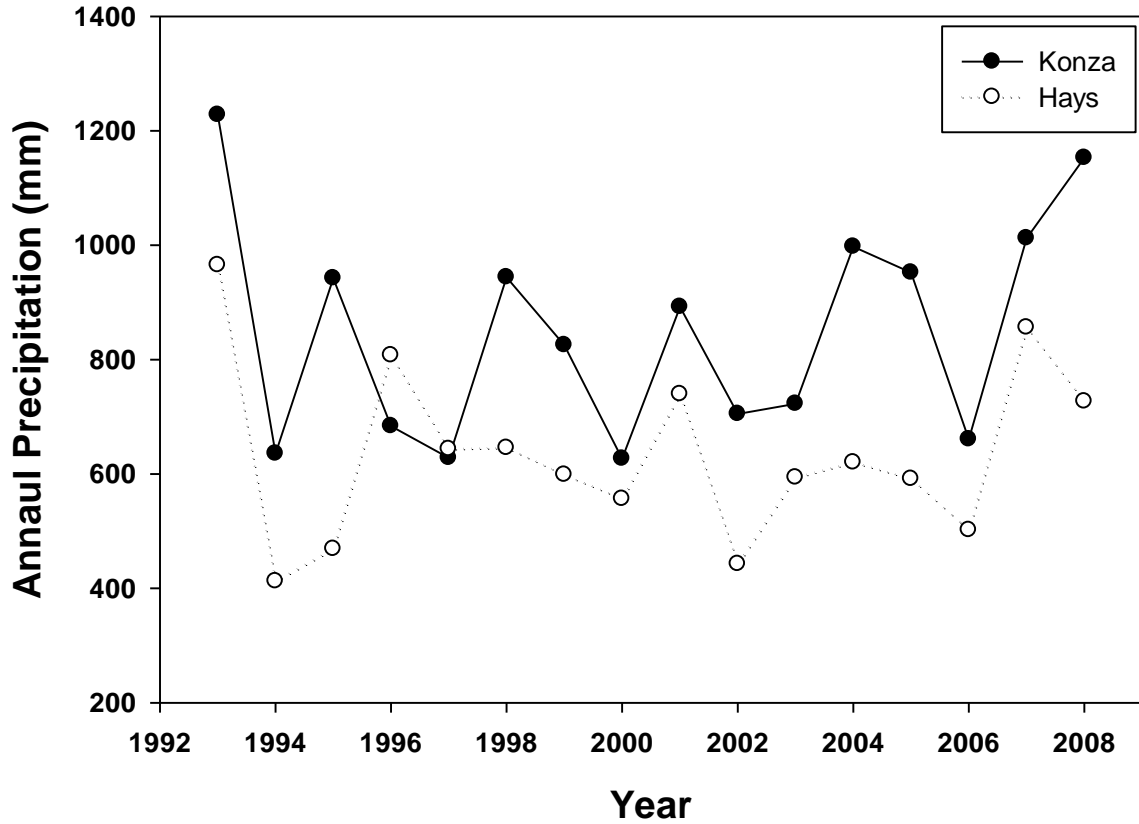


Figure 3.1 Annual precipitation (1993-2009) at Konza Prairie Biological Station (solid line) and Kansas State University Agricultural Research Center at Hays (dotted line).

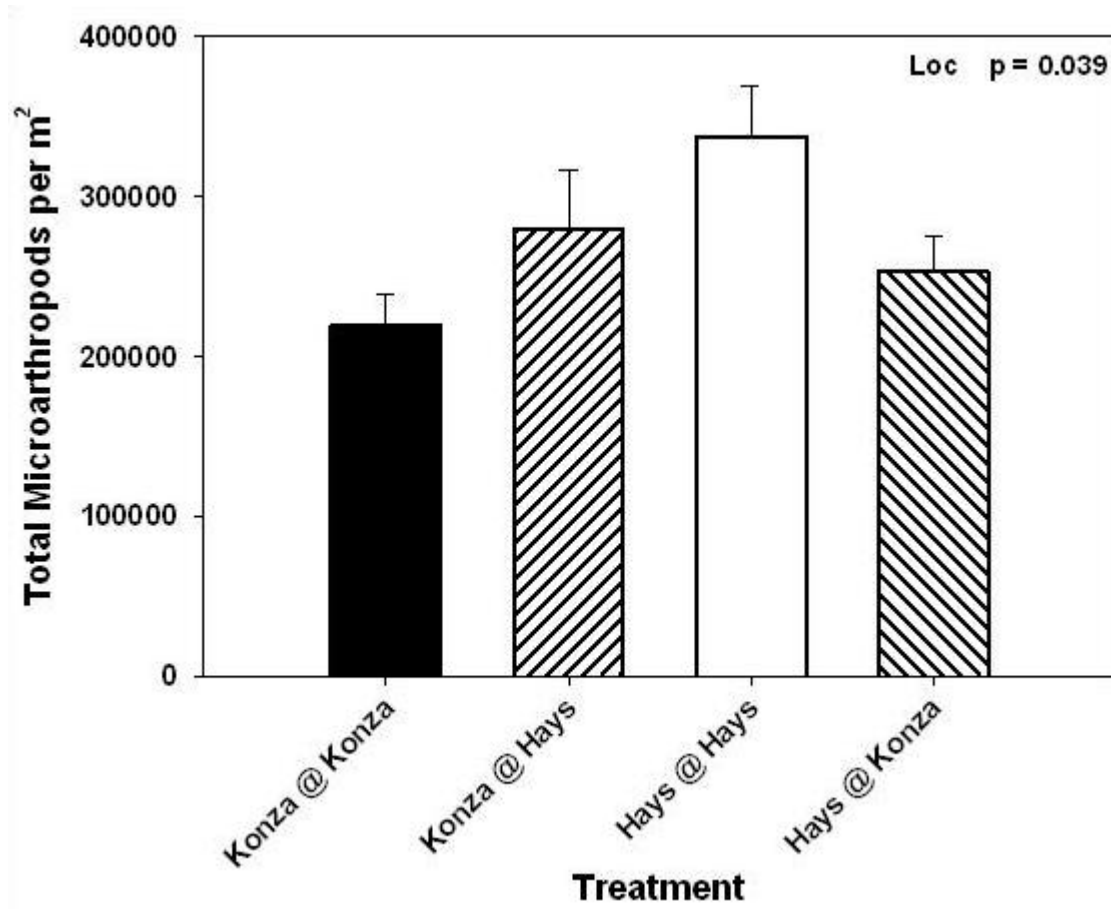


Figure 3.2 Total microarthropod densities (0-60 cm) from four combinations of soil core origin and incubation location. Error bars are ± 1 SE.

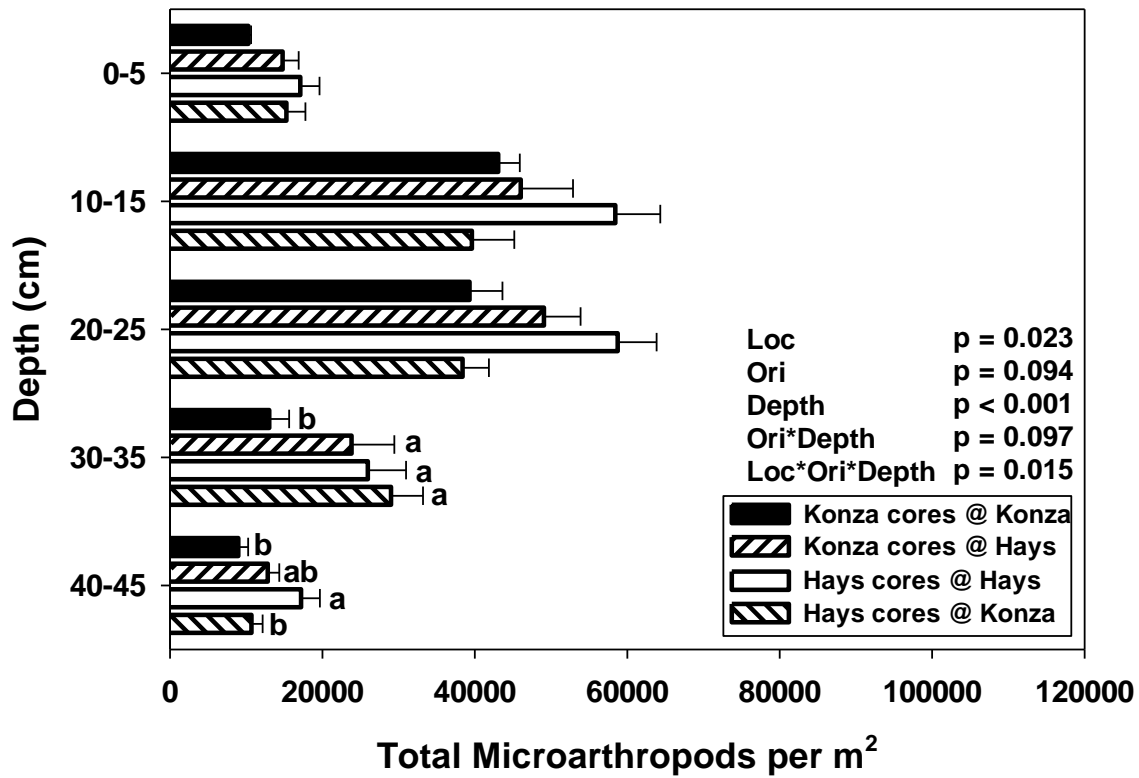


Figure 3.3 Average microarthropod densities from four combinations of soil core origin and incubation location by depth. Error bars are ± 1 SE. Lower-case letters indicate pairwise significant differences at $p < 0.05$, at the specified depth.

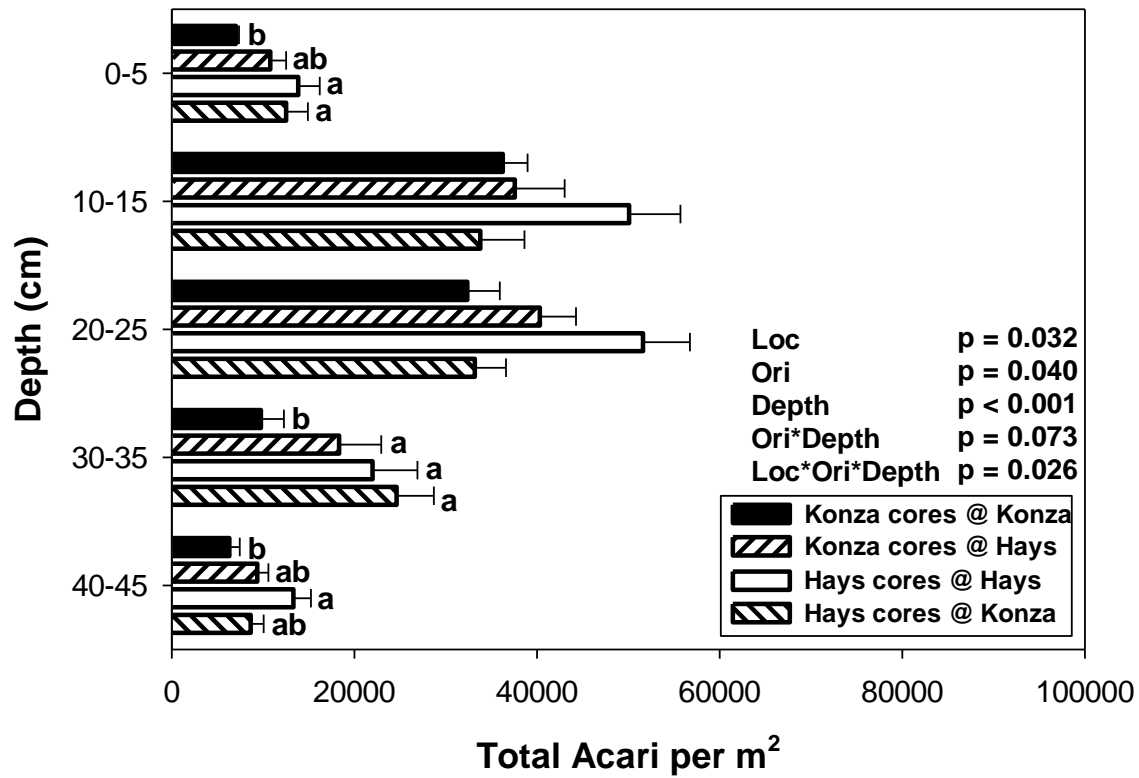


Figure 3.4 Average Acari densities from four combinations of soil core origin and incubation location by depth. Error bars are ± 1 SE. Lower-case letters indicate pair-wise significant differences at $p < 0.05$, at the specified depth.

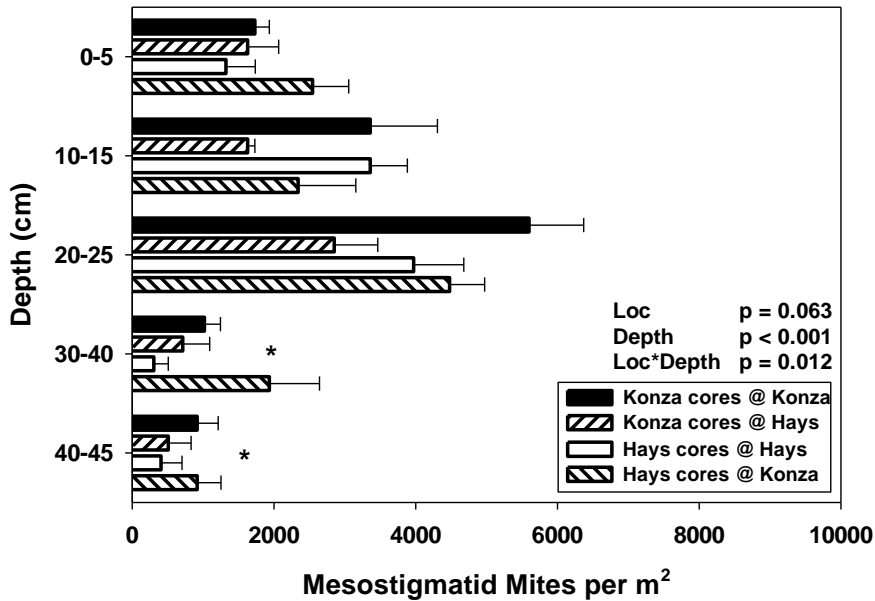
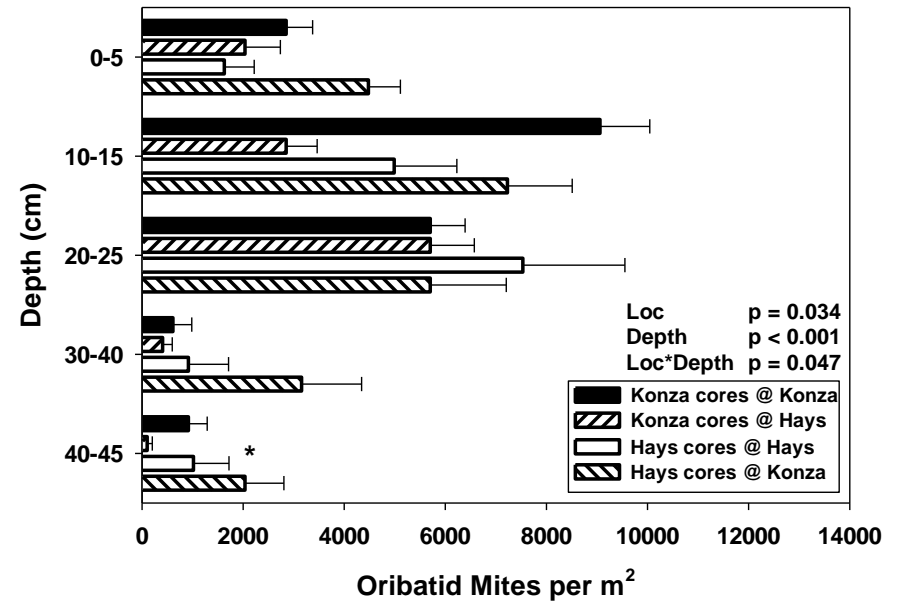
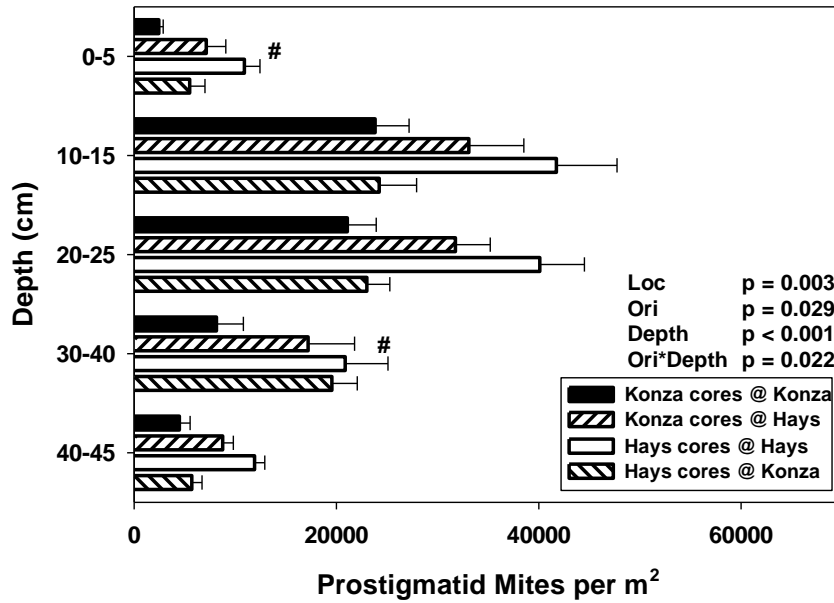


Figure 3.5 Average densities of prostigmatid mites (top left), oribatid mites (top right), and mesostigmatid mites (bottom left) from four combinations of soil core origin and incubation location by depth. Error bars are ± 1 SE. A number symbol (#) indicates significant ($p < 0.05$) origin effects and an asterisk (*) indicates significant location effects, at the specified depth.

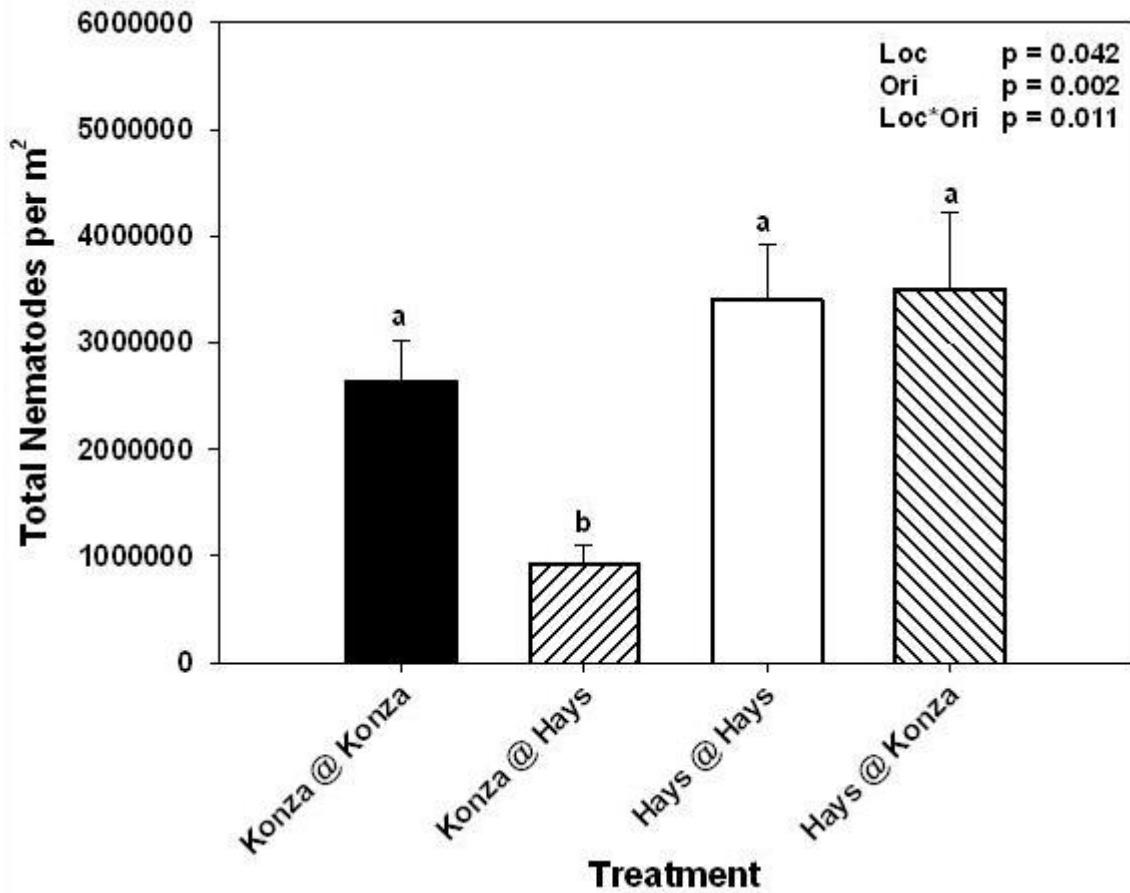


Figure 3.6 Average densities of nematodes from four combinations of soil core origin and incubation location. Error bars are ± 1 SE. Lower-case letters indicate pair-wise significant differences at $p < 0.05$, at the specified depth.

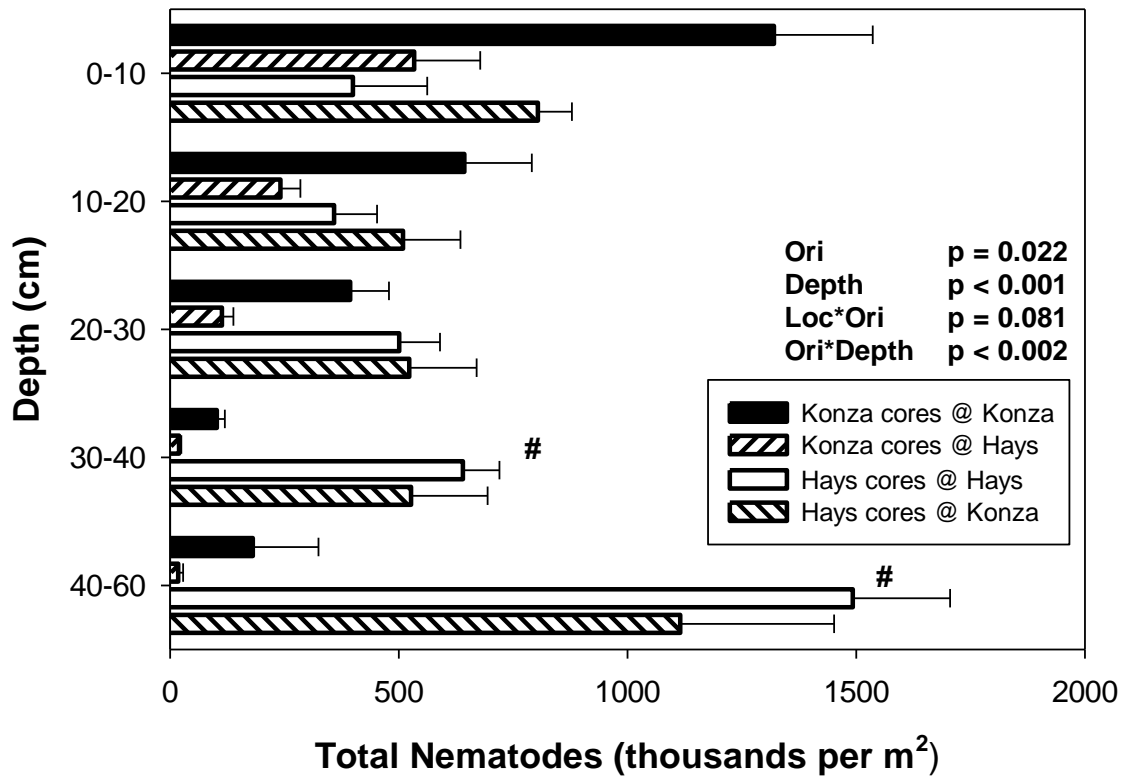


Figure 3.7 Average densities of nematodes from four combinations of soil core origin and incubation location by depth. Error bars are ± 1 SE. A number symbol (#) indicates significant ($p < 0.05$) origin effects, at the specified depth.

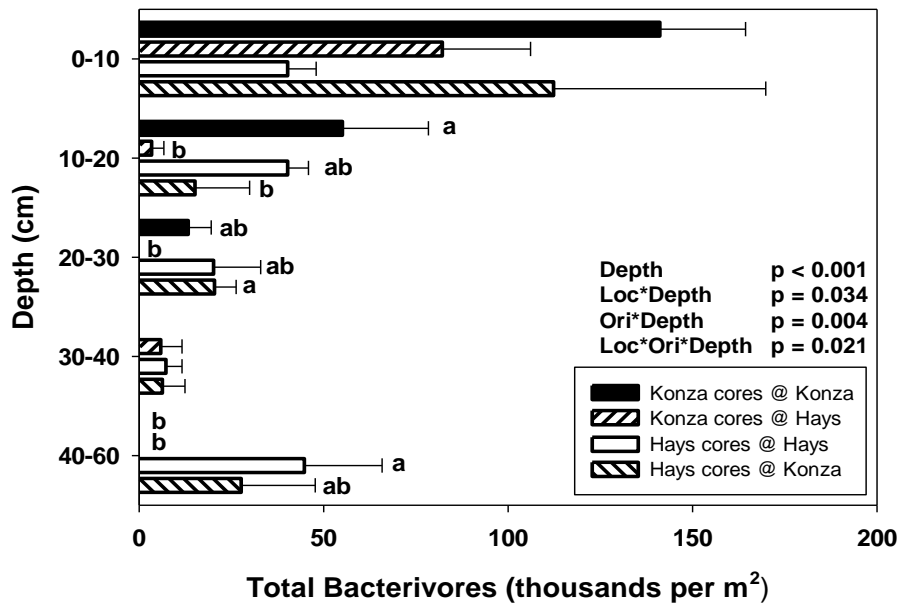
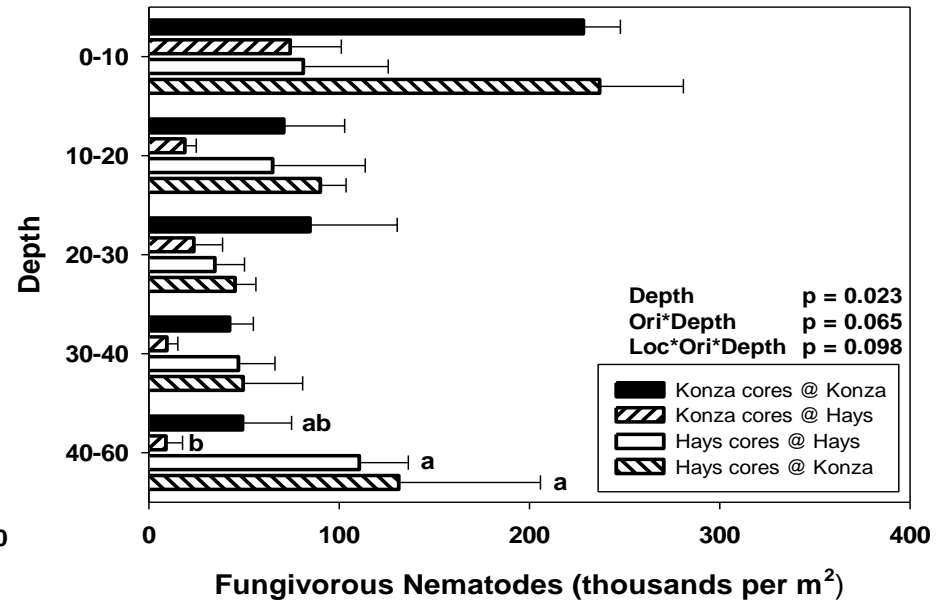
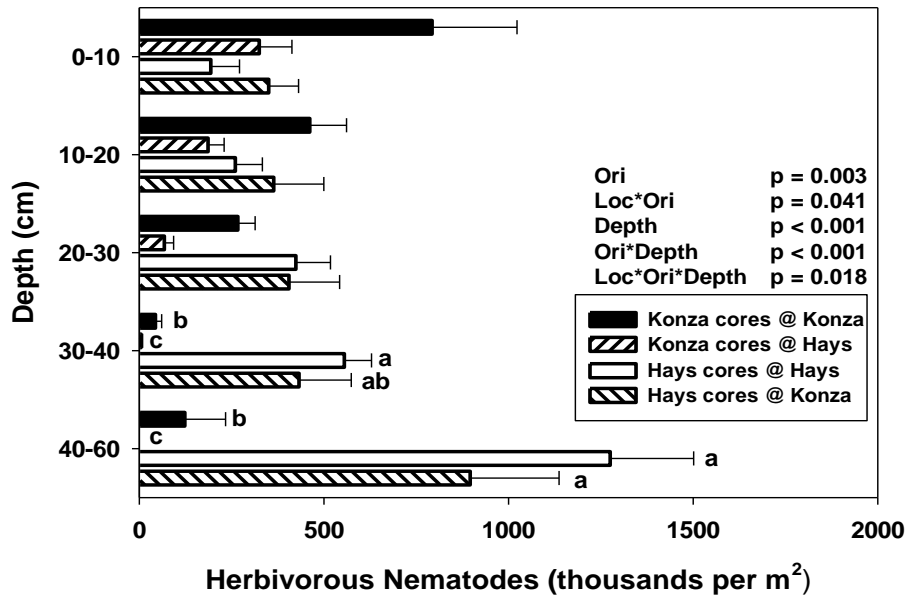


Figure 3.8 Average densities of herbivorous (top left), fungivorous (top right), and bacterivorous (bottom left) nematodes from four combinations of soil core origin and incubation location by depth. Error bars are ± 1 SE. Lower-case letters indicate pair-wise significant differences at $p < 0.05$, at the specified depth.

Chapter 4 - Conclusions

Contemporary global climate change is represented by unprecedented alterations in the global physical and chemical environment. In light of these changes, studies investigating long-term ecological responses to changes in precipitation regimes are becoming increasingly important. Grasslands are likely to be the most vulnerable to global climate change of any terrestrial ecosystem, due to their high dependence on soil water availability for primary productivity. In this thesis, I analyzed how climate change, specifically changes in mean annual precipitation and associated soil moisture content, affects plant and soil nutrient status, microarthropods, and nematodes in the Central Plains region of the United States

The first chapter explored the effects of both increased and decreased mean annual precipitation on belowground plant and soil nutrient status of soils conditioned to more arid and mesic environments. These parameters were assessed using a reciprocal core transplant between two locations across a strong natural precipitation gradient: Konza Prairie Biological Station (MAP=850 mm) and Kansas State University Agricultural Research Center at Hays (MAP=580 mm). Using a reciprocal core transplant between these two sites we were able to compare both “native” and “transplanted” intact plant-soil cores between sites and among sites to assess differences due to precipitation and how precipitation effects may vary with soil origin. Belowground plant biomass was shown to be positively correlated with increasing precipitation, with cores originating from Konza being the most affected by altered precipitation. While the carbon (C) concentrations within belowground plant biomass were unaltered by precipitation, nitrogen concentrations were drastically altered. Regardless of soil origin, greater nitrogen (N) concentrations were associated with more arid climates. As a result, the quality of belowground plant biomass, indexed as the C:N ratio, was greater under more arid conditions relative to more

mesic conditions. Furthermore, the total amount C and N stored within plant biomass was altered by precipitation. While C sequestration in roots was a function of belowground biomass, N sequestration was greatly dependent on tissue N concentrations and was significantly greater under more arid conditions. These results indicate that grassland soils conditioned to more mesic environments are more responsive to decreases in precipitation, compared to the response of soils conditioned to more arid environments.

The second chapter explored the effects of both increased and decreased mean annual precipitation on microarthropod and nematode densities conditioned to more arid and more mesic environments. To assess these changes, subsamples of the reciprocal transplant experiment mentioned above were taken and densities of both organism types were measured. Microarthropods, almost exclusively comprised of organisms in the order Acari, were altered by changes in precipitation. Greater densities of microarthropods were extracted from cores in the more arid environment, regardless of soil origin. Mites in the suborders Prostigmata, Oribatida, and Mesostigmata were the most numerous and the most responsive to changes in historic moisture status. Prostigmatid mites were significantly greater under more arid conditions, while greater densities of oribatid and mesostigmatid mites were extracted from soils in more mesic environments. Nematodes densities were also affected by changes in precipitation; however, these changes were only apparent in soils originating from the more mesic Konza site. Within Konza cores, greater densities of nematodes were extracted from cores incubating at the more mesic Konza site relative to the more arid Hays site. In light of this conclusion, we examined the three most abundant nematode families and found that nematodes in the family Criconeematidae were *Telotylenchidae* and altered and greater densities were recovered from soils located in more mesic climates. These results suggest shifts in both microarthropod and nematode communities

are likely to occur with the changing climate, and their functions within the soil profile have the potential to change, as well.

While these two studies specifically addressed climate change implications, it also provides additional information on belowground grassland studies, particularly the role of annual precipitation. These studies provide a baseline for other studies to analyze specific interactions associated with changes in precipitation. The results of this experiment gave rise to additional questions regarding long-term altered water availability. Specifically: Are there changes in microbial community structure, and how might this relate to changes in potential C and N mineralization rates? How long would it take for predicted shifts in plant communities, and would the soil fauna respond to changes in precipitation similarly to responses observed in *A. gerardii* dominated systems? Is the soil C and N at a new steady state or will further changes occur? Will densities or activities of soil fauna continue to change? These and many other questions remain to be addressed. Still, the results of this study emphasize the importance of research on climate change, particularly precipitation changes, and its relevance to ecosystem structure and functioning in the Central Plains region of the United.