

THE EFFECTS OF DISTURBANCE IN GRASSLAND  
PLANT COMMUNITIES

By

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PLANT COMMUNITIES

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Throughout the course of my graduate studies, I have come to appreciate the beauty and complexity of grassland landscapes. The evolution of grasslands, with near constant perturbation from fire, herbivory and climatic fluctuations, resulted in a highly resilient plant communities. J. Philip Grime, (Plant Strategies, Vegetation Processes, and Ecosystem Properties) separates plant perturbations into two categories. He describes stresses as events that prevent the production of biomass, and disturbance as events that destroy existing biomass. In that light, I measured mixed-grass and tallgrass plant community response to stress and disturbance.

The first chapter describes the effects of eastern redcedar canopy cover stress on tallgrass plant communities in central Oklahoma. This study was developed in collaboration by myself with Aaron Alford and Eric Hellgren, previously at Oklahoma State University and currently at Southern Illinois University-Carbondale, and David Engle as a comprehensive investigation of the effects of eastern redcedar on small mammal populations and plant communities. This chapter was written for submission to the journal *Ecosystems*.

The second chapter was developed in collaboration by myself with Philip Gipson and Don Althoff, at the Kansas State University Cooperative Fish and Wildlife Research Unit, and David Engle to investigate the influence of military tracked vehicle maneuvers on small mammal and plant communities at the Smoky Hills Bombing Air National

Guard Bombing Range in central Kansas. Funding was provided from the Construction Engineering Research Laboratory. The manuscript is written for submission to the journal *Oecologia*.

The third chapter was developed by myself and David Engle to investigate the influence of tracked vehicle maneuvers on livestock distribution and plant vertical structure at the Smoky Hills Bombing Air National Guard Bombing Range in central Kansas. Funding was provided from the Construction Engineering Research Laboratory. This chapter is written for submission to the journal *Rangeland Ecology and Management*.

The fourth chapter was a method developed by myself, Karen Hickman, David Engle, Jack Norland and Samuel Fuhlendorf to digitally measure visual obstruction in grasslands. The study was conducted at the Oklahoma State University Range Research Station near Stillwater, Oklahoma. The manuscript was accepted for publication in the journal *Rangeland Ecology and Management*.

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## CHAPTER I

# TALLGRASS PRAIRIE PLANT COMMUNITY DYNAMICS ALONG A GRADIENT OF *JUNIPERUS VIRGINIANA* CANOPY COVER

**Tallgrass Prairie Plant Community Dynamics Along a Gradient of *Juniperus virginiana* Canopy Cover**

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## Abstract

North American grasslands are reduced 75 percent from their historic pre-European settlement size, and continue to be converted to forested ecosystems through the process of woody encroachment. The conversion of grassland to forest influences both abiotic and biotic properties of the associated ecosystem by altering nutrient cycling, water use and light penetration thus influencing plant community dynamics. Therefore, we designed a study to examine the relationship between stand-level *Juniperus virginiana* canopy cover and the herbaceous plant community. We documented herbaceous plant species composition, abundance and biomass within tallgrass prairie invaded by *J. virginiana* with canopy ranging from 0% to 80% in central Oklahoma, USA. Herbaceous species richness declined as a function of increased canopy cover and subsequent loss of open space; however, the decrease in species richness closely followed a species area model. Further, relative composition among C<sub>3</sub>, C<sub>4</sub> and forb species groups did not change with increasing canopy cover. Herbaceous biomass declined with increasing canopy cover, and was most variable with intermediate canopy cover. While we did find a decline in species richness and biomass with increased canopy cover, the decrease followed species area relationships and was without immediate and substantial declines typical of ecological thresholds. Thus removing *J. virginiana* trees in areas with various canopy cover will allow the restoration processes to be explored and tested.

## Introduction

North American grasslands are substantially reduced from their historic pre-European settlement size (Samson and Knopf 1994), and continue to experience woody encroachment. Woody species encroachment into grassland ecosystems is widely documented (Bragg and Hulbert 1976; Van Auken 2000; Archer 1994) and results from many factors including fire suppression, grazing, climate change, and deliberate tree and shrub planting (Bragg and Hulbert 1976; Smeins and Merrill 1988; Archer et al. 1995; Fuhlendorf et al. 1996). The rates of eastern redcedar (*Juniperus virginiana* L.) encroachment in Oklahoma is as high as 120 ha\*day<sup>-1</sup> over a 45 year span (Engle et al. 1996). The conversion of grassland to forest influences both abiotic and biotic properties of the associated ecosystem by altering nutrient cycling, water use and light penetration (Schlesinger 1977; Archer et al. 2001; Norris et al. 2001; Darrouzet-Nardi et al. 2006). Under juniper (*Juniperus* spp.) canopies, reduced light penetration, litter accumulation, and altered soil properties suppress seed germination and seedling establishment, ultimately influencing the understory plant community (Yager 1999; Fuhlendorf et al. 1997).

Most studies have focused on plant level effects of woody species encroachment into grassland ecosystems. Under the crown of isolated *J. virginiana* trees, little bluestem (*Schizachryium scoparium* [Michx.] Nash) was replaced by Kentucky bluegrass (*Poa pratensis* L.) and *Carex* spp. emphasizing a shift from mid and tall C<sub>4</sub> grass species to mid and short C<sub>3</sub> grass and sedge species (Gehring and Bragg 1992). Total species richness decreased immediately under the crown of individual Ashe juniper trees

(*Juniperus ashei* Buckholz) compared to adjacent non-juniper locations (Fuhlendorf et al. 1997). Similar results were reported by Briggs et al. (2002) for individual trees, and these authors also reported species richness had a negative relationship with *J. virginiana* stand density. The decline or shift in species composition is a reflection of the decreased light penetration immediately under the tree crown (Fuhlendorf et al. 1997). However, light penetration at the stand scale can be spatially and temporally heterogeneous and therefore sufficient to meet photosynthesis demand of some herbaceous species, especially in the interspaces, but insufficient under tree crowns (Bartemucci et al. 2006). Therefore, stand-level species composition at various levels of *J. virginiana* canopy cover, in contrast to species composition beneath individual tree crowns, is difficult to predict.

The species area relationship (SAR) is one of the oldest and most studied concepts addressing diversity patterns. (Rosenzweig 1995), The most fundamental principle of the SAR is that species richness generally increases as a function of increasing sampling area and decreases with decreased sampling area. A classic example is that described by Williams (1964) in Great Britain where plant species richness increased with increasingly large sampling areas, until the species richness for the entire island had been recorded. In general, SAR can be used to predict the decrease or even the extinction of species as a function of the loss of habitat or suitable space and provides the basis for natural area and preserve design, disturbance implications, and species richness (MacArthur and Wilson 1967, Soulé et al. 1979, Palmer 1990, Lawrey 1991, Rosenzweig 1995). Additionally, the SAR is not dependant on the association or pattern of area reduced, but the relative amount of space sampled. This principle can be applied

to woody species encroachment into grassland ecosystems, where a change in species richness could be expected to occur at a level predicted by the SAR.

Woody encroachment into grassland environments generally reduces herbaceous production (Engle et al. 1987, Belkys 1994, Bates et al. 2000, Watson and Reid 2001), but herbaceous production does not always decline linearly with woody species establishment (Callaway 1995). Interactions between woody species and grassland production need to be examined on a species-by-species basis because of variation in canopy structure, nutrient uptake and release, and root/shoot ratio in tree and shrub species. Directly under the crown of individual *J. virginiana* trees, production was greatly reduced, but was unaffected beyond the drip line (Engle et al. 1987). Under dense stands of *J. virginiana*, production decreased nearly 99% compared to open grassland sites (Briggs et al. 2002). Although light penetration through the tree canopy is heterogeneous, light available within the herbaceous canopy can be expected to decrease as canopy cover of *J. virginiana* increases. The relatively even distribution of abundant light at low canopy cover would create the potential for high herbaceous production and low stand-level variability. Similarly, the relatively even distribution of low light penetration associated with high canopy cover would promote decreased production, but low variability. Conversely, the uneven distribution of light at moderate levels of canopy cover promotes highly variable moderate production. However little is information known about production at low and moderate levels of stand-level *J. virginiana* canopy cover.

The assemblage of *J. virginiana* stands create inherent heterogeneous environments with the non-uniform distribution of individual trees and the contrasting



properties under individual tree crowns, marginally open crown edges, and open interspaces. Most ecological studies fail to consider this inherent heterogeneity in their conclusions and appropriate implications (Wu and Loucks 1995). However, in the context of hierarchy theory, where a scaled view of ecological systems reveals interacting components at multiple levels (O'Neill et al. 1989), patchy environments exhibit emergent properties that are more than the summation of individual characteristics. Vertical structure in a stand, for example, influences air flow across a landscape. Size, shape and density of trees within a stand dictate the micro-patterns (direction and velocity) of wind through the trees (Heisler and Dewalle 1988). This pattern differs from predictions that sum the effect of individual trees on microclimate and its influence on plant community composition and production. Therefore, we designed a study to examine the relationship between stand-level *J. virginiana* canopy cover and the herbaceous plant community incorporating stand-level heterogeneity. We predict an additive effect on plant community properties as trees are added to the stand because the effect of a tree is limited to beneath the tree crown (not beyond the crown) (Engle et al. 1987). Specifically we hypothesize that: 1) herbaceous species richness will decline along the *J. virginiana* canopy cover gradient, but at a level predicted by the SAR; 2) species loss (predicted in #1) is greater among the C<sub>4</sub> graminoid and forb functional groups than the C<sub>3</sub> graminoid functional group as suggested by Gehring and Bragg (1992) and 3) herbaceous biomass will decline at a linear rate along the *J. virginiana* canopy gradient and the variation in biomass will have a unimodal distribution along the gradient. We addressed these hypotheses in terms of both the addition of *J. virginiana* canopy cover and the subsequent decreases in open space.

## Methods

We conducted this experiment on historic tallgrass prairie sites located approximately 18 km Southwest of Stillwater, Oklahoma USA. The region is dominated by a continental climate with an average of 204 frost-free days and 846 mm annual precipitation, 65% of which falls from May to October. Typical climax vegetation in the study area is characterized by little bluestem, indiangrass (*Sorghastrum nutans* (L.) Nash), switchgrass (*Panicum virgatum* L.), big bluestem (*Andropogon gerardii* Vitman), *Carex* spp. and perennial forbs. Old world bluestem (*Bothriochloa ischaemum*) and sericea lespedeza (*Lespedeza cuneata*) are locally abundant exotic invasive species. We selected 14 100 x 100-m locations situated on similar ecological sites (USDA 2006), where *J. virginiana* canopy cover ranged between zero and approximately 80 percent as determined by aerial photographs and ground verified with densitometer at 50 points at each location. A 49 x 49-m plot was established at each location with a buffer of similar vegetation around the perimeter. Within each plot, permanent grids were established with 16 evenly spaced sampling points where plant species composition and aerial cover along with litter cover, and bare ground were estimated within a 1 x 1-m frame in mid-summer. To estimate the level of species accumulation, species area curves were constructed using the list of species from each of the 16 sampling points at two locations with zero *J. virginiana* canopy cover. The order in which we organized the 16 frames was chosen randomly, using a random number generator, and repeated 8 times then averaged between the two locations. Regression techniques and the Akaike information criterion (AIC) (Burnham and Anderson 1998) were used to determine the best model. We used this curve as the standard to compare the species richness all locations with *J. virginiana* canopy. To

determine species abundance, aerial cover was estimated using cover classes and each cover class score was converted to a midpoint value for analysis (0-1%-0.5, 1-5%-3, 5-25%-15, 25-50%-37.5, 50-75%-62.5, 75-95%-85, 95-100%-97.5). A mean cover value was calculated for each species among the 16 sampling points to determine plot-level plant species abundance.

Detrended correspondence analysis (DCA) (Hill and Gauch 1980) was used to analyze plot-level plant species composition. The data were square-root transformed and the influence of rare species was down-weighted in the ordination analysis. Percent *J. virginiana* cover was treated as a supplemental variable, which does not constrain the analysis, and used to visually assess the relationship between cedar cover and plant species composition.

Visual obstruction was recorded within each location at 90 evenly spaced points using the Robel pole technique (Robel et al. 1970). Among the 14 locations, herbaceous vegetation was clipped to ground height at 150 sampling points then oven dried to a constant weight. Regression techniques were used to determine the relationship between visual obstruction and herbaceous biomass, and then used to determine herbaceous biomass at each of 14 locations and to determine the relationship between the herbaceous biomass and open space. The AIC selection method was used to determine the best fit model.

## **Results**

We examined herbaceous species data using only those observations from the two plots void of *J. virginiana* to construct the SAR for this tallgrass prairie. Herbaceous species/genera richness increased with increased sampling area from an average of nearly

9 species at 6% open space (1 m) to 27 species at 100% open space (16 m) (Fig. 1). The data fit a logarithmic species area relationship ( $r^2 = 0.99$ ), which shows a rapid accumulation of species with initial additions of open space, but additional species are added at a decreased level with increased sampling area.

We used the constructed species area curve to assess the rate at which we expect species richness to decline when open space decreased. When we examined the influence of *J. virginiana* canopy cover, species richness declined from 23 species at 14% canopy cover to 17 at 77% canopy cover (Fig. 2). However, this decline in richness tracks closely the decline predicted by the species area relationship and indicates that declines in species richness associated with *J. virginiana* encroachment are due to the loss of open space.

Increase in canopy cover, and subsequent loss of open space, resulted in a general decrease of species within the C<sub>4</sub> graminoid, C<sub>3</sub> graminoid and forb functional groups at the same rate of decline ( $P > 0.05$ ) (Fig. 3). We recorded 61 individual species or genera among the 14 locations, 39 were of which forbs, 17 were C<sub>4</sub> graminoids and 5 were C<sub>3</sub> graminoids. Individual species/genera abundance varied from location to location, and did not consistently increase or decrease along the *J. virginiana* canopy gradient. The DCA emphasizes the lack of any strong relationships between individual species and canopy cover (Fig. 4). Species/genera evenness had nearly no relationship ( $r^2 = 0.02$ ) with loss of open space (Fig. 5). The lack of differences in evenness and functional group abundances indicate that increasing *J. virginiana* canopy cover did not cause a shift in species composition at the stand level.

Herbaceous biomass decreased at a linear rate from approximately 5350 kg\*ha<sup>-1</sup> with 0% canopy cover to nearly 1520 kg\*ha<sup>-1</sup> with approximately 77% canopy cover (Fig.6). This is a 460 kg\*ha<sup>-1</sup> decline in herbaceous biomass with every 10% increase in canopy cover. The variation in biomass along the canopy gradient followed a unimodal distribution (Fig. 7). The C.V. for herbaceous biomass was relatively small at both low and high levels of canopy cover (25% and 24% respectively) and greatest (46%) at a moderate level of canopy cover.

## Discussion

Herbaceous species richness declined as a function of increased canopy cover and subsequent loss of open space; however, the decrease in species richness closely followed a species area model. This supports our initial hypothesis that the decrease in richness would be explained by the SAR. Previous reports indicate that woody encroachment into tall grass prairie substantially reduces species abundance by as much as 90% (Briggs et al. 2002, Lett and Knap 2005). However, a substantial decrease in species richness was reported when *J. virginiana* reached a critical density of approximately 1500 trees\*ha<sup>-1</sup>, when richness declined from approximately 27 species per 10-m<sup>2</sup> to 5 species (Briggs et al. 2002). This indicated that species richness did not follow a SAR, where the decline is gradually increasing rather than large decreases at a single point. The impact of *J. virginiana*, while substantial, is limited to the area directly beneath the crown of individual trees (Engle et al. 1987 Gehring and Bragg 1992); therefore the influence at the stand level is the summation of individual trees in a given location. When additional trees are added to the stand, additional herbaceous plant species are displaced consistent with the effect predicted by the SAR.

The decline in herbaceous species richness along the increasing *J. virginiana* canopy gradient was relatively uniform among the three functional groups measured. Additionally, species evenness was reasonably consistent along the canopy cover/open space gradient. This is contrary to our second hypothesis where we predicted that the decrease in herbaceous species would be greater in the C<sub>4</sub> graminoid and forb functional groups relative to the C<sub>3</sub> graminoid group. Kentucky bluegrass and *Carex* spp., in previous reports, were more abundant in the shaded area directly beneath the crown of individual *J. virginiana* trees (Gehring and Bragg 1992, Briggs et al. 2002). In the center of dogwood (*Cornus drummondii* C.A. Mey.) islands, an additional encroaching woody shrub, forb cover was greater than adjacent open sites (Lett and Knapp 2005). It is well understood that forest canopies intercept vast quantities of incoming solar radiation preventing much of the light from reaching the canopy of the understory plant community. Woody species that encroach into historic grassland ecosystems decrease the total available light available to understory prairie species (Scholes and Archer 1997, Siemann and Rogers 2003). However, forest canopies do not intercept the incoming solar radiation uniformly and influence the quality of light by allowing differing wavelengths to pass depending on the canopy species composition (Freyman 1968). The quantity and quality of light penetrating the tree canopy can alter the understory plant composition (Haugo and Halpern 2007). Our study indicates the influence of *J. virginiana* canopy on light quantity and quality is limited to beneath individual tree crowns.

Woody species, in addition to altering light regimes, influence the litter depth, soil moisture, nitrogen availability and soil biota which are likely to strongly influence

plant species composition (Griffiths et al. 2005, Huago and Halpem 2007). The roots of individual trees extend well beyond the dripline and transport nutrients back to the tree center and ultimately into the stems and leaves, suppressing herbaceous plant growth beyond the canopy. In western North America alligator juniper (*Juniperus deppana*) influenced vegetation in an area over three times that was attributed to tree canopy cover (Clary 1974). Through natural processes, the nutrients leach from the leaves into the underlying soil creating relatively fertile areas commonly known as islands of fertility (Hibbard et al. 2001). Plants, especially grasses, with the C<sub>3</sub> photosynthetic pathway are able to take advantage of this fertile soil and grow and reproduce vigorously. One-seeded juniper (*Juniperus monosperma*) suppressed vegetation nearly 5-m beyond the canopy, but increased production at the dripline (Arnold 1964). This effect is less likely to be as pronounced at the stand scale, where multiple root masses cross and compete for the same resources. *J. virginiana*, unlike other North American juniper species, does not produce fertile and unfertile zones extending beyond the tree, but rather influences vegetation directly under the canopy (Engle et al. 1987).

The lack of a compositional shift is further emphasized by the random arrangement of species in relation to canopy cover in the DCA. The distribution of *J. virginiana* seeds and establishment of seedlings is random across the landscape with the exception of increased abundance near frugivorous bird perch sites (Holthuijzen and Sharik 1984). Herbaceous plant species, in naturally established prairies, are also randomly distributed within ecological site boundaries. Therefore, the nearly complete removal of herbaceous species directly beneath individual tree crowns (Gehring and Bragg 1992) results in a random displacement of species at the stand level and explains

why there was not a shift in functional group abundance along the canopy/open space gradient. Even at high levels of canopy cover, sufficiently large patches of open space remain to support characteristically dominant prairie species. The resulting assemblage of species is therefore more a product of individual site characteristics (soil, slope, fire, grazing etc.) than of *J. virginiana* canopy cover.

The decrease in herbaceous biomass associated with *J. virginiana* was substantial, but directly proportional to the canopy cover/open space gradient. Further, the variation in biomass, as reflected by the C.V., was maximized at moderate levels of canopy cover. This provides evidence to support our third hypothesis that predicted a linear decline in herbaceous biomass along a *J. virginiana* canopy gradient, and a unimodal distribution of biomass variation. The addition of woody vegetation into grassland environments does not decrease the annual net primary production (ANPP) of the site. Rather it causes a shift from largely herbaceous biomass to woody production (Norris et al. 2001). Lett and Knapp (2005) reported nearly a 90% decrease in forb and graminoid ANPP in the center of shrub islands adjacent to open prairie locations. Directly under the crown of isolated trees, herbaceous ANPP decreased as much as 99% (Engle et al. 1987, Briggs et al. 2002). However, the influence of *J. virginiana* is reported to be limited to the area immediately beneath the crown (Engle et al. 1987, Gehring and Bragg 1992).

It is well understood that plants are dependent on light for photosynthesis and subsequent growth. Up to the light saturation point, plants typically have greater ANPP with increased light. This is especially true in North American's southern grasslands, where the dominant C<sub>4</sub> grasses have relatively high light saturation points. The



heterogeneous nature of *J. virginiana* stands creates areas under tree crowns with reduced light, but areas in the interspaces with direct light are capable of relatively high ANPP of herbaceous species. ANPP should be consistently high throughout the site in areas where there is minimal tree canopy cover given even distribution of nutrients. Conversely, in areas where canopy cover is nearly complete ANPP will be consistently low. However, with moderate canopy cover there are areas where shade limits production, but there are also areas where direct sunlight allows for high production creating a highly variable environment.

## **Conclusions**

The results of this study are relevant to studies of ecosystems not in equilibrium especially grasslands where woody encroachment is occurring. The ecological thresholds concept (Holling 1973, Westoby et al. 1989) provides an intellectual framework for understanding ecosystems not at equilibrium. These systems may experience transition through excessive negative feedback mechanisms which promote a series of degenerative thresholds and transitions. The stepwise process ultimately leads to a new state with a substantially different function than the original ecosystem (Briske et al. 2006). Grasslands cross the initial structure threshold when low densities of trees or shrubs alter natural disturbance patterns promoting further woody encroachment; however the successive species richness threshold is inconsistent among woody species. Several studies in western (Blackburn and Tueller 1970, Miller et al. 2000) and southwest (Archer 1989) North America reported that the species richness threshold was crossed at moderate levels of woody encroachment. Tall grass prairie in central North America is reported to cross the species richness threshold following *J. virginiana* encroachment

(Briggs et al. 2002). However, at the scale of our study, we did not find evidence to support this theory. While we did find a decline in species richness with increased canopy cover, the decrease followed the SAR and was without immediate and substantial declines typical of thresholds. To definitively test the species richness threshold theory, additional in-depth study will be necessary. Ecological thresholds imply that a return to the original condition will not occur without excessive anthropogenic inputs or exceed our management timeline. Removing *J. virginiana* trees in areas with various canopy cover will allow the restoration processes to be explored and tested.

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### Figure captions

Figure 1. A species area relationship constructed from two 50 x 50-m locations, void of *Juniperus virginiana*, in central Oklahoma. A total of 16-1 m<sup>2</sup> plots were sampled at each location

Figure 2. A species area relationship constructed with standard error for open grassland locations; and the relationship between species richness and loss of open space attributed to *Juniperus virginiana* canopy cover in central Oklahoma

Figure 3. The relationship between open space attributed to *Juniperus virginiana* canopy cover and species richness among three functional groups in central Oklahoma

Figure 4. Bi-plot of the detrended correspondence analysis of plot level herbaceous species abundance along a *Juniperus virginiana* canopy cover/open space gradient in central Oklahoma. The variation explained by *J. virginiana* (Cedar Cover) was 8.7% among all axes

Figure 5. The relationship between plot level herbaceous species evenness and the loss of open space attributed to *J. virginiana* canopy cover in central Oklahoma

Figure 6. The relationship between plot level herbaceous biomass and the loss of open space attributed to *J. virginiana* canopy cover in central Oklahoma

Figure 7. The relationship between plot level herbaceous biomass variation and the loss of open space attributed to *J. virginiana* canopy cover in central Oklahoma

Figure 1

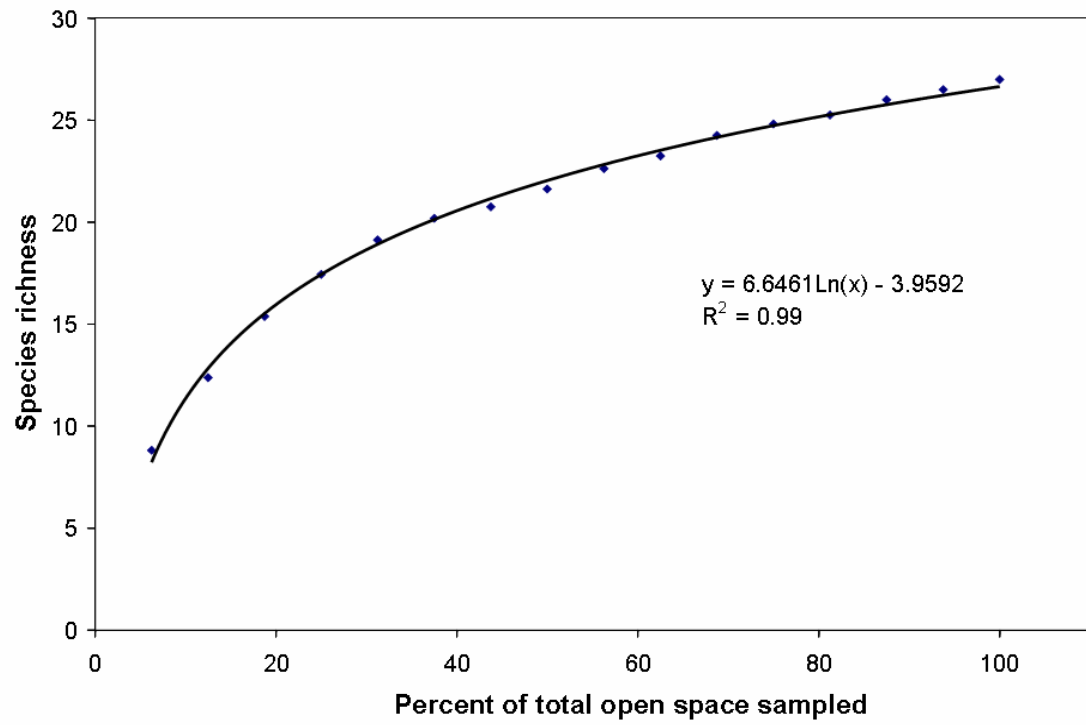


Figure 2

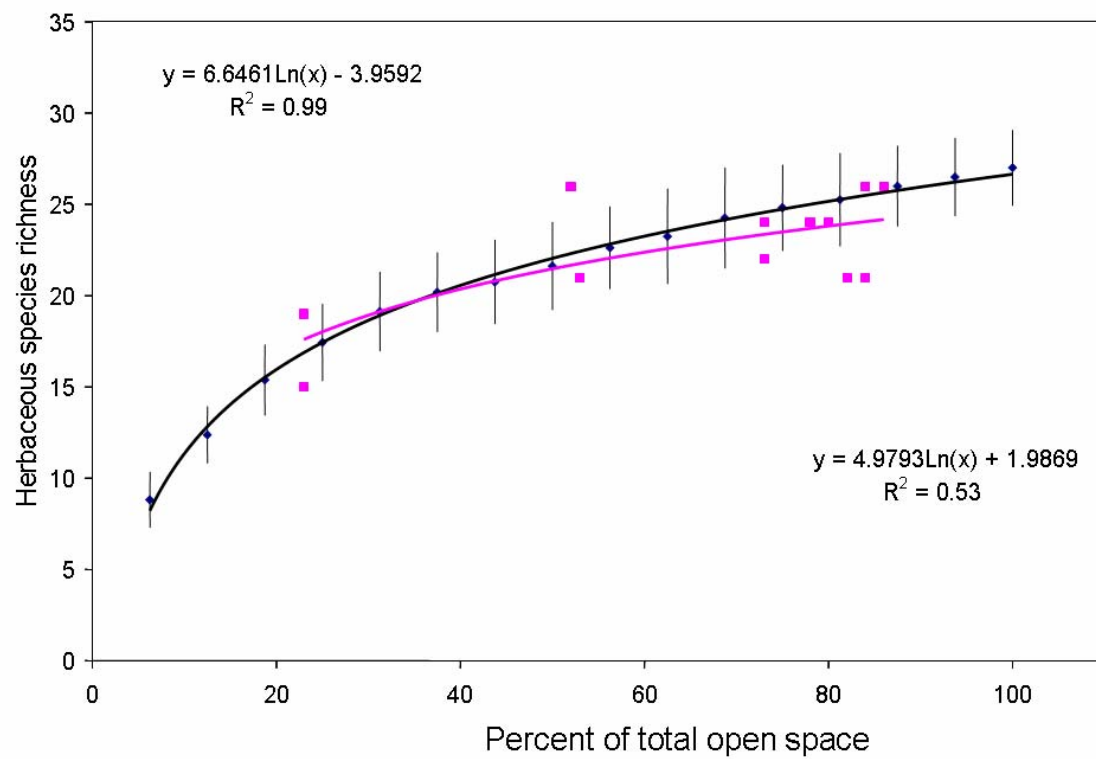


Figure 3

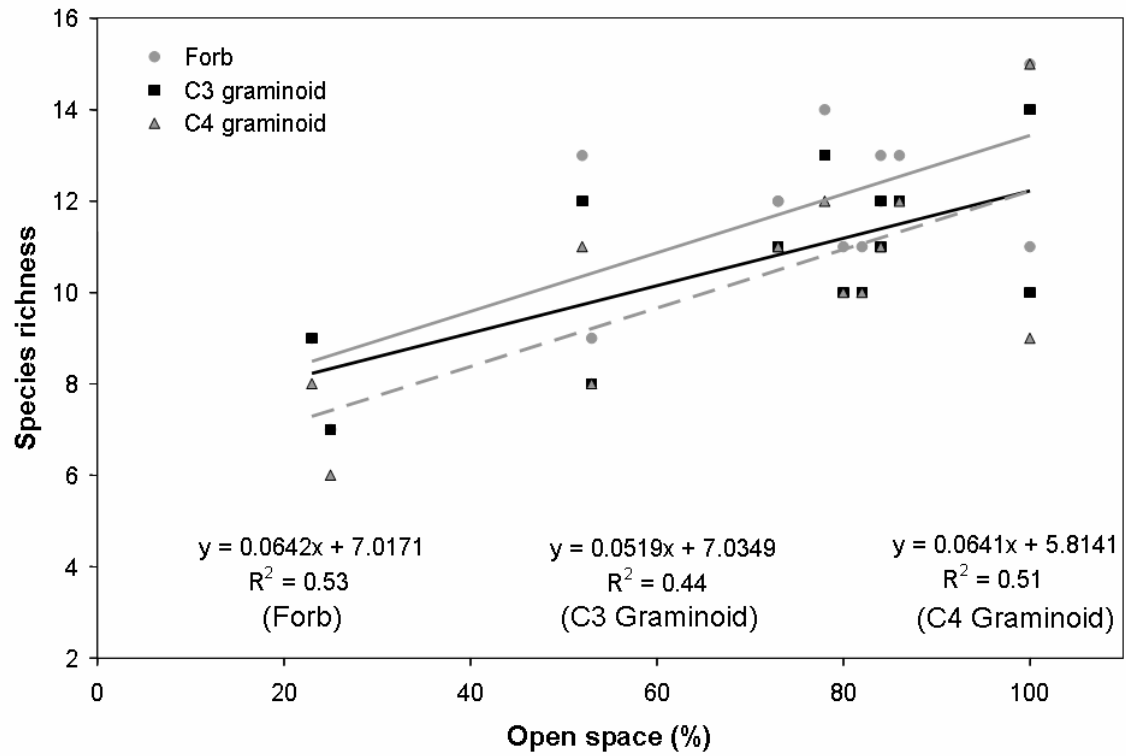
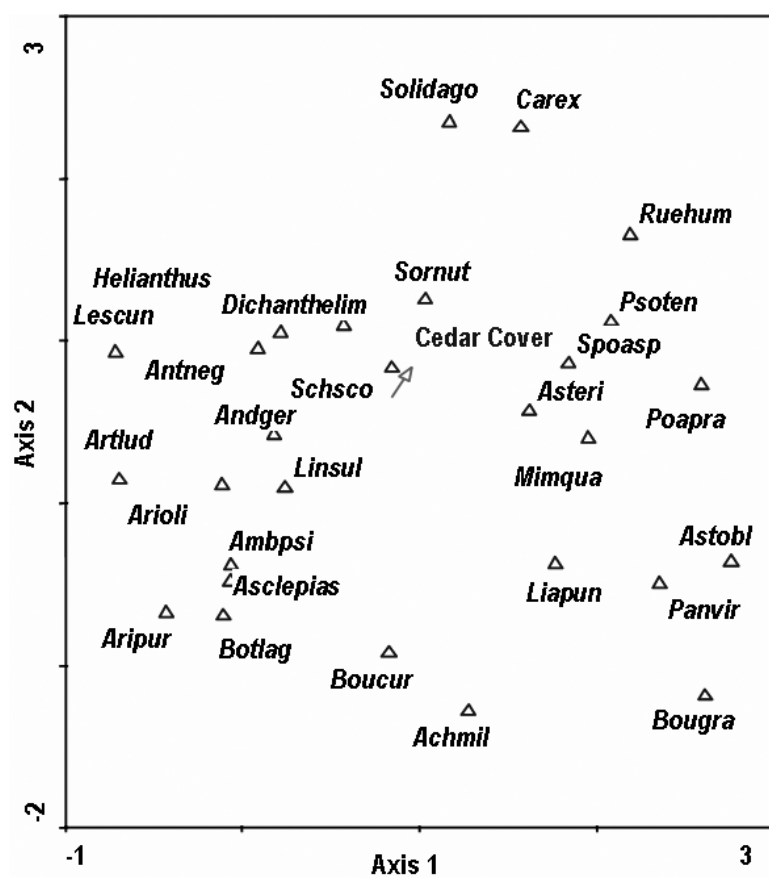


Figure 4



Axes	1	2
Eigenvalues	0.35	0.41
Cumulative variance	18.1	39.1
Total variation explained	8.7%	

Figure 5

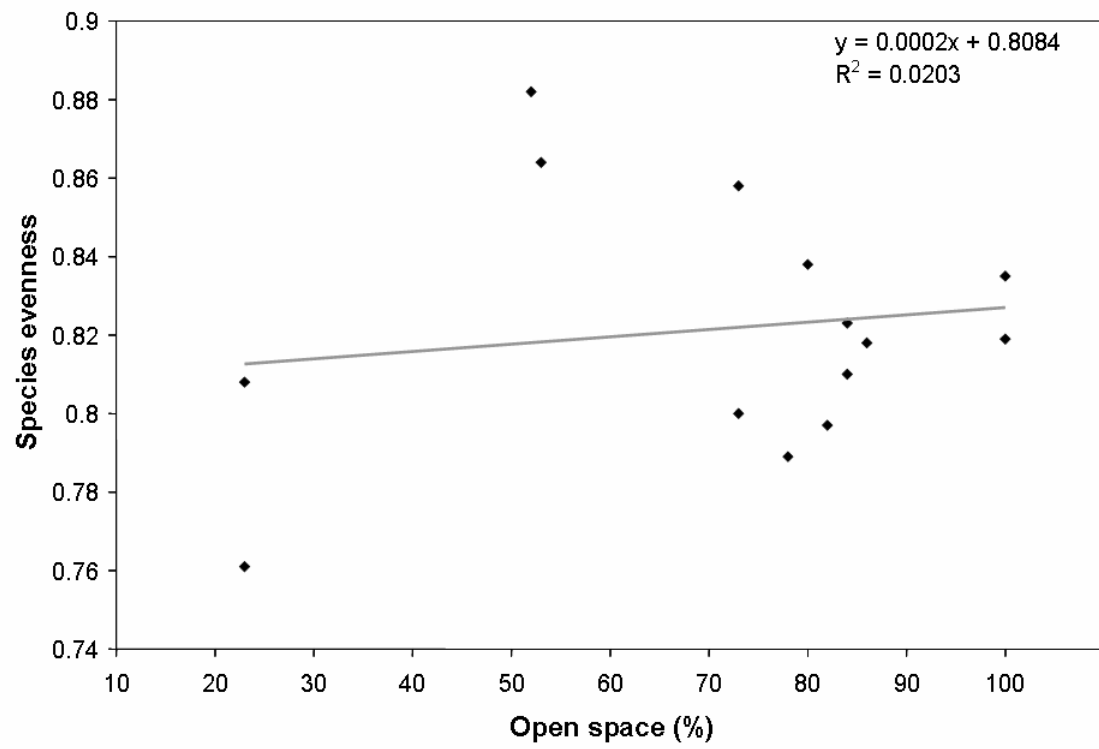


Figure 6

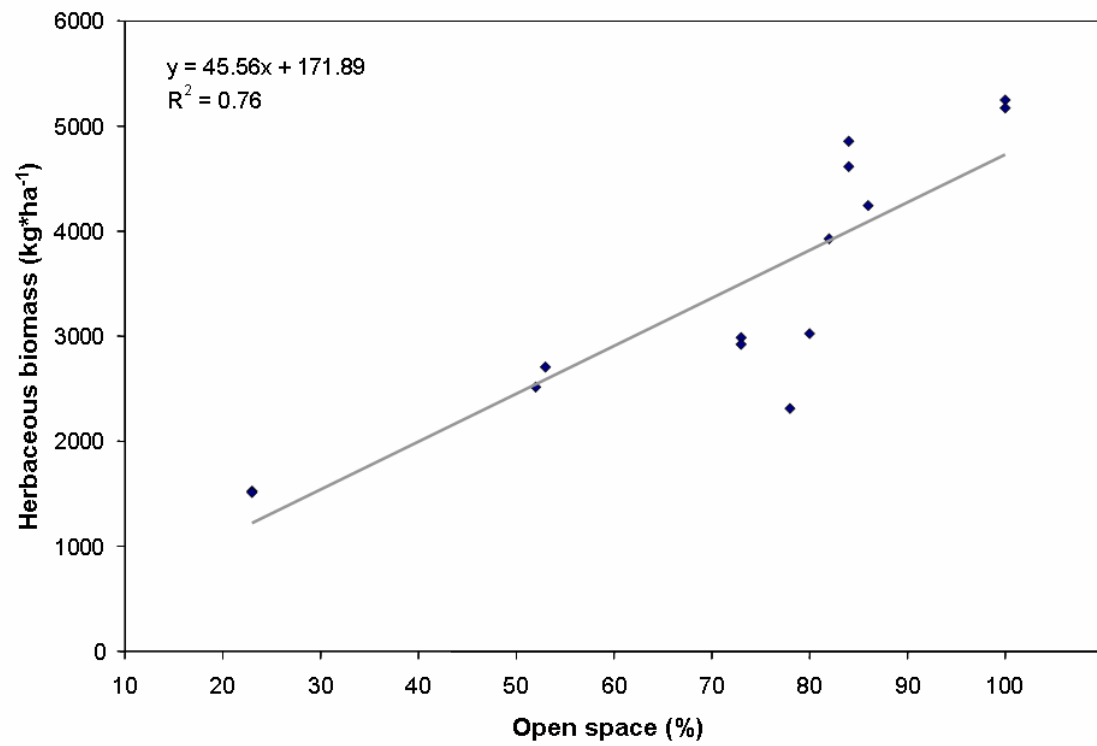
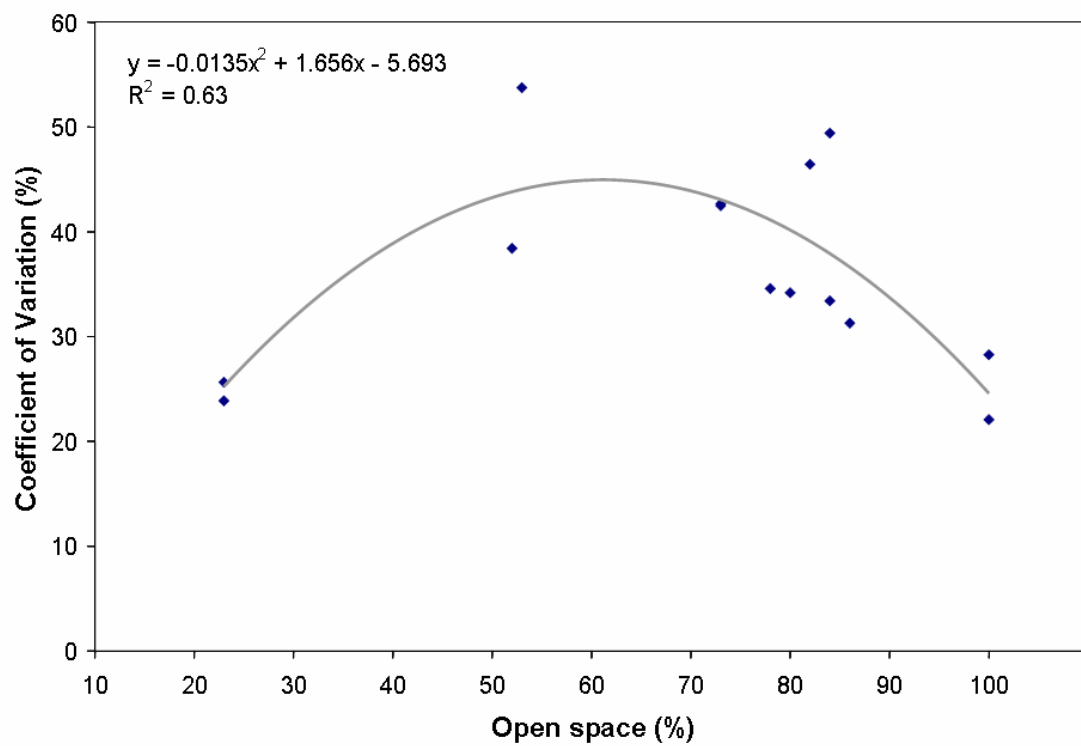




Figure 7



## CHAPTER II

# GRASSLAND PLANT COMMUNITY RESPONSE TO MULTI-SCALED ANTHROPOGENIC DISTURBANCE

# **Grassland plant community response to multi-scaled anthropogenic disturbance**

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Key words: grazing, hay harvest, resilience, resistance, soil disturbance, successional trajectory, tracked vehicles,

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## **Abstract**

Grassland ecosystems evolved with natural disturbance events on multiple spatial scales. The resulting plant communities are adapted to defoliation disturbance and are resistant to herbivory, but are less adapted to soil disturbance. Historic disturbance regimes are now largely replaced by anthropogenic activities, many of which at least partially mimic natural disturbance to plants and soil. While we have a good understanding of individual anthropogenic disturbances, it is unclear how plant communities respond when multiple disturbances are combined. Therefore, we used tracked vehicles as focal soil disturbance agents in a mesic mixed prairie to assess the relative influence of intense, focal soil disturbance on plant species composition and bareground within a matrix of either undisturbed prairie or prairie disturbed by grazing or hay harvest. Plant communities were resistant to both defoliation disturbances, but were less resistant to focal soil disturbance. Despite having different initial plant species composition, grazed and hayed communities followed similar successional trajectories following focal disturbance and recovered within two growing seasons. Plant species richness and bareground increased ( $P < 0.05$ ) following focal soil disturbance in both grazed and hayed communities, but the combination of focal soil disturbance and extensive defoliation disturbance did not have a greater effect ( $P > 0.05$ ) than focal soil disturbance alone. Also, the effect was short lived with recovery after two growing seasons. Our results suggest that anthropogenic disturbances can serve as proxies for natural disturbance.

## Introduction

Disturbance followed by recovery is a natural process common in biomes globally. The effects of disturbance on plant communities can be complex depending on the type, extent, severity and frequency of each disturbance (Sousa 1984). Often the vegetative response of an ecosystem to disturbance is separated into two categories. Ecosystem resistance refers to the ability of vegetation to resist change following perturbation, while ecosystem resilience is in reference to the time period necessary for a community to return to its pre-disturbance composition or state (Holling 1973, May 1973, Mitchell et al. 2000, Hirst et al. 2003). Grassland ecosystems evolved with frequent disturbance events and thus developed attributes that promoted resilience. Frequent broad-scale and non-selective disturbances such as fire enabled graminoid species to become the dominant vegetation in many grasslands due to protected growth points and relatively quick growth and reproduction compared to many shrub and tree species (Axelrod 1985). In North America's Great Plains region grazing by large ungulates often occurred in tandem with fire (Fuhlendorf and Engle 2001), but more selective in nature, and further emphasized the dominance of graminoid species with sub-dominate forb species (Axelrod 1985, Augustine and McNaughton 1998, Towne et al 2005). Recent investigations suggest that recovery following fire and grazing disturbances is rapid and takes as little as three growing seasons in tallgrass prairie which further emphasizes the ecosystem's resiliency (Fuhlendorf and Engle 2001, Fuhlendorf et al. *In Press*). However, both fire and grazing are above-ground disturbances acting to remove vegetative biomass, but largely left the soil and below-ground biomass unaltered which promoted relatively stable and high seral stage matrix grassland plant communities.

Biopedturbation, organism induced soil disturbance, is a factor influencing plant community composition (Mielke 1977, Whitford and Fenton 1999). Fossorial animals occupied much of the grassland region and at times were the most numerous and extensive herbivores in North America (Koford 1958). However, unlike large ungulate grazing, they existed in small unconnected colonies or complete isolation. The burrowing and mounding action of the animals regularly disturbed the soil and created small patches of bare ground which enabled sub-dominant forb and early seral species to be expressed and become locally abundant (Platt, 1975, Steuter et al. 1995, Whitford and Fenton 1999, Winters et al. 2002). Plant community composition favored early successional forb and grass species for up to eight years following prairie-dog burrow abandonment in tallgrass ecosystems (Coppock et al. 1983). Similarly, wallowing action of bison created isolated islands of exposed soil which promoted early seral vegetation species (Trager et al. 2004, Coppedge and Shaw 2000). This suggests that grasslands are only moderately resistant or resilient to soil disturbances. In an additional report from tallgrass prairie, Suding and Goldberg (2001) indicated that soil disturbances promote compositional changes more than above-ground disturbance. Historically however, both above-ground disturbances (fire and grazing) and at or below-ground disturbances occurred in tandem and promoted a species rich grassland biome. However, following European settlement, many natural disturbance regimes were altered or removed from the grassland landscape and replaced with anthropogenically derived disturbances.

Anthropogenic activities are commonplace within the current grassland landscape, many of which at least partially mimic natural disturbances. Fenced livestock grazing has all but completely replaced the migrating bison herds. However, the

influence of cattle and bison grazing on plant community composition was 85% similar, with differences in management playing a larger role in plant composition than grazing animal (Towne et al. 2005). Livestock grazing has numerous implementation strategies with varying intensities. For our purpose we consider it to be non-uniform and moderately applied throughout a growing season. This disturbance can result in a species rich and spatially heterogeneous plant community (Adler et al. 2001, Fuhlendorf and Engle 2004, Hickman et al. 2004). Conversely, hay harvest, the process of cutting and removing herbaceous biomass mechanically, is a uniform disturbance applied singly or at set intervals during the growing season. This type of disturbance can result in a species rich and spatially uniform plant community (Critchley et al. 2007) however; hay harvest does not have an analogous natural disturbance. Even though differences exist between grazing and hay harvest, both are defoliation disturbances typically applied at broad landscape scales, and are mostly limited to above-ground leaving the soil surface relatively unaltered.

Vehicular disturbance, similar to other anthropogenic disturbance, is wide spread throughout the grassland region (Webb 1983) and can destroy above-ground plant parts through trampling (Anderson et al. 2005). However, unlike livestock grazing and hay harvest, vehicle disturbances typically impact at fine-scales (Dale et al. 2005) and can extend to the soil surface and below-ground similar to the natural disturbance created by fossorial animals and bison wallowing. Multiple studies investigated the influence of individual anthropogenic disturbances such as livestock grazing (Fleischner 1994, Vavra et al. 1994, Vallentine 2001), hay harvest (Stampfli and Zeiter 1999, Bullock et al. 2001) and vehicular movements (Prosser et al. 2000, Althoff and Thien 2005, Anderson et al.

2005) on plant species composition resistance and resilience, however little is known about the interactions of above and below-ground disturbances or interactions between extensive and focal disturbances.

Recovery following anthropogenic disturbance is reported to be highly dependant on the original plant community (Larson et al 2001). While both livestock grazing and hay harvest can result in relatively stable and species rich plant communities, differences in the temporal and spatial pattern of disturbance can lead to differences in plant species composition. Grazing tends to favor grass species and hay harvest promotes forb abundance (Jog et al. 2006). Historically, it is thought that the interaction of natural extensive and intensive events such as drought, fire, grazing and prairie dog burrowing determined the plant community composition. However, with many of these disturbances removed from the ecosystem, understanding the implications of anthropogenic disturbance interactions on plant community succession and recovery is vital to maintain ecosystem stability.

Therefore we used tracked vehicles as disturbance agents in a mesic mixed prairie to assess the relative influence of intense, focal soil disturbance on plant species composition and bare ground within a matrix of either undisturbed prairie or prairie disturbed by grazing or hay harvest. We predicted that anthropogenic disturbances would mimic natural disturbances and deviate from original plant communities but then recover to non-disturbed composition. Further, due to different initial plant communities, the successional trajectories would be different for grazed and hayed landscapes. We also predicted that the implications of combined focal soil disturbance and extensive defoliation disturbances would be additive in both grazed and hayed communities.



## Methods

The study was located at the Smoky Hills Air National Guard Bombing Range (Smoky Hills Range, hereafter) about 10 km southwest of Salina, Kansas USA. The Smoky Hills Range is 14,000 ha comprised of sandstone formations intermixed with well formed silty loam soils. The climate is continental with the majority (51%) of the 802 mm annual precipitation occurring between May and August. July is the warmest month with a mean high temperature of 34°C and January is the coldest month with a mean high temperature of 3.9°C. The vegetation is classified as mixed-grass prairie with dominant grass species including: little bluestem (*Schizachyrium scoparium* (Michx.) Nash), big bluestem (*Andropogon gerardii* Vitman), indiangrass (*Sorghastrum nutans* (L.) Nash) and sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.). Grazing of domestic livestock occurs in a portion of the Smoky Hills Range beginning 1 May through 31 October annually. Hay harvest is conducted once in additional units between July 1 and July 31 annually. Current land management is consistent with the previous 25 years.

Disturbance experiments were conducted in six randomly selected grazed (n=6) and hayed (n=6) landscapes. Four 100 x 100-m plots were established on similar ecological sites within each landscape with a 50-m distance between plots. Extensive disturbance consisted of either grazed and non-grazed treatments or hayed and non-hayed treatments within grazed units and hayed units respectively. Focal soil disturbance consisted of a 39,000-kg tracked vehicle on a 2.8 km fixed pattern (Figure 1) within a 100-m plot in late winter 2006 prior to active spring growth (Table 1). A factorial combination of extensive defoliation and focal soil disturbance was randomly applied to each of the four plots within grazed and hayed units.

We estimated plant species composition and abundance and bare ground within 15 frames (1 x 1m) in each 100 x 100-m plot. Frames were arranged in three groups of five extending diagonally between opposite plot corners (Figure 1). To ensure that tracked vehicle disturbance locations were represented in sampling, three additional frames were randomly located at turn locations (Figure 1). To prevent unequal sampling among plots, we randomly discarded three frames from matrix locations. Sampling for plant species composition and bareground was conducted in late spring (1 to 15 June) in 2005, 2006 and 2007. Plant species canopy cover and bare ground were estimated with a modified cover class system (0-1%, >1-5%, >5-25%, >25-50%, >50-75%, >75-95%, and >95-100%). The midpoint values for each class were used in analyses. Plant nomenclature follows the National Plants Database (NRCS 2004).

Detrended correspondence analysis (DCA) was used to determine differences in plant species composition for each treatment and for differences between matrix and focal soil disturbance locations within treatments. DCA positions groups by compositional similarity, thus we used the mean site score and the standard deviation among treatment plots to assess the relative differences among treatments. The mean plant species cover for each plot and location within plots was square-root transformed prior to analysis.

One-way analysis of Variance (ANOVA) was used to determine if extensive disturbance and focal disturbance significantly ( $P < 0.05$ ) affected plant species richness and bare ground. Data from grazed and hayed communities were analyzed separately. Data were species richness from 15 frames within each treatment plot ( $n=6$ ) and for focal disturbance locations within each treatment plot ( $n=6$ ). The mean percent bare ground

from 15 frames within each treatment plot (n=6) and for focal disturbance locations within each treatment plot (n=6) was used for analysis. To increase homogeneity of variances, all percent bare ground values were arcsine transformed prior to analysis (Steel et al 1997).

## **Results**

Long-term grazing and hay harvest disturbances promoted two different plant communities (Figure 2). Both grazed and hayed communities were similarly dominated by tall C<sub>4</sub> grass species, but distinct differences within the sub-dominant community existed (Table 2). Subdominant plant species in the grazed community were characteristic of mid to late seral stages with few early seral species, while plants in the hayed community were early to mid seral species with few late seral plants. The area occupied within the ordination space was much greater within the hayed community, indicating greater variability in composition compared to the grazed community.

Prior to treatment, differences in plant species composition existed between the grazed and hayed community therefore we analyzed data from the two landscapes separately. Focal soil disturbance had an influence on plant species composition the first year following treatment. The changes were short-lived with similar plant species composition among treatments in both grazed and hayed communities the second growing season following focal soil disturbance. Also, in the effect was similar in both grazed and hayed communities, indicated by a separation of mean site scores along DCA axis 1 (Figure 3). Further, there was not a noticeable additive effect between focal soil disturbance and extensive defoliation disturbance on composition in either community. The shift in species composition at the plot level was due to the large compositional

change at the specific turn locations within plots containing focal soil disturbance. Compared to matrix locations, which consisted of perennial grasses and late seral forbs, turn locations were dominated by annual grass and early seral forb species in both grazed and hayed communities (Table 2).

The amount of bare-ground created by focal soil disturbance and extensive defoliation disturbance differed within grazed and hayed communities (Figure 4). The first year following treatment the amount of bare-ground increased similarly ( $P < 0.05$ ) in all disturbed plots within the grazed community. However, the amount of bare-ground was greatest ( $P < 0.05$ ) in plots with a combination of both focal soil disturbance and extensive defoliation disturbance. In contrast, within the hayed community the amount of bare-ground was influenced by focal soil disturbance ( $P < 0.05$ ) but did not show a greater response to the combination of focal soil disturbance and extensive disturbance. The second year following treatment, there were no differences ( $P > 0.05$ ) in the amount of bare-ground among treatments.

Focal soil disturbance increased plant species richness in both grazed and hayed communities (Figure 5). The first year following treatment, plots with focal soil disturbance and plots with focal soil disturbance and extensive defoliation disturbance had greater ( $P < 0.05$ ) plant species richness than only extensive defoliation disturbance or no disturbance plots. The turn locations within focal soil disturbance plots did not have high species richness, however the species assemblage was different compared to matrix locations, and added to the overall plot richness. Our study design was not sufficient to detect differences in species richness in plots with the interaction of focal soil disturbance and extensive defoliation disturbance ( $P > 0.05$ ) in both grazed and

hayed communities and the second year following treatment species richness was similar among treatments.

## **Discussion**

In an ecosystem adapted to periodic, intense disturbance, we imposed anthropogenic focal soil disturbance imbedded within extensive defoliation disturbances that were either analogous (i.e., grazing) or non-analogous (i.e., haying) to the natural disturbance regime. We predicted that grasslands would be resilient to anthropogenic disturbances that mimic natural perturbations. Our study revealed that despite having different initial plant community composition, successional trajectories in grazed and hayed communities merged following focal soil disturbance and then diverged and returned to pre-disturbance states within two growing seasons. Further, we have a good understanding of disturbances, both natural and anthropogenic, independently but we lack a complete understanding of combined disturbances or disturbances in differing contexts. The combination of both focal soil disturbance and extensive defoliation disturbance did not produce an additive effect in neither grazed nor hayed community suggesting grassland ecosystems are adapted to above-ground defoliation but not soil disturbances.

Despite having different initial starting points, grazed and hayed communities shared common successional trajectories with similar dominant annual grasses and forb species occurring at focal disturbance locations imbedded within grazed and hayed communities. This is contrary to many studies that indicate successional trajectory is highly dependent on initial floristic composition (Egler 1954, Noble and Slatyer 1980, del Moral 2007). In tallgrass prairie, vegetation change following focal soil disturbance was greater when perennial C<sub>3</sub> grasses, both native and exotic, were abundant (Dickson et al.

2008). Initial differences, as minor as a single species, can initiate succession that eventually results in two completely different plant communities (del Moral 2007). Often the key species linked to marked change, particularly following anthropogenic disturbance, is an exotic invasive species (Larson et al. 2001).

Characteristic of many invasive plant species, alterations of nutrient, water and light availability and disturbance regimes often occur following establishment, which modifies the environment making it less suitable for native species (Perrins et al. 1992, Thompson et al. 1995, Williamson and Fitter 1996). Often the modifications are such that successional threshold is crossed and hysteresis occurs with a new suite of species and recovery to the original plant community is not realized (Laycock 1991, Rietkerk and van de Koppel 1997, Suding et al. 2004, Briske et al. 2006). Cheatgrass establishment following perturbation in semi-arid regions of North America facilitates increased fire return intervals. The altered fire regime promotes additional cheatgrass establishment and other fire tolerant species eventually completely changing the community composition (Laycock 1991, Knapp 1996, D'Antonio 2000). While cheatgrass was present at our study location, it was not a dominant in either grazed or hayed landscapes pre or post-disturbance and hysteresis did not occur following focal or extensive disturbance individually or when combined.

The presence or absence of either extensive defoliation disturbance (i.e. grazing or hay harvest) did not alter the influence of the focal soil disturbance. This might reflect that regional grasslands, like many others, evolved with herbivory and are well adapted to defoliation disturbances, a historically relevant extensive disturbance. For example, species richness and diversity of Mediterranean grasslands remained high after centuries

of grazing and hay harvest (Garcia 1992). In Kansas tallgrass prairie, areas grazed by bison had higher species richness, evenness and diversity than ungrazed areas (Hartnett et al. 1996). Similarly, South African grasslands retained species diversity and species abundance despite decades of excessive herbivory (Harrison and Shackleton 1999). Grazing at multiple intensities had no noticeable influence on cover, density or production of forb species in a cool-season mixed-grass prairie (Biondini et al. 1998). Conversely, California grassland plant communities did not evolve with extensive grazing and show changes in composition from perennial to annual species following defoliation disturbance (Bartolome et al 2004). Thus, the plant community response to defoliation is largely dependant on evolutionary history.

Grasslands are not resistant to soil disturbance and experience large shifts in plant composition following both natural events such as prairie dog burrowing and anthropogenic events such as cultivation, but resilience following soil disturbance appears to be dependant on the extent and frequency of the disturbance. Fossorial animal disturbance is locally severe, but it is heterogeneously spaced throughout a colony. It is necessary that intact soil remains between individual mounds to support sufficient vegetation as food resources for the colony. Therefore, plant populations are in close proximity to disturbed areas and can re-colonize quickly. Additionally, following initial mound and burrow establishment, additional soil disturbance is minimal allowing plants in the interspaces to persist. Cultivation, in contrast, is predominantly a uniform disturbance with minimal undisturbed locations within a given location resulting in relatively large distances for re-colonization. Further, cultivation is more frequent than natural soil disturbance often occurring annually preventing many plants from persisting.

Many grasslands are less resilient to extensive soil disturbance and show greater resilience to focal soil disturbances. Mechanized soil disturbance in Australian grasslands was more influential on plant species composition than defoliation and water availability (McIntyre and Lavorel 1994) and one-time cultivation on small plots was more influential than grazing or fire, but recovery was relatively quick (Li et al. 2007). Following prairie dog removal, plant community composition and annual herbaceous production was similar to areas formerly grazed by bison within two years (Silva Cid et al. 1991). Shortgrass steppe was less resistant to tracked-vehicle disturbance than shrubland or woodland communities, but was more resilient with a shorter recovery period (Milchunas et al. 2000). In contrast, Kansas tallgrass prairie, even 35 years post extensive cultivation, go-back tallgrass prairie does not completely recover to match uncultivated communities, despite deliberate seeding (Kindscher and Tieszen 1998). Therefore, exposure to prolonged extensive soil disturbances might impose successional thresholds. Yet in our study, recovery was achieved within two growing seasons, indicating that a single-event focal anthropogenic disturbance did not create a restoration threshold in either grazed or hayed community indicating that focal anthropogenic disturbance can mimic natural disturbance events.

Climatic conditions often dictate the rate of recovery of plant communities. Under wet conditions we might see a prolonged recovery due to increased soil perturbation. Track vehicles, designed to move on a continuous circular track, are in contact with a larger surface area compared to wheeled vehicles, and decrease soil surface pressure and increases traction and mobility (Karafiath and Nowatzki 1978). However, when soil moisture content is high, the increased traction increases soil



disturbance. Rut depth from tracked vehicles under wet soil conditions was nearly twice the depth under dry conditions (Braunak and Williams 1993). Vegetation impact from tracked vehicles on wet soil was nearly 80% greater than on dry soil (Anderson et al. 2006). Before and immediately following focal soil disturbance soil conditions were dry due to well below normal precipitation (data not shown). Thus the tracked vehicle merely scraped the soil surface leaving roots and other below-ground plant structure intact. Further, above-normal precipitation the second growing season following focal disturbance provided an opportunity for rapid recovery. We anticipate that the recovery period would be different under alternative climatic conditions.

Combined disturbances often have an additive effect on plant communities; however, in both grazed and hayed landscapes, focal disturbance superseded both extensive disturbances and did not reveal any additive effects. This is not unique and many studies report that additive effects are highly dependant on the particular combination of disturbance. The application of both fire and grazing in grassland ecosystems results in greater species richness than either disturbance individually (Collins 1987, Noymeir 1995). Ant mounds within prairie dog colonies, in shortgrass steppe, had less vegetation than either mounds outside the colony or colonies without ant mounds demonstrating the additive effect of combined disturbances (Alba-Lynn and Detling 2008). Yet, in multiple grassland ecosystems, the combination of grazing and drought did not have a greater effect on plant communities than drought alone suggesting that compositional shifts only occur within the context of climatic conditions rather than herbivory (Biondini and Manske 1996, Biondidi et al 1998, Heitschmidt et al. 1999). Our study further demonstrates the grasslands resistance to defoliation disturbances.

Historical disturbance has been altered in grassland ecosystems, but using anthropogenic disturbances as proxies for natural disturbances is a way to maintain species diversity and system stability (Fuhlendorf and Engle 2001, Donlan et al. 2005, Fuhlendorf et al. *In Press*). While grasslands are not resistant to natural or anthropogenic soil disturbance, the disturbance process is meaningful to numerous small mammal and bird species. Annual grass and forb species, common to soil disturbance sites, provide a meaningful food resource to small mammal and bird species. Further, the alteration of ground cover provides essential habitat for many obligate grassland bird species. We conclude that overall the grassland plant community response to anthropogenic focal disturbance was similar to that of natural disturbance regimes.

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## Figure captions

Figure 1.

A. Focal disturbance pattern applied to grazed and hayed landscapes prior to active spring growth at the Smoky Hills Range near Salina, Kansas USA; B. Aerial photograph of a plot with focal disturbance with turn and matrix locations identified; C. Sampling pattern used to estimate plant species composition and bare ground within 100 x 100-m plots.

Figure 2.

Plot of the first two axes of a detrended correspondence analysis of plant species composition data. The plot represents mean site scores and bidirectional standard error for plots within grazed and hayed plant communities before focal soil disturbance and removal of extensive defoliation disturbance at the Smoky Hills Range near Salina, Kansas USA.

Figure 3.

Plots of the first two axes of detrended correspondence analysis of plant species composition data. The plots represent mean site scores and bidirectional standard error for plots within (a) grazed and (b) hayed plant communities and turn locations within (c) grazed and (d) hayed plant communities before focal soil disturbance and removal of extensive defoliation disturbance (-9 mo), 1 growing season (+3 mo) and 2 growing seasons (+15 mo) after focal soil disturbance and removal of extensive defoliation disturbance. Solid and dashed lines follow individual treatments throughout time.

Figure 4.

Mean plot level percent bare ground and standard error on (a) grazed and (b) hayed communities before focal soil disturbance and removal of extensive defoliation disturbance and two growing seasons following focal soil disturbance and extensive defoliation disturbance; and mean percent bare ground and standard error for turn locations within focal soil disturbance plots within (c) grazed and (d) hayed communities two growing seasons following focal soil disturbance and removal of extensive defoliation disturbance. Solid and dashed lines follow individual treatments throughout time.

Figure 5.

Mean plot level plant species richness and standard error in (a) grazed and (b) hayed plant communities before focal soil disturbance and removal of extensive defoliation disturbance and two growing seasons after focal soil disturbance and removal of extensive defoliation disturbance; and mean plant species richness and standard error for turn locations within focal soil disturbance plots within (c) grazed and (d) hayed communities two growing seasons following focal soil disturbance and removal of extensive defoliation disturbance. Solid and dashed lines follow individual treatments throughout time.

**Table captions**

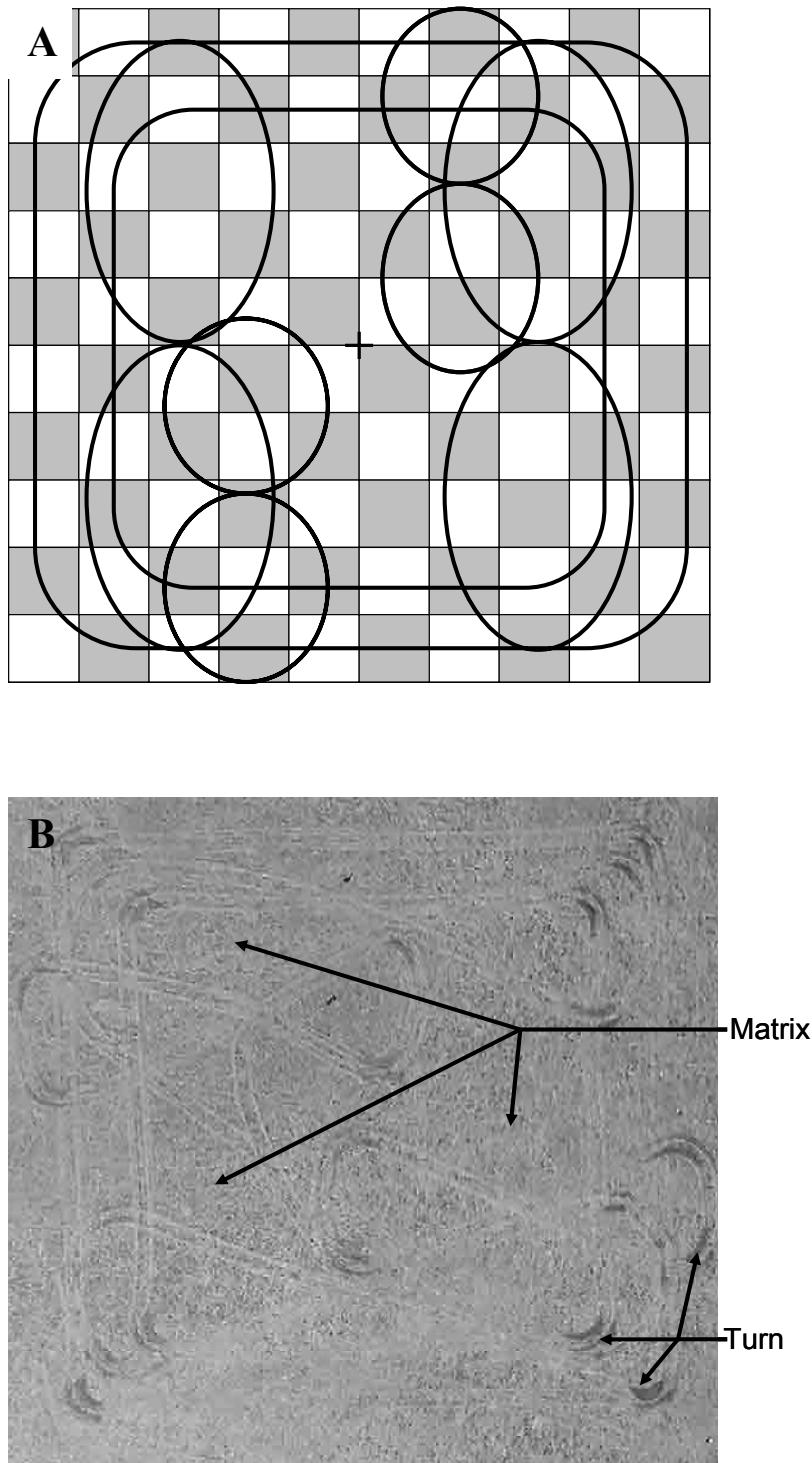
Table 1.

Timing of vegetation and ground cover sampling and application of focal soil disturbance and removal of extensive defoliation disturbance at the Smoky Hills Range near Salina, Kansas USA

Table 2.

The ten most abundant species (canopy cover mean and standard error) present at turn locations in plots with focal soil disturbance within grazed and hayed communities at the Smoky Hills Range near Salina, Kansas USA

Figure 1.



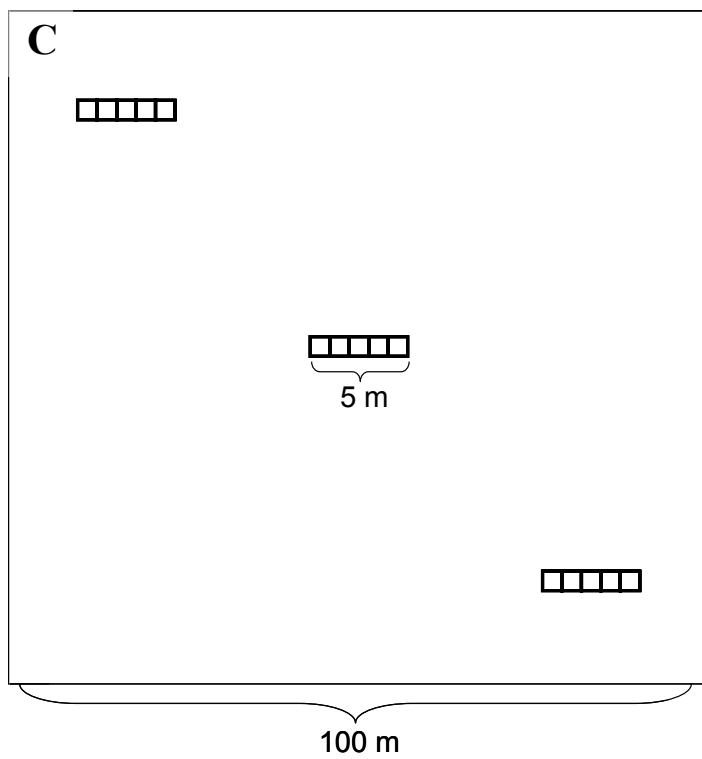


Figure 2.

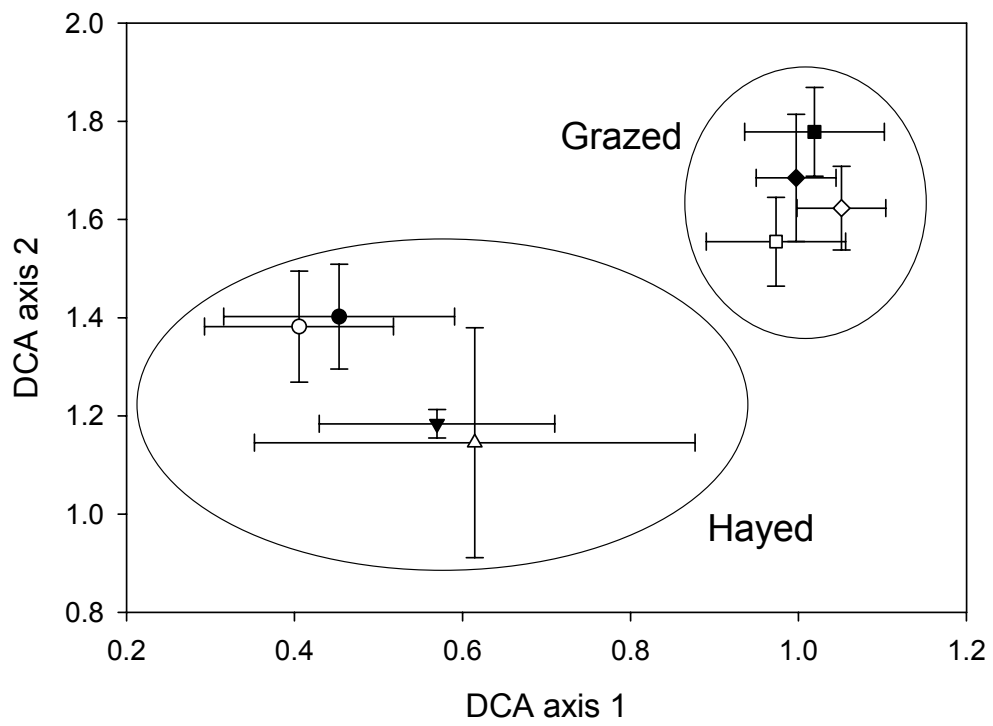




Figure 3.

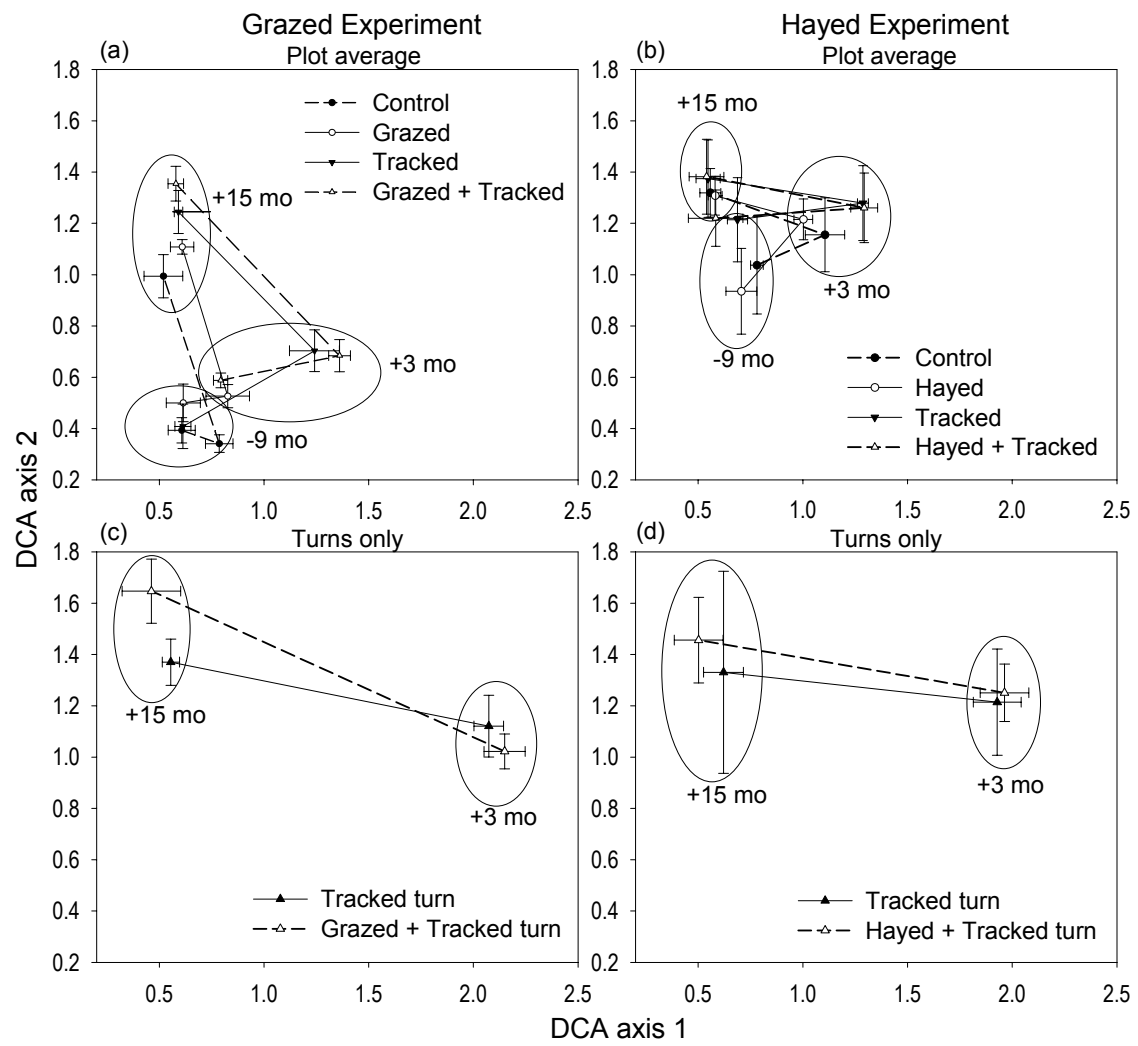


Figure 4.

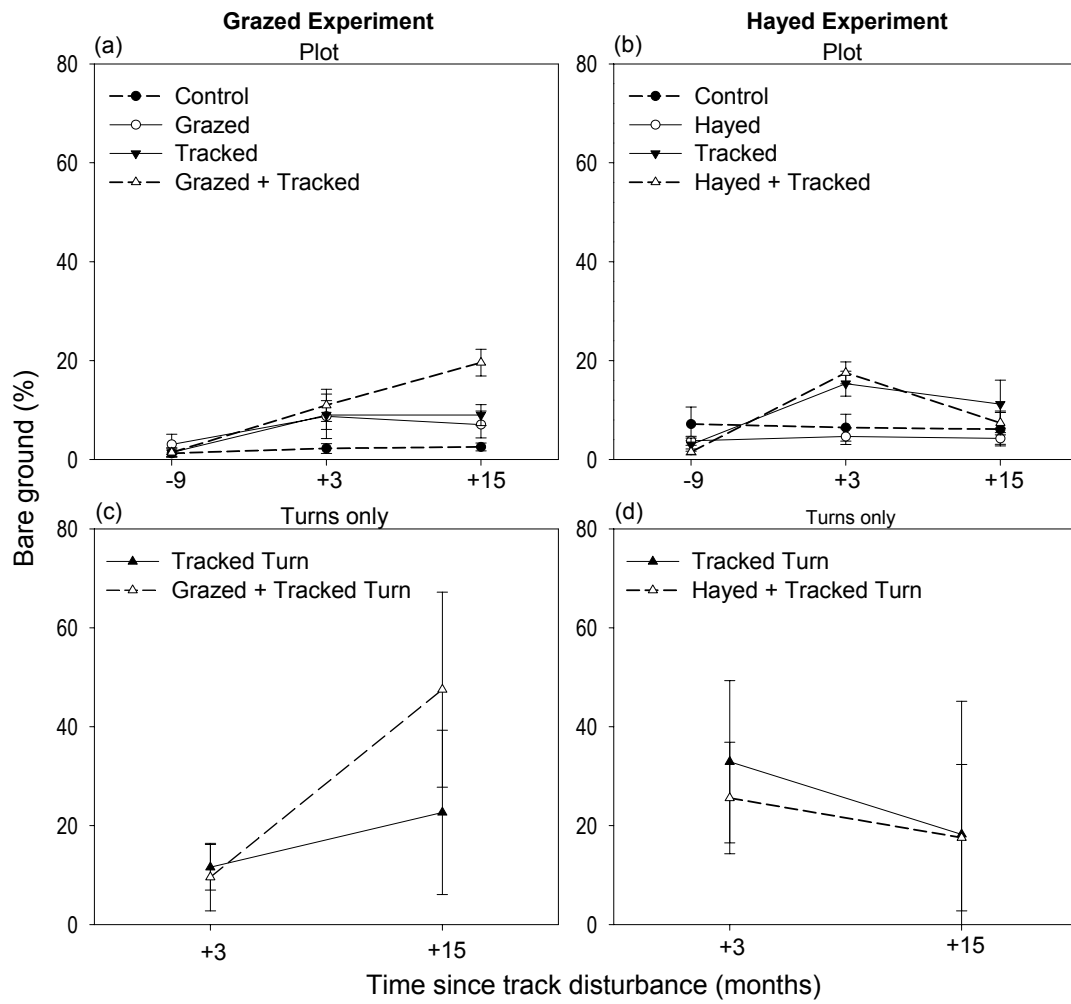


Figure 5.

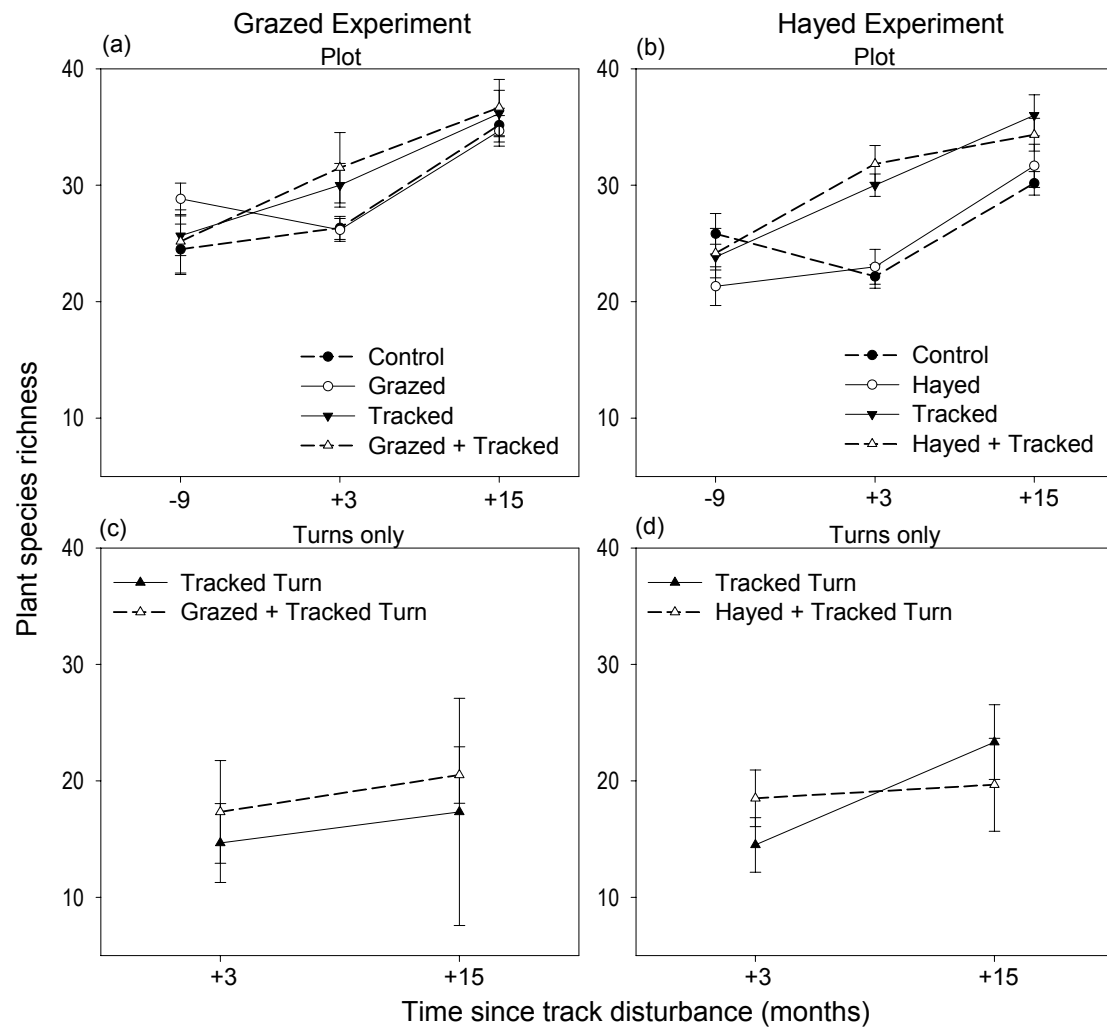


Table 1.

Event	Date
Pre-treatment sampling	June and September 2005
Focal soil disturbance	March 2006
Removal of extensive defoliation disturbance (in non-extensive treatment)	March 2006
Post-treatment sampling	June and September 2006, 2007

Table 2.

Grazed			Hayed		
Species	$\bar{X}$	Std. Err.	Species	$\bar{X}$	Std. Err.
<i>Panicum capillare</i>	18.5	4.7	<i>Panicum capillare</i>	16.8	6.3
<i>Aristida oligantha</i>	17.5	3.9	<i>Aristida oligantha</i>	45.9	4.3
<i>Ambrosia psilostachya</i>	8.3	3.1	<i>Erodium cicutarium</i>	13.9	4.3
<i>Croton capitatus</i>	8.1	2.4	<i>Erigeron strigosus</i>	3.1	3.8
<i>Schizachyrium scoparium</i>	5.6	2.4	<i>Ambrosia psilostachya</i>	6.8	3.7
<i>Erodium cicutarium</i>	3.4	2.3	<i>Schizachyrium scoparium</i>	5.4	3.2
<i>Erigeron strigosus</i>	2.3	1.8	<i>Andropogon gerardii</i>	5.3	2.9
<i>Eragrostis spectabilis</i>	2.3	1.6	<i>Dicanthelium wilcoxianum</i>	3.8	2.9
<i>Andropogon gerardii</i>	1.8	1.6	<i>Artemisia ludoviciana</i>	3.6	2.7
<i>Dicanthelium wilcoxianum</i>	1.4	1.5	<i>Croton capitatus</i>	3.3	2.5

## CHAPTER III

# ALTERED HERBIVORE DISTRIBUTION ASSOCIATED WITH FOCAL DISTURBANCE

## **Altered herbivore distribution associated with focal disturbance**

Department of Natural Resource Ecology and Management, Oklahoma State University

Key words: anthropogenic disturbance, heterogeneity, tracked vehicles, vegetation structure

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## ABSTRACT

Natural disturbances historically created structurally diverse patterns across the landscape and large herbivores concentrated herbivory in areas where disturbances decreased standing senesced biomass acting as grazing deterrents through decreased palatability and overall forage quality. However, following European settlement, many natural large-scale disturbance regimes that influence vegetation and herbivore grazing selection were altered or removed and replaced with fine-scale disturbances anthropogenic disturbances. It is unclear how fine-scale focal disturbance and alteration of vegetation structure influences livestock distribution and grazing.

Therefore we used tracked vehicles as disturbance agents in a mesic mixed-grass prairie to assess the influence of focal anthropogenic disturbance on livestock distribution and grazing. Track vehicle disturbance decreased the height of vegetation ( $P < 0.05$ ) but did not alter plant species composition. Cattle fecal pat density was greater ( $P < 0.05$ ) in locations with track vehicle disturbance. Little bluestem tiller height was shorter ( $P < 0.05$ ) in tracked locations than non-tracked locations in grazed treatments, but was not different in non-grazed locations the first growing season following disturbance. Fecal pat density and tiller height but were not different ( $P > 0.05$ ) between tracked and non-tracked locations following the second growing season. Therefore, we concluded that fine-scale focal anthropogenic disturbance does alter herbivore distribution and defoliation and can maintain structural heterogeneity, but the effect is ephemeral and does not create long-lasting grazing lawns.

## Introduction

Grassland ecosystems are naturally dynamic and dependant on regular disturbance to maintain species composition and function. Structural heterogeneity is a critical component of grassland management, enabling diverse assemblages of both animal and plant species (Fuhlendorf and Engle 2001, Limb et al. *In Press*). Natural disturbances such as fire, burrowing and foraging activity by fossorial animals, and bison wallowing historically created structurally diverse vegetation patterns, at multiple spatial and temporal scales, across the landscape (Coppock et al. 1983, Coppedge et al. 1999, Fuhlendorf and Engle 2001). Large herbivores responded to these events and concentrated herbivory in areas where disturbance decreased standing senesced biomass acting as grazing deterrents through decreased palatability and overall forage quality. McNaughton (1978) noted that when highly palatable grasses and forbs were in close proximity to less palatable species, consumption was lower than when they were distant. Canopy of sagebrush can act as a barrier to herbivores, therefore protecting more palatable understory species (Davis and Bonham 1979). However, following European settlement, many natural disturbance regimes that influence vegetation structure and herbivore grazing selection were altered or removed from grasslands and replaced with anthropogenic disturbances.

Anthropogenic activities, including military vehicle training exercises and livestock production, are commonplace within the current grassland landscape and partially mimic natural disturbance. Fenced livestock grazing has replaced migrating bison herds. However, in a study that controlled for species level variation, the influence of cattle and bison grazing on plant community composition was 85% similar, suggesting



that differences in management play a larger role in plant composition than the grazing animal (Towne et al. 2005). Vehicular disturbance, wide spread throughout grasslands, can destroy above-ground plant parts (Hirst et al. 2003), which effectively alters plant vertical structure and decrease grazing deterrents, similar to historical fire and fossorial animal disturbances. However, unlike fire, vehicle disturbance is typically fine-scale focal disturbance (Dale et al 2005) similar in many respects to natural disturbances created by fossorial animals and bison wallowing. Fine-scale focal disturbance and alteration of vegetation structure likely influences livestock distribution and preferential selection of grazing locations.

Therefore, we used tracked vehicles as disturbance agents in a mesic mixed-grass prairie to assess the influence of focal anthropogenic disturbance on livestock distribution, grazing, and vegetation structure. We predicted that grazing animals would preferentially graze locations disturbed by tracked vehicles, as a result of decreased senesced plant height acting as a grazing barrier, and maintain structural heterogeneity. We also predicted that this preference would persist for more than one growing season.

## **Methods**

The study was located at the Smoky Hills Air National Guard Bombing Range (Smoky Hills Range, hereafter) about 10 km southwest of Salina, Kansas USA. The Smoky Hills Range is 14,000 ha comprised of sandstone formations intermixed with well formed silty loam soils (Soil Conservation Service 1992). The climate is continental with the majority (51%) of the 802 mm annual precipitation occurring between May and August. July is the warmest month with a mean high temperature of 34°C and January is the coldest month with a mean high temperature of 3.9°C. The vegetation is classified as

mixed-grass prairie with dominant grass species including: little bluestem (*Schizachyrium scoparium* (Michx.) Nash), big bluestem (*Andropogon gerardii* Vitman), indiangrass (*Sorghastrum nutans* (L.) Nash) and sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.). Portions of the Smoky Hills Range are continuously grazed 1 May through 31 October each year with cow/calf pairs, with a density of 1 AUM\*2.8 ha<sup>-1</sup>.

In six pastures we established two 100 x 100-m plots on similar ecological sites (NRCS 2004) and drove a 39,000-kg track vehicle in a 2.8-km pattern simulating military tracked vehicle maneuvers, in March, prior to active spring growth (Figure 1). Following focal disturbance, we randomly selected one plot within each pasture and excluded grazing during the 2006 and 2007 growing seasons. This resulted in a pair of treatments (grazed and non-grazed) within each pasture. Within each grazed and non-grazed plot, a 2 x 25-m belt transect was established at a disturbed location (tracked) and at a random location at least 25 m distant to the 100 x 100-m disturbance plot (non-tracked).

The height of the tallest plant (grass or forb) was measured at 1-m intervals within the tracked and non-tracked transects, immediately following the focal disturbance, as an index to removing grazing barriers. Plant species composition and abundance was estimated in June 2006 within a 1 x 1-m frame placed at 3 random locations within the treatment and control transects. Plant species canopy cover were estimated with a cover classes (0-1%, >1-5%, >5-25%, >25-50%, >50-75%, >75-95%, and >95-100%). The midpoint of each class was used in analyses.

To estimate cattle distribution, fecal pats were counted within tracked and non-tracked transects within grazed plots, in early October, at the end of the grazing season.

Fecal pats are a common and non-intrusive means to estimate animal abundance and distribution (Neff 1968). To estimate defoliation intensity, height of the nearest green and actively-growing little bluestem tiller was recorded at 1-m intervals, in early October, along the centerline of each tracked and non-tracked transect. The height of little bluestem tillers was also measured in non-grazed plots to assess the effect of the tracked vehicle on above-ground plant growth.

We used a single-tailed t-test with pair-wise comparison of the mean tallest plant within each plot ( $n=12$ ). We pooled the grazed and non-grazed data to increase sample size because the mean height of the tallest plant, immediately following tracked vehicle disturbance, was not different ( $P < 0.05$ ) between grazed and non-grazed plots. The mean fecal pat count ( $n=6$ ) and mean height of little bluestem tillers ( $n=6$ ) in tracked and non-tracked locations were also compared using a single-tailed t-test with pair-wise comparison. Vegetation growth varies greatly year-to-year due to climatic fluctuations, thus statistical analysis was limited to within year comparisons. We used detrended correspondence analysis (DCA) (Hill and Gauch 1980) to compare the plant species composition between the in track and out of track locations using default settings within CANOCO<sup>®</sup> software. The mean plant species cover from three frames for tracked and non-tracked location was used for analysis.

## **Results**

Tracked vehicle disturbance decreased the height of vegetation ( $P < 0.05$ ) located in tracked locations nearly 20 cm and reduced the barrier to grazing compared to non-tracked locations (Figure 2). Despite large variation in plant height in non-disturbed locations, tracked vehicle disturbance resulted in fairly uniform vegetation height (Figure

2). However, the DCA did not reveal any differences in plant species composition between tracked and non-tracked locations on either axis in neither grazed nor non-grazed treatments (Figure 3). This suggests that a single focal disturbance was limited to vertical structure and did not influence plant species composition, which might influence grazing preference.

Cattle spent more time in tracked locations the first year following treatment as indicated by more fecal pats ( $P < 0.05$ ), but this preference was not evident the second year following treatment (Figure 4). Cattle preferentially defoliated little bluestem, in tracked locations, the first year following focal disturbance ( $P < 0.05$ ). The grazing preference for tracked locations did not continue the second year following treatment (Figure 5). Tracked vehicle disturbance in non-grazed plots did not decrease little bluestem tiller height ( $P > 0.05$ ) in either 2006 or 2007 (Figure 6). This indicates that herbaceous production was not influenced by tracked vehicle disturbance.

## **Discussion**

We disturbed mesic mixed-grass prairie with a tracked vehicle and grazed portions of the landscape with domestic livestock predicting that animals would preferentially graze the disturbed locations and maintain structural heterogeneity for multiple growing seasons. Our results indicate focal disturbance decreased vertical structure of vegetation and initially created structurally heterogeneous landscape. Structural heterogeneity did not persist throughout the first growing season in non-grazed treatments, but in the grazed treatment, focal disturbance attracted large ungulates, due to an increase in relative forage quality, and maintained a structural heterogeneity throughout the growing season. However, the response did not persist the second

growing season following focal disturbance. Fire, previous herbivory and prairie dog disturbances historically reduced standing plant structure, exposing relatively high quality forage, and consequently attracted herbivores (Coppock et al. 1983, Fuhlendorf and Engle 2001). The coupled fire-grazing disturbance maintains structural heterogeneity throughout the growing season (Fuhlendorf and Engle 2004, Fuhlendorf et al. 2006), where heterogeneity created by fire without grazing did not persist (Bidwell et al. 1990). Grazing animals select foraging locations based on many factors including forage quality, biomass, and optimization of both quality and quantity (Pinchak et al. 1991, Pyke 1984). Plant re-growth in heavily utilized areas is more palatable than adjacent non-utilized areas (McNaughton 1984, Illius et al. 1987), and thus promotes future utilization and the existence of heterogeneous landscapes often persisting for multiple growing seasons.

Grazing lawns, locations with repeated heavy grazing and short vegetation, often develop in large landscapes with adequate forage and persist for multiple seasons (McNaughton 1984, McNaughton 1986, Collins 1987, Coppedge et al 1998). The development of grazing lawns is especially prevalent in landscapes without periodic large scale disturbances such as fire to redistribute herbivores (McNaughton 1985, Karki et al. 2000). Many large herbivores repeatedly graze locations and maintain high-quality forage and restrict low-quality mature plant development in effort to maintain a proper balance between nutrient requirements and forage intake (Valentine 2001). Without new focal disturbances to attract cattle, we expected animal distribution and defoliation selection to favor the tracked locations the second year following disturbance and maintain landscape structural heterogeneity. However, in our study, grazing lawns did not develop and persist for multiple seasons.

If grazing pressure is not sufficient, to maintain a relatively short plant community, due to either insufficient animal densities or favorable plant growth conditions, large herbivores will not preferentially graze in these locations and large-scale structural heterogeneity, associated with grazing lawns and adjacent vegetation, will persist (Pfeiffer and Hartnett 1995). Growing-season precipitation in 2007 was well above normal at the Smoky Hills Range (data not presented) allowing vegetation to grow faster than grazing animals could consume, thus cattle were not able to maintain the short-stature and high-quality forage. The accumulation of tall and mature vegetation in tracked locations reduced the nutritional benefits to cattle for concentrating grazing in these locations. Thus, cattle stopped preferentially selecting the focally disturbed locations and prevented long-term grazing lawn development and reduced landscape structural heterogeneity.

Tracked vehicle disturbance often increases soil compaction and can reduce above-ground herbaceous production (Jorajuria et al. 1997, Althoff and Thein 2005). However, in our study, little bluestem production (height) was unaffected by tracked vehicle disturbance. The influence of tracked vehicle maneuvers on soil compaction and herbaceous above-ground production is strongly influenced by soil moisture. Tracked vehicle disturbance, on wet tallgrass prairie soil, decreased vegetation biomass nearly three times more than disturbance in areas with less soil moisture (Althoff and Thein 2005). Before and immediately following focal disturbance, in our study, soil conditions were dry due to well below-normal precipitation (data not shown). As a result, soil damage from focal disturbance was minimal and did not decrease plant growth.

Heterogeneity created by the tracked vehicle disturbance did not persist long into the growing season unless coupled with grazing.

### **Management implications**

Proper grazing management traditionally implied uniform animal distribution across the landscape, resulting in relatively uniform plant height and vertical structure (Fuhlendorf and Engle 2001, Holechek et al. 2001, Valentine 2001, Briske et al. 2008). Given the benefits of heterogeneity to livestock, wildlife and biodiversity (Sarnelle et al. 1993, Fuhlendorf and Engle 2001, Cummings et al. 2007, Limb et al. *In Press*), tracked vehicle disturbance coupled with grazing, is a potentially valuable tool to create maintain heterogeneity throughout a growing season. Because structural heterogeneity was not maintained beyond the first growing season, multiple tracked vehicle disturbance events might be necessary to maintain structural heterogeneity, especially in years with above-average precipitation and increased above-ground herbaceous production. Also, shifting the tracked vehicle disturbance location throughout the landscape over consecutive years should create a fine-scale shifting mosaic disturbance.

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## **Figure captions**

### **Figure 1**

Focal disturbance pattern (dark line) applied with a tracked vehicle to mixed-grass prairie at the Smoky Hill Range near Salina, KS. Dashed line represents a grazing enclosure surrounding the non-grazed treatment. Rectangles are belt transects located at tracked locations and at random non-tracked locations. Squares are plant species composition sampling locations within each belt transect. Comparisons were between tracked and non-tracked locations within grazing treatment plots.

### **Figure 2**

The mean height and standard error of the tallest plant (grass or forb) immediately following focal disturbance, in tracked and non-tracked locations pooled between grazed and non-grazed treatments.

### **Figure 3**

Plot depicting axis 1 and axis 2 of detrended correspondence analysis (DCA), using plant species canopy cover, three months after focal disturbance in grazed and non-grazed treatments. The plots represent site scores for tracked and non-track locations.

### **Figure 4**

The mean density and standard error of fecal pats located in tracked and non-tracked locations in at the end of the growing season in October 2006 and 2007.

Figure 5

The mean height and standard error of little bluestem tillers located in tracked and non-tracked locations within grazed treatment at the end of the growing season, in October 2006 and 2007.

Figure 6

The mean height and standard error of little bluestem tillers located in tracked and non-tracked locations within non-grazed treatments at the end of the growing season in October 2006 and 2007.

Figure 1

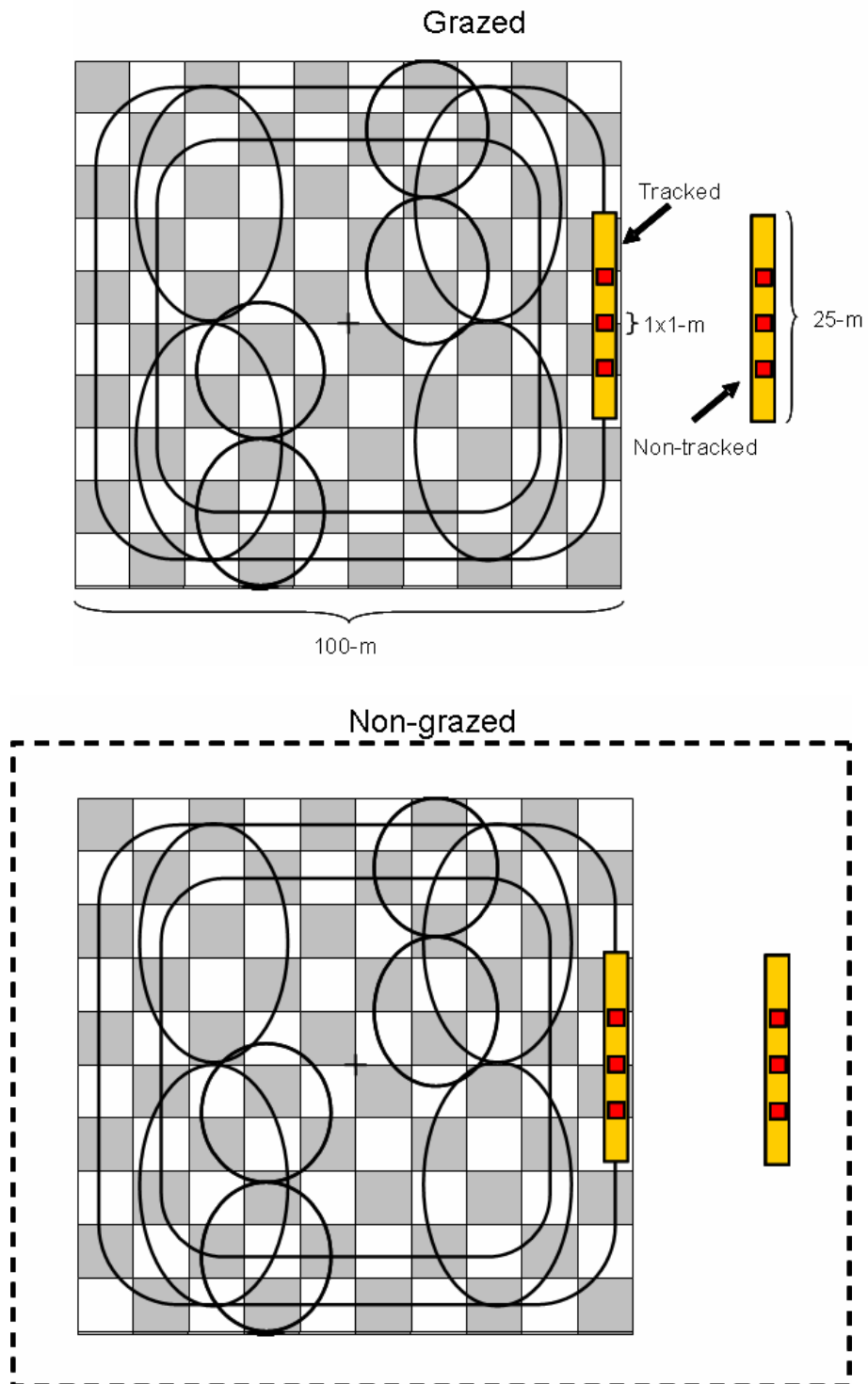


Figure 2

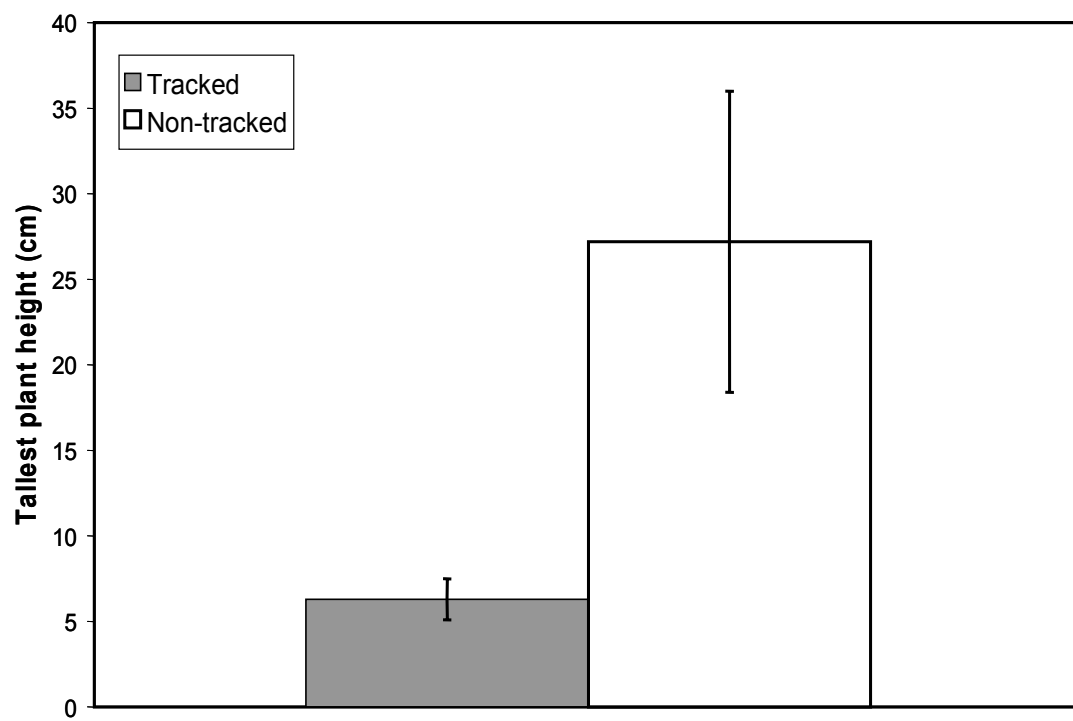


Figure 3

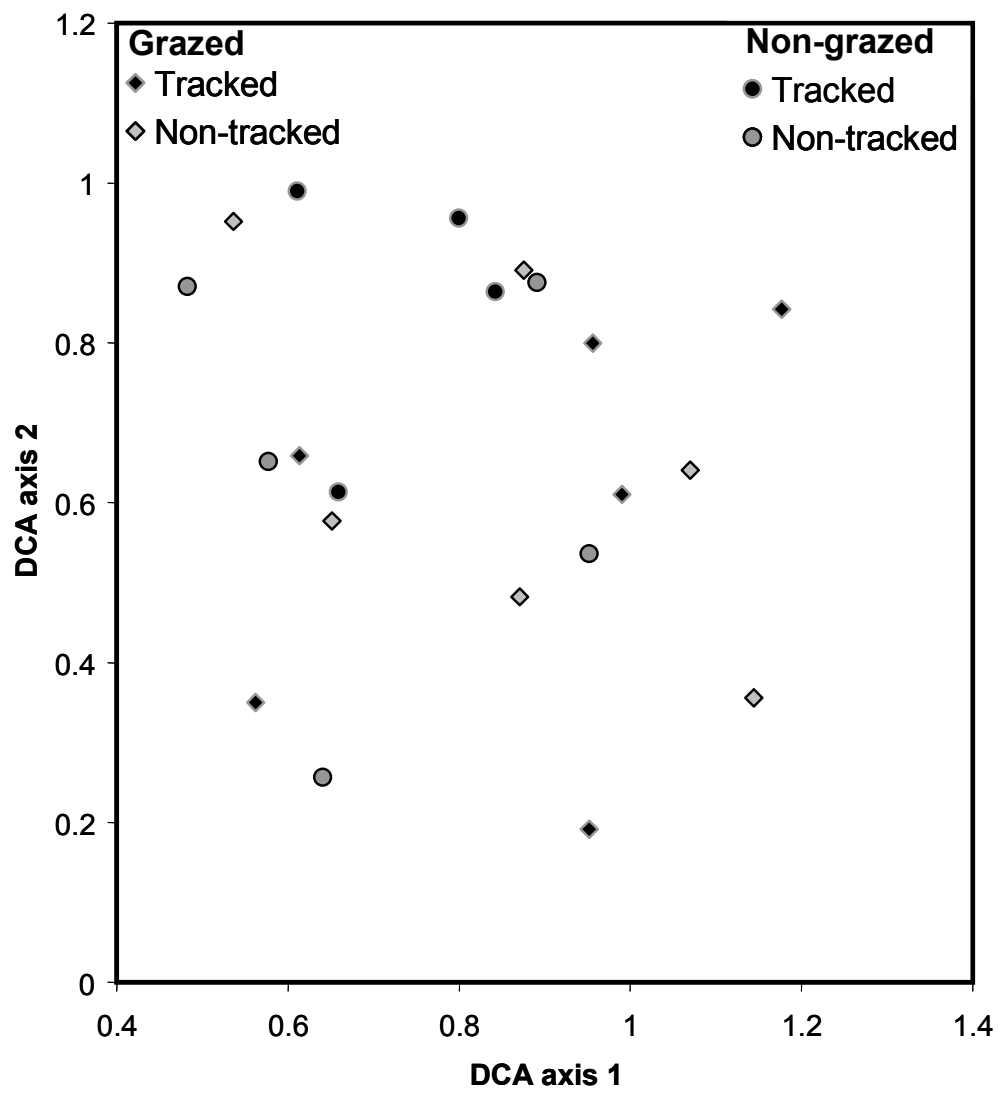




Figure 4

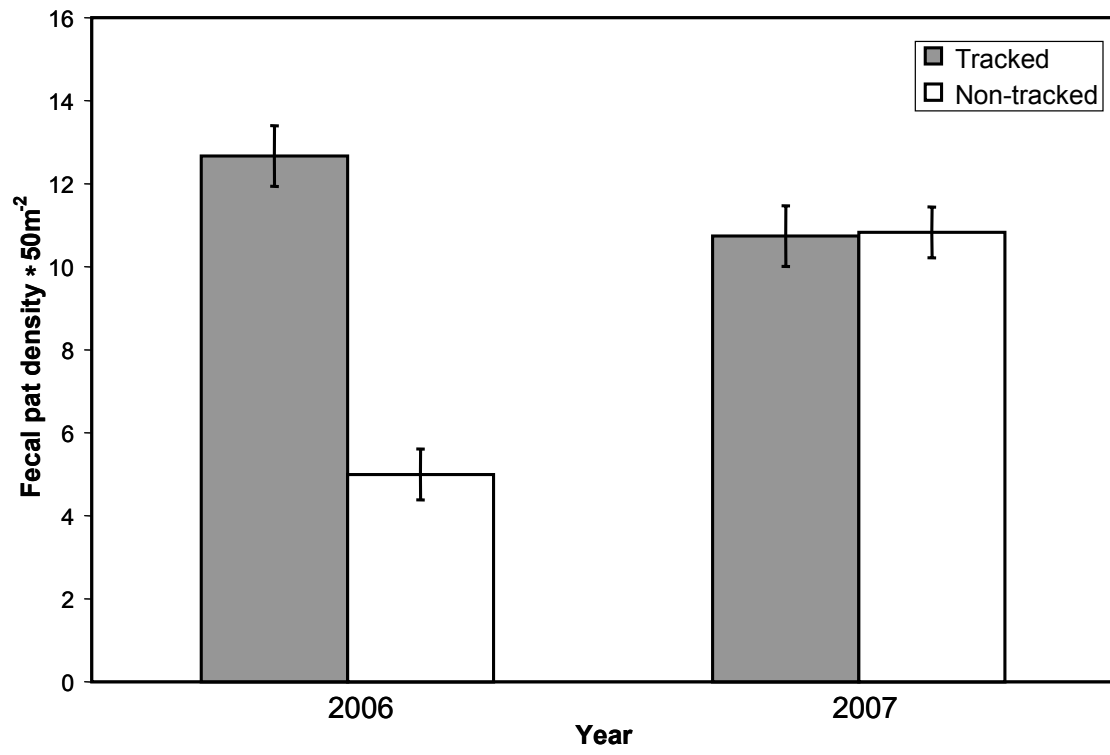


Figure 5

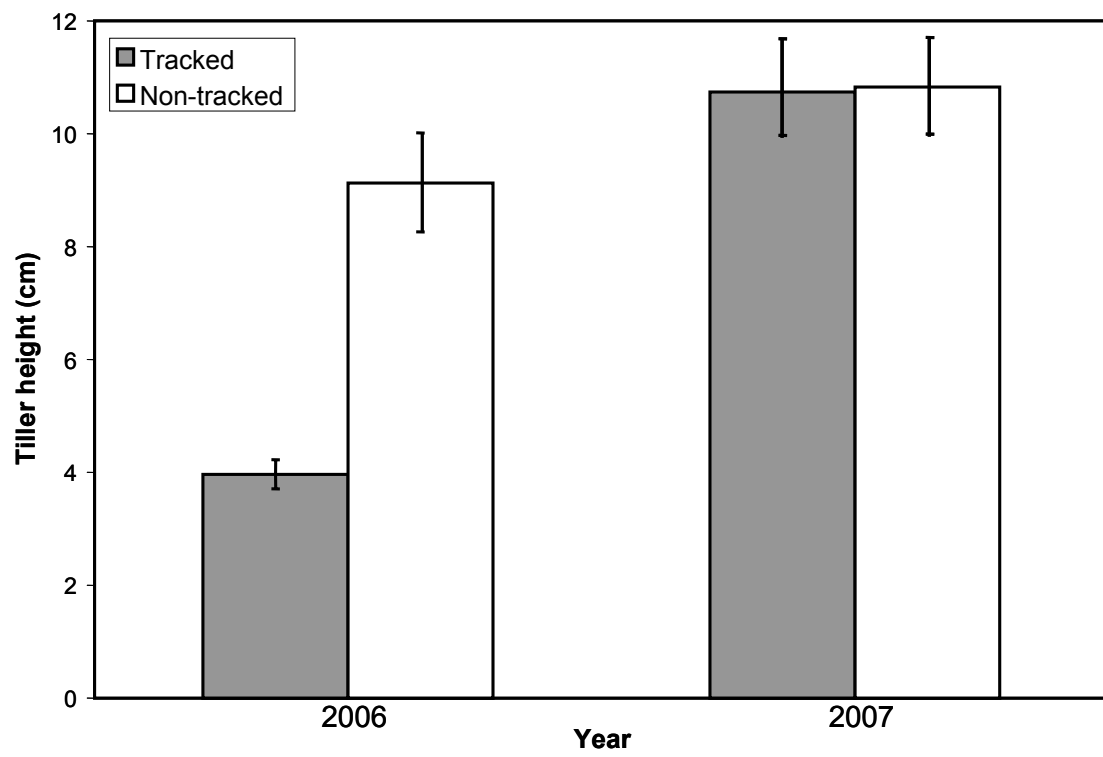
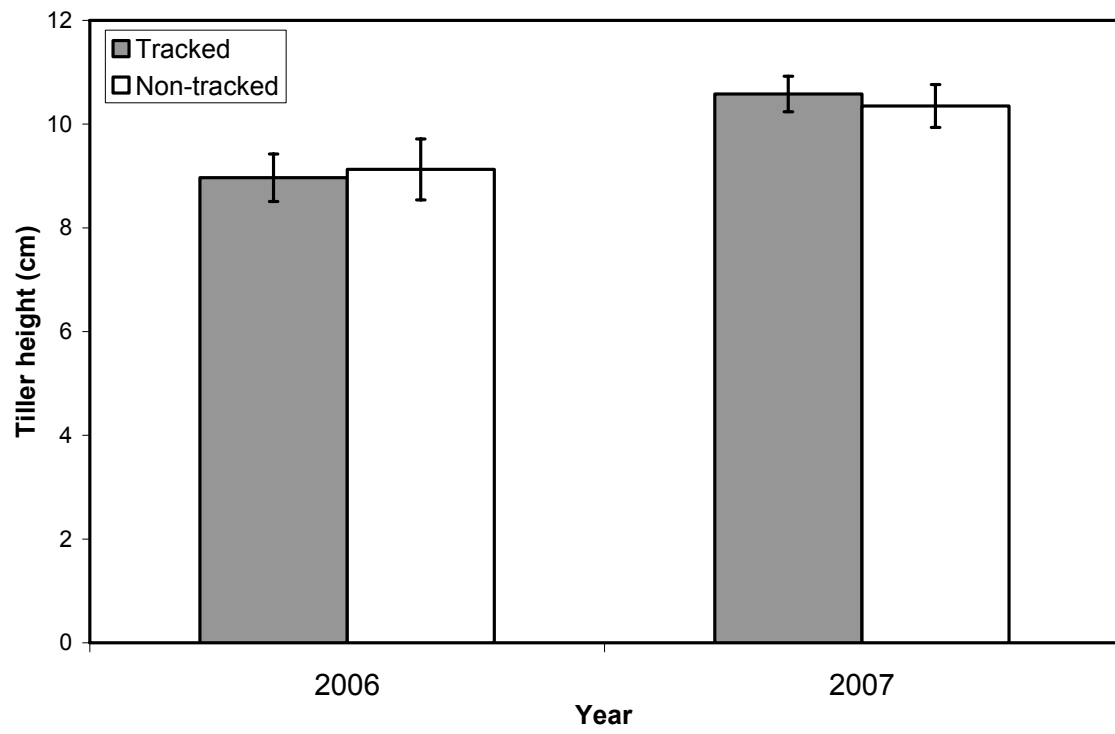


Figure 6



## CHAPTER IV

### DIGITAL PHOTOGRAPHY: REDUCED INVESTIGATOR VARIATION IN VISUAL OBSTRUCTION MEASUREMENTS FOR SOUTHERN TALLGRASS PRAIRIE

**Digital Photography: Reduced Investigator Variation in Visual Obstruction  
Measurements for Southern Tallgrass Prairie**

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Key Words: biomass, sampling variation, techniques, wildlife habitat

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## **Abstract**

Landscapes with structural heterogeneity or patchiness can support diverse and stable wildlife populations. Visual obstruction methods (i.e. Robel pole and Nudd's coverboard) are common and useful techniques for quantifying vegetation structure however, both rely on ocular estimations which can be highly variable between observers. Our objectives were to: (1) compare measurement and observer variation for visual obstruction among the two standard methods and the digital image method we developed using a digital camera; and (2) compare the performance of the Robel pole and digital image to estimate standing crop. The mean variation across the five observers using the digital image method (6.8%) was significantly lower ( $p < 0.05$ ) than both the Nudds' coverboard (32.1%) and the Robel pole (52.2). There were no significant differences among locations for the digital image method, however there were for both the Robel pole and Nudds' cover board ( $p < 0.05$ ). The digital image method provided a better estimate of standing crop ( $r^2 = 0.89$ ) compared to the Robel pole ( $r^2 = 0.68$ ), accounting for 21% more of the observed variation in biomass. Long-term research programs that utilize seasonal field technicians to quantify habitat structure with a visual obstruction method could benefit from implementing use of the digital image method we developed. The low measurement error observed with this technique relative to the more traditional methods compared in this study might limit year-to-year and within-year variability of habitat structure data collected by numerous technicians with a high annual turnover.

## **Introduction**

Landscapes with structural heterogeneity, i.e., patchy vegetation, as found in tallgrass prairie support diverse and stable wildlife populations (Roth 1976; McGarigal and McComb 1995). A variety of measurements of the two-dimensional vegetation structure from a vertical and horizontal perspective are used to assess wildlife habitat (Higgins et al. 2005) and are essential to many other ecological disciplines, including rangeland management. Visual obstruction methods from a vertical and horizontal perspective are common and useful techniques for quantifying vegetation structure (Robel et al. 1970; Nudds 1977; Higgins et al. 2005). Rapid and accurate description of vegetation structure is crucial to assessing wildlife habitat, and vegetation structure is especially important for avian habitat assessment (Roth 1976; Haensly et al. 1987; McGarigal and McComb 1995; Sutter and Brigham 1998).

Estimates of standing crop in tallgrass prairie (e.g., by clipping herbaceous vegetation) also provide essential information used in developing proper land management strategies. However, clipping herbaceous vegetation is labor intensive, and therefore clipping often is replaced with visual obstruction estimates such as the Robel pole or Nudds' coverboard (Vermeire and Gillen 2001; Higgins et al. 2005).

Because most of the common horizontal and vertical visual obstruction methods depend on ocular estimations of both vegetation height and density of the plant material, visual obstruction methods carry inherent potential to introduce excessive measurement error together with investigator variation (Schultz et al. 1961; Gotfryd and Hansell 1985; Block et al. 1987; Collins and Becker 2001; Higgins et al. 2005). For example, Hall and Max (1999) noted that observer variation represented 20% of the variation among visual

estimates of shrub twig length. That is not to say that when a visual obstruction technique is mastered and a limited number of technicians collect the data, accurate and reliable results are not possible (Volesky et al. 1999; Ganguli et al. 2000; Collins and Becker 2001; Vermeire and Gillen 2001). However, accuracy using ocular sampling methods can be compromised by high technician turnover and inexperienced labor.

Increasing the sample size is often the approach used to overcome large measurement error together with observer variation, but increased sample size translates into increased sampling time and costs. Other techniques for measuring habitat structure, such as the cone of vulnerability (Kopp et al. 1998), can reduce measurement error and observer variation (Harrell and Fuhlendorf 2002), but they are limited to a few habitat types, and they are labor intensive. Photography (aerial and satellite images) along with radar and LIDAR (Light Detection and Ranging) has been used to map and monitor vegetation change through time (Mullerova 2004; Boyd and Svejcar 2005; Higgins et al. 2005), but remote sensing has not yet been used to measure horizontal visual obstruction in tallgrass prairie. Hence, our objectives were to: (1) compare measurement variation (precision) for horizontal visual obstruction among the two standard methods (Robel et al. 1970; Nudds 1977) and the digital image method we developed using a digital camera at a typical tallgrass prairie site in Oklahoma; and (2) compare the performance of the Robel pole and digital image to estimate standing crop at the same site. Ideally, the digital image technique would have the following attributes: 1) low measurement variance (high precision), 2) ease of use, and 3) low cost. We discuss these attributes as they relate to sampling vegetation structure and mass with a digital camera on rangelands.



## Methods

Development of the protocol for the digital horizontal visual obstruction method involved capturing a series of digital images of vegetation using a tripod mounted Canon PowerShot® A520 camera (4 megapixels) and standard factory lens placed at a distance of 4 m from the sampling point and at a camera lens height of 1 m, similar to that described for the Robel pole (Robel et al. 1970). Tallgrass prairie vegetation was photographed, on calm days, using white plastic sheeting fastened to a 1- x 1-m frame positioned as a backdrop to the sampled vegetation point (Fig. 1A). Height reference points spaced at 0.1m were marked on each vertical side of the board using a 2.5-cm black dash. Vegetation and backdrop occupying the camera viewfinder were maximized. Digital images were imported into CS2 (Adobe Systems Inc, San Jose, CA) and cropped such that only the 1 x 1-m backdrop and vegetation remained in the field of view. We used the Adobe Photoshop® software threshold function in the image menu to convert the color images to binary black and white images. The threshold value determined the amount of luminance (amount of light reflected from an object) necessary to convert an individual pixel to either black or white with all values higher than the threshold value converted to white while the lower values are converted to black. Those pixels above the threshold values corresponded to the white background whereas lower values were vegetation and shadow. We selected one threshold setting for all images (128), which was often the default setting, to reduce unnecessary variation. Threshold values below 128 did not convert all of the color pixels to black based on the original color photograph, and values over 128 often converted white pixels to black. After conversion to a binary image (Fig. 1B) the histogram feature was used to provide the percentage of black and

white pixels in each image. We defined visual obstruction as the percent black pixels in each image tallied by the software.

To assess measurement variation (precision) among the three horizontal visual obstruction methods (i.e. Robel pole, Nudd's coverboard, digital image method) and to compare the performance of the Robel pole relative to the digital image to estimate standing crop, we conducted a study in a 3-ha tallgrass prairie remnant in Payne County, Oklahoma (lat 36°10'N long 97°5'W). Ten vegetation sampling locations were systematically selected to maximize structural heterogeneity along the continuum found within the study area. Horizontal visual obstruction measurements using standard techniques for the Robel pole and Nudds' coverboard (Robel et al. 1970; Nudds 1977) and the digital image method were recorded independently by five technicians, four times in rapid sequential order (20 observations per method) at the same point within each of the ten sampling locations. The digital image backdrop and camera were removed after each individual image, and were re-centered at the same location in an effort to sample the same vegetation structure. The height and line of site among observers for all methods were done at 1 m in height and 4 m from the sampling point. The technicians were inexperienced with visual obstruction; however they did receive instruction on proper use of the three visual obstruction methods in the classroom and in field demonstrations.

The variability (precision) of multiple measurements from the same observer was estimated using coefficient of variation (CV). A CV was calculated for each observer using the four different readings at each location for all method-location combinations. The measurement variability among the three methods and the ten locations was tested

using repeated measures analysis of variance. In the repeated measures analysis the five observers (experimental units) were treated as replications with the ten locations and the three methods treated as fixed variables. Locations were treated as fixed rather than random variables because locations were selected to represent different cover levels rather than being a random selection of the locations, and we wanted to infer whether measurement variability within each method is different at the selected locations (Schabenberger and Pierce 2002). Repeated measures analysis was used because measurements over the ten locations from the same five observers could be correlated. The SAS/STAT® software procedure PROC MIXED (SAS Institute 2004) was used for the analysis because the variance and covariance structures present can be modeled. The Akaike information criterion (AIC) was used to guide the selection of the variance-covariance model used in the analysis (Burnham and Anderson 1998). The unstructured covariance model had the lowest AIC value among various other covariance models tried and was selected for the final analysis. The probability levels for the multiple comparisons tests were adjusted using the Tukey procedure.

To estimate the number of samples required to adequately measure the horizontal visual obstruction of the study location, sample adequacy for each method was estimated at 95% confidence and within 10% of the true mean using the equation  $n=(t_{\alpha}SD)^2/(\alpha \bar{X})^2$  where  $a$  = accuracy and  $\alpha$  = precision (Zar 1984). Specific sampling protocols vary with different vegetation types, however our objective was to provide an estimate of sample adequacy; not to estimate the visual obstruction for our study site.

To compare the Robel pole and digital image processing methods of estimating herbage mass, we measured horizontal visual obstruction at 50 locations. We then

determined herbage mass at these locations using a 0.25- x 0.5-m frame centered directly in front of the Robel pole and digital image backdrop. All Robel pole measurements were by a single observer to minimize observer variation. Clipped herbage was bagged and dried at 50° C until mass stabilized (8-9 days). The data on herbage mass as a function of visual obstruction was fitted with polynomials using regression (SPSS 2005) with the AIC used for model selection.

## **Results**

Measurement variation (precision) varied greatly among the three methods for this tallgrass prairie site. The CV values averaged over the 10 locations were significantly lower for the digital image method (6.8%) compared to both the Nudds' coverboard (32.1%) and the Robel pole (52.2%) ( $p < 0.05$ ) (Fig. 2). The CV among the locations was significantly different along with the interaction between the location and method ( $p < 0.05$ ). Comparisons of the mean CV values between each location within a method found that there were no significant differences between locations for the digital method ( $p > 0.05$ ) (Fig. 2). There were significant differences between some locations for both the Nudds and Robel method ( $p < 0.05$ ). Significant differences between the various locations within the Nudds and Robel method are most likely the reason for the interaction of location and method. Based on the data recorded and assuming that the sites selected for measurement were representative of the tallgrass prairie site, 20 samples would have been needed for the digital image technique to adequately sample the horizontal visual obstruction at our study location (95% confidence) compared to 158 and 233 for the Robel pole and Nudds' cover board respectively.

The regression model with the best fit between the digital image obstruction and herbage mass was the linear model (root mean square error [RMSE] = 3.8). The best fit model between the Robel pole obstruction and herbage mass was the quadratic model (RMSE = 12.1) (Fig. 3). Values of zero excluded the logarithmic model from the analysis of the Robel pole. The digital image method provided a better estimate of herbage mass, as determined by horizontal visual obstruction ( $r^2=0.89$ ,  $p < 0.001$ ), compared to the Robel pole ( $r^2= 0.68$ ,  $p < 0.001$ ), accounting for 21% more of the observed variation in biomass (Fig. 3). Others (Robel et al.1970; Ganguli, et al. 2000; Vermeire and Gillen 2001) reported similar  $r^2$  values for the Robel pole. The digital image method estimates herbaceous biomass more reliably than the Robel pole for tallgrass prairie. Residuals for the digital image method are more evenly distributed at all standing crop values than the Robel pole. This suggests that it is a more robust method, and not biased toward low, medium or high standing crop values.

## **Discussion**

Long-term research programs that utilize seasonal field technicians to quantify habitat structure with a horizontal visual obstruction method could benefit from implementing the digital image method we developed. The low measurement variation with this technique relative to the traditional horizontal visual obstruction methods has the ability to limit year-to-year and within-year measurement variability for tallgrass prairie. The digital method is probably not prone to the affects of high annual technician turnover since the method is not dependent on trained technicians asked to visually estimate obstruction.

The digital image technique used to estimate horizontal visual obstruction was relatively rapid and produced low measurement variation (high precision) in comparison to the two standard visual methods for tallgrass prairie. The time required to measure visual obstruction, at a given sampling point, is comparable among the three methods tested (15 seconds per sample), however additional lab analysis is required for the digital image method to convert the digital image. Once imported, each image required an average of 30 seconds to complete the analysis process. However, the additional lab analysis time required is relatively small compared to the additional field time required (8X and 12X, respectively) by the Robel pole and Nudds' coverboard. Overall, landscape level sampling with the digital image method requires less time due to the reduced sample size required to accurately estimate horizontal visual obstruction.

The strong relationship between clipped herbaceous biomass and the digital method points to how this method may be better related to the actual horizontal vegetation structure than the other methods. Both the Nudds and Robel method have both been criticized for being estimates and not accurately reflecting the actual vegetative structure (Higgins et al. 2005). A standard method of measuring actual cover is debated with no accepted way of accessing accuracy (Booth et al. 2006; Laliberte et al. 2007). In fact, Booth et al. (2006) used a digital image as a known standard for a 2-dimensional study of different cover estimation methods.

Horizontal visual obstruction produced by the digital image is relative to the size of the backdrop, which must be noted when reporting the measurements, similar to reporting the size quadrat used for estimating plant species density or biomass. Backdrops other than 1m x 1m might be better suited in other ecosystems (eg. shortgrass

prairie or sagebrush steppe) thus, sampling protocol is site specific and will need to be developed accordingly to account for unique vegetation and landscape conditions. Other investigators have used digital image techniques with colored backdrops and color recognition software to estimate vegetation measurements (Boyd and Svejcar 2005); however, we found the white backdrop and converted black vegetation in the foreground to be a simple and reliable combination for digital horizontal visual obstruction estimates. However, with white backdrops shadows cast by the surrounding vegetation and crew members relative to the sun are major drawbacks to the digital image method, so careful backdrop placement is necessary, along with timing sampling efforts with the position of the sun.

The total cost of field equipment for this technique was \$600. Digital cameras, similar to the camera used in this experiment, range in price between \$100 and \$300 (U.S. currency). The image processing software is readily available through most software suppliers or can be purchased directly from the manufacture for \$300. The backdrop, frame and camera tripod totaled \$35 dollars, and can be used for multiple years. This relatively low cost would easily fit into most sampling budgets, especially when considering the labor savings over several sampling seasons.

### **Management implications**

Relatively large sample sizes for sampling adequacy are common with traditional visual obstruction methods (Higgins et al 2005). Given that the digital method studied here had low measurement variability (high precision) compared to the other popular methods, it is the more desirable visual obstruction method. The decreased sample size

for accurate measurements allows enables land managers to monitor additional sites with little or no increased cost and effort which promotes greater habitat quality.



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### **Figure captions**

Figure 1. Example of a digital image (1A) imported to Adobe Photoshop®. The color image was converted to black and white (1B).

Figure 2. Mean coefficient of variation from the five observers for each method by location. Only positive standard deviation bars are shown to reduce clutter in the graph. Letters following the three methods in the legend indicate statistical difference among the methods ( $p < 0.05$ ).

Figure 3. Lines fit by linear and polynomial regression estimating herbage standing crop (dry weight) with two methods of visual obstruction (digital image, top, and Robel pole, bottom). The digital image method utilizes the number of black and white pixels to determine percent cover.

Figure 1.

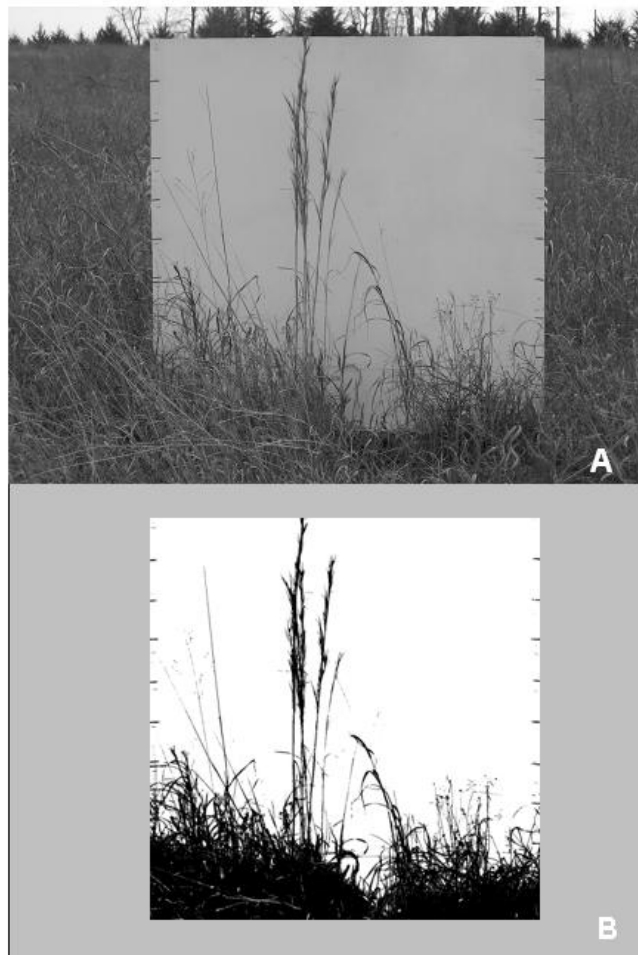


Figure 2.

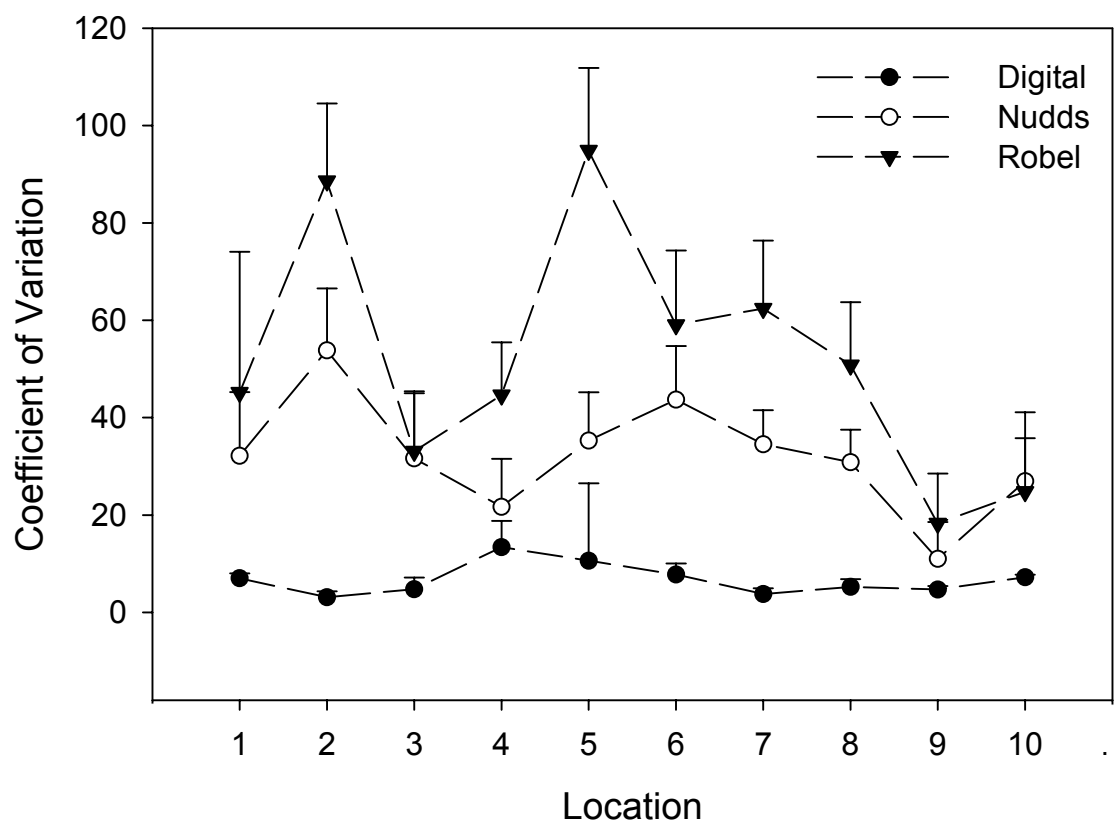
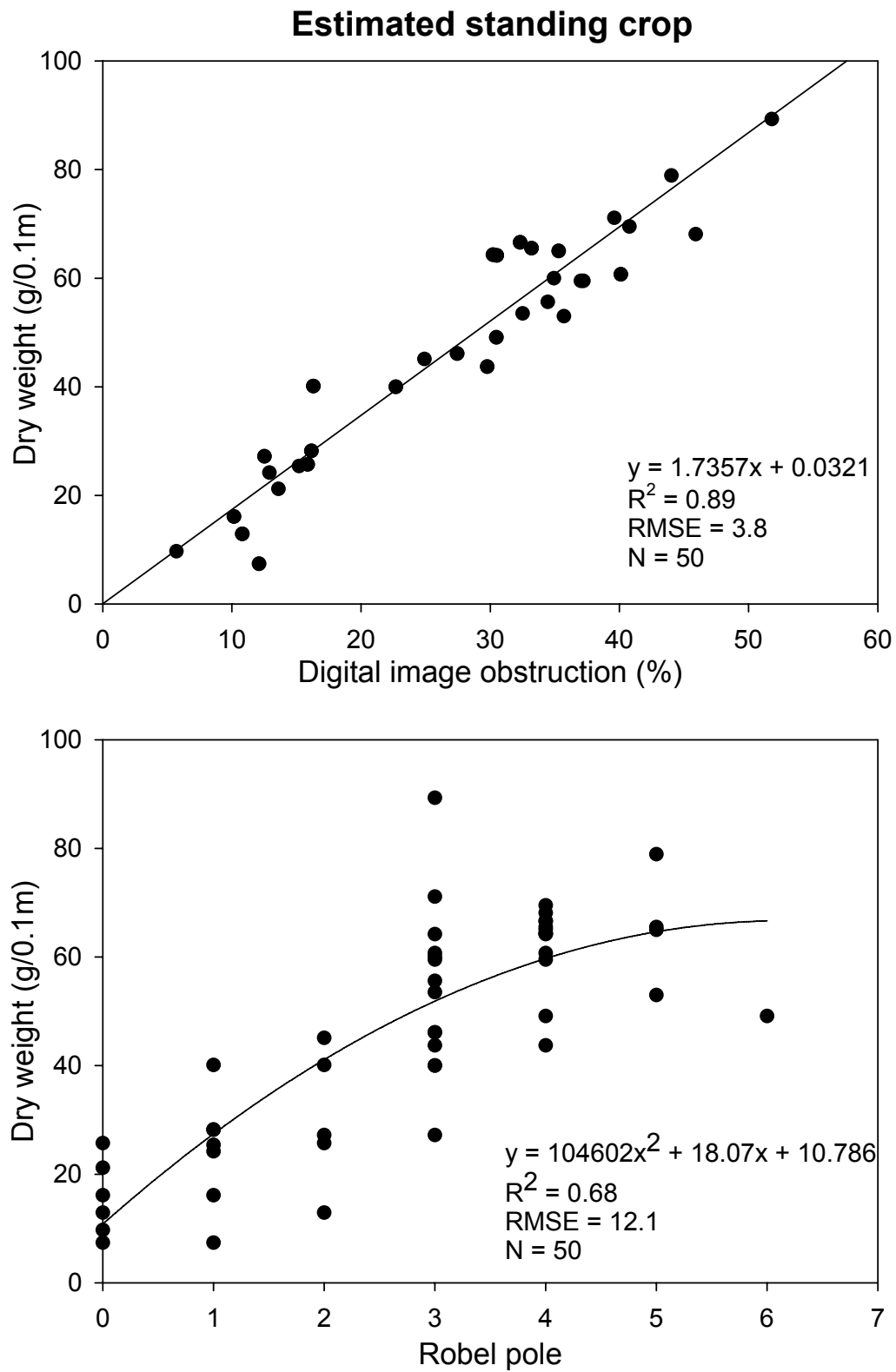


Figure 3.



VITA

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Dissertation: THE EFFECTS OF DISTURBANCE IN GRASSLAND PLANT  
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Major Field: Natural Resource Ecology and Management

Scope and Method of Study: We examined vegetation dynamics and livestock grazing in response to stress and disturbance on rangelands in two different studies, one in north central Oklahoma and one in central Kansas. The study in north central Oklahoma measured the herbaceous plant community response to stress along a gradient of increasing eastern redcedar (*Juniperus virginiana*) canopy cover in tallgrass prairie. The study in central Kansas investigated the plant community and livestock grazing response to anthropogenic disturbance in native mixed-grass prairie.

Findings and Conclusions: In the north central Oklahoma study, plant species richness declined with increased eastern redcedar canopy cover. However, the rate of decline in species richness closely followed that which was predicted by a species-area relationship. Furthermore, the decline was uniform among C<sub>3</sub>, C<sub>4</sub> and forb species groups. Annual herbaceous above-ground production declined with increasing eastern redcedar canopy cover, but was most variable at intermediate canopy cover. These results indicate that eastern redcedar reduces species richness. However, canopy cover up to 80% does not impose an ecological threshold. In the central Kansas study, we used tracked vehicles to impose anthropogenic focal soil disturbance within a mixed-grass landscape extensively disturbed with livestock grazing or hay harvest. In both landscapes focal soil disturbance had a larger influence on plant community composition than either livestock grazing or hay harvest. Moreover, combined focal and extensive disturbance did not have a greater effect than focal disturbance alone. Despite differences in initial plant species composition, successional trajectories following focal soil disturbance were similar between grazed and hayed communities, and both plant communities recovered from focal soil disturbance within two growing seasons. Tracked vehicle disturbance attracted preferential livestock grazing, which promoted structural heterogeneity within the plant community. However, the effect was ephemeral and only lasted one growing season.

ADVISER'S APPROVAL: Terrence G. Bidwell

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