

Effects of white-tailed deer herbivory on remnant tallgrass prairie plant communities

By

Copyright 2016

Courtney E. Masterson

Submitted to the graduate degree program in Ecology and Evolutionary Biology and the Graduate Faculty of the University of Kansas in partial fulfillment of the requirements for the degree of Master of Arts.

Chairperson, Helen Alexander

Bryan Foster

Craig Freeman

Aaron Reed

Date Defended: April 29, 2016

The Thesis Committee for Courtney E. Masterson
certifies that this is the approved version of the following thesis:

Effects of white-tailed deer herbivory on remnant tallgrass prairie plant communities

Chairperson, Helen Alexander

Date approved: July 20, 2016

Abstract

White-tailed deer (*Odocoileus virginianus*) abundance is increasing across North America as habitat is created and populations are protected from predation. Their preferred habitat, the forest edge, surrounds many remnant prairie fragments, providing access to small plant populations that may be sensitive to deer herbivory. This thesis investigated the effects of deer herbivory on plant communities in tallgrass prairie remnants as well as the perennial *Helianthus* species contained therein. In the community-focused study, I found that white-tailed deer exclusion from study plots over two years led to reduced herbivory but did not change the overall richness, diversity, or community composition of the sites. The edge and interior prairie plots contained distinctly different plant communities, and the edge plots experienced greater counts of herbivory on favored species than the interior plots. Woody species abundance was reduced by deer herbivory, a potentially important result given the effects of woody plant colonization on prairie fragments. *Helianthus* herbivory was higher at the edge of the prairie than in the interior. These latter results led to a more focused study of deer herbivory on *Helianthus* using two study methods: exclusion of deer in the prairie and artificial herbivory on stems off site. White-tailed deer remove the apical meristem from plants, often causing the plant to branch. Branching may lead to the production of multiple inflorescences, possibly providing a reproductive benefit through overcompensation. These studies investigate *Helianthus* response to herbivory to determine if the effect on the plant's fitness is negative or positive, overall. In the prairie study, stems protected from herbivory were taller and less likely to branch than those exposed to deer herbivory. *Helianthus* in the exclosures were more likely to produce inflorescences, but there was no difference in the number of inflorescences produced by protected vs. damaged reproductive stems. The same general conclusions were drawn from the artificial herbivory study. However,

the herbivory treatment was imposed across the entire rhizome on all stems produced by the plant. In this study, rhizomes with herbivory grew more branches per stem than undamaged rhizomes. Still, there was no evidence of increased reproduction in damaged plants. Thus, deer herbivory may alter the morphology and reproduction of perennial *Helianthus*, potentially having a long-term effect on their abundance in plant communities. Continuing both studies would reveal the long-term effect of deer herbivory on both prairie plant communities and the population dynamics of individual species. Continued increase of white-tailed deer populations may pose a threat to favored browse species in fragmented plant communities. However, herbivory may play an important role in succession in grasslands. As conservationists consider the management of white-tailed deer in protection of remnant ecosystems, it will be important to consider both the positive and negative effects of herbivory.

Acknowledgments

My advisor, Helen Alexander, provided immeasurable help with study design, field work conundrums, and the review of dozens of manuscripts including everything from small grants to thesis chapters. Her flexibility and support, even at the busiest times, was truly appreciated.

I am grateful for my patient committee members, Bryan Foster, Craig Freeman, and Aaron Reed. Their assistance and encouragement over the years made this research possible.

At The University of Kansas – I thank Caleb Morse for working with me to identify countless plant specimens and for never kicking me out of the herbarium. I also thank John Kelly for his invaluable advice on my statistical analysis. The conversations shared and time spent in the field with Robert Hagan shaped this research immeasurably. Kelly Kindscher provided support through friendly conversation, advice and prairie walks. Dean Kettle, Bruce Johanning, and Vaughn Salisbury at the KU Field Station provided research support and kind advice. Finally, to my fellow graduate students Daphne Mayes, Kathy Denning, Theo Michaels, Terra Lubin, David Hall - Thank you sincerely for your support and advice on this project. Thank you for sharing your work with me. You inspire me *constantly*.

In the field – I thank Lloyd Fox for introducing me to deer management, letting me tag along on his adventures, and providing a connection with deer and people who love them. I also share my deep appreciation of Larry Rizzo for inspiring my work and patiently advising me on everything from prairie ecology to deer/human conflict. Thank you to Frank Norman, as well, for pushing me to succeed and testing my skills.

This project would not have been possible without the support of Matt Garrett and the Johnson County Parks and Recreation Department. While they provided the funds to build the deer enclosures, their greatest contribution was boots on the ground, sweat equity, and genuine interest in the effect of deer on the land they manage. They are true allies and conservationists.

I was assisted by dozens of undergraduate students, master naturalists, educators and prairie enthusiasts. I was touched by their interest in my work, their patience, and their tenacity. I couldn't have finished this work without them. There are too many to name but a great debt is owed to Linda Lehrbaum, Bill Fessler, Stephen Giambrone, Jay Antle, Kim Bellemere, Ginger Werp, Nathan Stotts, Jim Kilmer, Olympus Aviles, Emily Lomaka, Che-Ling Ho, and Haley Bagshaw. You're all rock stars.

Thank you to my family and friends for their patience and love through nine years of college. Let's make up for lost time!

Most importantly, I share a whole-hearted thank you to my husband, Ryan Riedel. Your support made all of this possible. Thank you for your patience with the ticks, poison ivy, and seeds all over the house! Thank you for being my home. Thanks for *everything*. We made it!

Table of Contents

Abstract	iii
Acknowledgments.....	v
Thesis Introduction	1
Chapter 1: Role of edge effects, deer herbivory, and their interaction on tallgrass prairie remnants	4
Introduction.....	4
Methods	6
Study Area Description.....	6
Deer Management and Population Estimation	7
Paired Deer Exclosure and Control Plots.....	8
Vegetation Sampling and Herbivory.....	9
Statistical Analysis.....	10
Deer Population Estimates	10
Analysis of Vegetation and Herbivory	11
Results.....	13
Deer Density Surveys	13
Herbivory	13
Vegetation Analysis	14
Guilds and focal species.....	15
Discussion.....	16
Prairie fragments: edge/interior communities and deer herbivory.....	16
Future directions	20

Chapter 2: Response of perennial sunflowers, <i>Helianthus pauciflorus</i> and <i>Helianthus hirsutus</i> , to natural and artificial herbivory.....	22
Introduction.....	22
Methods: <i>Helianthus</i> Prairie Exclosure Study.....	25
Study Species.....	25
Study Area Description.....	25
Deer Management.....	25
Deer Exclosures.....	26
Vegetation Sampling and Herbivory.....	26
Methods: <i>Helianthus</i> Artificial Herbivory Study.....	27
Study Area Description.....	27
Deer Exclosures.....	27
Vegetation Sampling.....	27
Statistical methods.....	29
Results: <i>Helianthus</i> Prairie Exclosure Study.....	29
Herbivory.....	29
Morphology.....	30
Reproduction.....	31
Results: <i>Helianthus</i> Artificial Herbivory Study.....	31
Rodent herbivory.....	31
Morphology.....	32
Reproduction.....	32
Discussion.....	33

Future Directions	34
Thesis Conclusions	36
References.....	38
Appendix.....	66

Tables

Table 1: Deer survey results.	45
Table 2: ANOVA Results, Herbivory Effects.	45
Table 3: ANOVA Results, Vegetation Analysis.....	46
Table 4: SIMPER Analyses, by species.....	46
Table 5: SIMPER analyses, by guild.	47
Table 6: PERMANOVA Analyses.	48
Table 7: PERMDISP Analyses.	49
Table 8: Focal Species Analyses.....	49
Table 9: <i>Helianthus</i> stem height.	50
Table 10: Stem diameter of <i>Helianthus</i>	50
Table 11: Branching in <i>Helianthus</i>	50
Table 12: Inflorescences in <i>Helianthus</i>	51
Table 13: Branching in <i>Helianthus</i>	51

Figures

Figure 1: Site maps	52
Figure 2: Exclosure plot diagram.....	53
Figure 3: Exclosure photos.	53
Figure 4: Deer vs. Rodent Herbivory.....	54
Figure 5: Herbivory Effects.	55
Figure 6: Richness and Diversity.....	56
Figure 7: MDS Plots.	57
Figure 8: Woody Differences.....	58
Figure 9: <i>Helianthus</i> Differences.....	59
Figure 10: Diagram of artificial herbivory plot.	60
Figure 11: <i>Helianthus</i> herbivory.....	61
Figure 12: <i>Helianthus</i> stem height.....	62
Figure 13: <i>Helianthus</i> stem diameter.....	62
Figure 14: <i>Helianthus</i> inflorescence diameter.	63
Figure 15: Branching by stem in <i>Helianthus</i>	63
Figure 16: Branching by rhizome in <i>Helianthus</i>	64
Figure 17: <i>Helianthus</i> inflorescence by stem.....	65

Thesis Introduction

Plant-animal interactions play an important role in the structure and sustainability of ecosystems, worldwide. Historically vast, contiguous landscapes are now highly fragmented as human development reaches every corner of Earth. Iconic herbivore populations, like the bison of North America and the rhinoceros of Africa, are significantly affected by shrinking habitats and have reached critically low numbers. In fact, approximately 60% of all large herbivore species are facing extinction (Ripple *et al.* 2015).

However, some herbivores are more suited to human-inhabited landscapes than others.

Generalist herbivores may continue to thrive despite habitat destruction and may coexist with humans in developed areas. In these cases, human-wildlife conflict becomes a great concern.

Sharing space with wildlife populations often leads to great financial loss in the form of damaged crops, gardens, and other properties. For example, elephants (*Elephas maximus*) damage greater than \$3 million USD in crops and damage over 10,000 homes in India each year (Bist 2006).

There are also health expenses as interactions with wildlife often mean increased disease prevalence and vehicle accidents.

White-tailed deer (*Odocoileus virginianus* Zimmerman) are adept at coexisting with humans.

Despite extensive habitat modification, perhaps because of it, deer populations continue to grow in the Midwestern United States. Their numbers are estimated to be at an all-time high, possibly due to the steadily shrinking popularity of hunting (Enck *et al.* 2000) and the increase in habitat and food available to the species. Deer prefer the forest edge and browse for food heavily for much of the growing season, whether in natural areas, cropland, or urban/suburban areas.

The focus of this thesis is the tallgrass prairie, one of the most endangered, terrestrial ecosystems in the world. Prairies are often fragmented into small islands surrounded by a deciduous forest or developed area matrix. Tallgrass prairie now covers less than 1% of its original range on the continent (Howe 1994, Samson and Knopf 1994), and less than 1% of its original range in northeastern Kansas (Kindscher et al. 2005). Forest edges abutting prairies provide habitat well suited to white-tailed deer, potentially affecting how these herbivores use the prairie.

Deer are known to affect tree, shrub, and forb populations in woodlands (Russel *et al.* 2001). In the presence of large deer populations, tree recruitment is greatly reduced, and forb abundances drop dramatically (Rooney 1997, Augustine and Frelich 1998). Unpalatable species may dominate the plant community (Tilghman 1989). Much less is known about white-tailed deer effects in grasslands. Recent studies have provided some direction with regard to which prairie species are favored by deer, but little has been revealed about the long-term effects of increased herbivory pressure on these browsed populations (Spotswood *et al.* 2002, Anderson *et al.* 2001, Gooch 2009, Nisi *et al.* 2015).

This suite of studies marks the beginning of a long-term investigation into the effects of deer herbivory on tallgrass prairie plants, both as a community (Chapter 1) and at the species level (Chapter 2). For Chapter 1, I set up paired deer exclosures/control plots at edge and interior locations of two prairies. Using this experimental design, I can address several questions on the effects of white-tailed deer herbivory, as well as location (edge vs. interior) effects, on plant communities. Is the edge plant community different than the interior plant community? Are deer

targeting the edge plants with herbivory more often than the interior plants? Does deer herbivory alter the composition of the plant communities, at the edge and interior of the prairie? For Chapter 2, I focus on *Helianthus*, a genus known to be favored browse for white-tailed deer. Deer feeding typically removes the apical meristem. Using both exclosure/control plots in one prairie and an artificial herbivory study, I address the response of these perennial plants to deer herbivory. Questions include: Does deer herbivory alter plant morphology, such as increased branching? If so, do morphological changes on damaged plants lead to changes in inflorescence number or size? Overall, does deer herbivory have a net positive or negative effect on plant reproduction?

Increased study of deer is important because they have been implicated in the extirpation of forbs in tallgrass prairies (for example, in the Kansas City metropolitan area, personal communications - Matt Garrett, Johnson County Parks and Recreation, Larry Rizzo, Missouri Department of Conservation). Management of deer populations has the potential to promote the conservation of sensitive plant species. However, managing large mammal populations comes with great difficulty as there are many stakeholders with opposing views, and there is a great expense to the process. In sum, understanding the impact of white-tailed deer on prairie fragments will not only provide insight into their role in this important ecosystem, it will also provide some information on how we might better manage deer populations to meet our conservation goals.

Chapter 1: Role of edge effects, deer herbivory, and their interaction on tallgrass prairie remnants

Introduction

The worldwide loss of contiguous ecosystems challenges ecologists to investigate the effects of fragmentation on natural communities. Fragmentation is broadly expected to affect ecosystem function and global biodiversity negatively (Rands *et al.* 2010, Haddad *et al.* 2015). Potential contributions to these losses include decreased patch size, increased isolation from other fragments, and an increasing edge to interior ratio. Fragmented plant communities are also vulnerable to altered abiotic and biotic pressures. The former can include altered light intensity, temperature, vapor pressure (Pohlman *et al.* 2007), and changed wind intensity (Laurence 2000). Examples of the latter include changes to pollination and seed set (Aizen and Feinsinger 1994), altered incidence of fungal disease (Johnson and Haddad 2011), and reduced tolerance of herbivory (Shaw *et al.* 2015). All these factors, as well as variation in seed dispersal, can lead to the development of distinct edge and interior plant communities.

Edge and interior plant communities are often differentially utilized by animals. For example, some herbivores prefer forest edges, as it provides a balance of shelter (predator evasion, breeding grounds, nurseries) and variable, nutritious food sources (Alverson *et al.* 1988, Yahner 1988). Given that herbivores can potentially alter the richness, diversity, and structure of plant communities (Amsberry and Maron 2006, Bagchi and Ritchie 2010, Heirro *et al.* 2011), it is important to evaluate the effect of herbivory on edge and interior plant communities in habitat fragments.

Edge effects, including the potential differential influence of herbivores in edge vs. interior plant communities, are particularly relevant for conservation of the North American tallgrass prairie. Such prairies are among the most endangered ecosystems in the world with remaining prairie remnants occupying less than 1% of its original range (Samson and Knopf 1994). These remnants are highly fragmented and, especially on the eastern edge of the prairie region, are often surrounded by a deciduous forest matrix. The predominance of forest/prairie ecotones surrounding prairie remnants can have many effects on the prairie plant community, including altered biomass (Reichman *et al.* 1993), invasion of interior communities by edge species, and altered herbivory (Briggs *et al.* 2002, van der Hoek *et al.* 2002, Anderson 2006, Batzli and DeJaco 2013). White-tailed deer (*Odocoileus virginianus* Zimmerman), the most abundant wild ungulate in North America (Rooney 2001), favor the ecotone habitat between grassland and woodland systems (Alverson *et al.* 1988, Côté *et al.* 2004).

Deer populations in North America have increased dramatically since the early 1900s due to increased habitat and restricted hunting (McShea *et al.* 1997, Côté *et al.* 2004). While the effects of deer in the deciduous forests of the U.S. are well studied (Fletcher *et al.* 2001, Webster *et al.* 2005, Urbanek *et al.* 2012, Bressette *et al.* 2012), the effects of this large herbivore in prairies are relatively unknown (Anderson 2006). Unlike the historically abundant bison (*Bison bison* Linnaeus), deer forage preferably on forbs and woody species (Anderson *et al.* 2001). Englund and Meyer (1986) found that deer rarely cause mortality in target plant species in woodland studies, although it is likely that some highly favored species may be completely eliminated. Deer may show preferences for plants with higher nitrogen content and those in burned areas (Nisi *et al.* 2015). Further, deer are known to favor members of the genus *Helianthus*

(Asteraceae), a suite of species well represented in the tallgrass prairie (Englund and Meyer 1986, Anderson *et al.* 2001, Gooch 2009). Still, the long-term effects of large deer populations on tallgrass prairie plant communities are poorly understood. Insight into these relationships would allow for a greater understanding of the role deer play in prairie preservation and management.

Utilizing two remnant prairies in eastern Kansas, U. S., and experimental deer exclosures, I address three questions. First, does the vegetation at the prairie edge differ from that of the interior? Second, what is the effect of excluding deer on the plant community? Third, are there interactions between location (edge vs. interior) and deer herbivory (i.e., Do deer preferentially feed in the different locations? Are the plant community responses to herbivory similar at the edge and the interior?)?

Methods

Study Area Description

The study was conducted on two remnant prairies, both owned and managed by Johnson County Parks and Recreation Department, in northeastern Kansas, U. S. One site, Ogg Prairie (3 ha or ~ 8 acres, ~ GPS coordinates: 38.990845, -94.799225), is located in Shawnee Mission Park (Lenexa, KS). Lenexa is part of the suburban area surrounding Kansas City, Kansas, and is located approximately 25 km southwest of downtown Kansas City. The other site, Kill Creek Prairie (~ 8 ha or 20 acres, ~ GPS coordinates: 38.917885, -94.974586), is located in Kill Creek Park (Olathe, KS), a rural area approximately 17 km south-southwest of Ogg Prairie.

Both sites are managed with controlled burning (annually or biennially at Ogg Prairie, approximately biennially at Kill Creek Prairie). The prairies also are managed for invasive plant species and woody succession using spot herbicide spraying and mowing. Areas directly adjacent to study plots were not managed for invasive species for the duration of the study.

Both sites exhibit high native plant species richness that is comparable to other high quality prairie remnants in the region. Kill Creek Prairie is estimated to contain nearly 200 plant species while Ogg Prairie contains approximately 125 species (Personal communication, C. Freeman, R. L. McGregor Herbarium, University of Kansas). These counts include native and nonnative species.

Deer Management and Population Estimation

White-tailed deer are common in northeastern Kansas. Deer in the park surrounding Ogg Prairie (Shawnee Mission Park) are managed via annual culling only if the population is estimated to exceed 20 deer/mi² (0.08 deer/ha) in fall spotlight/distance surveys. Deer at Kill Creek Prairie are not directly managed; however private land bordering Kill Creek Park may be hunted in accordance with state regulations. Deer were often observed browsing for food and bedded down in the study prairies during plant data collection. These prairies are likely heavily utilized by deer.

Deer population sizes were estimated using spotlighting surveys over multiple years. The spotlight/distance surveys were conducted by trained biologists and field assistants experienced in this type of data collection. Observations started approximately 30 minutes after sunset each

night of the survey in the fall seasons (2014: 10/27, 10/28, 10/29; 2015: 10/26, 10/27, 11/2). A spring survey was also conducted for comparison (2015: 4/20, 4/21, 4/22). Spotlighting was conducted along transects from a platform raised above the cab of a pickup truck traveling 10-15 mph (16-24 kph). For each cluster of deer, data were collected on the number of animals, approximate age, sex, and behavior, as well as the distance from the truck and angle of incidence

Spotlighting was conducted on multiple park roads surrounding each prairie and in adjacent areas. Survey effort was defined by the number of kilometers traveled each night (Table 1). In fall 2015, for example, the effort at Kill Creek Park was 19.5 km and 41 km for Shawnee Mission Park. The difference was due to the larger size of Shawnee Mission Park (648 ha) compared to Kill Creek Park (358 ha).

Paired Deer Exclosure and Control Plots

Ten paired experimental areas were established from September 2013 through June 2014 across two remnant prairie sites (six at Kill Creek Prairie, four at Ogg Prairie) (Figs. 1, 2). Each experimental area consisted of a fenced deer exclosure plot and an unfenced control plot. Plots were randomly assigned to “exclosure” or “control” within each paired area. The control and exclosure plot were adjacent to each other, in a split plot design, to reduce variation between plots beyond the treatment. Analyses of the baseline data revealed no statistical differences between the control and exclosure plots for the variables studied. Five of the 10 paired plots were located on the prairie edge (in the prairie but at the ecotone next to the forest); the other five were located in the prairie interior.

The deer exclosures were 6 m² and 2.75 m tall (Fig. 3). The corners were supported with 3 m long fence posts and guy lines. The fencing material was either fire resistant wire mesh or heavy duty plastic deer fencing of the same dimensions. Plastic fencing was removable to allow for controlled burning. The fencing was zip tied to the fence posts and closed with zip ties to allow for entry during data collection. All damage to exclosures was repaired regularly. No evidence of deer entry was observed during the study.

Vegetation Sampling and Herbivory

Four 1m² quadrats were established in each control and exclosure plot, totaling 8 quadrats per paired experimental area. Each quadrat was 1 m from the closest plot perimeter and 1 m from each adjacent quadrat (Fig. 2). Vegetation in the quadrats were sampled biannually in the spring (April-May) and fall (August-September). Control and exclosure plots within the same paired experimental area were sampled within 48 hours of each other to reduce variation due to temporal differences. Field counts and identification were conducted by one observer with the recording assistance of volunteers. Staff members of the R.L. McGregor Herbarium (University of Kansas) provided assistance with identification of plant samples.

Each season, for each quadrat, every stem was identified to at least the genus level and counted. Grasses and sedges were only counted if they produced inflorescence, and then the abundance of those species were defined as equal to the number of its inflorescences in the quadrat. Each counted stem was also examined for damage from herbivory. Deer herbivory on plants was identified by characteristic torn tissue, unique to ruminant damage, due to their lack of upper

incisors. Damage from deer was readily distinguished from rodent herbivory because rodents remove tissue from plants using clean, angular cuts (Fig. 4).

To estimate aboveground biomass in each plot, I visually estimated percent cover of three categories (live biomass, dead biomass (litter), and bare ground) in each season. The sum of cover equaled 100%. In fall 2015, another percent cover category, woody cover, was also estimated. This cover was separate from the live biomass category, which included all live biomass including woody species, allowing the sum of all cover categories to exceed 100%.

For analyses excluding woody plants and woodland plant species (see analyses on richness), a woodland species was defined as one that grows in part to full shade and in open woodland to dense woodland. Decisions were based on personal observations and information in botanical guide books. None of the herbaceous species occupying prairie interiors were defined as woodland species.

Statistical Analysis

Deer Population Estimates

Spotlight/distance survey data were analyzed using Distance software (Version 6, 2009, Bishop *et al.* 2009) with the assistance of Kansas Department of Wildlife Parks and Tourism Big Game Manager, Lloyd Fox. Multiple models were run simultaneously with this software; the half normal/Cosine models are reported in the Results section.

Analysis of Vegetation and Herbivory

Past work in this region noted that sunflowers (*Helianthus spp.*) were favored browse for white-tailed deer (personal communications, Larry Rizzo, Missouri Department of Conservation, see Appendix, Englund and Meyer 1986). I thus analyzed herbivory on *Helianthus* species in the quadrats as an indicator of the effectiveness of the exclosure. All perennial *Helianthus* species at the site (*H. pauciflorus* Nutt. [stiff sunflower], *H. hirsutus* Raf. [woodland sunflower]) were analyzed as a single group because of intergrading morphologies that caused difficulties in identification of some individuals. Both species grow rhizomatously, producing annual shoots.

Statistical analyses on response variables were initially conducted in two ways: 1) a focus on the last year of the study (2015) and 2) a change from baseline (= initial) conditions (i.e., 2015 data subtracted from 2014 data). Preliminary analyses on the baseline data for several vegetation and herbivory response variables revealed no significant differences between the treatments in that season. The change from baseline analyses potentially allowed for an investigation of response variables while taking into account the variation in initial conditions from plot to plot. However, late spring 2014 erection of the exclosures left vegetation exposed to deer during a period of potentially high herbivory (nutritious new growth). Because herbivory was observed on vegetation that was later caged, this likely led to a reduced response due to treatment in analyses of the change variable. I thus present only 2015 analyses.

Analyses were completed in Minitab 17 (2010) unless otherwise indicated (see community analyses below). I used general linear models with a split plot design, allowing for tests of main effects of location (edge vs. interior), treatment (control vs. exclosure), the interaction, and the

plot. Interactions of main effects were not common and are only reported if a significant effect was found. Plots from both prairies were included for all analyses, but prairie was not considered as a factor due to a lack of replication. For all general linear models, normality was assessed by examining the residual plots. When data were not distributed normally, transformations were attempted to normalize the data. If further modification was necessary, non-parametric analyses were used on the original data (Kruskal-Wallis).

For community composition data, community dissimilarity among plots was estimated using the Bray–Curtis dissimilarity index based on relative abundance of stem counts of each taxonomic unit. I used Permutational Analysis of Variance (PERMANOVA) and Permutational Analysis of Multivariate Dispersions (PERMDISP; Anderson 2006, Anderson *et al.* 2008) to evaluate treatment and location effects on plant community composition. Similarity Percentages analyses (SIMPER) were also conducted to determine the contribution of species to communities in each location and to compare those communities qualitatively.

With both PERMANOVA and PERMDISP it is possible to investigate treatment effects on community composition due to centroid shifts and changes in mean distance to the centroid (beta diversity) (Anderson *et al.* 2008). To investigate potential within-whole-plot effects on species composition in response to location, treatment and location*treatment, I used split-plot PERMANOVAs in combination with PERMDISP and ordination diagrams (per Anderson *et al.* 2008). To investigate between whole plot effects of location, I used a 1-way PERMANOVA. PERMANOVA, PERMDISP and SIMPER analyses were performed using PRIMER-E (version 6.1.13) and PERMANOVA + for PRIMER 6 (version 1.0.3, Anderson *et al.* 2008). Analyses

randomly generated 9,999 permutations of Bray-Curtis dissimilarity matrix in the calculation of the reported p values.

For portions of the community analyses concerning guilds, genera were sorted into guilds defined by Kindscher and Wells (1995). These prairie guilds were as follows: warm season graminoids (C4 grasses), cool-season graminoids (C3 grasses and sedges), annuals and biennials, ephemeral spring forbs, spring forbs, summer/fall forbs, legumes, and shrubs. I added a tree and woody vine category to account for the added species found at the prairie/forest ecotone.

Results

Deer Density Surveys

Deer populations estimated at each site revealed an estimated 2.7, 1.5, and 2.25 times more deer at Kill Creek Prairie than Ogg Prairie, respectively for the fall 2014, spring 2015 and fall 2015 seasons (Table 1). . The furthest deer observed from the truck at Kill Creek and Ogg Prairie were 438 m and 291 m, respectively.

Herbivory

Deer exclosures were effective in restricting deer herbivory, reducing damage to protected plants to nearly 0% across all plots. Herbivory damage inside of the exclosures, while rare, was identified as rodent or arthropod damage.

In fall 2015, the percentage of all stems with herbivory was 9 x higher in the control plots than in the exclosures ($p=0.018$, Table 2, Figure 5). In spring 2015, a larger proportion of *Helianthus*

stems experienced herbivory in the control than in the exclosure treatments (spring: $p=0.048$, Table 2). The same trend was found in the fall season, when 18% of *Helianthus* in the edge control plots were targeted by herbivores, while 0% of stems were damaged in the paired exclosures. This pattern was observed in the interior plots as well. In fall 2015 there was also a trend towards a greater effect of the treatment (i.e., greater proportion of *Helianthus* eaten in the control treatment) at the edge plots over the interior plots (location*treatment, $p=0.103$).

Vegetation Analysis

I found no significant differences between control and exclosure plots for richness, diversity (e^H), or community composition. However, differences due to location were often found. In spring and fall 2015, the edge plots had significantly higher richness than the interior plots (Table 3, Fig. 6). However, when woodland species were removed from analyses, there was no longer a significant difference in the richness of the locations. In spring 2015, the edge plots were more diverse than the interior plots (Table 3). This trend continued into the fall season but was not statistically significant.

The community composition, as analyzed by PERMANOVA, differed between edge and interior communities across all seasons except fall 2014 (Fig. 7, Table 6). For all seasons and years, the largest contribution to this difference was the higher *Helianthus* species abundance in edge vs. interior plots (see Table 4 for similarity percentages analyses [SIMPER results], by species).

Each season, there was a significant difference in the mean distance to the group centroid for the two prairies, meaning that the plant communities in the plots of one prairie are more similar to

each other than the plots in the other prairie (see Fig. 7 – MDS Plots, Table 7). For each season, the plots for Kill Creek were more dissimilar to one another than those of Ogg Prairie. In spring 2015, there was also a significant difference in communities due to location, within the prairies.

Guilds and focal species

Guilds: In general, differences among guilds were most evident between edge and interior plots. In spring and fall 2015, the edge community contained significantly greater abundance of tree species (Location - spring $F_{1,14}=23.03$, $p < 0.001$, $F_{1,14}=35.21$, $p < 0.001$), as expected. By the fall season, the interior was defined by grasses and legumes while the edge plots were dominated by annuals and late summer/fall forbs (See SIMPER analysis by guild, Table 5).

Woody vegetation: With the abundance of all woody species combined into a single category (reducing complications due to relatively low incidence of individual woody species), I found multiple instances of significant treatment effects. In spring 2015, there were significantly more woody stems in the exclosures ($p=0.050$, Table 8). The same was true in fall 2015 (location $p=0.02$, treatment $p=0.001$, Table 8, Fig. 8 A).

I found no significant differences between the treatment groups for woody percent cover (taken only in fall 2015, Table 8), though there was a trend for more woody cover in the edge exclosure compared to the edge control plots (Mean/SE: Control 20.97/7.75, Exclosure 25.14/6.67). As expected, there was a significant difference in woody cover between locations ($p \leq 0.001$, Table 8, Fig. 8). Woody plants covered 9 x more area in the edge control plots than the interior control plots.

***Helianthus* species:** In the spring of 2015, the edge plots contained 15 x more *Helianthus* stems than the interior plots ($p=0.015$, Table 8). In fall 2015, I found a significant difference in the edge and interior responses to treatment (location*treatment, $p=0.026$, Table 8, Fig. 9) with a greater treatment effect at the edge. Interestingly, there was a higher abundance of *Helianthus* in edge control plots when compared to the edge exclosures. Quadrats in the control edge plots contained an average of 35 stems of *Helianthus* in fall 2015, compared to an average of 25 stems found in exclosure quadrats.

Discussion

Prairie fragments: edge/interior communities and deer herbivory

Prairie fragments have greater edge to interior ratios than contiguous grasslands, and thus interior habitat may be limited. This is of conservation concern because as shown in this study, edge and interior plant communities are distinct, with full-sun, dry soil dependent plants typically restricted to the interior. These interior species could be lost in small fragments if population sizes drop due to shrinking suitable habitat. Prairie fragments are also increasingly exposed to high deer densities. Past studies on forests and grasslands (Fletcher *et al.* 2001, Webster *et al.* 2005, Urbanek *et al.* 2012, Bressette *et al.* 2012) have largely focused on the negative conservation consequences of deer, in particular deer feeding on favored species leading to shifts in plant community composition. By creating large experimental exclosures, I was able to address this issue in prairie remnants.

Exclosures were effective at reducing herbivory, providing evidence of increased feeding on favored species at the prairie/forest edge plots (Fig. 5 B). Approximately 7-8% of all stems were

damaged in study plots open to deer, comparable to the intensity of herbivory in similar studies (1.3 to 10.5%, Harris 2012). In this two year study, I did not find shifts in plant community due to deer exclusion. However, I did observe a possible positive conservation consequence of deer herbivory: reduced woody colonization (with differences most evident in the edge plant communities, Fig. 8). In Africa, herbivory from large animals, such as elephants, giraffe, and rhinoceros, have been found to suppress the spread of palatable woody species in savannahs but increase the relative abundance of unpalatable woody species (Gordijn *et al.* 2012). It is possible that white-tailed deer reduce the movement of favored woody species into the prairie by targeting those species while browsing (Russell *et al.* 2001, Gooch 2009). Van der Hoek *et al.* (2002) suggested that shrubs on the prairie facilitate or encourage white-tailed deer movement into the prairie but also provide forage (See also Gooch 2009). They found that shrub species favored by deer had relatively low abundance compared to those that deer left undisturbed. Woody colonization of grasslands is an important conservation issue in North America, as it threatens the open habitat required for most prairie species. Woody plant populations are difficult to remove and pose one of the greatest challenges to prairie management.

Sunflower species are known to be favored by deer (Masterson Chapter 2, Englund and Meyer 1986, Anderson *et al.* 2001). *Helianthus* were always more abundant at the prairie edge (Table 8), and a greater proportion of *Helianthus* stems at the edge was damaged by deer, in fall 2015 (Figure 5 B). However, surprisingly, deer herbivory increased the abundance of *Helianthus* stems at the forest edge, as seen in the greater number of stems in control vs. exclosure plots. This may be the product of clonal integration, an adaptation in rhizomatous plants that may allow for shoot production along the rhizome in response to disturbance sensed by other ramets in the genet (see Hems and Mattson 1992, Wilsey 2002).

Clonal integration is a well-studied tolerance response (Callaghan *et al.* 1992, Gao *et al.* 2014). It is noteworthy that the increase in *Helianthus* abundance in response to deer herbivory was only significant in edge plots. This result could be due to a greater intensity of herbivory on *Helianthus* at the edge. However, the lack of response in interior plants could also be a reflection of the limitations imposed by clonal integration. Water and nutrients, resources more limited in the prairie interior, have been found to restrict rhizome shoot production after damage (He *et al.* 2011, Wolfer and Straile 2012). Another explanation for the lack of effect of herbivory on *Helianthus* abundance in the interior could be the relatively low abundance of sunflowers in those plots as compared to edge plots (i.e., low sample size).

Beyond changes to abundance, deer herbivory also affected the morphology and reproduction of perennial *Helianthus* (Masterson Chapter 2). Damage from deer causes these forbs to branch, providing an opportunity for increased inflorescence counts. However, *Helianthus* in the prairie rarely succeeded in producing inflorescences post herbivory because of continual deer browse (Masterson Chapter 2). Because deer herbivory may cause an increase in the abundance of *Helianthus* stems (potentially energy input from the rhizome) and an increased number of branches, it is possible that pressure from deer herbivory could have a negative effect on the long-term survival of individual plants. Both of these tolerance responses are “expensive,” utilizing stored energy from the rhizome that may be important to overwintering. This question could be addressed by a multi-year artificial herbivory study where rhizomes are transplanted with enough space between them to accommodate their spread.

To evaluate these and other vegetation changes due to herbivory, longer term observations are needed. This is particularly important because many prairie plants can live for decades (Keeler 1991, Wagenius *et al.* 2012). It is also interesting that Harris (2012) found deer herbivory increased richness and diversity in newly planted prairie restorations, conflicting with deer effects in established prairies (Anderson 2001, 2006). Adding study sites to recently established prairies would help us to understand the variance in deer effects between prairie remnants and restorations.

It is important to note that the deer population in the study areas has been higher than historic numbers for many years (personal communication, Lloyd Fox). The effect of deer on sensitive species therefore would likely have already taken its toll before the exclosures were erected. With the continuation of this study, I will be able to identify the return of any sensitive plant species to exclosed areas. I will also be able to record changes to the abundance of species favored by deer such as high nitrogen legumes (Nisi *et al.* 2015), sensitive forbs (see Gooch 2009), and members of the *Asteraceae*. It is interesting to note that land managers have seen the return of sensitive plant species to some prairies once deer populations in the area are managed, including *Lithospermum* (puccoons) and *Erythronium* species (fawn lilies) (personal communication, Matt Garrett, Field Biologist for Johnson County Parks and Recreation, Kansas). Finally, it would also be interesting to compare herbivory in prairies of high deer abundance and low deer abundance. In forest systems, deer herbivory is thought to be dependent on the density of the herbivore and which species deer selectively browse, as it varies by location (Côté *et al.* 2005). Studying multiple prairies of varying deer density would highlight the differences in herbivory as deer density increases.

Future directions

In addition to long-term studies on the effects of deer herbivory, there are many other opportunities for future work in this field. Three areas of particular interest include a more comprehensive understanding of increased richness in ecotone areas, spatiotemporal deer behavior in prairies, and the effects of deer herbivory at multiple spatial scales.

First, I found the richness of the plant community to be greater at the prairie/forest edge, supporting the findings of similar studies (Valett *et al.* 2010 (forest/cropland and forest/developed land), Jacot *et al.* 2012 (meadow/forest)). However, when woodland species are removed from the analysis, there are no significant differences in the richness between locations. This provides evidence that increased richness at the edges is due to the colonization of woodland species into the prairie as opposed to differences in numbers of prairie species at the two locations. Ideally, a study comparing forest to prairie plant communities would incorporate forest interior sampling, allowing for a better understanding of which species inhabit the ecotone and which species are colonizing the prairie from the forest interior. For example, Łuczaj and Sadowska (1997) found that grassland richness in the Carpathian Foothills (Poland) was greater than adjacent forest richness, but both were lower than the richness of the shared ecotone. This may be true of the tallgrass prairie/deciduous forest ecotone, as well.

Second, studying the behavior of deer on the prairie would shed more light on how deer select plants, the seasonality of their diet, and the other resources provided to them by the plant community (e.g., shelter, nursery). In the field, I observed an intriguing pattern of herbivory. It appeared that deer browsed the edge plant community heavily in the early spring, which drove

the branching of *Helianthus* stems. In the summer, they seemed to turn their attention to interior prairie, like *Rosa* and *Rubus*, when those plants produce highly nutritious fruit. Finally, deer herbivory seemed to increase at the ecotone again in the late summer months as *Helianthus* produced inflorescences. These patterns were seen in the community data for *Helianthus* but not for *Rosa* and *Rubus*, probably because interior sampling plots contained few of these species. Data collection targeted on the deer feeding patterns might provide an important complement to this study. The spatiotemporal behavior of deer species is well studied in some regions through long-term field observation and radio-telemetry studies (see Klaver *et al.* 2008, Monteith *et al.* 2010, Massé and Côté 2013). However, these studies focus on regional movements across seasons and rarely, if ever, address deer use of grassland systems.

Finally, there is a need for further research on a range of spatial scales reflecting the varying size of prairie remnants. Deer are capable of utilizing hundreds of kilometers of habitat and likely affect plants at a landscape level. It is possible that deer use of remnant prairies is contingent on the surrounding land use and seasonal food availability. Grund *et al.* (2002) found that deer preferentially use protected areas (parks, conservation areas) and occupy reduced home ranges in urban areas. In general, I would expect that deer in urban areas would be forced into prairie remnants in the region while rural prairies would experience less pressure from deer herbivory (the urban Ogg Prairie had, for example, very high densities prior to the start of culling in 2009). My studies would have to be expanded into several additional prairies to address the differences in deer herbivory in urban vs. rural prairie remnants.

Chapter 2: Response of perennial sunflowers, *Helianthus pauciflorus* and *Helianthus hirsutus*, to natural and artificial herbivory

Introduction

On average, terrestrial plants accrue 18% damage in the field due to invertebrate and vertebrate herbivores (Cyr and Pace 1993). As sessile organisms, plants have developed defensive traits in response to this pressure, including resistance and tolerance (Strauss and Agrawal 1999, Martin et al. 2015). The latter may be particularly significant for long-lived perennials as the impacts of herbivory may affect the plant for multiple years (Loe et al. 2007, Lehdal and Agren 2015).

Tolerance can be described as the mechanisms by which plants regrow or reproduce after damage from herbivores (i.e., accommodating the herbivore). A more succinct definition would be endurance through damage (Pujalon et al. 2011).

In the presence of herbivores, tolerance has been shown to provide a fitness advantage to plants (Tiffin 2000). However, tolerance is not expressed until the individual plant experiences damage, which may never occur (Agrawal 2000). If an herbivore does visit the plant, it may remove a significant amount of vegetative and/or reproductive tissue on the first visit. If the plant survives this visit from a predator, the plant may expend significant energy in a tolerance response to the damage, potentially increasing the plant's reproductive success when compared to an undamaged plant (overcompensation, see below) (Agrawal 2000).

The most common form of tolerance observed in plants is compensatory growth, or growth in response to damage (Belsky *et al* 1993). A particularly common and well-studied example of

compensatory growth is that which occurs after apical meristem damage (AMD, Wise and Abrahamson 2008, Klimesova *et al.* 2014). The apical meristem, the meristematic tissue found at the tips of shoots and roots, is responsible for primary growth or elongation. It is potentially more nutritious and palatable than older parts of the plant making it more attractive to herbivores (Benner 1988). When this tissue is removed from a plant, meristem tissues in other areas are activated, leading to branching, adventitious shoot growth, or other compensatory growth (Haukioja and Koricheva 2000).

Tolerance through compensatory growth ranges in magnitude across plant species, from negative effects to overcompensation. With regard to reproduction after damage from herbivory, Wise and Abrahamson (2008) found that AMD increased the number of branches produced by perennial goldenrod but did not lead to increased flower/inflorescences production (see also Spirko and Rossi 2015). However, other studies provide evidence of overcompensation to AMD, i.e., improved reproductive success in damaged plants (Belsky, 1986, Paige and Whitham 1987, Aarssen 1995).

The extent of plant response to herbivory is an important conservation question at the ecotone of the tallgrass prairie and the deciduous forest in North America, where white-tailed deer (*Odocoileus virginianus* Zimmerman) are increasing in abundance. Most past studies on deer herbivory focused on woodland systems and revealed important effects of herbivory. For example, Englund and Meyer (1986) found that deer are unlikely to cause mortality on targeted plants when browsing; rather deer focus on apical meristem removal, which may lead to change in plant growth, plant structure, or reproduction. Other studies revealed that plants browsed by

deer may be smaller and less likely to flower than those protected from deer (Augustine and Frelich 1998, Knight 2004).

Less is known about differential deer herbivory on plant species. Nisi *et al.* (2015) found that deer prefer legumes with relatively high nitrogen content and for plants in recently burned areas. Gooch (2009) found that deer preferentially browse certain prairie species, such as species of *Erigeron*, *Penstemon*, *Gaillardia*, and *Oenothera*. Tolerance could explain why some plant species that are palatable to white-tailed deer have persisted in areas of high deer density in eastern North America (Martin *et al.* 2015).

My research focused on the effects of herbivory on plant growth, morphology, and reproduction with the goal of understanding how deer foraging affects prairie plant ecology. I chose *Helianthus* as a study genus because it is known favored forage of white-tailed deer (Masterson Chapter 1, personal communication, Larry Rizzo, Natural Historian, Missouri Department of Conservation, Englund and Meyer 1986, Gooch 2009). Perennial plants commonly respond to AMD, the type of damage inflicted by deer, by branching. My studies explore the compensation of *Helianthus* to herbivory pressure, focusing on plant size, branching patterns, and subsequent number of reproductive structures. Ultimately, given our understanding of AMD and compensation, I ask whether the net effect of herbivory on *Helianthus* is negative or positive.

Methods: *Helianthus* Prairie Exclosure Study

Study Species

The perennial *Helianthus* species at the site (*H. pauciflorus* Nutt. [stiff sunflower], *H. hirsutus* Raf. [woodland sunflower]) were analyzed as a single group because of intergrading morphologies that caused difficulties in identification of some individuals.

Study Area Description

The study was conducted at Kill Creek Prairie, a remnant prairie (~ 8 ha or 20 acres) owned and managed by Johnson County Parks and Recreation Department, in Northeastern Kansas, U. S. This site lies within Kill Creek Park (Olathe, KS) in a rural area approximately 30 km southwest of Kansas City, Kansas (~ GPS coordinates: 38.917885, -94.974586).

The prairie is managed with a combination of controlled burning (approximately biennially), spot herbicide spraying, and mowing. Areas directly adjacent to the study plots (see below) were unmanaged for the duration of the study. Kill Creek Prairie is highly diverse, containing approximately 200 native and naturalized plant species (Personal communication, C. Freeman, R. L. McGregor Herbarium, University of Kansas).

Deer Management

Deer at Kill Creek Prairie were unmanaged; however, private land bordering the park may be hunted in accordance with state regulations. Deer populations were estimated to be 0.209, 0.14, and 0.198 deer per hectare in surveys conducted in Fall 2015, Spring 2015, and Fall 2014 respectively (Table 1, see Masterson, Chapter 1 for more details).

Deer Exclosures

Three experimental plots were established in June 2014 at the forest/prairie ecotone (Figs. 1 A, 2). Each plot consisted of a fenced deer exclosure treatment and an adjacent unfenced control. I placed plots at the prairie edge in areas that contained *Helianthus*. Each half of the plot was randomly assigned to a treatment: control or exclosure. The exclosure treatment excluded large mammals from the plant community through the erection of deer fencing. The deer exclosures were 6 m² and 2.75 m tall (Fig. 3). The corners were supported with 3 m long fence posts and guy lines. The fencing was heavy duty plastic deer fencing (2.54 cm mesh). All damage to exclosures was repaired regularly. No evidence of deer entry was observed, during the study (for more details on the deer exclosures, see Masterson, Chapter 1).

Vegetation Sampling and Herbivory

In order to evaluate the differences between the plant communities, four 1m² quadrats were established in each control and exclosure, totaling 8 quadrats per paired experimental area (Fig. 2). In both 2014 and 2015, 15 *Helianthus* stems per quadrat were tagged in spring (June and May, respectively) and revisited in the fall (August and September). Specific dates were: spring 2014 (June 19-July 2), fall 2014 (September 9 – October 6th), spring 2015 (May 2-June 10), fall 2015 (Aug 25-Sept 6). When greater than 15 *Helianthus* stems were present in the spring, study stems were chosen haphazardly. Fewer *Helianthus* stems were tagged if there were fewer than 15 were available in the quadrat. In each season, data were collected on height (to the top node), stem diameter (just below the lowest node), height of location on stem or branch where each herbivory event was observed, number of herbivory events, number of branches, and number of

inflorescences. The control and exclosure treatments within a plot were sampled within 48 hours of each other to reduce variation due to time.

Methods: *Helianthus* Artificial Herbivory Study

Study Area Description

The study was conducted at the Kansas University Field Station, approximately 10 km north of Lawrence, Kansas, U. S. (~39.050161, -95.187551) and 25 km from Kill Creek Prairie.

Deer Exclosures

The deer exclosure at this site was a permanent construction of metal deer fencing and posts, with an entry point through a heavy duty gate. The fenced area was 55 x 25 m and approximately 3 m tall. No sign of deer activity was observed in the exclosure during the study.

Vegetation Sampling

Rhizomes were dug from Kill Creek Prairie (March 2014) and stored in an outdoor lath house during site preparation. In July 2014, the rhizomes were weighed and transplanted into the study site in random order at 2 m intervals in 6 rows spaced 2.5 m apart (Fig. 10). The rhizomes were overwintered in the ground. Rhizome locations were examined for emerging stems in May 2015. Surviving rhizomes were ranked by rhizome weight, and sequential groups of four rhizomes were randomly assigned to a treatment group. Treatment groups were control, spring herbivory (May), fall herbivory (August), and both spring and fall herbivory (May and August).

Spring and fall herbivory was imposed on May 13 – 15, 2015 and August 27 – 29, 2015, respectively. Artificial herbivory treatments were applied within 48 hours to reduce variation due

to time. To remove tissue, artificial herbivory was conducted with a white-tailed deer skull to replicate the damage enacted by deer. The directional force applied by deer was also simulated to produce a visually comparable tearing pattern on the plant stem. I removed the top node, or if the plant had branched, the top nodes on the top branches of the plant. For an unbranched plant, for example, approximately 5 cm of the main stem was removed. This simulates what I frequently observed in prairies where deer bite off only the top portion of a plant. See Fig. 4 for pictures of deer herbivory and how it differs from rodent herbivory that also occurred naturally in the plot.

Due to time limitations in the fall, I was unable to complete treatment on all plants assigned to these groups, leading to unequal samples sizes (spring only: $N = 30$), fall only ($N = 8$), spring and fall ($N = 10$), and control ($N = 33$). Although analyses were done on the full factorial study, my focus has been on the control vs. spring herbivory comparisons.

Size, herbivory, and reproductive data were collected for each rhizome location just prior to the spring herbivory treatment (May 13-15), June 23 – 25, just prior to the fall treatment (August 27-29), and on October 10-15, 2016. Measurements were made on diameter of growth (greatest distance between two stems from the same rhizome), stem count, height of each stem, height of herbivory, number of herbivory events, number of branches, and number of inflorescences. See Prairie Enclosure section above for details on how measurements were made.

Statistical methods

Analyses were completed in Minitab 17 (2010) unless otherwise indicated. For continuous variables in the prairie exclosure study, I used general linear models, testing main effects of treatment, plot, and the interaction. For the artificial herbivory study, analyses were conducted on the complete factorial design unless otherwise noted. Results of analyses on interactions of main effects were only reported if a significant effect was found. Stem count was a helpful covariate in the artificial herbivory study and was used for all morphology analyses. When data were not distributed normally, transformations were attempted to normalize the data. If further modification was necessary, non-parametric analyses were used on the original data (Kruskal-Wallis). Normality was assessed by examining the residuals plots. Binary data (presence/absence) were analyzed using binary logistic regression.

Results: *Helianthus* Prairie Exclosure Study

Herbivory

Late spring erection of deer exclosures meant that deer had access to the *Helianthus* stems until the second week of June 2014. I found no difference in the probability of herbivory occurring for 2014 for the control vs. the exclosure treatment, but for stems with herbivory, there was a significant interaction between the treatment and plot factors, for the number of times a stem was damaged by deer herbivory. The control plots consistently experienced a higher intensity of herbivory than the exclosed areas, with variance in the magnitude of response from plot to plot (Interaction $F_{1, 155}=4.09$, $p=0.019$).

In 2015, plants in the control treatment were more likely to experience herbivory than those in the exclosures (Fig. 11, Percent damaged stems: Plot 1 - Pearson χ^2 (DF=1) =17.58, $p < 0.001$, Plot 2 - Control sample size too small for chi square test, Plot 3 - Pearson χ^2 (DF=1) =26.99, $p < 0.001$).

Morphology

In fall 2014, there were no significant differences in the height of plants in the control and exclosure treatments. As noted earlier, late spring erection of cages meant deer had access to the *Helianthus* stems; many stems in the exclosure experienced herbivory prior to being protected. By spring 2015, there was a significant interaction of treatment and plot for plant height with greater height in exclosure treatments but variation among plots (Table 9, Fig. 12 A). The same pattern was observed in fall 2015 (Table 9, Fig. 12 B).

I found that stem diameter was sometimes larger in the control plots, but with variation from plot to plot, leading to a significant interaction term in fall 2015 (Table 10). Similar results were seen in spring 2015 ($p = 0.063$, interaction term, Table 10).

Stems in the control plots were more likely to branch than those in the exclosures in both 2014 and 2015 (Table 11). For example, in fall 2015, 43% of stems in the control treatment branched, only 14% in the exclosures branched. There were no significant differences in the number of branches produced by stems due to the treatment.

Reproduction

Stems in the exclosures were significantly more likely to have an inflorescence at the end of the growing season, in both 2014 and 2015 (Table 12). For example, in fall 2015, protected stems were 2.02 times more likely to produce inflorescences than those in the control treatment (averaged across all plots).

In both 2014 and 2015, there were no significant differences in the number of inflorescences produced per stem due to treatment, when only stems with inflorescences were considered. In fall 2015, there was a relationship between treatment and plot for inflorescence diameter (Fig. 14, $F_{2,82}=2.64$, $p=0.078$).

Results: *Helianthus* Artificial Herbivory Study

Rodent herbivory

An unexpected variable in this study was heavy rodent herbivory. Damage from rodent herbivory was easily distinguished from other form of damage because rodents remove tissue from plants using clean, angular cuts (Fig. 4). Rodent-affected rhizomes were defined as those with greater than 50% of their stems damaged by rodents. Rodent herbivory was significantly higher in the control group than in the spring herbivory treatment group (count of rodent herbivory events per rhizome, Kruskal-Wallis, $p=0.002$). As a consequence, initial analyses on plant morphology and growth were done both with and without inclusion of rodent-affected rhizomes. Given that both sets of analyses gave similar results, I only present analyses for the full data set.

Morphology

Neither the diameter of growth or stem count were affected by the herbivory treatments or the starting rhizome weight.

Rhizomes subject to spring herbivory had a lower maximum height (defined as the height of the tallest node of an individual stem produced by a rhizome) than those in the control group ($F_{1,76}=6.06$, $p=0.016$), consistent with the findings of the prairie exclosure study. Control rhizomes were 1.25 times taller than those in the spring herbivory treatment.

Herbivory in the spring also led to a higher probability that rhizomes had branching stems (see Table 13). 70% of the 30 rhizomes in the spring treatment had stems that branched while 30% of the 33 rhizomes in the control treatment had stems that branched. This general pattern is consistent with the prairie exclosure study results.

When considering only rhizomes with branched stems, those with spring herbivory grew 4 x more branches per stem than those in the control group (Fig. 15, $F_{1,35}=9.69$, $p=0.062$). This result was not seen in the field study. The spring treatment also led to significantly more branched stems per rhizome than found in the control (Fig. 16, total branched stems/stem count, $F_{1,35}=32.67$, $p<0.001$).

Reproduction

Only 27 rhizomes produced inflorescences across all treatment groups (N=11 of 33 for control, N=15 of 30 for spring, N=0 of 8 for fall, N=1 of 10 for spring and fall). Analyses on solely the control and spring herbivory treatment groups revealed a trend for more inflorescences per stem

on control rhizomes than in the spring treatment, but these differences were not statistically significant (Fig. 17).

Discussion

As white-tailed deer populations exceed historic numbers in the U.S. (Schmitz and Sinclair 1997) it is increasingly important to understand their effects on plant communities. Shrinking ecosystems, like the tallgrass prairie, are of particular interest because of their relationship to the deer's favored habitat, forest edge. Recent work documents that deer are browsing heavily in fragmented, remnant prairies (Côté *et al.* 2004, Gooch 2009), but few studies have focused on effects of deer herbivory on prairie species. This study addresses this gap of knowledge using both a field experiment (where deer access, but not herbivory on individual stems, was controlled) and a field artificial herbivory study. Importantly, both studies provided similar results. Herbivory led to shorter plants that branched more often, providing the opportunity to produce more inflorescences when compared to plants without herbivory. However, there was no increase in reproduction with herbivory in either study. In the prairie, this lack of compensation is likely because deer herbivory in the prairie was intense throughout the growing season, often resulting in a loss of both apical meristem tissue in the spring and later reproductive tissue in the fall. Somewhat surprisingly, the artificial herbivory experiment also saw no significant increase in inflorescences even though the spring only herbivory treatment occurred months prior to fall reproduction. Thus, despite increased branching in damaged stems, herbivory had neutral (artificial herbivory effects) to negative (prairie enclosure study) effects on *Helianthus* reproduction. Wise and Abrahamson (2008) found that a plant's ability to

overcompensate when damaged was somewhat dependent on competition and resource availability in its environment, suggesting directions for future experiments.

It is interesting that in the artificial herbivory study plants produced many more branches in response to herbivory than expected based on the results of the prairie study. Although this difference was only marginally significant ($p = 0.062$), it is important to consider because it may be due to a disparity in study design. In the artificial herbivory study, the treatment was imposed on all stems produced by a rhizome, while the field study focused on response of a single stem. This difference in herbivory intensity may have led to the varying response between the two studies. Wise and Abrahamson (2008) explain that apical meristem loss induces the activation of axillary meristems, increasing the number of active meristems on the plant. It is likely that as more AMD is experienced by a rhizome, more meristem tissue will be activated.

Future Directions

Strauss and Agrawal (1999) recognized five mechanisms involved in plant tolerance to herbivory: increased net photosynthetic rate after damage, high relative growth rates, increased branching or tillering after release of apical dominance, pre-existing high levels of carbon storage in roots for allocation to above-ground reproduction, and the ability to shunt carbon stores from roots to shoots after damage. My research on *Helianthus* addressed one of these mechanisms, branching patterns, leaving ample opportunities for further investigation.

I recommend further inquiry into two additional aspects of perennial *Helianthus* tolerance of herbivory. First, does deer herbivory lead to increased asexual reproduction in perennial prairie

plants? In chapter 1, I described an unexpected response of *Helianthus* to deer herbivory, as the abundance of stems increased in prairie control areas. It is possible that this response is the result of compensatory asexual reproduction. Further research on the asexual response of perennial prairie plants, such as perennial *Helianthus*, to herbivory damage would help us to understand the extent of their tolerance to herbivory. Investment in rhizome structures during heavy herbivory years, for example, may allow the population to “hang on” until the habitat is more hospitable. Studies of other species provide some evidence that damage to a plant’s reproductive organs may lead to investment in another mode of reproduction. For example, Buchanan (2015) found that AMD increased asexual reproduction (in this case, clone number) in water hyacinth. However, other studies showed that rhizome growth or structure, often related to asexual reproduction, was not increased with herbivory. Specifically, Rooney (1997) found no significant difference between the inter-nodal rhizome lengths of *Maianthemum canadense* plants growing in natural refugia from deer (on top of large boulders) and those exposed to deer herbivory.

A second opportunity for future research is investigating the effect of artificial herbivory methodology on study results. My artificial herbivory results may have been affected by my methods of inflicting damage to the plants. Although use of the deer skull simulated the tearing action, it is noteworthy that Liu *et al.* (2012) found herbivore saliva has a stimulating effect on growth in damaged plants. A closer emulation of deer herbivory may provide more insight into the morphological responses of perennial plant species to this pressure.

Thesis Conclusions

The rapid decline of natural ecosystems has altered many relationships between plants and animals. As human infrastructure encroaches on remnant tallgrass prairie fragments and our focus turns to conservation, it becomes increasingly important to understand how herbivores utilize this plant system. Native spaces may act as oases for wildlife, leading to increased herbivory pressure on fragmented plant communities (Grund *et al.* 2002, Urbanek 2005). Van Dyke *et al.* (2012) found that elk (*Cervus elaphus* Linnaeus), used human modified landscapes more heavily (46% higher) than control areas over time. A broader study revealed that deer were one of few wildlife species that did not discriminate in their use of ranges with varying levels of human disturbance and activity (Markovchick-Nicholls *et al.* 2008). It is therefore of interest to examine effects of deer herbivory across both natural and transformed landscapes.

As white-tailed deer populations grow to unprecedented numbers throughout much of North America, pressure from deer herbivory must be considered as a factor in prairie conservation. Deer may significantly affect the morphology and reproductive success of prairie plants. Though deer are adept at utilizing urban areas for food and other resources, they continue to use remaining natural areas heavily (Waller and Alverson 1997, Côté *et al.* 2004, Gooch 2009). Further observations of deer behavior in fragmented ecosystems will provide insight on how this herbivore might be managed to increase conservation success.

My community-level study (Chapter 1) laid the groundwork for an extended investigation into the effects of deer herbivory on tallgrass prairie remnants. At current densities, deer show favor for certain plant species in the studied prairies. Although plant compositional changes were

generally not apparent with two years of enclosure, it is possible that over time, deer will have an impact on the abundance of particular species in a community. This is of particular concern as deer populations will likely continue to grow if unchecked. However, one aspect of plant composition (i.e., abundance of woody species) was altered by deer herbivory, and coverage of these species may change with deer pressure. This effect, in contrast to the potential negative effects of herbivory on target prairie species, supports the idea that disturbance from these herbivores aids in the persistence of prairie remnants. To my knowledge, this is the only ongoing study of the effects of deer browse on remnant prairie communities in the United States, making it of importance to informing deer management and prairie conservation practices. I plan to continue data collection to be able to address the long-term effects of deer herbivory on this fractured grassland ecosystem.

Through observation of a favored genus, *Helianthus* (Chapter 2), I found that deer impact the morphology and reproductive structures of perennial plants. Branching and increased shoot production are expenditures to targeted plants but may provide a reproductive benefit, at certain herbivore densities. In these studies, inflorescences produced post herbivory were comparable in size to those grown on undamaged *Helianthus* stems. However, in the prairie *Helianthus* study, stems in the control plots were less likely to produce inflorescences than protected stems. Deer may potentially reduce the lifespan of perennial plants through repetitive apical meristem damage, altering the abundance of favored species in communities over time. It is clear that continued study is necessary to reveal the “hidden” effects of intense herbivory. Ultimately, investigating deer use of fragmented landscapes will be important to sustaining prairie ecosystems and other conservation targets.

References

- Aarssen, L. W. 1995. Hypotheses for the evolution of apical dominance in plants: implications for the interpretation of overcompensation. *Oikos* 74: 149–156.
- Agrawal, A. A. 2000. Overcompensation of plants in response to herbivory and the by-product benefits of mutualism. *Trends in Plant Science* 5(7): 309-313.
- Aizen, M. A., Feinsinger, P. 1994. Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest, Argentina. *Ecology* 75(2): 330-351.
- Alverson, W. S., Waller D. M., Solheim, S. L. 1988. Forests too deer: edge effects in Northern Wisconsin. *Conservation Biology* Vol 2, No. 4: 348-358.
- Amsberry, L. K., Maron, J. L. 2006. Effects of herbivore identity on plant fecundity. *Plant Ecol* 187: 39-48.
- Anderson, R. C., Corbett, E. A., Anderson, M. R., Corbett, G. A., Kelley, T. M. 2001. High white-tailed deer density has negative impact on tallgrass prairie forbs. *The Journal of the Torrey Botanical Society* 128(4): 381-392.
- Anderson R.C. 2006. Evolution and origin of the central grassland of North America: climate, fire, and mammalian grazers. *Journal of Torrey Botanical Society* 133: 626-647.
- Anderson, M. J., Gorley, R.N., Clark, K.R. 2008. PERMANOVA + for PRIMER: Guide to Software and Statistical Methods, PRIMER-E. Plymouth, UK.
- Augustine, D. J. Frelich, L. E. 1998. Effects of white-tailed deer on populations of an understory forb in fragmented deciduous forests. *Conserv. Biol.*, 12: 995-1004.
- Bagchi, S., Ritchie, M. E. 2010. Herbivore effects on above- and belowground plant production and soil nitrogen availability in the Trans-Himalayan shrub-steppes. *Oecologia Ecosystem Ecology* 164: 1075-1082.
- Batzli, G. O., DeJaco, C. E. 2013. White-tailed deer (*Odocoileus virginianus*) facilitate the development of nonnative grasslands in central Illinois. *Am. Midl. Nat.* 170: 323-334.
- Belsky, A. J. 1986. Does herbivory benefit plants? A review of evidence. *Am. Nat.* 127: 870-892.
- Belsky, A. J., Carson, W. P., Jensen, C. L., Fox, G. A. 1993. Compensatory growth: herbivore optimization or red herring? *Evolutionary Ecology* 7(1): 109-121.
- Benner, B. L. 1988. Effects of apex removal and nutrient supplementation on branching and seed production in *Thlaspi arvense* (Brassicaceae). *American Journal of Botany* 75: 645–651.

- Bishop, J.R.B. and Marques, T.A. 2009. Distance 6.0. Release "2". Research Unit for Wildlife Population Assessment, University of St. Andrews, UK. <http://www.ruwpa.st-and.ac.uk/distance/>
- Bist, S.S. 2006. Elephant conservation in India – an overview. *Gajah* 25: 27–35.
- Bressette, J. W., Beck, H., Beauchamp, V. B. 2012. Beyond the browse line: complex cascade effects mediated by white-tailed deer. *Oikos* 121: 1749-1760.
- Briggs J., A. Knapp, and B. Brock. 2002. Expansion of woody plants in tallgrass prairie: a fifteen year study of fire and fire-grazer interactions. *American Midland Naturalist* 147: 287-294.
- Buchanan, A. L. 2015. Effects of damage and pollination on sexual and asexual reproduction in a flowering clonal plant. *Plant Ecol* 216: 273-282.
- Callaghan, T. V., Carlsson, B. A., Jónsdóttir, I. S., Svensson B. M., Jonasson, S. 1992. Clonal plants and environmental change: introducing the proceedings and summary. *Oikos* 63 (3): 341-347.
- Côté, S. D., Rooney, T. P., Tremblay, J. Dussault, C., Waller, D. M. 2004. Ecological impacts of deer overabundance. *Annu. Rev. Ecol. Evol. Syst.* 35: 113-147.
- Cyr, H., Pace, M. L. 1993. Magnitude and patterns of herbivory in aquatic and terrestrial ecosystems. *Nature* 361: 148-150.
- Englund, J. V., Meyer, W. J. 1986. The impact of deer on 24 species of prairie forbs. *The Prairie: Past, Present, and Future: Proceedings of the Ninth North American Prairie Conference*: 210-212.
- Enck J. W., Decker D. J., Brown T. L. 2000. Status of hunter recruitment and retention in the United States. *Wildl. Soc. Bull.* 28: 817–24.
- Fletcher, J. D., Shipley, L. A., McShea, W. J., Shumway, D. L. 2001. Wildlife herbivory and rare plants: the effects of white-tailed deer, rodents, and insects on growth and survival of Turk's cap lily. *Biological Conservation* 101: 229-238.
- Gao, Y., Wang, D., Xing, F., Liu, J., Wang, L. 2014. Combined effects of resource heterogeneity and simulated herbivory on plasticity of clonal integration in a rhizomatous perennial herb. *Plant Biology* 16 (2014): 774-782.
- Gooch, S. J. 2009. Effects of white-tailed deer herbivory on a tallgrass prairie remnant. ProQuest Dissertations Publishing. Order No. MR60623.

- Gordijn, P. J., Rice, E., Ward, D. 2012. The effects of fire on woody plant encroachment are exacerbated by succession of trees of decreased palatability. *Perspectives in Plant Ecology, Evolution and Systematics* 14: 411-422.
- Grund, M. D., McAninch, J. B., Wiggers, E. P. 2002. Seasonal movements and habitat use of female white-tailed deer associated with an urban park. *J. Wildlife Management* 66(1): 123-130.
- Haddad, N. M., Brudvig, L. A., Clbert, J., Davies, K. F., Gonzales, A., Holt, R. B., Lovejoy, T. E., Sexton, J. O., Austin, M. P., Collins, C. D., Cook, W. M., Damschen, E. I., Ewers, R. M., Foster, B. L., Jenkins, C. N., King, A. J., Laurance, W. F., Levey, D. J., Margules, C. R., Melbourne, B. A., Nicholls, A. O., Orrock, J. L., Song, D. X., Townshend, J. R. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *PNAS* 111(9): 3484-3493.
- Harris, P. 2012. The role of deer browsing on plant community development and ecosystem functioning during tallgrass prairie restoration. Order No. 1566897 Southern Illinois University at Carbondale, 2014. Ann Arbor: *ProQuest*. Web. 5 June 2016.
- Haukioja, E., Koricheva, J. 2000. Tolerance to herbivory in woody vs. herbaceous plants. *Evolutionary Ecology* 14: 551-562.
- He, W. M., Alpert, P., Yu, F. H., Zhang, L. L., Dong, M. 2011. Reciprocal and coincident patchiness of multiple resources differentially affect benefits of clonal integration in two perennial plants. *J. of Ecology* 99: 1202-1210.
- Hermes D. A. and Mattson W. J. 1992. The dilemma of plants: to grow or defend. *Quart. Rev. Biol.* 67: 283-335.
- Hierro, J. L., Clark, K. L., Branch, L. C., Villarreal, D. 2011. Native herbivore exerts contrasting effects on fire regime and vegetation structure. *Oecologia Community Ecology* 166: 1121-1129.
- Howe, H. F. 1994. Managing species diversity in tallgrass prairie: assumptions and implications. *Society of Conservation Biology* 8(3): 691-704.
- Jacot, K., Eggenschwiler, L., Beerli, C., Bosshard, A., Suter, M. 2012. Significance of different types of meadow edges for plant diversity in the Swiss Alps. *Agriculture, Ecosystems & Environment* 153: 75-81.
- Johnson, B. L., Haddad, N. M. 2011. Edge effects, not connectivity, determine the incidence and development of a foliar fungal plant disease. *Ecology* Vol. 92, No. 8: 1551-1558.
- Keeler, K. H. 1991. Survivorship and recruitment in a long-lived prairie perennial, *Ipomoea leptophylla* (Convolvulaceae). *American Midland Naturalist* 126(1): 44-60.

- Kindscher, K., Wells, P. V. 1995. Prairie plant guilds: an ordination of prairie plant species based on ecological and morphological traits. *Vegetatio* 117:29-50.
- Kindscher, K., Busby, W. H., Delisle, J. M., Dropkin, J., Freeman, C. C. 2005. A natural areas inventory of Douglas, Johnson, Leavenworth, Miami, and Wyandotte counties in Northeast Kansas. Open-File Report No. 124. Kansas Biological Survey, Lawrence, KS. 79 pp.
- Klaver, R. W., Jenks, J. A., Deperno, C. S., Griffin, S. L. 2008. Associating seasonal range characteristics with survival of female white-tailed deer. *J. of Wildlife Management* 72(2): 343-353.
- Klimesova, J., Malikova, L., Rosenthal, J. Smilauer, P. 2014. Potential bud bank responses to apical meristem damage and environmental variables: matching or complementing axillary meristems. *PloS One* 9(2): e88093 doi:10.1371/journal.pone.0088093.
- Knight, T. M. 2004. The effects of herbivory and pollen limitation on a declining population of *Trillium grandiflorum*. *Ecol. Appl.* 14(3): 915–928.
- Laurence, W. F. 2000. Do edge effects occur over large spatial scales? *Trends in Ecology and Evolution* 15: 134-135.
- Lehndal, L., Ågren, J. 2015. Herbivory differentially affects plant fitness in three populations of the perennial herb *Lythrum salicaria* along a latitudinal gradient. *PLoS ONE* 10(9): e0135939. doi:10.1371/journal.pone.0135939.
- Liu, J., Wang, L., Wang, D., Bonser, S. P., Sun, F., Zhou, Y., Gao, Y., Teng, X. 2012. Plants can benefit from herbivory: stimulatory effects of sheep saliva on growth of *Leymus chinensis*. *PloS One* 7(1): e29259.
- Loe, G., Torang, P., Gaudeul, M., Agren, J. 2007. Trichome production and spatiotemporal variation in herbivory in the perennial herb *Arabidopsis lyrata*. *Oikos* 116: 134-142.
- Łukasz, L., Sadowska, B. 1997. Edge effect in different groups of organisms: vascular plant, bryophyte and fungi species richness across a forest-grassland border. *Folia Geobotanica & Phytotaxonomica* 32(4): 343-353.
- Markovchick-Nicholls, L., Regan, H. M., Deutchman, D. H., Widyanata, A., Martin, B., Noreke, L., Hunt, T A. 2008. Relationships between human disturbance and wildlife land use in urban habitat fragments. *Conservation Biology* 22(1): 99-109.
- Martin, L. J., Agrawal, A. A., Kraft, C. E. 2015. Historically browsed jewelweed populations exhibit greater tolerance to deer herbivory than historically protected populations. *Journal of Ecology* 103: 243-249.

- Massé, A., Côté, S. D. 2013. Spatiotemporal variations in resources affect activity and movement patterns of white-tailed deer (*Odocoileus virginianus*) at high density. *Canadian Journal of Zoology* 91: 252-263.
- McShea, W. J., Rappole, J. H., Underwood, H. B. 1997. *The Science of overabundance: deer ecology and population management*. Washington [D.C.]. Smithsonian Institution Press.
- Minitab 17 Statistical Software. 2010. [Computer software]. State College, PA: Minitab, Inc. (www.minitab.com)
- Monteith, K. L., Bleich, V. C., Stephenson, T. R., Pierce, B. M., Conner, M. M., Klaver, R. W., Bowyer, R. T. 2011. Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life-history characteristics. *Ecosphere* 2(4): art47. doi:10.1890/ES10-00096.1.
- Nisi, A. C., Hernandez, D. L., English, L. P., Rogers, E. S. 2015. Patterns of selective herbivory on five prairie legume species. *The American Midland Naturalist* 173(1): 110-121.
- Paige, K. N., Whitham, T. G. 1987. Overcompensation in response to mammalian herbivory: the advantage of being eaten. *American Naturalist* 129:407-416.
- Pohlman, C. L., Turton, S. M., Goosem, M. 2007. Edge effects of linear canopy openings on tropical rain forest understory microclimate. *Biotropica* 39(1): 62-71.
- Puijalon, S., Bouma, T. J., Douady, C. J., Groenendaal, J., Anten, N. P. R., Martel, E., Bornette, G. 2011. Plant resistance to mechanical stress: evidence of an avoidance-tolerance trade off. *New Phytologist* 191: 1141-1149.
- Rands, M. R. W., Adams, W. M., Bennun, L., Butchart, S. M. H., Clements, A., Coomes, D., Entwistle, A., Hodge, I., Kapos, V., Scharlemann, J. P. W., Sutherland, W. J., Vira, B. 2010. Biodiversity conservation: Challenges beyond 2010. *Science* 329: 1298–1303.
- Riechman, O. J., Benedix Jr., J. H., Seastedt, T. R. 1993. Distinct animal-generated edge effects in a tallgrass prairie community. *Ecology* 74(4): 1281-1285.
- Ripple, W. J., Newsome, T. M., Wolf, C., Dirzo, R., Everatt, K. T., Galetti, M., Hayward, M. W., Kerley, G. I. H., Levi, T., Lindsey, P. A., Macdonald, D. W., Malhi, Y., Painter, L. E., Sandom, C. J., Terborgh, J., Valkenburgh, B. 2015. Collapse of the world's largest herbivores. *Sci. Adv.* 1: doi: 10.1126/sciadv.1400103.
- Rooney, T. P. 1997. Escaping herbivory: refuge effects on the morphology and shoot demography of the clonal forest herb *Maianthemum canadense*. *J. Torrey Bot. Soc.*, 124: 280-285.
- Rooney, T. P. 2001. Deer impacts on forest ecosystems: a North American perspective. *Forestry* 74(3): 201-208.

- Rowe, H. I., Fargione, J., Holland, J. D. 2013. Prairie restorations can protect remnant tallgrass prairie communities. *American Midland Naturalist* 170: 26-38.
- Russell, Francis Leland., Zippin, David B. and Norma L. Fowler. 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: a review. *American Midland Naturalist* 146(1): 1-26.
- Samson, F., Knopf, F. 1994. Prairie conservation in North America. *BioScience* 44: 418-421.
- Saunders, D. A., Hobbs, R. J., Margules, C. R. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5 (1): 18-32.
- Schmitz, O.J. and Sinclair, A.R.E. 1997. Rethinking the role of deer in forest ecosystem dynamics. Pages 201-223 in W.J. McShea, H.B. Underwood, and J.H. Rapploe, editors. *The Science of Overabundance: Deer Ecology and Population Management*. Smithsonian Books, Washington D.C., USA.
- Shaw, R. G., Wagenius, S., Geyer, C. J. 2015. The susceptibility of *Echinacea augustifolia* to a specialist aphid: eco-evolutionary perspective on genotypic variation and demographic consequences. *Journal of Ecology* 103(4): 809-818.
- Spirko, L. S., Rossi, A. M. 2015. Manner of apical meristem destruction affects growth, reproduction, and survival of sea oxeye daisy. *Journal of Botany* 2015: 480891.
- Spotswood, E., Bradley, K. L., Knops, J. M. H. 2002. Effects of herbivory on the reproductive effort of 4 prairie perennials. *BioMed Central Ecology* 2: 2.
- Strauss, S. Y., Agrawal, A. A. 1999. The ecology and evolution of plant tolerance to herbivory. *TREE* 14(5): 179-185.
- Tiffin, P. 2000. Mechanisms of tolerance to herbivore damage: what do we know? *Evolutionary Ecology* 14: 523-536.
- Tilghman, N. G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. *J. Wildl. Manage.*, 53: 524-532.
- Urbanek, R. E. 2005. Ecological and societal impacts of suburban white-tailed deer: a case study in the Chicago metropolitan area. ProQuest Dissertations Publishing. Order No. 3514106.
- Urbanek, R. E., Nielsen, C. K., Glowacki, G. A., Preuss, T. S. 2012. Effects of white-tailed deer (*Odocoileus virginianus* Zimm.) herbivory in restored forest and savanna plant communities. *The American Midland Naturalist* 167(2): 240-255.

- Vallet, J., Beaujouan, V., Pithon, J., Roze, F., Daniel, H. 2010. The effects of urban or rural landscape context and distance from the edge on native woodland plant communities. *Biodivers Conserv* 19: 3375-3392.
- Van der Hoek, D. J., Knapp, A. K., Briggs, J. M., Bokdam, J. 2002. White-tailed deer browsing on six shrub species of tallgrass prairie. *Great Plains Research* 12: 141-156.
- Van Dyke, F., Fox, A., Harju, S. M., Dzialak, M. R., Hayden-Wing, L. D., Winstead, J. B. 2012. Response of elf to habitat modification near natural gas development. *Environmental Management* 50: 942-955.
- Wagenius, S., Dykstra, A. B., Ridley, C. E., Shaw, R. G. 2012. Seedling recruitment in the long-lived perennial *Echinacea augustifolia*: a 10-year experiment. *Restoration Ecology* 20(3): 352-359.
- Waller, D. M., Alverson, W. S. 1997. The white-tailed deer: a keystone herbivore. *Wildlife Society Bulletin* 25(2): 217-226.
- Webster, C. R., Jenkins, M. A., Rock, J. H. 2005. Long-term response of spring flora to chronic herbivory and deer exclusion in Great Smoky Mountains National Park, USA. *Biological Conservation* 125 (3): 297-307.
- Wilsey, B. 2002. Clonal plants in a spatially heterogeneous environment: effects of integration on Serengeti grassland response to defoliation and urine-hits from grazing animals. *Plant Ecology* 159: 15-22.
- Wise, M. J., Abrahamson, W. G. 2008. Applying the limiting resource model to plant tolerance of apical meristem damage. *American Naturalist* 172(5): 635-647.
- Wolfer, S. R., Straile, D. 2012. To share or not to share: clonal integration in a submerged macrophyte in response to light stress. *Hydrobiologia* 684: 261-269.
- Yahner, R. H. 1988. Changes in wildlife communities near edges. *Conservation Biology* 2(4): 333-339.

Table 1: Deer survey results.

Spotlight/distance survey results from Kill Creek Park and Shawnee Mission Park, for each year of the studies.

Year/Location	Estimated Population		CI (95%) - Deer/ha		Effort (km)	AIC
	Deer/ha	Deer/Acre	Upper Bound	Lower Bound		
Fall 2015						
Kill Creek Park	0.21	54.01	0.09	0.48	19.50	646.46
Shawnee Mission Park	0.08	19.80	0.05	0.12	41.00	607.29
Spring 2015						
Kill Creek Park	0.14	36.23	0.07	0.27	9.65	134.33
Shawnee Mission Park	0.09	23.91	0.01	1.09	13.70	81.12
Fall 2014						
Kill Creek Park	0.20	53.01	0.13	0.30	29.60	925.70
Shawnee Mission Park	0.10	23.39	0.06	0.15	40.70	693.70
Fall 2013						
Shawnee Mission Park	0.07	19.04			40.90	673.69

Table 2: ANOVA Results, Herbivory Effects.

Number of stems with herbivory/total number of stems (top table) and number of stems of *Helianthus* with herbivory/total number of stems of *Helianthus* (bottom table).

Source	Herbivory / Abundance							
	Spring 2015				Fall 2015			
	df	MS	F	p	df	MS	F	p
Treatment	1	0.02	1.68	0.42	1	131.28	1278.31	0.02
Location	1	0.01	3.70	0.10	1	1.74	0.16	0.70
Treatment*Location	1	0.01	3.30	0.09	1	0.10	0.01	0.93
Whole plot	2	0.01	1.93	0.18	2	39.80	3.00	0.10
Error	14	0.00			10	13.28		
Source	<i>Helianthus</i> Herbivory / <i>Helianthus</i> Abundance							
	Spring 2015				Fall 2015			
	df	MS	F	p	df	MS	F	p
Treatment	1	2179.46	177.84	0.05	1	498.78	3.24	0.32
Location	1	40.10	0.07	0.79	1	324.58	4.99	0.07
Treatment*Location	1	12.26	0.02	0.89	1	153.83	3.23	0.10
Whole plot	2	110.81	0.18	0.84	2	100.98	2.12	0.17
Error	14	631.95			10	47.67		

Table 3: ANOVA Results, Vegetation Analysis.

Richness analyses (top table) diversity or effective number of species (e^H) (bottom table).

	Richness							
	Spring 2015				Fall 2015			
Source	df	MS	F	p	df	MS	F	p
Treatment	1	0.43	0.12	0.78	1	2.01	1.60	0.43
Location	1	70.25	4.56	0.05	1	52.25	6.15	0.03
Treatment*Location	1	3.40	0.19	0.67	1	1.25	0.13	0.73
Whole plot	2	23.99	1.36	0.29	2	118.68	12.08	0.00
Error	14	17.60			14	9.82		
	Diversity (e^H)							
	Spring 2015				Fall 2015			
Source	df	MS	F	p	df	MS	F	p
Treatment	1	0.00	0.00	0.99	1	3.06	1.96	0.40
Location	1	126.49	4.57	0.05	1	39.28	2.24	0.16
Treatment*Location	1	5.45	0.17	0.69	1	1.56	0.08	0.79
Whole plot	2	57.81	1.82	0.20	2	105.92	5.16	0.02
Error	14	31.78			14			

Table 4: SIMPER Analyses, by species.

	Average abundance	Contribution %	Cumulative %
--	-------------------	----------------	--------------

SPRING 2014

Average Dissimilarity = 78.93%

	Edge	Interior		
<i>Helianthus</i> species	3.99	0.71	7.56	7.56
<i>Solidago</i> species	1.27	4.58	7.14	14.7
<i>Galium circaeans</i>	3.14	0	5.94	20.64
<i>Helianthus pauciflorus</i>	1.66	1.01	3.29	23.92
<i>Rosa arkansana</i>	0	1.55	3.19	27.11
<i>Echinacea pallida</i>	1.48	0.78	2.86	29.97

FALL 2014

Average Dissimilarity = 73.43%

	Edge	Interior		
<i>Helianthus</i> species	5.28	0.85	9.93	9.93
<i>Schizachyrium scoparium</i>	0.68	3.22	5.86	15.79
<i>Solidago</i> species	2.23	2.95	5.67	21.46
<i>Andropogon gerardii</i>	1.91	2.77	4.55	26.01
<i>Comandra umbellata</i>	2.55	0.21	4.44	30.45

<i>Galium circaezans</i>	1.88	0	4.11	34.56
--------------------------	------	---	------	-------

SPRING 2015

Edge Interior

Average Dissimilarity = 79.92%

<i>Helianthus</i> species	5.91	1.61	8.48	8.48
<i>Solidago</i> species	0.96	4.11	6.8	15.28
<i>Galium circaezans</i>	3.4	0.19	6.05	21.33
<i>Comandra umbellata</i>	1.96	0.37	3.88	25.21
<i>Rosa</i> species	0	1.44	3.22	28.43
<i>Lespedeza violacea</i>	0.14	1.50	2.84	31.27

FALL 2015

Edge Interior

Average Dissimilarity = 73.42%

<i>Helianthus</i> species	5.79	1.48	7.96	7.96
<i>Solidago</i> species	0.62	3.84	5.88	13.85
<i>Galium circaezans</i>	3.08	0	5.70	19.55
<i>Sorghastrum nutans</i>	0.74	2.20	3.32	22.87
<i>Schizachyrium scoparium</i>	0.81	2.21	3.05	25.91
<i>Bouteloua curtipendula</i>	0.47	1.74	2.95	28.86

Table 5: SIMPER analyses, by guild.

	Average abundance	Contribution %	Cumulative %
--	-------------------	----------------	--------------

SPRING 2014

Edge Interior

Average Dissimilarity = 29.71%

Annual	3.31	1.07	16.09	16.09
Legume	2.31	3.53	13.37	29.46
C3 Grass	2.85	1.77	12.93	42.38
Tree	2.73	1.10	12.13	54.52
Spring Forb	4.22	3.36	8.87	63.39

FALL 2014

Edge Interior

Average Dissimilarity = 37.91%

C4 Grass	3.66	1.41	17.41	17.41
Summer/Fall Forb	3.88	3.52	14.23	31.64
Spring Forb	1.56	3.07	13.4	45.03
Legume	1.17	2.72	13.17	58.2
C3 Grass	6.79	6.69	8.22	66.42

SPRING 2015

Average Dissimilarity = 36.85%

	Edge	Interior		
Annual	3.66	1.41	17.41	17.41
Spring Forb	3.88	3.52	14.23	31.64
Woody Shrub	1.56	3.07	13.4	45.03
Legume	1.17	2.72	13.17	58.2
Summer/Fall Forb	6.79	6.69	8.22	66.42

FALL 2015

Average Dissimilarity = 34.68%

	Edge	Interior		
<i>C4 Grass</i>	2.37	4.96	17.33	17.38
<i>Annual</i>	3.64	1.86	13.61	30.99
<i>Legume</i>	1.31	2.58	11.75	42.74
<i>Spring Forb</i>	2.1	2.31	10.85	53.59
<i>Summer/Fall Forb</i>	6.7	5.38	10.76	64.35
<i>C3 Grass</i>	2.86	2.62	9.53	73.88

Table 6: PERMANOVA Analyses.

PERMANOVA analyses by species (top table) PERMANOVA analyses by guild (bottom table).

	PERMANOVA by Species							
	Spring 2015				Fall 2015			
	df	MS	Pseudo F	p	df	MS	Pseudo F	p
Treatment	1	236.66	0.23	0.98	1	662.81	0.78	0.65
Location	1	6057.00	2.99	0.01	1	6267.30	4.49	0.01
Treatment*Location	1	501.28	0.49	0.85	1	505.33	0.59	0.81
Whole plot	9	4947.80	4.83	0.00	9	3876.90	4.56	0.00
Error	8	1023.90			8	849.86		
	PERMANOVA by Guild							
	Spring 2015				Fall 2015			
	df	MS	Pseudo F	p	df	MS	Pseudo F	p
Treatment	1	233.48	0.66	0.61	1	234.58	0.89	0.48
Location	1	906.65	1.88	0.10	1	1132.10	3.05	0.03
Treatment*Location	1	43.82	0.12	0.95	1	130.74	0.49	0.76
Whole plot	9	1057.60	2.98	0.00	9	911.33	3.45	0.00
Error	8	354.61			8	264.29		

Table 7: PERMDISP Analyses.

PERMDISP analyses by location (top table) PERMDISP analyses by prairie (bottom table).

	PERMDISP by Species - Location					
	Spring 2015			Fall 2015		
Source	df	F	p	df	F	p
Group Factor	1	7.68	0.01	1	0.19	0.65
Error	18			18		
	PERMDISP by Species - Prairie					
	Spring 2015			Fall 2015		
Source	df	F	p	df	F	p
Group Factor	1	48.63	0.00	1	43.62	0.00
Error	18			18		

Table 8: Focal Species Analyses.

Woody percent cover analyses (top table), Combined woody abundance (Trees, shrubs, woody vines) (middle table), *Helianthus* species abundance (bottom table).

	Woody Percent Cover (square root transformed)							
	Spring 2015				Fall 2015			
Source					df	MS	F	p
Treatment					1	0.29	0.46	0.62
Location					1	32.96	17.49	0.00
Treatment*Location					1	0.63	0.30	0.59
Whole plot					2	7.02	3.32	0.07
Error					14	4.09		
	Combined Woody Abundance							
	Spring 2015				Fall 2015			
Source	df	MS	F	p	df	MS	F	p
Treatment	1	1.29	162.23	0.05	1	3.49	906328.01	0.00
Location	1	8.84	1.87	0.19	1	11.09	6.82	0.02
Treatment*Location	1	0.01	0.00	0.97	1	0.00	0.00	1.00
Whole plot	2	4.70	0.84	0.45	2	1.17	0.61	0.56
Error	14	5.61			14	1.93		
	<i>Helianthus</i> Abundance							
	Spring 2015				Fall 2015			
Source	df	MS	F	p	df	MS	F	p
Treatment	1	20.17	0.70	0.56	1	82.94	0.75	0.55
Location	1	3595.70	7.69	0.02	1	977.03	30.69	0.01
Treatment*Location	1	29.00	0.05	0.82	1	110.82	6.78	0.03
Whole plot	2	529.67	0.97	0.40	2	143.71	8.80	0.01
Error	14	548.01			10	16.33		

Table 9: *Helianthus* stem height.

ANOVA results for edge prairie study plots, spring and fall 2015.

Source	<i>Helianthus</i> Stem Height							
	Spring 2015				Fall 2015			
	df	MS	F	p	df	MS	F	p
Treatment	1	23213.40	7.61	0.11	1	7056.46	3.69	0.18
Plot	2	7929.70	2.59	0.28	2	70.42	0.03	0.97
Treatment*Plot	2	3058.10	15.64	<0.001	2	2375.91	5.90	0.00
Error	320	195.50			248	403.02		

Table 10: Stem diameter of *Helianthus*.

ANOVA results in edge prairie study plots, spring and fall 2015.

Source	<i>Helianthus</i> Stem Diameter							
	Spring 2015				Fall 2015			
	df	MS	F	p	df	MS	F	p
Treatment	1	0.00	0.06	0.84	1	0.12	1.80	0.30
Plot	2	0.08	4.32	0.19	2	0.31	3.84	0.21
Treatment*Plot	2	0.02	2.79	0.06	2	0.08	6.55	0.00
Error	320	0.01			265	0.01		

Table 11: Branching in *Helianthus*.Probability of branching in *Helianthus* stems in edge prairie study plots, fall 2014 and fall 2015.

Source	Branching							
	Fall 2014				Fall 2015			
	df	Adj Mean	X2	p	df	Adj Mean	X2	p
Regression	5	9.03	45.14	0.00	5	36.62	36.62	<0.001
Treatment	1	3.45	3.45	0.06	1	9.24	9.24	0.00
Plot	2	17.61	35.21	<0.001	2	3.26	6.52	0.04
Treatment*Plot	2	3.19	6.39	0.04	2	0.84	1.67	0.43
Error	272	1.25			248	1.05		

Table 12: Inflorescences in *Helianthus*.

Probability of *Helianthus* stems producing an inflorescence in edge prairie study plots, fall 2014 and fall 2015.

	Inflorescence							
	Fall 2014				Fall 2015			
Source	df	Adj Mean	X2	p	df	Adj Mean	X2	p
Regression	5	2.092	10.46	0.063	5	7.235	36.18	<0.001
Treatment	1	6.6794	6.68	0.01	1	4.125	4.12	0.006
Plot	2	0.556	1.11	0.573	2	5.129	10.26	0.042
Treatment*Plot	2	1.0358	2.07	0.355	2	1.495	2.99	0.224
Error	286	0.8044			248	1.176		

Table 13: Branching in *Helianthus*.

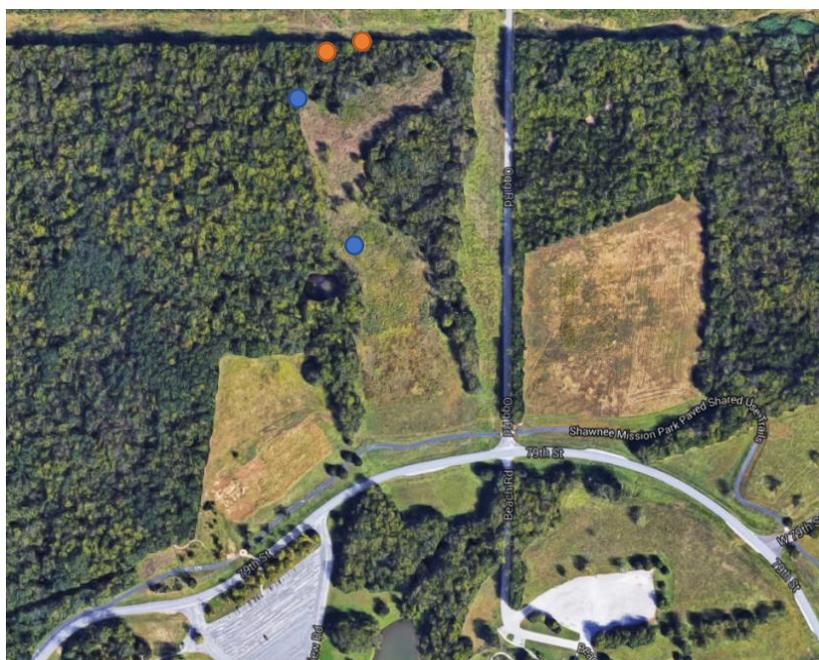
Probability of branching in *Helianthus* rhizomes in artificial herbivory study, fall 2015.

	Branching			
	Fall 2015			
Source	df	Adj Mean	X2	p
Regression	4	9.99	39.95	<0.001
Stem Count	1	26.02	26.02	<0.001
Spring	1	14.65	14.65	<0.001
Fall	1	0.04	0.04	0.83
Spring * Fall	1	0.00	0.00	0.99
Error	76	0.95		



Remnant, ~ 20 acres ● - Edge paired plot ● - Interior paired plots

1 A) Kill Creek Park, Olathe, Kansas



Remnant ~ 8 acres ● - Edge paired plots ● - Interior pairs plots

1 B) Ogg Prairie, Shawnee Mission Park, Lenexa, Kansas

Figure 1: Site maps

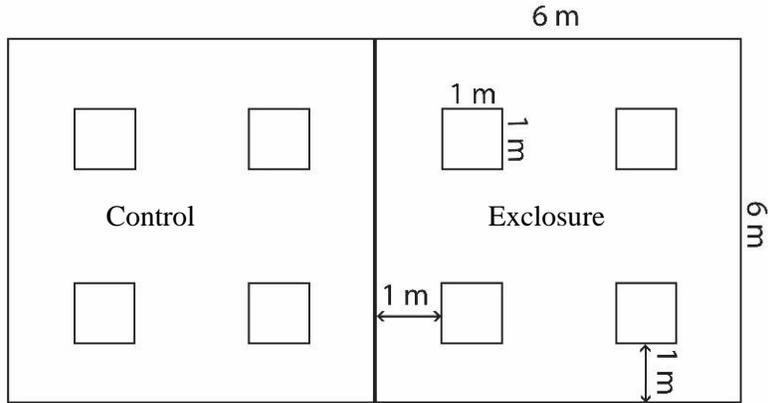


Figure 2: Exclosure plot diagram.

Diagram showing the spatial relationship between control and exclosure plots and the relative location of the sampled quadrats.



Figure 3: Exclosure photos.

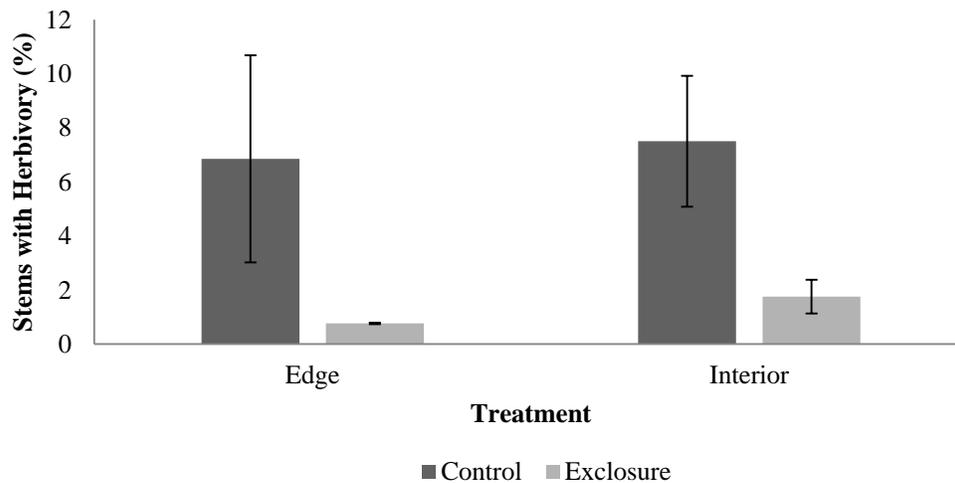
Left - differences in the abundance of *Helianthus* inflorescences due to treatment. Right – view of entire exclosure, interior plot Kill Creek Prairie.



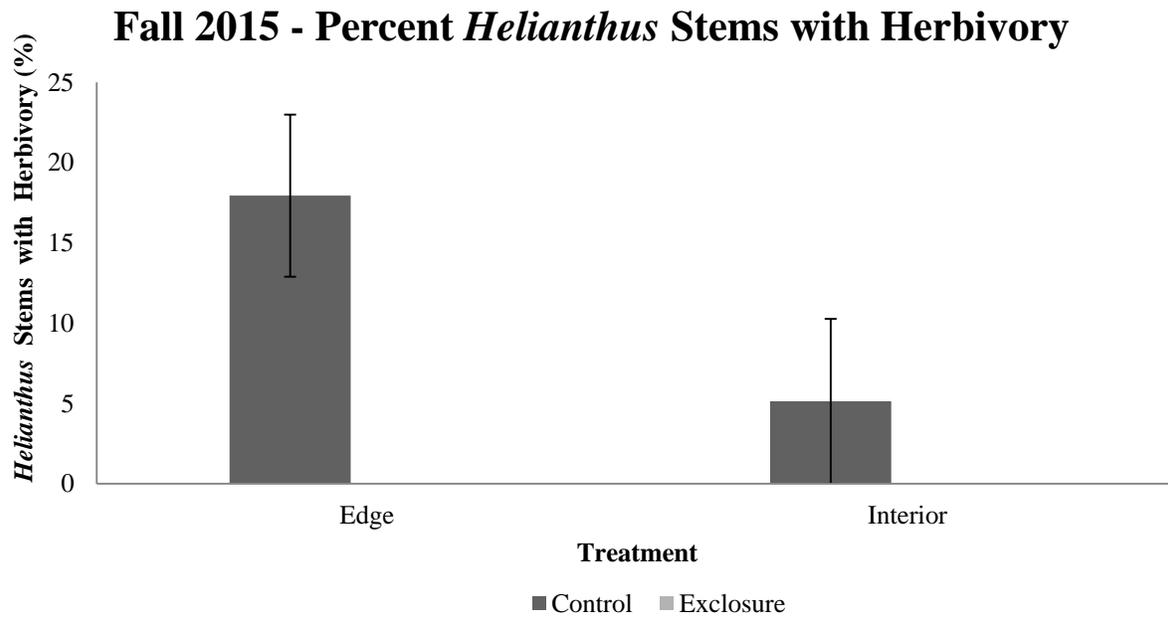
Figure 4: Deer vs. Rodent Herbivory.

Left - deer herbivory is torn in appearance and typically over 10cm high. Right - rodent herbivory is typically clean cut at an angle and below 10cm high. Rodents are also limited by stem diameter and stem toughness (seldomly found on woody stems).

Fall 2015 - Percent Stems with Herbivory

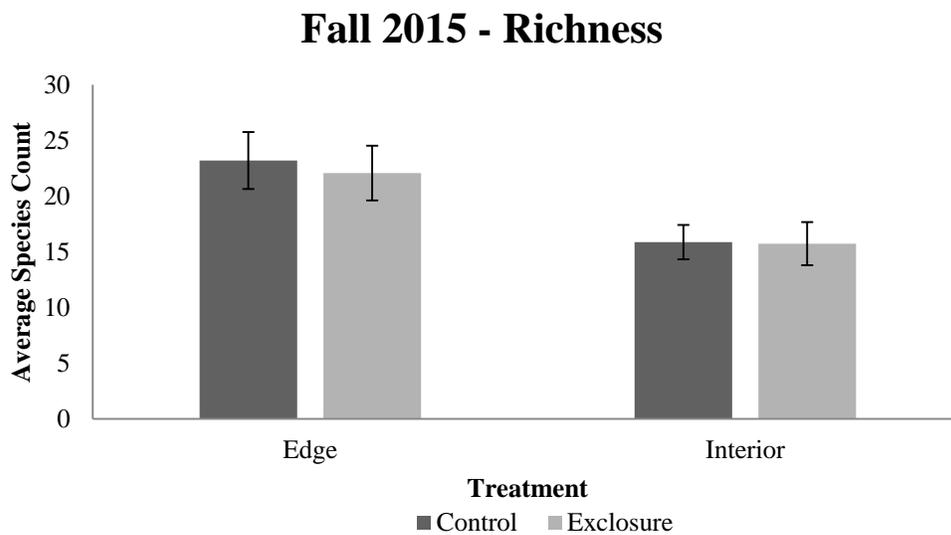


5 A) Average percent of stems with herbivory, comparing locations and treatments (+/- 1 SE)

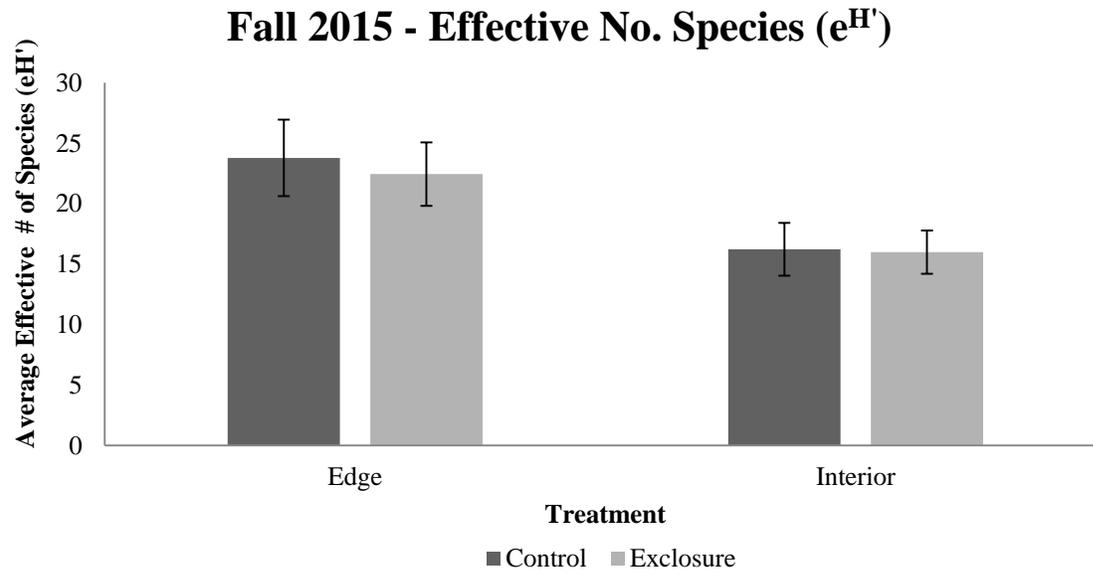


5 B) Average percent of *Helianthus* stems with herbivory, comparing locations and treatments (+/- 1 SE)

Figure 5: Herbivory Effects.



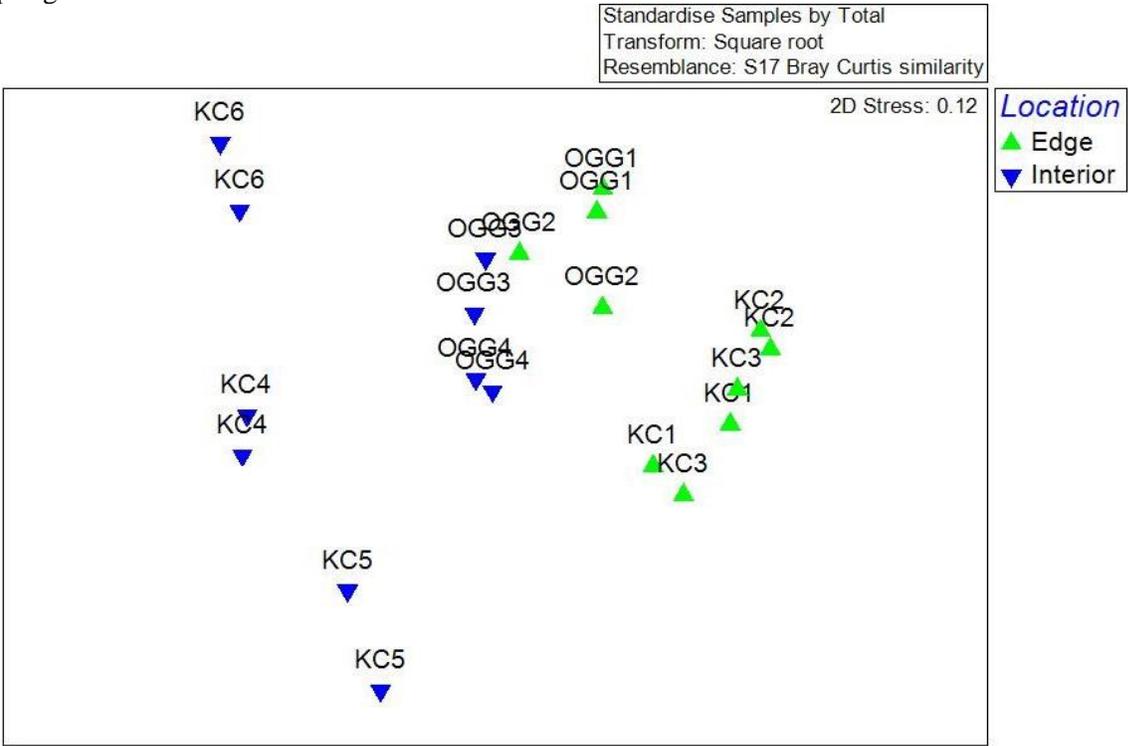
6 A) Average richness of plant communities, comparing locations and treatments (+/- 1 SE)



6 B) Average diversity ($e^{H'}$) of plant communities, comparing locations and treatments (± 1 SE)

Figure 6: Richness and Diversity.

Spring 2015



Fall 2015

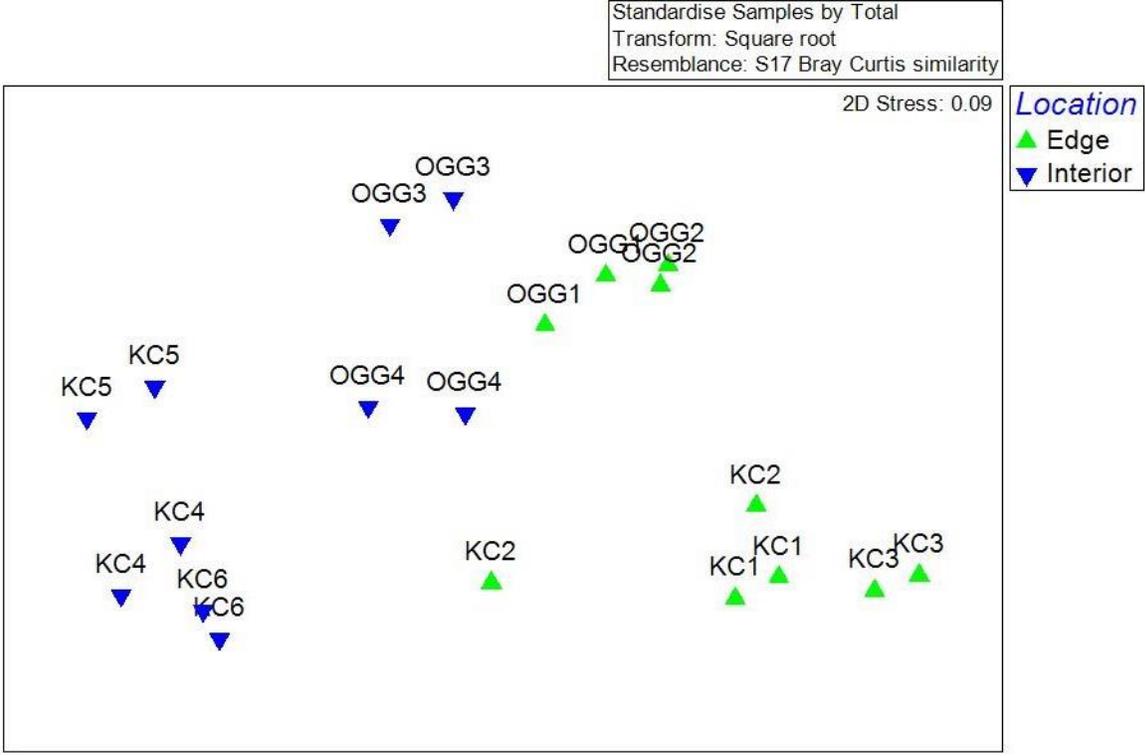
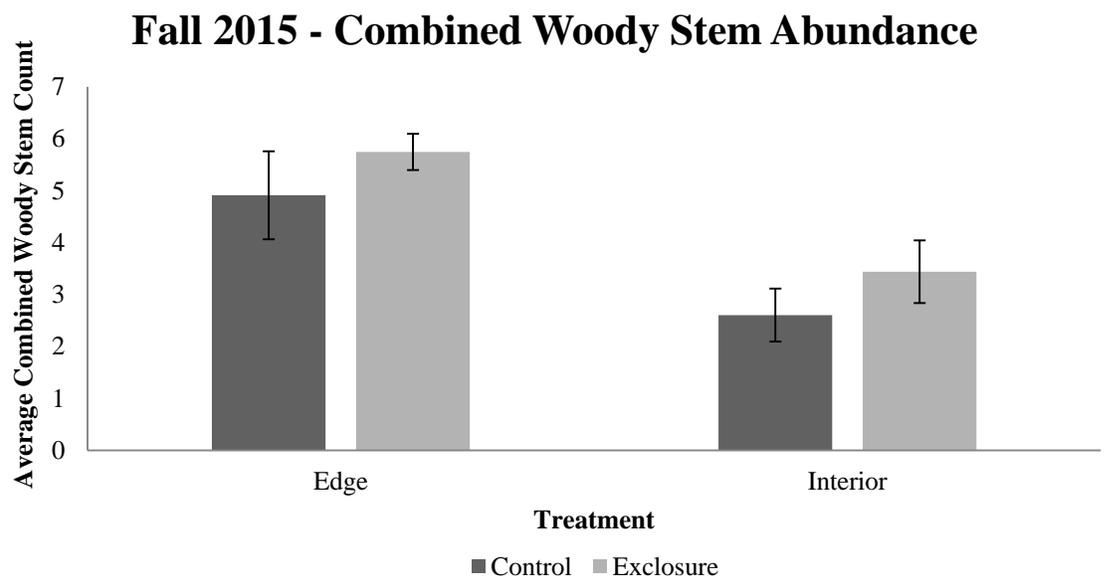
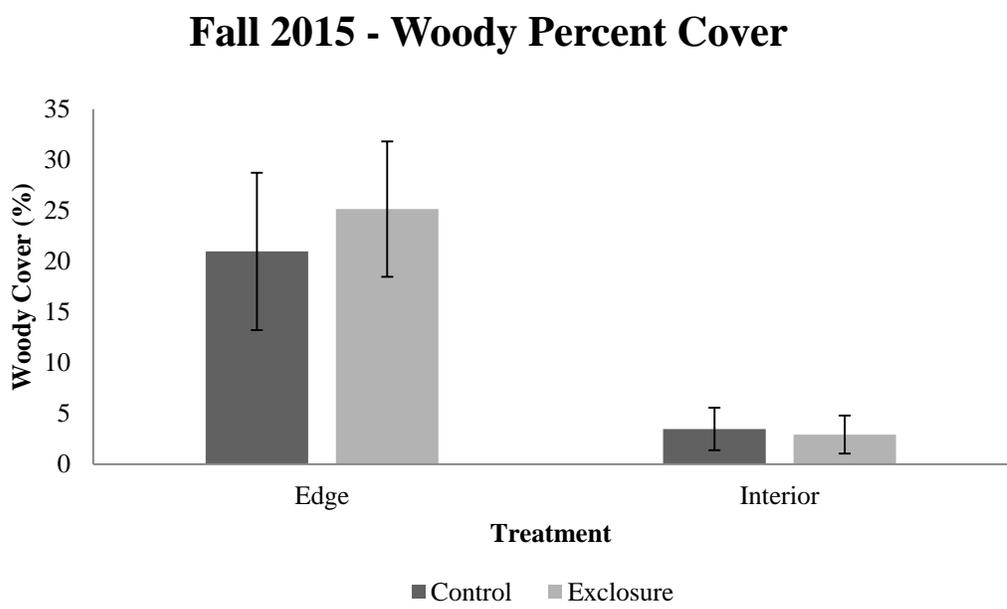


Figure 7: MDS Plots.



8 A) Average combined woody stem abundance, comparing locations and treatments (+/- 1 SE)



8 B) Average woody percent cover, comparing locations and treatments (+/- 1 SE)

Figure 8: Woody Differences.

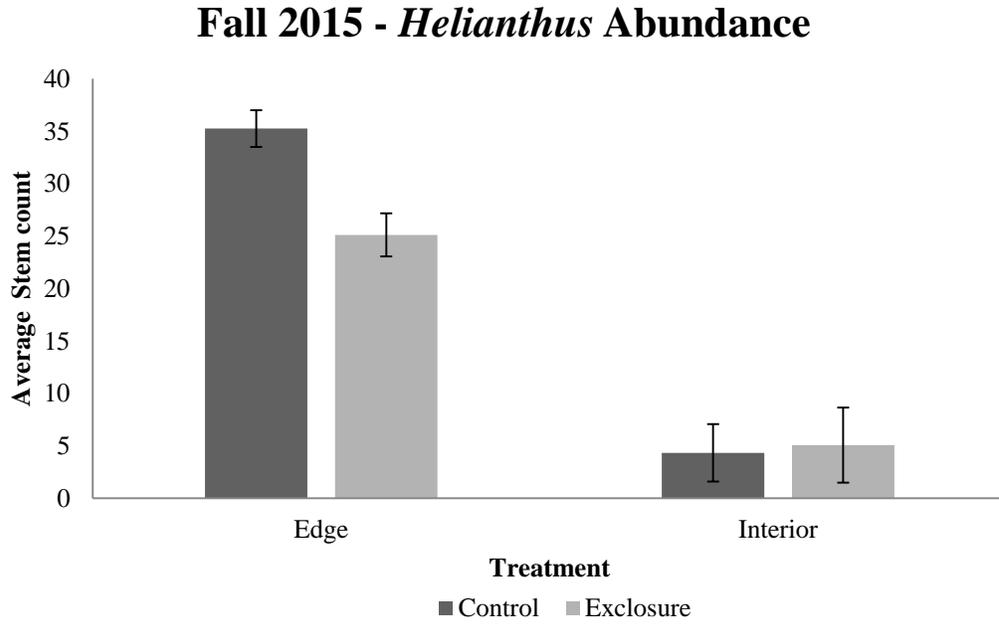


Figure 9: *Helianthus* Differences.

Average *Helianthus* abundance, comparing locations and treatments (± 1 SE)

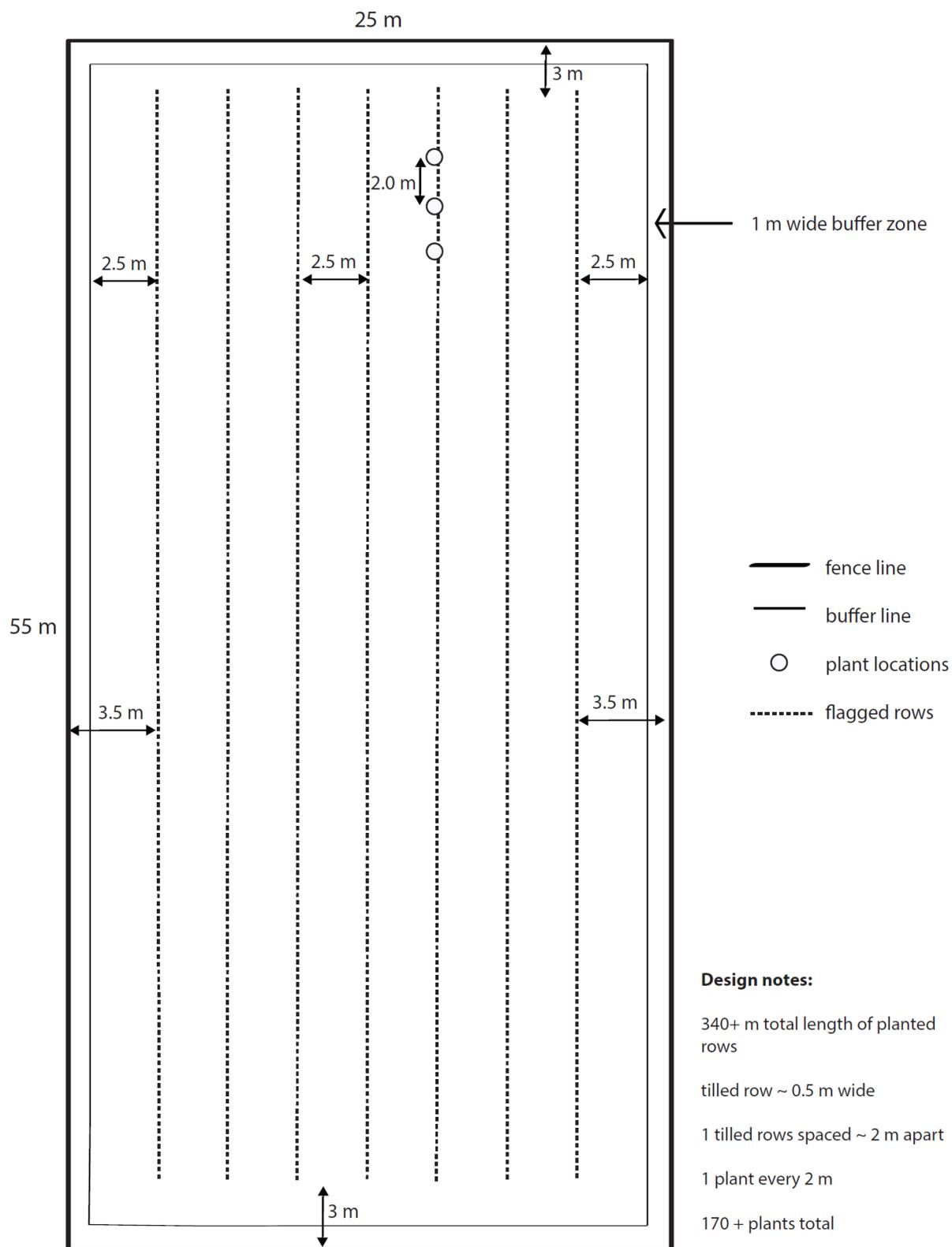


Figure 10: Diagram of artificial herbivory plot.

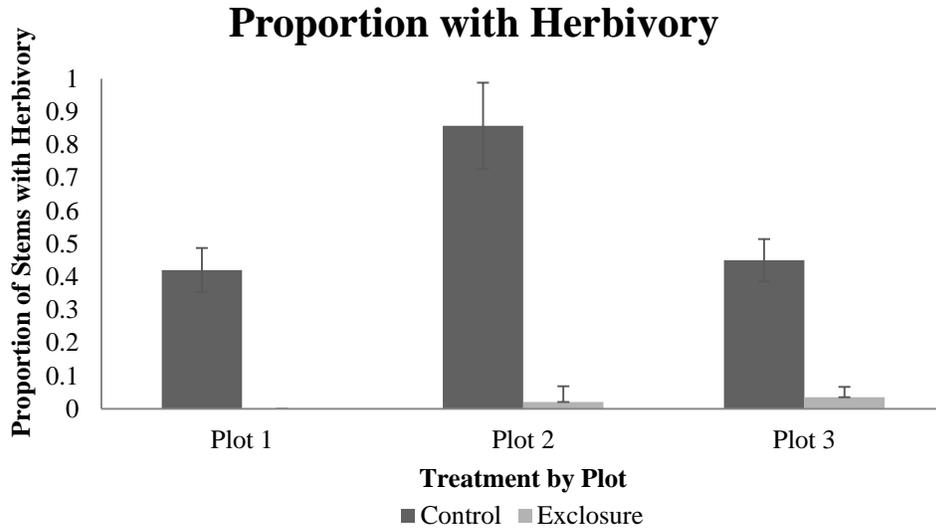
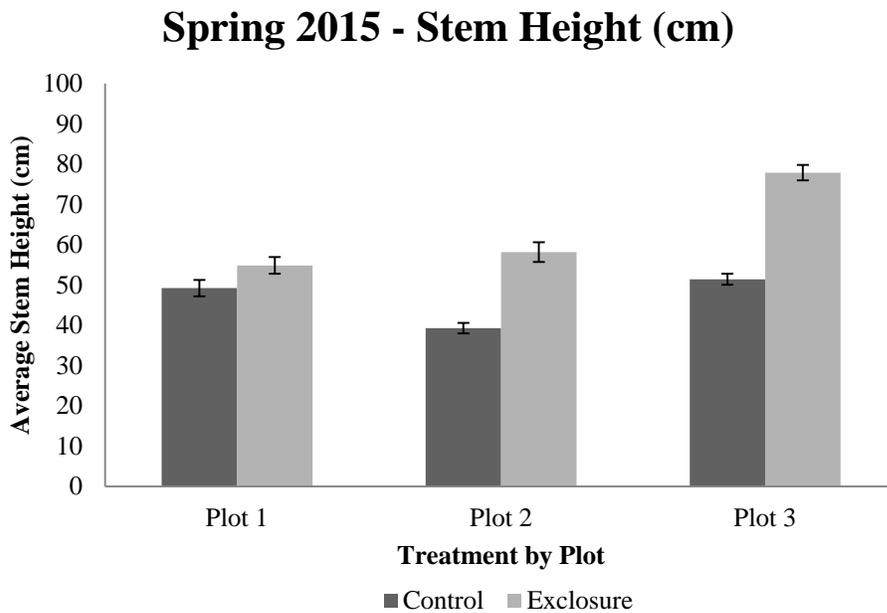
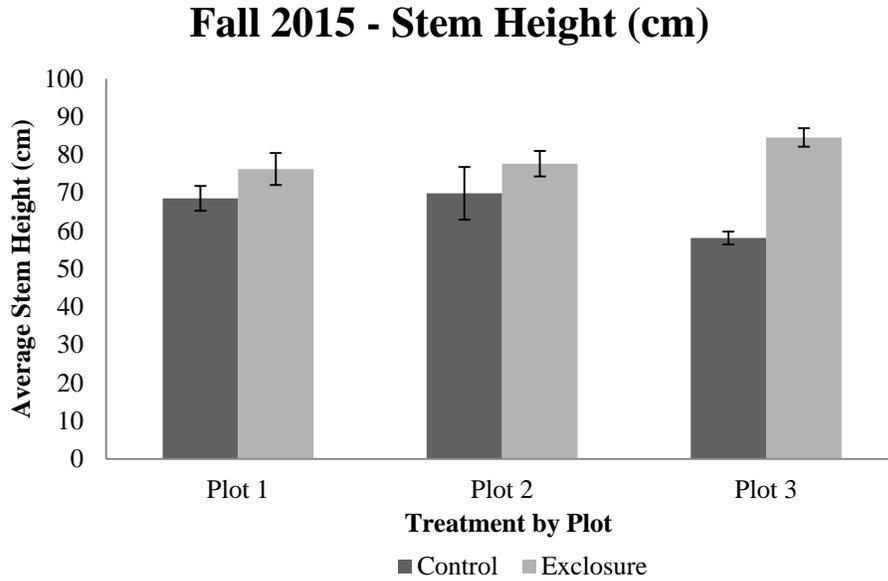


Figure 11: *Helianthus* herbivory.

Proportion of perennial *Helianthus* stems with deer herbivory in edge study plots, in remnant prairies (\pm 1 SE)



12 A: *Helianthus* stem height in edge prairie study plots, spring 2015. Significant plot*treatment interaction. (\pm 1 SE)



12 B: *Helianthus* stem height in edge prairie study plots, fall 2015. (+/- 1 SE)

Figure 12: *Helianthus* stem height.

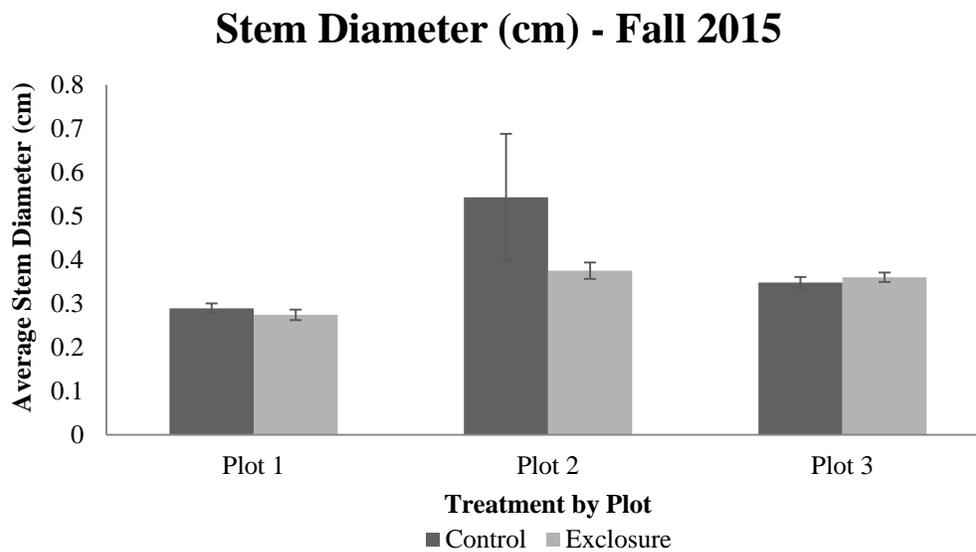


Figure 13: *Helianthus* stem diameter.

Stem diameter for *Helianthus* stems in fall 2015, edge plots in remnant prairie (+/- 1 SE).

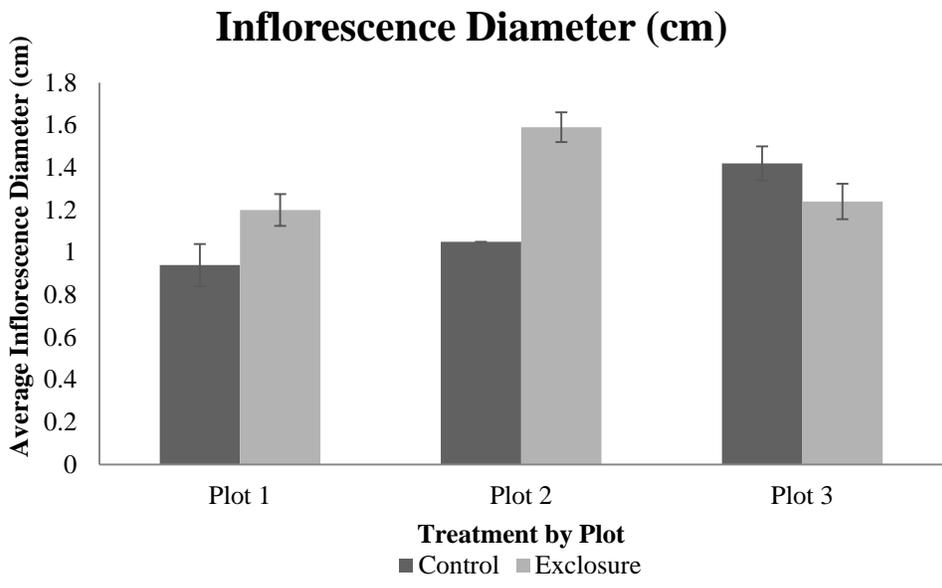


Figure 14: *Helianthus* inflorescence diameter.

Inflorescences diameter for *Helianthus* stems in fall 2015, edge plots in remnant prairie (+/- 1 SE).

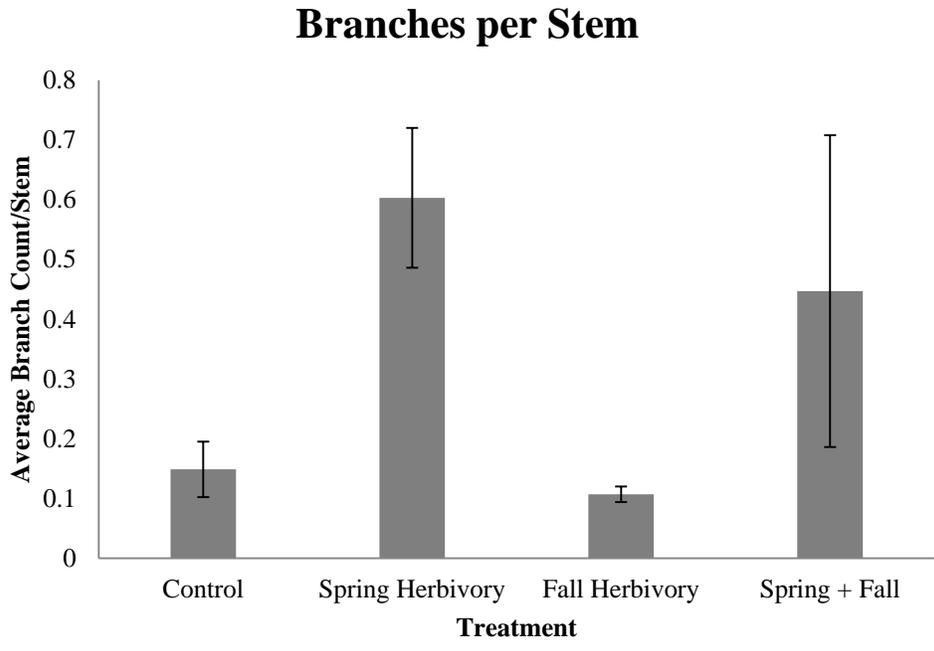


Figure 15: Branching by stem in *Helianthus*.

Number of branches per stem, by treatment, in artificial herbivory study. (+/- 1 SE)

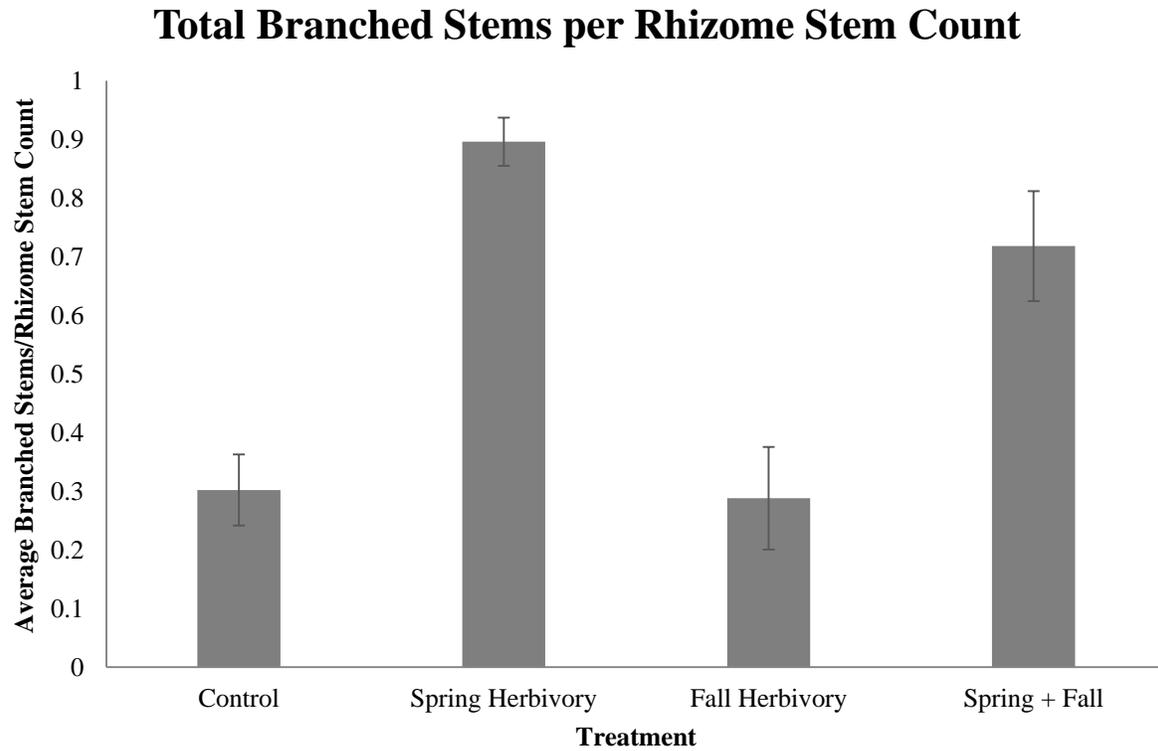


Figure 16: Branching by rhizome in *Helianthus*.

Number of branched stems standardized by the number of stems per rhizome and separated by treatment for the artificial herbivory study. (+/- 1 SE)

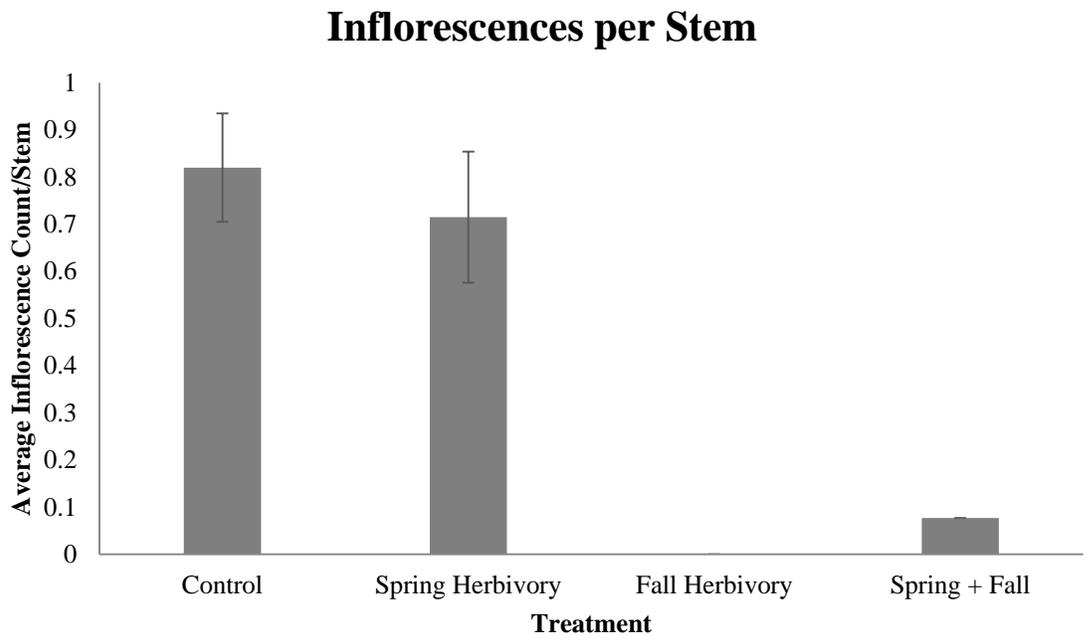


Figure 17: *Helianthus* inflorescence by stem.

Number of inflorescences per stem, separated by treatment, for artificial herbivory study (+/- 1 SE). Small sample size reduced statistical power of study but there was a trend toward a greater number of inflorescences per stem in the control treatment, consistent with the prairie study.

Appendix

Data from exclosures in Swope Park, Kansas City, MO - 2009 Missouri Department of Conservation, Natural Historian – Larry Rizzo

Two deer exclosures were installed at Rocky Point glade/woodland in Swope Park in March, 2009 to measure the increasing impact of deer browsing on the native flora. Exclosures are fenced squares 25' per side and approximately seven feet high. Immediately adjacent to each exclosure is an equal-sized unfenced square marked with flags which represents a control area accessible to deer. Exclosures and control plots were surveyed monthly from May through October. Blooms were counted for each species of plant found in the plots. Two parameters were summarized for assessing the impact of deer browse on plant reproduction and abundance. The first measures one species only—woodland sunflower (*Helianthus hirsutus*)—an important and dominant woodland plant highly favored by deer. The second measure is a comprehensive summation of all species of plants at all plots for the entire sampling season.

Measure #1—Woodland Sunflower: Abundance of woodland sunflower. Numbers are from the July and August sampling periods.

Exclosure #1: 183 total blooms	Control #1: 71 total blooms
Exclosure #2: 183 total blooms	Control #2: 29 total blooms

Exclosure #1 = 2.58 X more blooming plants than control plot
Exclosure #2 = 6.31 X more blooming plants than control plot

Total blooms in exclosures = 366 or 78.5% of total
Total blooms in control plots = 100 or 21.5%

Measure #2—Total Number of Blooms: Total numbers of all blooms from all species of plants from all sampling periods (May-October).

Exclosure #1: 831 total blooms	Control #1: 189 total blooms
Exclosure #2: 403 total blooms	Control #2: 189 total blooms

Exclosure #1 = 4.40 X more blooms than control plot
Exclosure #2 = 2.13 X more blooms than control plot

Total blooms in exclosures = 1,234 or 76.6% of total
Total blooms in controls = 378 or 23.4%

**Helianthus Inflorescence Counts by Treatment
Summer 2009**

