

THE INTERACTION OF FIRE AND GRAZING IN
OKLAHOMA *ARTEMISIA FILIFOLIA* SHRUBLAND

By

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THE INTERACTION OF FIRE AND GRAZING IN
OKLAHOMA *ARTEMISIA FILIFOLIA* SHRUBLAND

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CHAPTER I

FIRE-RESILIENCY OF A NORTH AMERICAN *ARTEMISIA* (ASTERACEAE) SHRUB:
IMPLICATIONS FOR RESTORATION OF A CRITICAL ECOSYSTEM PROCESS

**Fire-resiliency of a North American *Artemisia* (Asteraceae) shrub:
implications for restoration of a critical ecosystem process**

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Abstract

Question: Is *Artemisia filifolia* (Asteraceae) a fire-resilient shrub or is it similar to most other *Artemisia* shrub species in North American which are considered fire-sensitive?

Location: Cooper Wildlife Management Area, Woodward County, Oklahoma, USA.

Methods: Data on *Artemisia filifolia* plant density and structural characteristics (percent cover of live and dead shrubs, shrub height, shrub canopy area, and shrub volume) were collected in areas that had been burned once at one-half, one, two, three, four and five years after an initial burn and compared to data collected in areas that had not been burned. Data on density and structural characteristics of *Artemisia filifolia* also were collected in areas that had been burned twice at one-half, one, and four years after being burned the second time.

Results: Density of *A. filifolia* was not affected by one or two fires and structural characteristics, although initially altered by fire, recovered to levels characteristic of unburned areas in one to four years after burning.

Conclusions: Unlike most North American *Artemisia* shrub species, our research suggests that *A. filifolia* is highly resilient to the effects of fire. Therefore, use of prescribed fires for the restoration and maintenance of ecosystem processes and properties is appropriate in *A. filifolia* shrublands of the southern Great Plains in North America.

Keywords: density; disturbance ecology; ecosystem maintenance; fire-dependent; fire-influenced; Great Plains; prescribed fire; resprouting; vegetation structure; woody plant.

Nomenclatural Reference: (USDA-NRCS, 2009b)

Introduction

Explanations for the distribution of biomes, ecosystems and plant communities commonly emphasize the role of climate (Clements 1936; Holdridge 1947; Prentice 1990; Prentice et al. 1992), but there is increasing recognition of the profound influence that fire has on the global distribution of vegetation (Bond and Keeley 2005; Bond et al. 2005). Indeed, fire has influenced properties and processes of the “Earth system” as far back as the first appearance of terrestrial plant life in the fossil record (Bowman et al. 2009; Pausas and Keeley 2009). In biomes that have recurring fires, plant functional type and life-history traits are used to categorize woody plants based on their response to this and other disturbances such as wind, avalanches and flooding (Verdú 2000; Bell 2001; Allen 2008). Individuals of resprouting species persist in fire-prone environments by renewing growth from buds that survive the fire, such as belowground buds that are insulated from the heat of a fire by soil (Bellingham and Sparrow 2000; Bond and Midgley 2001). In contrast to resprouters, individuals of reseeding species are killed by fire, but persistence of these species in fire-prone environments requires recruitment by seed dispersed from adjacent undisturbed populations or seeds that survive fire events in belowground seed banks (Keeley and Zedler 1978; Bell 2001).

In North America, the genus *Artemisia* (Asteraceae) includes 13 species of shrubs distributed from the central Great Plains to the Pacific Coast (Shultz 2006). *Artemisia* species are often the dominant species in their respective ecosystems and *Artemisia* shrublands constitute the largest semi-arid vegetation type in North America, occupying in excess of 63.7×10^6 ha (West 1983a; West 1983b). Most *Artemisia* shrub species in North America are incapable of resprouting following fires that remove aboveground biomass and their only means for recolonizing burned areas is through the import of small, wind-blown seeds from adjacent unburned areas or from plants that escaped exposure to fire within burned areas (USDA Forest Service 2009). A large body of evidence indicates that populations of the non-sprouting *A. tridentata* may require 50–120 years for recovery to pre-fire levels of density and foliar cover (Baker 2006).

Artemisia filifolia, a 6–18 dm tall shrub, occurs in 11 states of the central and western United States (Shultz 2006). Within the central and southern Great Plains of North America, *A. filifolia* can be the dominant species on sandy soils, achieving foliar cover of 20–50% (Collins et al. 1987; Gillen and Sims 2006), and *A. filifolia* shrublands occupy approximately 4.8 million ha of this region (Berg 1994). In North America, the conservation and restoration of *Artemisia* shrublands are of concern to conservationists because of the high number of wildlife species that are associated with or obligates of these habitats, including several declining species (Knick et al. 2003; Rowland et al. 2006; Meinke et al. 2008). In particular, *A. filifolia* shrublands in the central and southern Great Plains provide important habitat for declining grassland and shrubland bird species including the lesser-prairie chicken (*Tympanuchus pallidicinctus*) and Cassin’s sparrow (*Aimophila cassinii*) both of which are species of conservation concern (Cannon and Knopf 1981; Rodgers and Sexson 1990; Woodward et al. 2001; Hagen et al. 2005; Pitman et al. 2006; Doxon 2009).

The importance of Great Plains rangelands in the conservation of global biodiversity has been recognized (Knopf and Sampson 1997; Samson et al. 2004), and there also is a growing realization that many of these ecosystems are undergoing a conversion to woodland and forest because the influence of fire as a recurring ecosystem process has been reduced or eliminated (Briggs et al. 2005; Engle et al. 2007; Van Auken, 2009). Use of prescribed fire has the potential to restore ecosystem properties and processes and enhance rangeland habitats in the Great Plains (Sieg 1997; Fuhlendorf et al. 2009; Scheintaub et al. 2009), but the adoption of prescribed fire as an effective management tool in *A. filifolia* shrublands of the southern Great Plains is hindered by a lack of published information on the effects of fire on this ecosystem’s dominant species, *A. filifolia*.

In light of the demonstrated importance of recurring fires to the maintenance of many Great Plains ecosystems, we conducted a study on the fire resiliency of *A. filifolia* in the southern Great Plains of North America. We define resiliency as the amount of time required to return to a state, following disturbance, which approximates the pre-disturbance state. This definition corresponds to the definition

for resilience provided by Pimm (1984) and the definition of engineering resilience provided by Holling (1996). The results of our study should be useful to land managers who need to know if prescribed fire is an appropriate tool for the restoration and management of *A. filifolia* shrublands. Our objectives were to: 1) determine if the density of *A. filifolia* was altered by single spring fires; 2) characterize the response of *A. filifolia* structural characteristics (canopy cover, height, canopy area and canopy volume) relative to years since being burned; and 3) determine if being burned twice affected density and structural characteristics of *A. filifolia* differently than being burned once.

Methods

Study site

The study site was the Hal and Fern Cooper Wildlife Management Area (Cooper WMA) in Woodward County, Oklahoma, USA (99°30'05"W, 36°32'10"N). The long-term (1940-2008) average annual precipitation at the National Oceanic and Atmospheric Administration Fort Supply weather station was 59.9 cm (www.ncdc.noaa.gov). The annual total precipitation and percent deviation from the long-term average for 2005, 2006, 2007 and 2008 was 72.5 cm (121%), 40.5 cm (68%), 77.0 cm (129%) and 55.3 cm (92%), respectively. About 63% of the study site was characterized by soils in the Eda-Tivoli soil complex (USDA-NRCS 2009c), and all sampling occurred in areas occupied by this soil complex. These loamy fine sands and fine sands are rapidly permeable, mixed, thermic Lamellic (Eda part) and Typic (Tivoli part) Ustipsamments that occur as undulating to rolling dunes with slopes of 3–12% (USDA-NRCS 2009a). Vegetation of the study region was an *Artemisia* shrubland with the dominant species being *A. filifolia* (Collins et al. 1987; Gillen and Sims 2004). Herbaceous vegetation was a diverse mixture of grasses and forbs including the perennial tall, mid-height and short grasses such as *Andropogon hallii*, *Schizachyrium scoparium*, *Eragrostis trichodes*, *Paspalum setaceum* and *Bouteloua gracilis*. Prior to and during this study, all study pastures were annually grazed by yearling steers (*Bos*

taurus) from 1 April to 15 September. Stocking level in all pastures was approximately 6.85 ha per animal unit (1 steer = 0.6 animal unit) and cattle had free access to all areas of each pasture. Prior to the prescribed fires described in this study, no fires had occurred in the study pastures at least since the property was purchased by the State of Oklahoma in 1992.

Study design

The study was conducted in five pastures of 406–848 ha (mean = 608 ha; Appendix Fig. 1). During 1999–2001, prescribed fires were used to create 14 separate 4-ha patches within these pastures during a study of the effects of spring (April) and autumn (November) fires on *A. filifolia* (Vermeire 2002; Appendix Fig. 2, Appendix Table 3). During 2003–2008, three of the pastures were treated with larger spring (March–May) fires such that approximately one-third of each pasture was burned. Mean size of the patches burned during 2003–2008 was 195 ha and ranged from 83 to 415 ha (Appendix Fig. 3, Appendix Table 1). Thus, we were able to sample areas that had not been burned, areas that had experienced only one fire during 2003–2008, and areas that had experienced two fires, first during 1999–2001 and again during 2003–2008. For areas that were burned twice, time between the two burns ranged from 5 to 8 years (mean = 6.4 years).

Sampling – areas burned once and unburned areas

For sampling purposes, each pasture was divided into three approximately equal-sized patches; patch boundaries in patch-burn pastures corresponded with fire breaks delineating individual burn units (Appendix Fig. 3). Four 100-m transects were randomly located in Eda-Tivoli soils within each patch (n = 12 transects per pasture; Appendix Fig. 4, Appendix Table 2) and all transects were located so that they did not occur within the 4-ha patches burned during 1999–2001 in conjunction with the research

conducted by Vermeire (2002). From 21 May to 16 June in 2006–2008, we quantified density of *A. filifolia*, percent canopy cover of live and dead *A. filifolia*, shrub height, canopy area, and volume. Density of *Artemisia filifolia* was determined by counting the number of individual plants within ten 10-m² belt transects (1 x 10 m) along each transect (Fig. 1). Percent canopy cover of live and dead *A. filifolia* was estimated to the nearest 5% within a 0.10-m² rectangular plot (0.20 x 0.50 m) placed on the ground at each 10-m interval along each transect. Finally, at each 10-m interval along each transect, the nearest individual *A. filifolia* was identified for measurement of shrub height, canopy area, and volume (Fig. 1). *Artemisia filifolia* plants with multiple stems arising from the ground surface were considered a single plant if no stem was > 20 cm from another stem at the ground surface. Stems that were > 20 cm from another stem at the ground surface, and it could be determined that they were not connected at near-surface soil depths, were considered separate plants. We determined the height of the selected individual by measuring distance from the ground surface to the highest living foliage. We measured greatest canopy widths of the selected individual perpendicular and parallel to the transect; width measurements also were determined solely on the presence of living foliage. Shrub canopy volume was calculated as:

$$\text{shrub canopy volume} = (\text{shrub canopy area}) * (\text{shrub height}) \quad (1)$$

where

$$\text{shrub canopy area} = [(\text{canopy width 1}) * (\text{canopy width 2}) * (3.1416)]/4 \quad (2)$$

Sampling – areas burned twice

Using aerial photos and centroid coordinates of burned plots provided by Vermeire (pers. comm.), we located all eight areas that had been first burned during 1999–2001 by Vermeire (2002) and had been burned a second time during 2003–2008 (Appendix Fig. 2, Appendix Table 3). During 1999–2001, four of those areas had been burned in the autumn (November) and four in the spring (April). At each of the

eight areas burned by Vermeire (2002) and re-located by us, we established two parallel 100-m transects, 50 m apart, at the centroid coordinates provided by Vermeire to achieve a sampling effort similar to our sampling of plants that had been burned once. From 25 June to 27 June 2008, we measured shrub density, shrub height and the two shrub canopy widths along each transect using the same methodology as described previously; due to time constraints at the end of the field season, we did not measure percent canopy cover of live and dead shrubs.

Analysis

We treated percent cover of live shrubs and dead shrubs, density, height, canopy area, and volume as response variables. We used the GLIMMIX procedure in SAS (SAS Institute 2007) to conduct all analyses using mean transect values for each year (2006–2008). For data from areas burned once, response variables were modeled as a function of time since fire. Models incorporating unequal variance components for areas burned once and areas burned twice were selected by optimizing the fit statistics as well as slope parameter significance. Following a Type III test of fixed effects, pair-wise comparisons of response variable transect means in each time since fire category (one-half, one, two, three, four and five years) were compared with transect means from unburned areas utilizing Dunnett's method for multiple comparisons (Dunnett 1955). Data from areas burned once and areas burned twice were analyzed using an analysis of covariance model with burn frequency (burned once or burned twice) as the class variable and time since fire as the covariate, incorporating pasture and patch as random effects (Milliken and Johnson 2002). Because we did not collect data on percent cover of live and dead shrubs for plants exposed to two fires, a comparison of the two best fit models (one for areas burned once, the other for areas burned twice) was not possible for these variables.

Results

In areas that were burned once, percent canopy cover of live shrubs at one-half year post-fire was lower ($P < 0.01$) than percent canopy cover of live shrubs in unburned areas, but there was no significant difference ($P \geq 0.39$) between unburned areas and burned areas that were from one to five years post fire (Table 1). The highest values of live shrub cover occurred at three, four and five years post-fire, but those values were not significantly higher ($P \geq 0.39$) than the values for unburned areas. Percent canopy cover of dead shrubs in areas that were burned once was lower ($P < 0.01$) at one-half, one, two and three years post fire but did not differ ($P \geq 0.36$) from unburned areas at four and five years post fire. In areas that were burned once, there was no difference ($P \geq 0.72$) in shrub density for all time since fire categories (one-half, one, two, three, four and five years post-fire) compared with areas that had not been burned. Shrub height and shrub canopy volume of plants that were exposed to one fire were both lower ($P \leq 0.04$) at one-half, one, two and three years post-fire than unburned plants but did not differ ($P \geq 0.97$) from unburned plants at four and five years post-fire. The tallest *A. filifolia* individual encountered in the three years of the study was 190 cm and was located in an unburned control pasture. Shrub canopy area of plants exposed to one fire was lower ($P \leq 0.01$) at one-half, one and two years post-fire relative to unburned plants. At three, four and five years post fire, shrub canopy area of plants exposed to one fire did not differ ($P \geq 0.45$) from unburned plants.

For plants that had been exposed to only one fire, a quadratic model best described the relationship between percent cover of live shrubs and time since fire while a linear model best described the relationship between percent canopy cover of dead shrubs and time since fire (Fig. 2; Table 2). There was no relationship between shrub density and time since fire, and the difference between the model for plants that were burned once and the model for plants that were burned twice was marginally significant ($P = 0.051$) (Fig. 3a; Table 2). The relationship of time since fire with both shrub height and shrub

canopy area was best described by a quadratic equation, and there were no differences ($P \geq 0.141$) between the best models of plants burned once and plants burned twice (Fig. 3b,4a; Table 2). The relationship between shrub canopy volume and time since fire was best described by a linear model, and there was no difference ($P = 0.595$) between the best models for plants burned once and plants burned twice (Fig. 4b; Table 2).

Discussion

Our results demonstrate that *A. filifolia* was highly resilient to fire at our study site. Structural characteristics of *A. filifolia* (canopy cover, height, canopy area and canopy volume) were readily altered by fire but they recovered to levels similar to unburned plants within one to three years. Additionally, we could not demonstrate that fire altered the density of this species. This is similar to what has been found with woody plants in other fire-influenced ecosystems such as South African savanna (Higgins et al. 2007), Brazilian savanna-forest transitional communities (Hoffman et al. 2009), North American *Quercus havardii* (Fagaceae) shrublands (Harrell et al. 2001; Boyd and Bidwell 2002) and North American *Prosopis glandulosa* (Fabaceae) savanna (Ansley et al. 2008). Low mortality resulting from fire, as indicated by no change in shrub density, is the likely mechanism explaining the lack of a relationship between time since fire and shrub density in our study of plants exposed to one and two fires. The only previous experimental work on the response of *A. filifolia* to fire documented a very low rate of post-fire mortality, approximately 4%, and positive correlations between resprouting ability and shrub height, canopy area and canopy volume were identified (Vermeire 2002). A theoretical basis for larger or older plants having greater post-disturbance resprouting vigor, because they have greater belowground reserves that can be mobilized for re-growth of aboveground foliage, has been elucidated (Iwasa and Kubo 1997), and empirical evidence of this has been provided for woody plants in the Mediterranean Basin (Malanson

and Trabaud 1988; Konstantinidis et al. 2006), Australia (Hodgkinson 1998), South America (Gurvich et al. 2005) and North America (Dacy and Fulbright 2009).

In Vermeire's (2002) study, *A. filifolia* plants achieved 80% of their pre-fire height and canopy area and 62% of their canopy volume after two growing seasons following a single fire (two years was the greatest amount of time that had passed between when plants were burned and when data were collected in that study). In our study, shrub height, canopy area, and canopy volume of plants exposed to only one fire were 77%, 59% and 46%, respectively, of unburned plants at two years post-fire. For plants exposed to two fires in our study, shrub height, canopy area, and canopy volume were 85%, 68% and 50%, respectively, of unburned plants at two years post-fire. Although not statistically different from unburned plants, the high values of percent canopy cover of live shrubs at three, four and five years post-fire for plants exposed to only one fire in our study are especially notable. The rapid recovery of *A. filifolia* structural characteristics following fire may be explained in part by a post-fire environment that is conducive to growth of this species. This has been demonstrated in North American tallgrass prairie, a fire dependent C₄ grassland, where post-fire re-growth of the shrub *Cornus drummondii* (Cornaceae) was enhanced by post-fire changes in the plant microclimate including increased soil temperature and increased light availability at the soil surface (Heisler et al. 2004). Plant physiological traits, such as net photosynthesis, maximum photosynthesis, stomatal conductance, and light saturation point can all be enhanced in *C. drummondii* shoots that resprout following fire (McCarron and Knapp 2003).

The fire-resiliency of *A. filifolia* that we have demonstrated differs substantially from other North American *Artemisia* shrub species such as *A. arbuscula*, *A. nova*, *A. pygmaea* and *A. rigida*, which are all typically killed by fire (USDA Forest Service 2009). The *A. tridentata* complex (*A. t.* ssp. *parshii*, *A. t.* ssp. *tridentata*, *A. t.* ssp. *vaseyana* and *A. t.* ssp. *wyomingensis*), one of the most widespread of North American *Artemisia* shrubs, is a non-sprouting species that is considered fire-sensitive, requiring as much as 50–120 years for recovery to pre-fire levels of density and foliar cover (Baker 2006). The inability of *A. tridentata* to resprout after a top-killing fire and the relatively short-lived viability of *A. tridentata*

seeds in soil seed banks (Young and Evans 1989) explain in part why this species does not recover rapidly following exposure to fire. A substantial threat to *A. tridentata* ecosystems in western North America is increased fire frequencies driven by increased levels of fine fuel load and fuel continuity as a result of exotic grass invasions (Knick and Rotenberry 1997; Brooks et al. 2004; Baker 2006).

The contrast in response of North American *Artemisia* shrub species to fire is illustrative of a fundamental dichotomy in woody plant functional response to disturbances. The response of woody plants to disturbances that remove aboveground biomass lend them to being classified into one of two functional groups: resprouters and reseederers (Keeley and Zedler 1978; Verdú 2000; Bell 2001). Resprouters persist in disturbance-prone environments through the ability of individuals to survive the disturbance event while reseederers persist through their ability to recruit new members into the population following the disturbance event, either through seed dispersal from outside the disturbed area or through seed banks that are present within the disturbed area (Bond and Midgley 2001; Pausas and Verdú 2005). Shrubs can be extremely long-lived (Vasek 1980) and population dynamics of resprouters, which can survive as individuals through disturbance events, may differ greatly from that of reseederers, whose populations can only be maintained if recruitment following a disturbance event is successful in spite of the effects of weather, competition and predation on seed and seedling survival (Bond and Midgley 2003).

While our results for *A. filifolia* differ greatly from what has been found for most North American *Artemisia* shrub species, they are not surprising when *A. filifolia* is considered within its environmental context. The temperate grasslands of North America's central and southern Great Plains are part of Earth's most extensive fire-dependent ecosystems, C₄ grasslands and savannas (Bond and Keeley 2005; Bond et al. 2005). Indeed, the few North American *Artemisia* shrub species in addition to *A. filifolia* that are capable of resprouting after fire, such as *A. californica* in coastal sage scrub of California (Malanson and Westman 1985) and *A. cana* in the Great Plains (White and Currie 1983), are typically found in ecosystems that are strongly fire-influenced or outright fire-dependent. Nevertheless, others have

cautioned that ecosystem components, such as woody plants, should not be considered completely fire-adapted but instead should be considered adapted to particular fire regimes (Pausas and Keeley 2009). If the frequency of disturbance is such that there is not enough time to allow a plant to store sufficient belowground energy reserves, which are necessary for post-fire resprouting, then post-disturbance resprout vigor may be reduced or precluded (Vilà and Terradas 1995; Bellingham and Sparrow 2000). We studied the response of *A. filifolia* after, at most, two fires and the shortest interval between those fires was five years. It remains to be seen how *A. filifolia* would respond after a greater number of fires and fires that occur with a shorter fire return interval. Fires that occurred at our study area during the period of 2003–2008 were all spring fires, and it is possible that *A. filifolia* would be affected differently by fires that occur at other times of the year. However, Vermeire's (2002) study suggested there was no difference between effects of one spring or one autumn fire on *A. filifolia* mortality.

There is increasing interest in the use of fire to enhance habitat heterogeneity across landscapes to achieve conservation objectives (Brockett et al. 2001; Fuhlendorf et al. 2006; Parr and Andersen 2006; Bird et al. 2008; Fuhlendorf et al. 2009). Nevertheless, current attitudes concerning the conservation of western North American *Artemisia* ecosystems typically regard both wildfires and prescribed fires as antithetical to the conservation of these ecosystems and their constituent organisms (Nelle et al. 2000; Baker 2006; Beck et al. 2009). In contrast to *Artemisia* shrub species and *Artemisia* ecosystems of western North America, *A. filifolia* shrublands in the central and southern Great Plains should benefit greatly from the increased use of fire as an ecosystem management tool. The patchwork of contrasting vegetation structure resulting from the prescribed burns that have been conducted at Cooper WMA has been shown to have a profound influence on the composition of passerine communities at this site (Doxon 2009). *Artemisia filifolia* shrublands are important habitat for the declining lesser-prairie chicken (Cannon and Knopf 1981; Woodward et al. 2001; Hagen et al. 2005; Pitman et al. 2006) whose habitat requirements differ at various times of the year; i.e., nesting hens require vegetation structure that differs from what is optimal for a hen with a brood of chicks, while both are different from what is required at

leks where mating occurs (Hagen et al. 2004). Further research needs to be conducted to determine if lesser prairie chickens would benefit from the type of landscape-scale heterogeneity created by the patchy application of fire at Cooper WMA. A particularly important consequence of the use of fire in *A. filifolia* shrublands and other grasslands of the North American Great Plains is that it precludes the conversion of these C₄ herbaceous/shrubland communities to C₃ woody plant communities. Fire exclusion in North America since the time of Euro-American settlement has facilitated the invasion of Great Plains grasslands by non-sprouting trees in the genus *Juniperus* (Cupressaceae) (Coppedge et al. 2001; Briggs et al. 2002; Engle et al., 2007), including the invasion of *J. virginiana* in *A. filifolia* shrublands. The deleterious effect of the invasion and spread of *Juniperus* spp. into Great Plains grasslands has been well documented for herbaceous plants, passerine birds and lesser prairie chickens (Gehring and Bragg 1992; Fuhlendorf et al. 1997; Fuhlendorf et al. 2002; Briggs et al. 2002; Engle et al. 2007).

In conclusion, our results provide evidence that *A. filifolia* is highly resilient to the effects of fire. *Artemisia filifolia* density does not change after one or two fires, and *A. filifolia* structural characteristics return to levels characteristic of unburned areas within a period of one to four years. These results contrast greatly with most other North American *Artemisia* shrub species that are considered highly fire sensitive. The high fire resiliency of *A. filifolia*, the dominant species of the ecosystems in which it is found, indicates that *A. filifolia* shrublands are a fire-dependent ecosystem and suggests that the use of fire for ecosystem maintenance will achieve conservation objectives in the North American southern Great Plains.

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Table 1. Mean \pm SE of response variables at one-half, one, two, three, four and five years post-fire for *Artemisia filifolia* plants that were exposed to only one fire at Cooper Wildlife Management Area, Oklahoma, USA. *P*-values were generated from pair-wise comparisons of each time since fire category with plants from unburned areas.

Response variable	Time since fire (years)						Unburned plants
	0.5	1	2	3	4	5	
% cover live shrubs	5.12 \pm 1.18 <i>P</i> < 0.01	9.78 \pm 2.18 <i>P</i> = 0.39	13.46 \pm 3.14 <i>P</i> = 1.00	18.35 \pm 2.50 <i>P</i> = 0.48	18.14 \pm 2.58 <i>P</i> = 0.56	17.92 \pm 2.89 <i>P</i> = 0.71	13.96 \pm 0.90
% cover dead shrubs	3.66 \pm 0.81 <i>P</i> < 0.01	3.32 \pm 0.94 <i>P</i> < 0.01	5.24 \pm 1.58 <i>P</i> < 0.01	7.31 \pm 1.42 <i>P</i> \leq 0.01	10.94 \pm 1.68 <i>P</i> = 0.36	11.26 \pm 2.78 <i>P</i> = 0.83	14.29 \pm 0.95
Shrub density (plants/10 m ²)	5.46 \pm 0.53 <i>P</i> = 0.72	5.73 \pm 0.58 <i>P</i> = 0.99	6.39 \pm 0.54 <i>P</i> = 0.99	5.94 \pm 0.57 <i>P</i> = 1.00	6.18 \pm 0.58 <i>P</i> = 1.00	6.54 \pm 1.05 <i>P</i> = 1.00	6.07 \pm 0.33
Shrub height (dm)	3.97 \pm 0.28 <i>P</i> < 0.01	4.84 \pm 0.28 <i>P</i> < 0.01	5.61 \pm 0.29 <i>P</i> < 0.01	6.35 \pm 0.25 <i>P</i> = 0.03	7.05 \pm 0.31 <i>P</i> = 0.99	7.38 \pm 0.34 <i>P</i> = 1.00	7.24 \pm 0.15
Shrub canopy area (dm ²)	19.46 \pm 2.86 <i>P</i> < 0.01	32.87 \pm 4.31 <i>P</i> < 0.01	43.33 \pm 5.40 <i>P</i> < 0.01	62.97 \pm 4.73 <i>P</i> = 0.45	72.12 \pm 7.21 <i>P</i> = 1.00	73.59 \pm 9.25 <i>P</i> = 1.00	72.36 \pm 3.20
Shrub canopy volume (dm ³)	106.36 \pm 30.27 <i>P</i> < 0.01	195.42 \pm 39.26 <i>P</i> < 0.01	299.68 \pm 52.70 <i>P</i> < 0.01	475.97 \pm 50.68 <i>P</i> = 0.04	594.81 \pm 80.04 <i>P</i> = 0.97	682.70 \pm 120.40 <i>P</i> = 1.00	653.58 \pm 37.85

Table 2. Best fit models describing the relationship between *Artemisia filifolia* response variables and time since fire (tsf) at Cooper Wildlife Management Area, Oklahoma, USA. *P*-values were generated from comparisons between models for plants burned only once and models for plants burned twice. Percent cover data for live and dead shrubs were not collected for plants burned twice.

Response variable	Fire history	Model system	<i>P</i> -value
% cover live shrubs	plants burned once	$y = 0.65 + 9.26(\text{tsf}) - 1.15(\text{tsf})^2$	not applicable
% cover dead shrubs	plants burned once	$y = 1.81 + 2.07(\text{tsf})$	not applicable
Shrub density (plants/10 m ²)	plants burned once plants burned twice	$y = 6.01 + 0(\text{tsf})$ $y = 6.77 + 0(\text{tsf})$	<i>P</i> = 0.051
Shrub height (dm)	plants burned once plants burned twice	$y = 3.17 + 1.57(\text{tsf}) - 0.15(\text{tsf})^2$ $y = 3.62 + 1.57(\text{tsf}) - 0.15(\text{tsf})^2$	<i>P</i> = 0.141
Shrub canopy area (dm ²)	plants burned once plants burned twice	$y = 8.42 + 23.57(\text{tsf}) - 2.05(\text{tsf})^2$ $y = 10.69 + 23.57(\text{tsf}) - 2.05(\text{tsf})^2$	<i>P</i> = 0.682
Shrub canopy volume (dm ³)	plants burned once plants burned twice	$y = 38.12 + 134.23(\text{tsf})$ $y = 59.61 + 134.23(\text{tsf})$	<i>P</i> = 0.595

Fig. 1. Diagrammatic representation of *A. filifolia* sampling efforts along 100-m transects at Cooper Wildlife Management Area, Oklahoma, USA.

Percent cover live and dead shrubs were quantified within 0.10-m² plots, shrub density was quantified within 10.0-m² belt transects, and shrub height and shrub canopy widths were quantified for the shrub nearest to each 10-m interval along the transect.

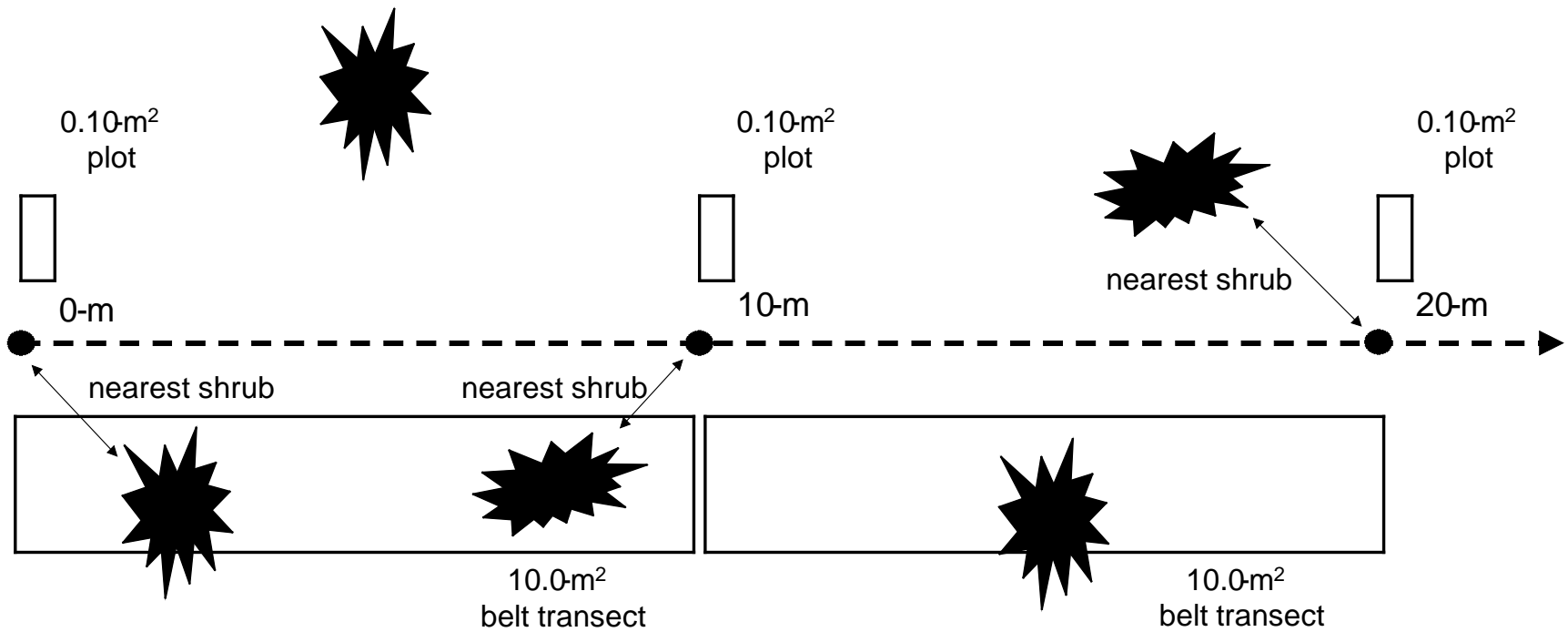
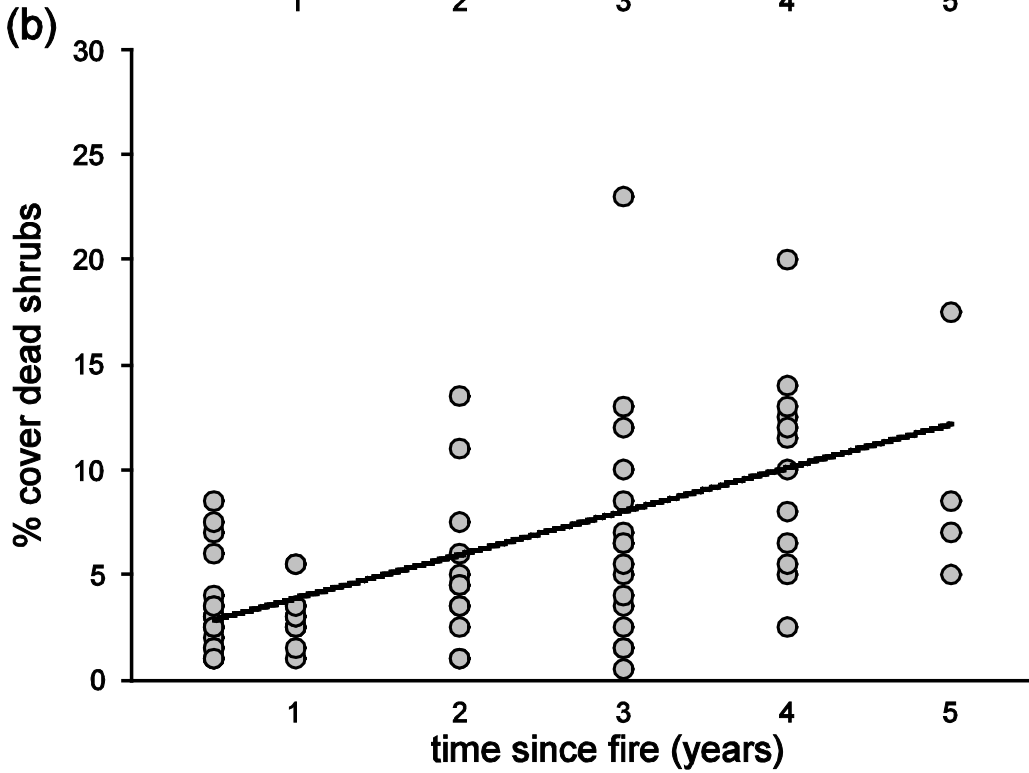
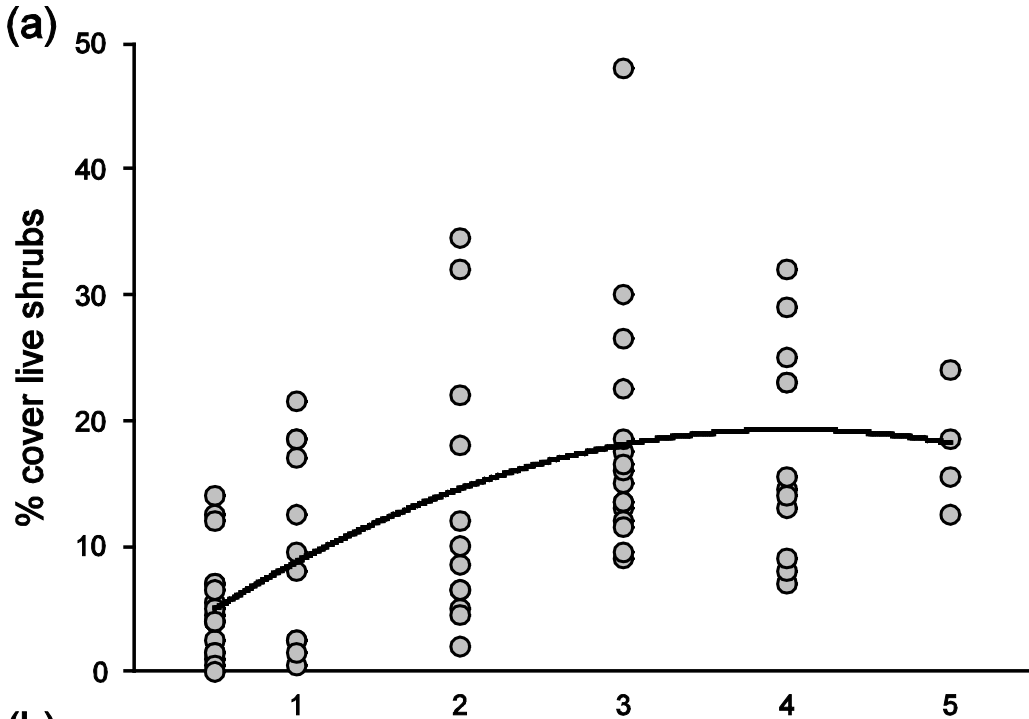
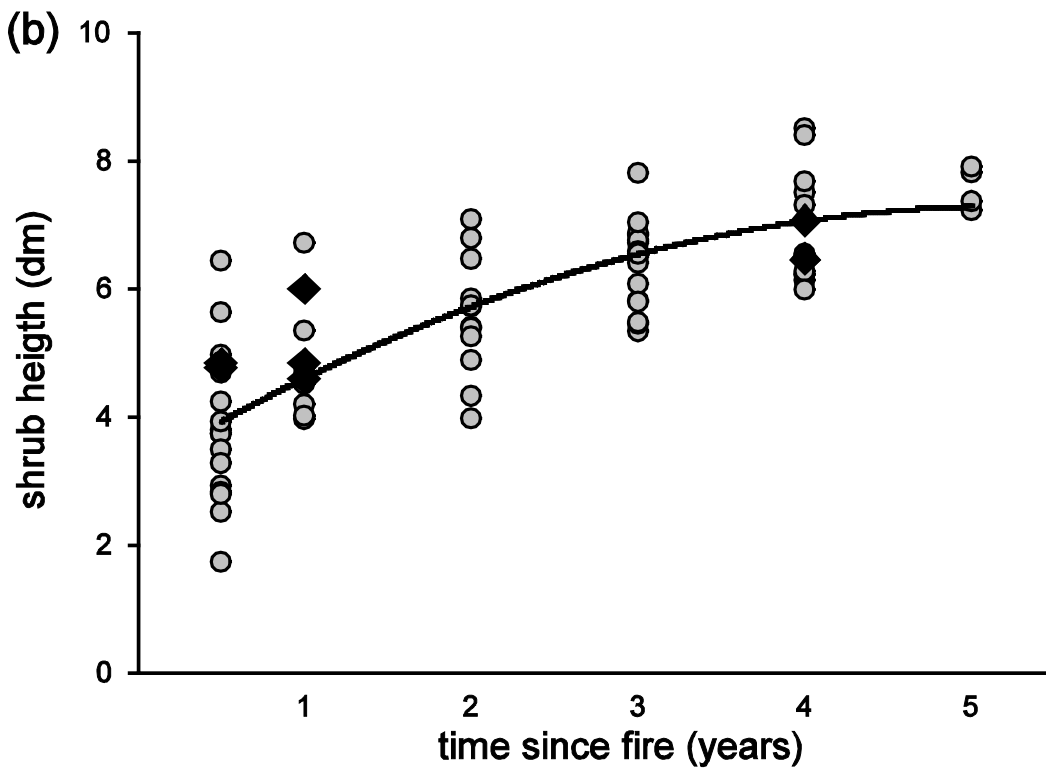
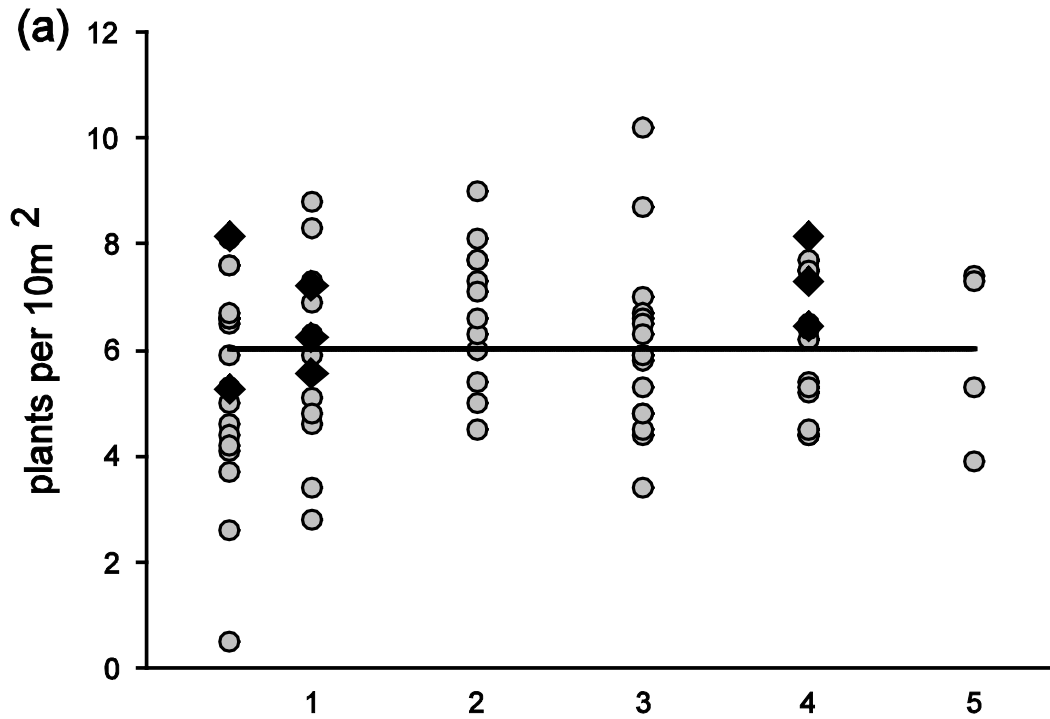


Fig. 2. Mean transect values from all sample years (2006–2008) of percent cover of live (a) and dead (b) *Artemisia filifolia* shrubs in areas burned once at one-half, one, two, three, four and five years post-fire at Cooper Wildlife Management Area, Oklahoma, USA. Best fit models describe the relationship between response variables and each time since fire category (see Table 2).



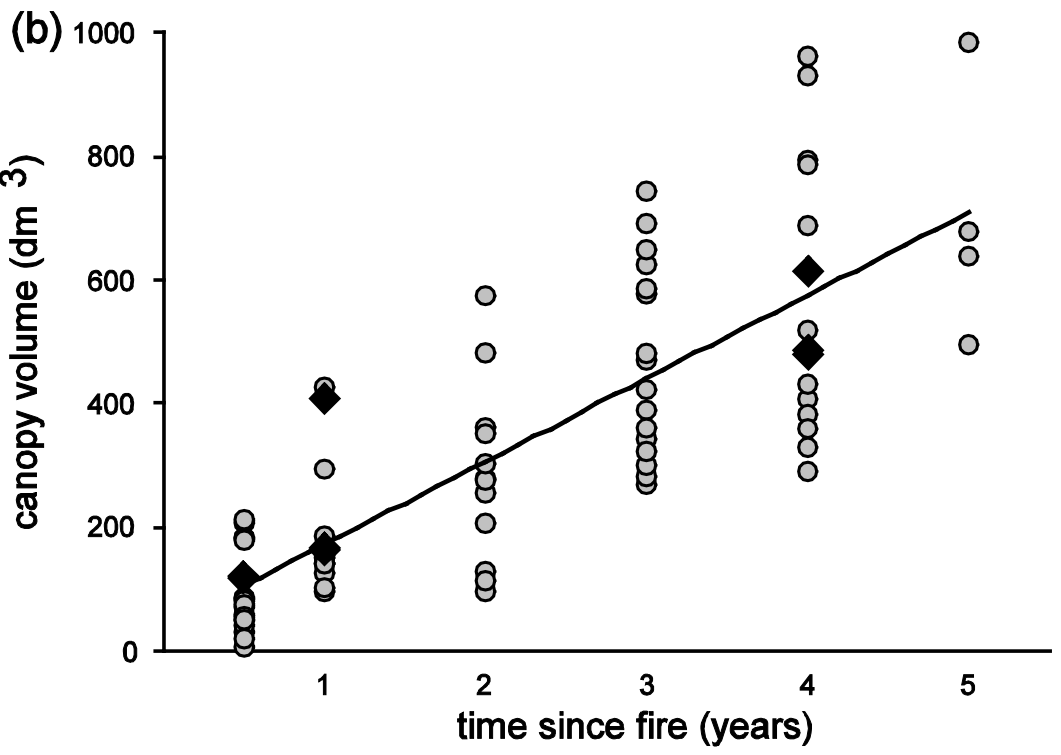
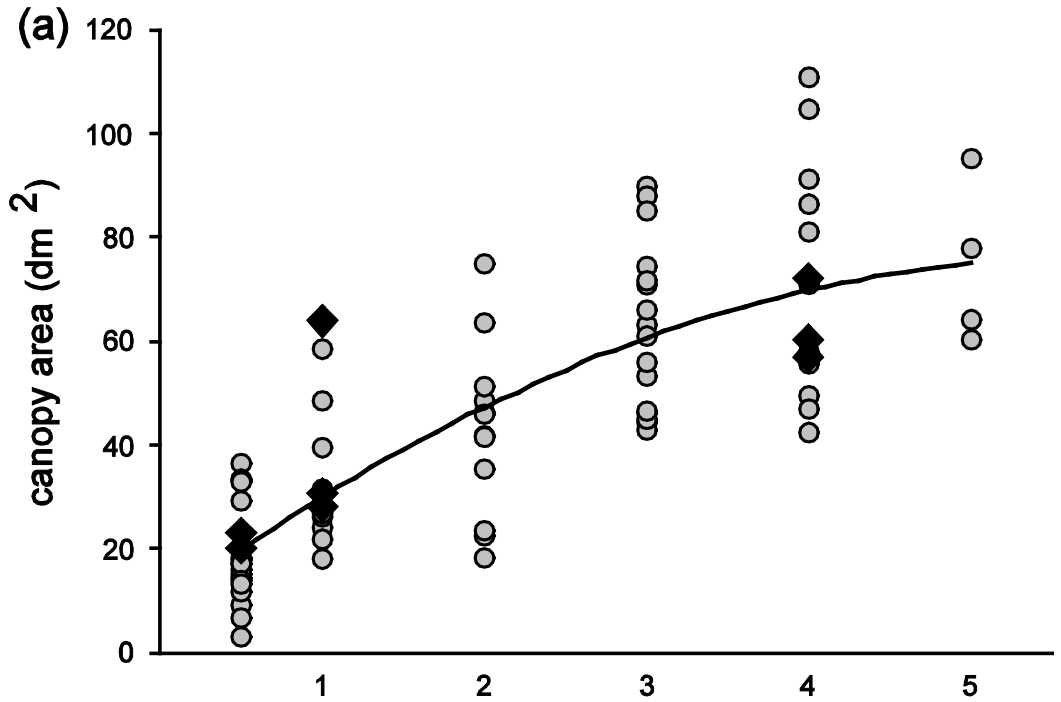
○ transect data for plants burned once
 — best fit model for plants burned once

Fig. 3. Mean transect values from all sample years (2006–2008) of *Artemisia filifolia* density (a) and shrub height (b) at one-half, one, two, three, four and five years post-fire for plants exposed to only one fire (circles) and plants exposed to two fires (diamonds) at Cooper Wildlife Management Area, Oklahoma, USA. Best fit models describe the relationship between response variables and each time since fire category for plants exposed to only one fire. Best fit models for plants exposed to two fires were statistically similar to models for plants exposed to only one fire (see table 2).



- transect data for plants burned once
- best fit model for plants burned once
- ◆ transect data for plants burned twice

Fig. 4. Mean transect values from all sample years (2006–2008) of *Artemisia filifolia* shrub canopy area (a) and shrub canopy volume (b) at one-half, one, two, three, four and five years post-fire for plants exposed to only one fire (circles) and plants exposed to two fires (diamonds) at Cooper Wildlife Management Area, Oklahoma, USA. Best fit models describe the relationship between response variables and each time since fire category for plants exposed to only one fire. Best fit models for plants exposed to two fires were statistically similar to models for plants exposed to only one fire (see table 2).



- transect data for plants burned once
- best fit model for plants burned once
- ◆ transect data for plants burned twice

CHAPTER II

RESTORATION OF THE FIRE-GRAZING INTERACTION IN *ARTEMISIA FILIFOLIA* SHRUBLAND OF THE SOUTHERN GREAT PLAINS, NORTH AMERICA

**Restoration of the fire-grazing interaction in *Artemisia filifolia* shrubland of
the Southern Great Plains, North America**

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Running Title: Fire-grazing interaction in *Artemisia* shrubland

Word Count: 6833

Summary:

1. Patterns of landscape heterogeneity are likely crucial to the maintenance of biodiversity in central North American shrublands and grasslands, yet management practices in these ecosystems typically seek to homogenize landscapes.
2. We conducted research in *Artemisia filifolia* (Asteraceae) shrublands located in the North American southern Great Plains to determine the effect of restoring the fire-grazing interaction on vegetation structure. Data were collected for three years in replicated pastures grazed by cattle (*Bos taurus*) where the fire-grazing interaction had been restored (treatment pastures) and in pastures that were grazed but remained unburned (control pastures).
3. The effect of the fire-grazing interaction on heterogeneity (variance) of vegetation structure was assessed at scales of 12.5 m² – 609 ha.
4. Most measurements of vegetation structure within treatment pastures differed from control pastures for one to three years after being burned but were thereafter similar to the values found in unburned control pastures.
5. Treatment pastures were characterized by a lower amount of total heterogeneity and a lower amount of heterogeneity through time.
6. Heterogeneity of vegetation structure tended to decrease as the scale of measurement increased in both treatment and control pastures with the exception that treatment pastures exhibited much higher heterogeneity at the patch scale (mean patch size = 202 ha) of measurement.
7. Patch-scale heterogeneity in treatment pastures tended to be higher than in the control pastures, to increase through the three years of the study, or both.
8. *Synthesis and applications.* Vegetation structure in *Artemisia filifolia* shrublands of our study were readily altered by the fire-grazing interaction, but they also demonstrated substantial resilience to these effects. The fire-grazing interaction also changed the total amount of heterogeneity characterizing this system, the scale at which heterogeneity in this system was

expressed and the amount of heterogeneity expressed through time. Restoration of the fire-grazing interaction resulted in a shifting mosaic of habitat conditions that is likely important to the conservation of biodiversity within this ecosystem.

Key Words: heterogeneity, patch-burn, pyric-herbivory

Introduction

Understanding effects of heterogeneity on the structure and function of ecological communities and landscapes has been deemed a critical component of biodiversity conservation (Christensen, 1997; Wiens, 1997). In contrast to the hypothesized importance of heterogeneity, a primary objective of range management has been the uniform distribution of grazing animals in space and time (Williams, 1954; Bailey, 2004; Holecheck et al., 2004), which may in fact homogenize rangeland landscapes (Knopf and Sampson, 1997; Fuhlendorf and Engle, 2001). An alternative rangeland management practice known as patch-burning is based on the evolutionary interaction of fire and grazing known as pyric-herbivory with the goal of manipulating animal distribution through the application of discrete fires that attract animals to different locations. This approach is intended to approximate historic cycles of disturbance and rest across multiple scales (Fuhlendorf and Engle, 2001; Fuhlendorf et al., 2009). The interaction between fire and large grazers is described by a model in which both positive and negative feedbacks create a shifting mosaic of out-of-phase landscape patches that differ in vegetation structure and composition, the amount of herbaceous biomass and levels of forage quality (Fuhlendorf and Engle, 2004; Fuhlendorf et al., 2009). High levels of forage utilization in recently burned patches, and concomitant low levels of forage utilization in adjacent patches that have not burned recently, have been suggested to result in a landscape mosaic of herbaceous biomass (fuel) that determines the location and behavior of subsequent fires within a landscape (Kerby et al., 2007; Savadogo et al., 2007; Fuhlendorf et al., 2009). The cycles of

disturbance and rest driven by the fire-grazing interaction replicate historical dynamics of landscape heterogeneity that are likely crucial for the maintenance of biodiversity in rangeland ecosystems (Fuhlendorf et al., 2009).

Land managers are more likely to adopt a novel management strategy if they are able to confidently predict the outcome of their actions within the context of the ecosystems that characterize the landscapes they manage. Currently, most research on restoration of the fire-grazing interaction has been conducted in mesic tallgrass prairies of central North America. Our research, however, was conducted in a shrub-dominated region characterized by a drier climate where information on the fire-grazing interaction is limited (but see Vermeire et al., 2004). The objectives of our research were to: 1) determine the response of vegetation structural characteristics (bare ground, litter, live and dead vegetation, live and dead grass, live and dead forbs, live and dead shrubs, vegetation height and vegetation visual obstruction) to increasing time since being burned; 2) determine the relationship between heterogeneity in vegetation structural characteristics and scale-of-observation within pastures managed in a traditional manner (control pastures: moderate grazing without patch-burning) and pastures where the fire-grazing interaction had been restored (treatment pastures: moderate grazing with patch burning); and 3) determine the amount of patch-scale heterogeneity in vegetation structural characteristics in control pastures and treatment pastures.

Materials and Methods

Study site

The study site was the Hal and Fern Cooper Wildlife Management Area (Cooper WMA) in Woodward County, Oklahoma, USA (99°30'05"W, 36°32'10"N). The long-term (1940-2008) average annual precipitation at the National Oceanic and Atmospheric Administration Fort Supply cooperative weather station (www.ncdc.noaa.gov) was 59.9 cm. The annual total precipitation and percent deviation from the

long-term average for 2005, 2006, 2007 and 2008 was 72.5 cm (121%), 40.5 cm (68%), 77.0 cm (129%) and 55.3 cm (92%), respectively. The majority of the study site, approximately 63%, was characterized by soils in the Eda-Tivoli soil complex (USDA-NRCS, 2009a), and all sampling occurred in areas occupied by this soil complex. These loamy fine sands and fine sands are rapidly permeable, mixed, thermic Lamellic (Eda component) and Typic (Tivoli component) Ustipsamments which occur as undulating to rolling dunes with slopes of 3–12% (USDA-NRCS, 2009b). Vegetation of the study region was considered an *Artemisia* shrubland with the dominant species being the shrub *A. filifolia* (Asteraceae; Collins et al., 1987; Gillen and Sims, 2004). Herbaceous vegetation was a diverse mixture of grasses and forbs including perennial tall, mid-height and short grasses such as *Andropogon hallii*, *Schizachyrium scoparium*, *Eragrostis trichodes*, *Paspalum setaceum* and *Bouteloua gracilis*. Common forbs included *Ambrosia psilostachya*, *Commelina erecta*, *Croton texensis* and *Eriogonum annuum*.

Prior to and during this study, all study pastures were annually grazed by yearling steers (*Bos taurus*) from 1 April to 15 September. Stocking level in all pastures was approximately 6.85 ha per animal unit (1 steer = 0.6 animal unit) and cattle had free access to all areas of each pasture. During 1999–2001, prescribed fires were used to create 14 separate 4-ha patches within the study pastures during research of the effects of patch-burning on the distribution of grazing cattle (Vermeire et al., 2004; Appendix Fig. 2, Appendix Table 3). Prior to the prescribed fires conducted during 1999–2001 and those described below in this study, no fires had occurred in the study pastures at least since the property was purchased by the State of Oklahoma in 1992.

Study design

The study was conducted in five pastures of 406–842 ha (mean = 608 ha; Appendix Fig. 1). During 2003–2008, three of the pastures (hereafter treatment pastures) were treated with spring (March-May) prescribed fires such that approximately one-third of each pasture was burned (Appendix Fig 3, Appendix

Table 1). Mean size of the patches burned during 2003–2008 was 195 ha and ranged from 83 to 415 ha. The remaining two pastures have had no fires from 2003 to 2008 and were considered control pastures.

Sampling

For sampling purposes, each pasture was divided into three approximately equal-sized patches; patch size was thus proportional to pasture size (Appendix Fig. 3, Appendix Table 1). Patch boundaries in treatment pastures corresponded with fire breaks delineating individual burn units. Four 100-m transects were randomly located in Eda-Tivoli soils within each patch ($n = 12$ transects per pasture; Appendix Fig. 4, Appendix Table 2); the 4-ha patches that had been burned during 1999–2001 (Vermeire et al., 2004) were visible on aerial photos and all transects were located so that they did not occur within them. From 21 May to 16 June in 2006–2008, we quantified the following vegetation structure variables to the nearest 5% within a 0.10-m² rectangular plot (0.20 x 0.50 m) placed on the ground at each 10-m interval along each transect ($n=10$ plots per transect). Vegetation structure variables were: percent bare ground; percent cover of litter; live and dead vegetation; live and dead grass; live and dead forbs; and live and dead shrubs. Litter was considered to be any dead or senesced plant material that was horizontally-arranged and in contact with the ground or in contact with other litter that was itself in contact with the ground. Dead vegetation, dead grass, dead forbs and dead shrubs were considered to be any dead or senesced plant material in each respective category that was not horizontally-arranged and in contact with the ground; i.e., standing dead plant biomass not in the litter category. We also measured vegetation height and visual obstruction at 10-m intervals along each transect using a visual obstruction pole modified from Robel et al. (1970; $n=10$ placements of the pole per transect). The visual obstruction pole was marked in 1-cm increments and observations were made two meters from the pole one meter above the ground surface. One observation was made from each of the four cardinal directions at each placement of the pole ($n=4$ observations per placement of the pole; $n=40$ observations per transect). Vegetation height was

determined by recording the highest point at which vegetation crossed between the observer and the pole. Visual obstruction was determined by recording the lowest point at which the pole was visible.

Analysis

Mixed-model analyses were conducted using the GLIMMIX procedure in SAS (SAS Institute, 2007).

We treated all vegetation structure measurements (percent bare ground; percent cover of litter, live and dead vegetation, live and dead grass, live and dead forbs, live and dead shrubs; vegetation height and visual obstruction) as response variables and calculated mean transect values for each year (2006–2008).

Following a significance test of fixed effects, pair-wise comparisons of response variable transect means in each time since fire category (one-half, one, two, three, four and five years) as well as transect means from unburned patches within patch-burned pastures were compared with transect means from the unburned control pastures utilizing Dunnett's method for multiple comparisons (Dunnett, 1955).

Additionally, response variables were modeled as either linear or quadratic functions of time since fire.

All percent cover response variables were modeled using a beta distribution with a logit link function, vegetation height was modeled with a normal distribution and vegetation visual obstruction was modeled with a gamma distribution and a log link function.

To assess heterogeneity, a hierarchical model was used to compute variance component estimates across all years (2006-2008) for all variance components associated with spatial scale (quarter-point, point, transect, patch and pasture) and temporal (2006-2008) variables for vegetation height and vegetation visual obstruction data. Restricted maximum likelihood (REML; Harville, 1977) variance components were estimated for vegetation height data which assumed a normal distribution while residual pseudo likelihood (REPL; Wolfinger and O'Connell 1993) variance components were estimated for vegetation visual obstruction data which assumed a gamma distribution. The quarter-point, the smallest scale of measurement in our study, represents a scale of approximately 12.5 m² (the area circumscribed by

the four readings around each placement of the visual obstruction pole). The point scale accounts for the data from the ten pole placements along each 100-m transect while the transect scale accounts for the data from the four transects in each patch. The patch scale (mean patch size = 202 ha) accounts for the data from the three patches in each pasture and the pasture scale (mean pasture size = 608 ha) accounts for the data from the pastures in the treatment (n=3) and control (n=2) categories. The sum of all scale and temporal variance estimates for vegetation height and vegetation visual obstruction provided the total amount of variance for each variable within treatment and control categories. Finally, to assess heterogeneity at the patch scale during each year of the study, we calculated REML and REPL variance component estimates at the patch level for each of the three years (2006, 2007 and 2008) of the study in the control and treatment pastures.

Results

Multiple comparisons of response variables at each time-since-fire category (one-half, one, two, three, four and five years) from the treatment pastures with the same variables from unburned control pastures indicate that all measurements of vegetation structure returned to levels that were not significantly different from those of unburned control pastures within four years after being burned (Table 1). Percent cover of dead shrubs and vegetation visual obstruction in treatment pastures differed ($P \leq 0.04$) from control pastures for three years post-fire. Percent bare ground, percent cover of litter and dead vegetation, and vegetation height in treatment pastures differed ($P \leq 0.03$) from control pastures for two years post-fire. Percent cover of dead grass, dead forbs and live shrubs in treatment pastures differed ($P \geq 0.01$) from control pastures for one-half of a year post-fire. Within the treatment pastures, there were relationships ($P \leq 0.04$) between most vegetation structural characteristics (bare ground, litter, live and dead vegetation, live and dead grass, live forb, live and dead shrub, vegetation height and vegetation visual obstruction) and time-since-fire (one-half, one, two, three, four and five years post-fire; Table 2). For

percent bare ground and percent cover of live forbs, the relationship with time-since-fire was negative ($P \leq 0.04$; Table 2). For all other measurements of vegetation structure except percent cover of dead forbs, there was a positive relationship with time-since-fire ($P \leq 0.04$; Table 2); percent cover of dead forbs was not related ($P = 0.28$) to time-since-fire (Table 2).

The REML and REPL variance estimates for all spatial scale (quarter-point, point, transect, patch and pasture) and temporal (2006- 2008) variables and the total amount of variance for vegetation height and vegetation visual obstruction response variables in the treatment and control pastures are provided in Table 3. The total variance in vegetation height was 1151 in the treatment pastures and 1289 in the control pastures (Table 3). The total variance in vegetation visual obstruction was 260 in the treatment pastures and 572 in the control pastures (Table 3). In both treatment and control pastures, variation in vegetation height (Fig. 1) and vegetation visual obstruction (Fig. 2) tended to decrease as the scale of measurement increased. In the treatment pastures, however, that trend was interrupted by a substantial amount of variation at the patch scale. Treatment pastures also were characterized by less variance through time than the control pastures (Table 3). For most measurements of vegetation structure (litter, live and dead vegetation, live and dead grass, dead forbs, live and dead shrubs, and vegetation height), variance at the patch level was relatively constant throughout the three years of the study in the control pastures (Figs. 3b, 4–5, 6b, 7, and 8b). Conversely, variance at the patch level in the treatment pastures was either greater than in the control pastures, increased through the three years of the study, or both (Figs. 3–8).

Discussion

Artemisia filifolia shrublands at our study site were resilient to the fire-grazing interaction as an ecosystem process. We define resiliency as the amount of time required to return to a state, following disturbance, which approximates the pre-disturbance state. This definition corresponds to the definition

for resilience provided by Pimm (1984) and the definition of engineering resilience provided by Holling (1996). Nearly all vegetation structural measurements in the treatment pastures were readily altered by fire-grazing interaction but recovered to levels similar to those characteristic of the unburned control pastures within one to three years. These results may not be unexpected when these shrublands are considered within their environmental context. The temperate grasslands and shrublands of North America's central and southern Great Plains are part of Earth's most extensive fire-dependent ecosystems, C₄ grasslands and savannas (Bond and Keeley, 2005; Bond et al., 2005). A particularly important consequence of the use of fire in *A. filifolia* shrublands of the southern Great Plains is that it precludes the conversion of these shrub-dominated communities to communities dominated by non-sprouting, fire-sensitive trees. Fire exclusion in many areas of North America since the time of Euro-American settlement has facilitated the invasion of central and southern Great Plains grasslands and shrublands by members of the genus *Juniperus* (Cupressaceae) (Fuhlendorf et al., 1996; Coppedge et al., 2001; Briggs et al., 2002; Engle et al., 2007).

Use of anthropogenic fire as a means of creating or enhancing landscape heterogeneity for conservation purposes has been described and critiqued (Brockett et al., 2001; Parr and Andersen, 2006), but in areas where fire and large grazers coevolved, the heterogeneity that results from the restoration of the fire-grazing interaction is likely of critical importance to biodiversity conservation (Fuhlendorf and Engle, 2001; Hamilton, 2007; Fuhlendorf et al., 2009). Consistent with previous research on the fire-grazing interaction (Fuhlendorf and Engle, 2004; Fuhlendorf et al., 2006), recently-burned patches in our study were characterized by high amounts of bare ground and low amounts of litter and live grass (Table 1). Previous research on the fire-grazing interaction has documented an increase in the percent cover or standing crop of forbs in patches that have been recently-burned and heavily grazed (Coppedge et al., 1998; Fuhlendorf and Engle, 2004; Vermeire et al., 2004). In North American tallgrass prairie, grazing of perennial grasses results in higher soil temperatures and higher levels of light available to associated forbs (Fahnestock and Knapp, 1993; Fahnestock and Knapp, 1994). The greater availability of resources

available to forbs when their neighboring grasses are grazed is thought to explain the increased growth, reproduction and abundance of tallgrass prairie forbs in grazed patches (Fahnestock and Knapp, 1993; Fahnestock and Knapp, 1994; Hartnett et al., 1996; Damhoureyeh and Hartnett, 1997). In more arid regions of the Great Plains, however, competition for belowground resources such as soil moisture may drive plant community dynamics to a greater extent than competition for the aboveground resource of light which can be of critical importance in tallgrass prairie (Scheintaub et al., 2009). Meek et al (2008) did not record a change in percent cover of forbs following summer patch-burns in a semi-arid region of Texas, USA. Their research period was characterized by drought conditions and they hypothesized that climatic variability may play a role in determining vegetation responses to patch-burning in arid and semi-arid regions (Meek et al., 2008). Our results from a region where water is a more-limited resource, relative to mesic tallgrass prairie, demonstrated a negative relationship between percent cover of live forbs and time-since-fire in the treatment pasture, with the highest cover of forbs occurring during the growing season immediately after a spring burn (Table 1). The negative relationship between percent cover of live forbs and time-since-fire in our study contrasted the positive relationship we found between percent cover of live grass and time-since-fire. This suggests that forbs in the *A. filifolia* shrubland of our study site may indeed be competing with grasses for resources and that the fire-grazing interaction allows forbs a period of release from such competition.

Patterns of landscape heterogeneity are important because they influence ecosystem processes (Turner, 1989). For instance, variable patterns of herbaceous biomass have been shown, both theoretically and empirically, to influence the processes of fire (Kerby et al., 2007; Savadogo et al., 2007) and herbivory (Archibald et al., 2005; Mouissie et al., 2008) across landscapes. A relationship between heterogeneity (i.e. variance) and scale, whereby heterogeneity decreases as the scale of measurement, or grain size, increases, has been described by Wiens (1989) and subsequently demonstrated by Fuhlendorf and Smeins (1999). Large herbivore distribution and foraging activities occur within a hierarchy of spatial scales and consumption of plant matter typically occurs at the smallest scale in the hierarchy, the

micropatch (Senft, 1989). Selective and repeated grazing of micropatches, which may be driven by the positive feedback of enhanced forage quality within the micropatch, can create persistent patterns of heterogeneity in grazed ecosystems (Bakker et al., 1983; Ring et al., 1985; Hobbs et al., 1991). Ungrazed ecosystems may have an inherent level of abiotic heterogeneity which contribute to small scale dynamics associated with plant populations and communities, and the imposition of grazing-induced heterogeneity on top of this may alter the amount or scale of heterogeneity (Fuhlendorf and Smeins, 1999; Mouissie et al., 2008).

Our results demonstrate that the fire-grazing interaction altered the scale at which heterogeneity occurs within *A. filifolia* shrublands at our study site. In the absence of a fire-grazing interaction, i.e. in the control pastures, most of the heterogeneity characteristic of this ecosystem (74%–79%; Table 3) was found at the smallest scales we measured, the quarter-point and point, while a minimal amount of the total heterogeneity was found at the patch scale ($\leq 2\%$; Table 3). Conversely, restoration of the fire-grazing interaction in the treatment pastures of our study site resulted in the amount of heterogeneity at the quarter-point and point scales to decrease to 65–66% of the total, while patch-scale heterogeneity increased to 18%–26% of the total (Table 3). Our results also suggest that, while the treatment pastures are characterized by an altered scale of spatial heterogeneity, they are also characterized by less total heterogeneity and less heterogeneity through time than the control pastures (Table 3). This reduced level of heterogeneity through time could indicate greater temporal stability associated with increased spatial heterogeneity at some scales. A relationship between spatial and temporal heterogeneity has been described for aquatic systems where greater community stability in stream insects through time was associated with greater variability in stream-bottom substrate (Brown, 2003).

The patchwork of contrasting vegetation structure at the patch-scale resulting from the restoration of the fire-grazing interaction at our study site has been shown to have a substantial influence on the composition of passerine communities at this site (Doxon, 2009), similar to what has been found in North American tallgrass prairie (Fuhlendorf et al., 2006; Coppedge et al., 2008) and Serengeti grasslands

in East Africa (Nkwabi et al., 2010). The influence of the fire-grazing interaction on the heterogeneity of primary production across landscapes has been shown to influence other secondary consumer trophic guilds as well (Yarnell et al., 2007; Engle et al., 2008).

Our study demonstrated that restoration of the fire-grazing interaction in *A. filifolia* shrublands of the North American southern Great Plains readily alters vegetation structure of this vegetation type but also that it is resilient to these effects. We also demonstrated that restoration of the fire-grazing interaction changed the scale of heterogeneity within this system, which has important implications for population and community dynamics of higher trophic levels. There have been numerous calls for the implementation of heterogeneity-based management as a means of conserving biodiversity in the North American Great Plains (Knopf and Sampson, 1997; Fuhlendorf et al., 2006; Toombs and Roberts, 2009) and our study demonstrates that restoration of the fire-grazing interaction is a viable means of doing this in *A. filifolia* shrublands.

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Table 1. Mean \pm SE of vegetation structure response variables for time since fire categories of one-half, one, two, three, four and five years post-burn in patches that had been burned within treatment pastures, as well as unburned patches in treatment pastures and in control pastures at Cooper Wildlife Management Area, Oklahoma, USA. *P*-values are from Dunnett's multiple comparisons of each time-since-fire category with control pastures. Bold-face font indicates significance at the $\alpha = 0.05$ level.

Response variable	Time since fire (years)						Unburned treatment	Unburned control
	.5	1	2	3	4	5		
bare ground	47.39 ± 3.74 <i>P</i> < 0.01	27.04 ± 3.82 <i>P</i> = 0.03	31.37 ± 4.12 <i>P</i> < 0.01	21.04 ± 3.03 <i>P</i> = 0.50	18.22 ± 3.22 <i>P</i> = 0.98	17.74 ± 5.29 <i>P</i> = 1.000	14.85 ± 2.02 <i>P</i> = 1.000	15.84 ± 1.54
litter	24.86 ± 3.59 <i>P</i> < 0.01	29.72 ± 4.90 <i>P</i> = 0.16	25.29 ± 4.52 <i>P</i> = 0.02	35.11 ± 4.56 <i>P</i> = 0.58	38.15 ± 5.42 <i>P</i> = 0.96	45.00 ± 9.75 <i>P</i> = 1.00	40.01 ± 3.42 <i>P</i> = 0.97	43.28 ± 2.29
live veg.	43.36 ± 3.10 <i>P</i> = 0.33	48.94 ± 3.93 <i>P</i> = 1.00	45.37 ± 3.90 <i>P</i> = 0.86	55.75 ± 3.36 <i>P</i> = 0.63	60.76 ± 3.78 <i>P</i> = 0.10	53.38 ± 6.76 <i>P</i> = 1.00	47.53 ± 2.45 <i>P</i> = 0.95	50.16 ± 1.60
dead veg.	15.66 ± 2.08 <i>P</i> < 0.01	32.19 ± 3.37 <i>P</i> < 0.01	36.83 ± 3.47 <i>P</i> = 0.03	41.52 ± 3.05 <i>P</i> = 0.31	48.82 ± 3.60 <i>P</i> = 1.00	48.62 ± 6.33 <i>P</i> = 1.00	50.24 ± 2.34 <i>P</i> = 1.00	48.33 ± 1.59
live grass	24.19 ± 2.80 <i>P</i> = 0.18	31.83 ± 4.08 <i>P</i> = 1.00	29.55 ± 3.88 <i>P</i> = 1.00	38.62 ± 3.66 <i>P</i> = 0.52	43.21 ± 4.38 <i>P</i> = 0.13	41.02 ± 7.73 <i>P</i> = 0.83	29.64 ± 2.50 <i>P</i> = 0.97	32.08 ± 1.77
dead grass	11.14 ± 1.78 <i>P</i> < 0.01	25.51 ± 3.10 <i>P</i> = 0.07	26.52 ± 3.12 <i>P</i> = 0.12	34.50 ± 2.89 <i>P</i> = 1.00	40.28 ± 3.48 <i>P</i> = 0.73	39.87 ± 6.15 <i>P</i> = 0.98	36.38 ± 2.18 <i>P</i> = 1.00	35.32 ± 1.44
live forb	18.28 ± 2.94 <i>P</i> = 0.87	15.72 ± 3.32 <i>P</i> = 1.00	11.44 ± 2.62 <i>P</i> = 0.88	11.35 ± 2.27 <i>P</i> = 0.78	10.97 ± 2.55 <i>P</i> = 0.79	10.88 ± 4.37 <i>P</i> = 0.98	15.07 ± 2.00 <i>P</i> = 1.00	14.91 ± 1.31
dead forb	3.01 ± 0.52 <i>P</i> < 0.01	7.92 ± 1.31 <i>P</i> = 1.00	6.35 ± 1.11 <i>P</i> = 0.99	5.49 ± 0.86 <i>P</i> = 0.58	4.83 ± 0.91 <i>P</i> = 0.30	7.50 ± 2.18 <i>P</i> = 1.00	7.77 ± 0.81 <i>P</i> = 0.99	7.16 ± 0.50
live shrub	5.32 ± 1.29 <i>P</i> < 0.01	9.00 ± 1.97 <i>P</i> = 0.34	13.29 ± 2.54 <i>P</i> = 1.00	18.44 ± 2.65 <i>P</i> = 0.52	19.39 ± 3.18 <i>P</i> = 0.45	18.85 ± 5.27 <i>P</i> = 0.91	13.83 ± 1.79 <i>P</i> = 1.00	13.95 ± 1.34
dead shrub	3.42 ± 0.85 <i>P</i> < 0.01	3.13 ± 1.00 <i>P</i> < 0.01	5.25 ± 1.28 <i>P</i> < 0.01	6.90 ± 1.26 <i>P</i> < 0.01	10.14 ± 1.77 <i>P</i> = 0.21	9.71 ± 3.10 <i>P</i> = 0.71	13.17 ± 1.28 <i>P</i> = 0.84	15.05 ± 0.89
veg. height	13.76 ± 7.27 <i>P</i> < 0.01	21.12 ± 7.56 <i>P</i> < 0.01	36.95 ± 7.62 <i>P</i> < 0.01	51.66 ± 7.48 <i>P</i> = 0.77	54.48 ± 7.97 <i>P</i> = 0.99	57.52 ± 10.00 <i>P</i> = 1.00	60.39 ± 7.10 <i>P</i> = 0.99	57.61 ± 6.81
veg. visual obstruction	2.17 ± 0.66 <i>P</i> < 0.01	4.34 ± 1.34 <i>P</i> < 0.01	5.51 ± 1.70 <i>P</i> < 0.01	9.27 ± 2.84 <i>P</i> < 0.04	10.64 ± 3.36 <i>P</i> = 0.39	12.48 ± 4.53 <i>P</i> = 1.00	15.65 ± 4.65 <i>P</i> = 1.00	14.24 ± 4.15

Table 2. Best fit models describing the relationship between response variables and time since fire at Cooper Wildlife Management Area, Oklahoma, USA. Predicted values from these models need to be inverse-linked to restore original units (percent cover, cm). P-values indicate significance level of linear trends or observed significance of the highest-order term of quadratic models.

Response variable	Distribution	Link function	Model system	P-value
bare ground	beta	logit	$y = -0.2595 - 0.3025(\text{tsf})$	< 0.01
litter	beta	logit	$y = -1.1948 + 0.1787(\text{tsf})$	0.04
live vegetation	beta	logit	$y = -0.4576 + 0.2265(\text{tsf})$	0.02
dead vegetation	beta	logit	$y = -1.4584 + 0.3491(\text{tsf})$	< 0.01
live grass	beta	logit	$y = -1.4088 + 0.3431(\text{tsf})$	< 0.01
dead grass	beta	logit	$y = -2.2085 + 0.8317(\text{tsf}) - 0.0962(\text{tsf})^2$	0.03
live forb	beta	logit	$y = -1.5136 - 0.1603(\text{tsf})$	0.04
dead forb	beta	logit	no significant relationship	–
live shrub	beta	logit	$y = -3.3954 + 1.0205(\text{tsf}) - 0.1229(\text{tsf})^2$	0.02
dead shrub	beta	logit	$y = -3.8072 + 0.4577(\text{tsf})$	< 0.01
vegetation height	normal	none	$y = 12.4678 + 11.8803(\text{tsf})$	< 0.01
vegetation visual obstruction	gamma	log	$y = 0.3723 + 0.8852(\text{tsf}) - 0.0953(\text{tsf})^2$	0.02

Table 3. Restricted maximum likelihood (vegetation height) and residual pseudo likelihood (vegetation visual obstruction) variance component estimates for vegetation height and vegetation visual obstruction in treatment and control pastures at Cooper Wildlife Management Area, Oklahoma, USA. Variance component estimates are for all scale (quarter-point, point, transect, patch and pasture) and temporal (2006, 2007 and 2008) variables as well as the total amount of variance.

Vegetation structure response variable	Heterogeneity variable	Estimates for control pastures	Estimates for treatment pastures
Vegetation height	time	165	11
	pasture	24	0
	patch	3	298
	transect	85	91
	point	372	274
	quarter-point	640	477
	total amount of variation in vegetation height	1289	1151
Vegetation visual obstruction	time	124	21
	pasture	3	0
	patch	10	47
	transect	9	21
	point	102	53
	quarter-point	324	118
	total amount of variation in vegetation visual obstruction	572	260

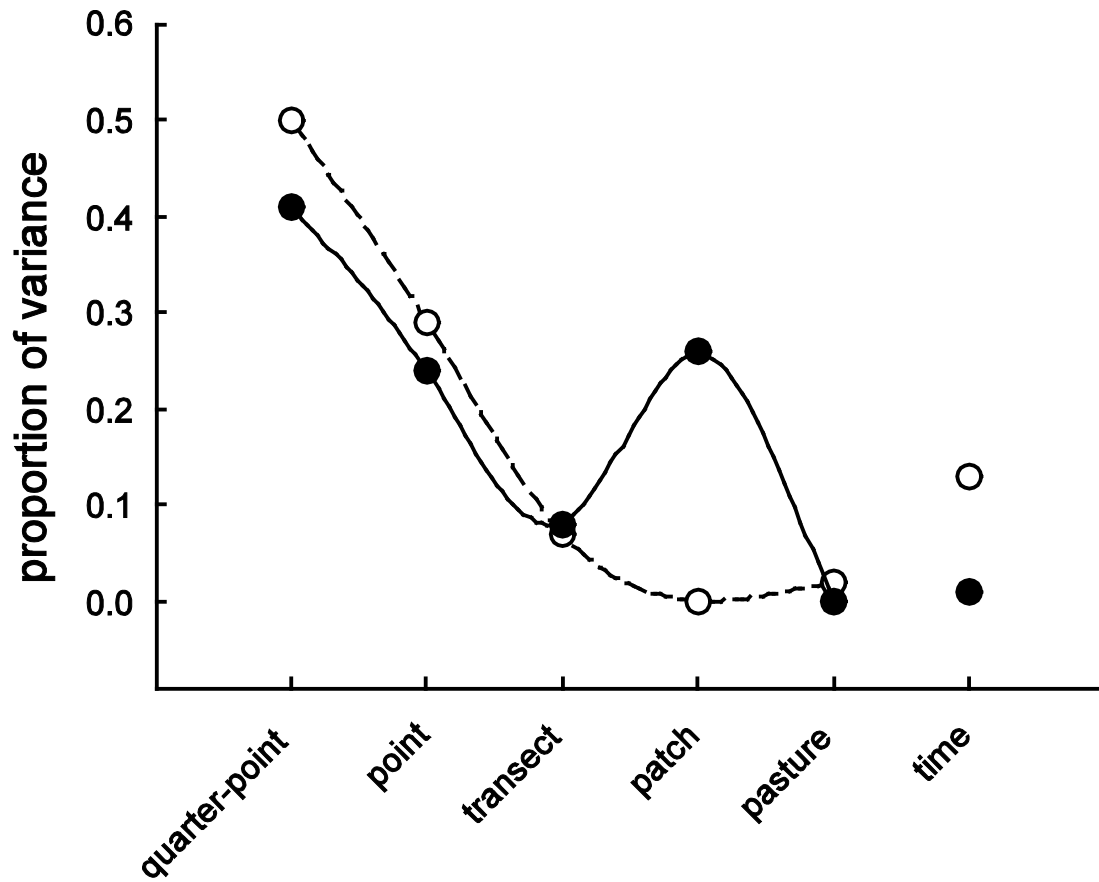


Fig. 1. Proportion of total variation (derived from restricted maximum likelihood estimates of variance components) contributed by all scale (quarter-point, point, transect, patch and pasture) and temporal (2006-2008) variables for vegetation height in treatment pastures (closed circles) and control pastures (open circles) at Cooper Wildlife Management Area, Oklahoma, USA.

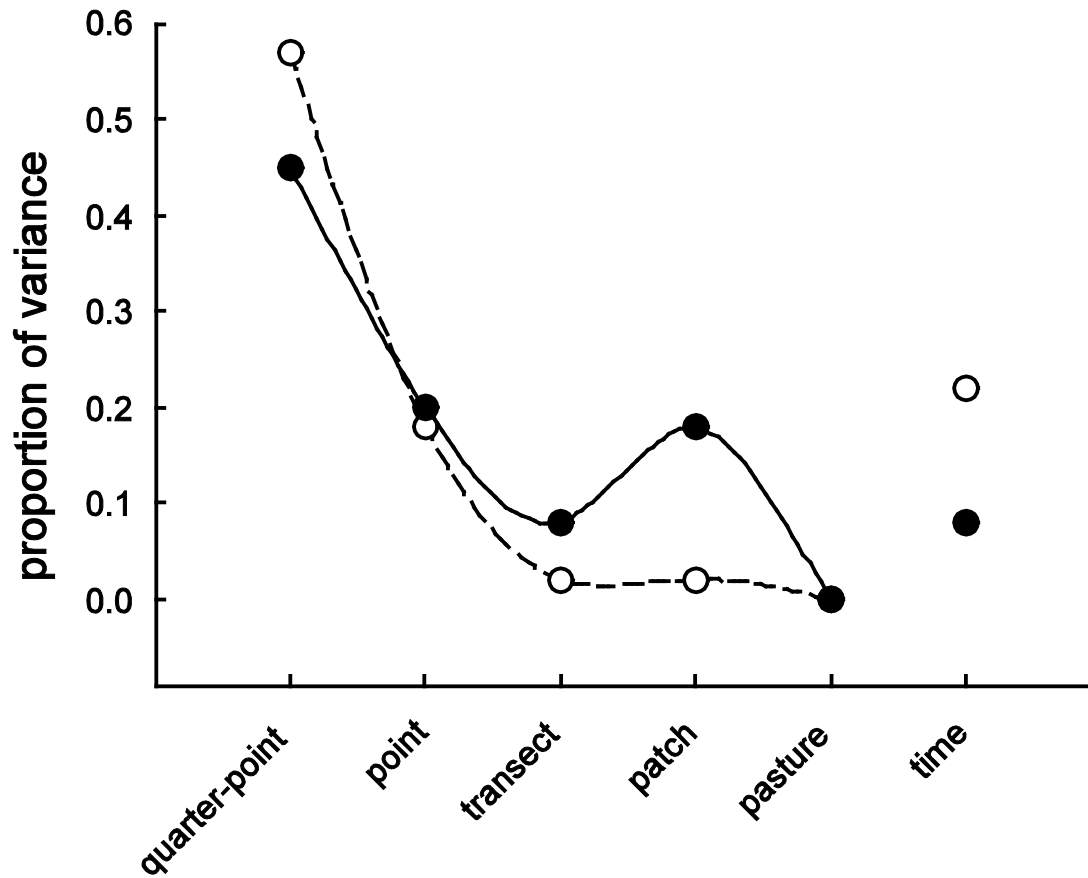


Fig. 2. Proportion of total variation (derived from residual pseudo likelihood estimates of variance components) contributed by all scale (quarter-point, point, transect, patch and pasture) and temporal (2006-2008) variables for vegetation visual obstruction in treatment pastures (closed circles) and control pastures (open circles) at Cooper Wildlife Management Area, Oklahoma, USA.

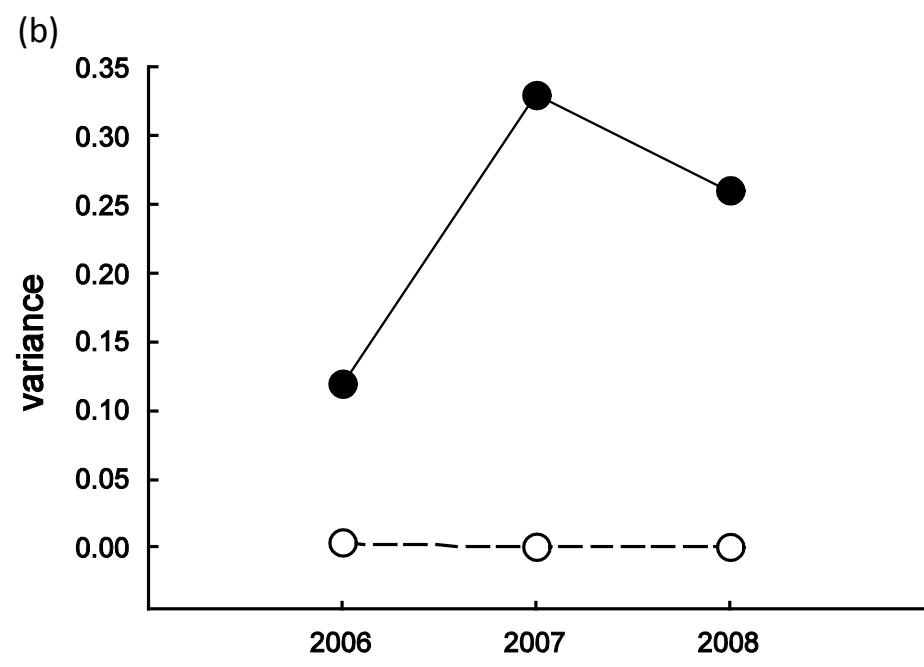
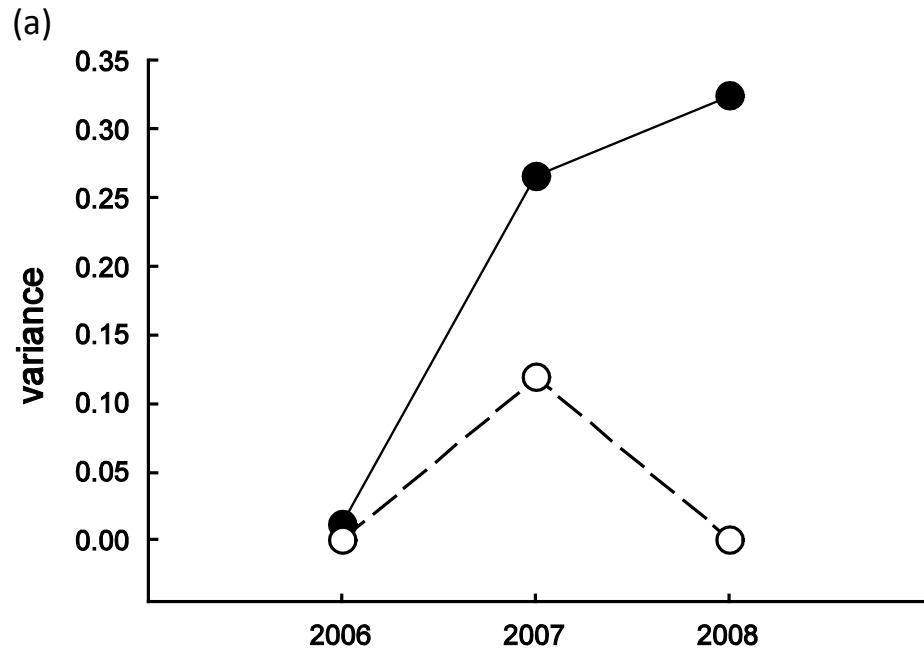


Fig. 3. Patch-scale variation (derived from restricted maximum likelihood variance estimates) in (a) percent bare ground and (b) percent cover litter for treatment pastures (closed circles) and control pastures (open circles) during each year of the study at Cooper Wildlife Management Area, Oklahoma, USA.

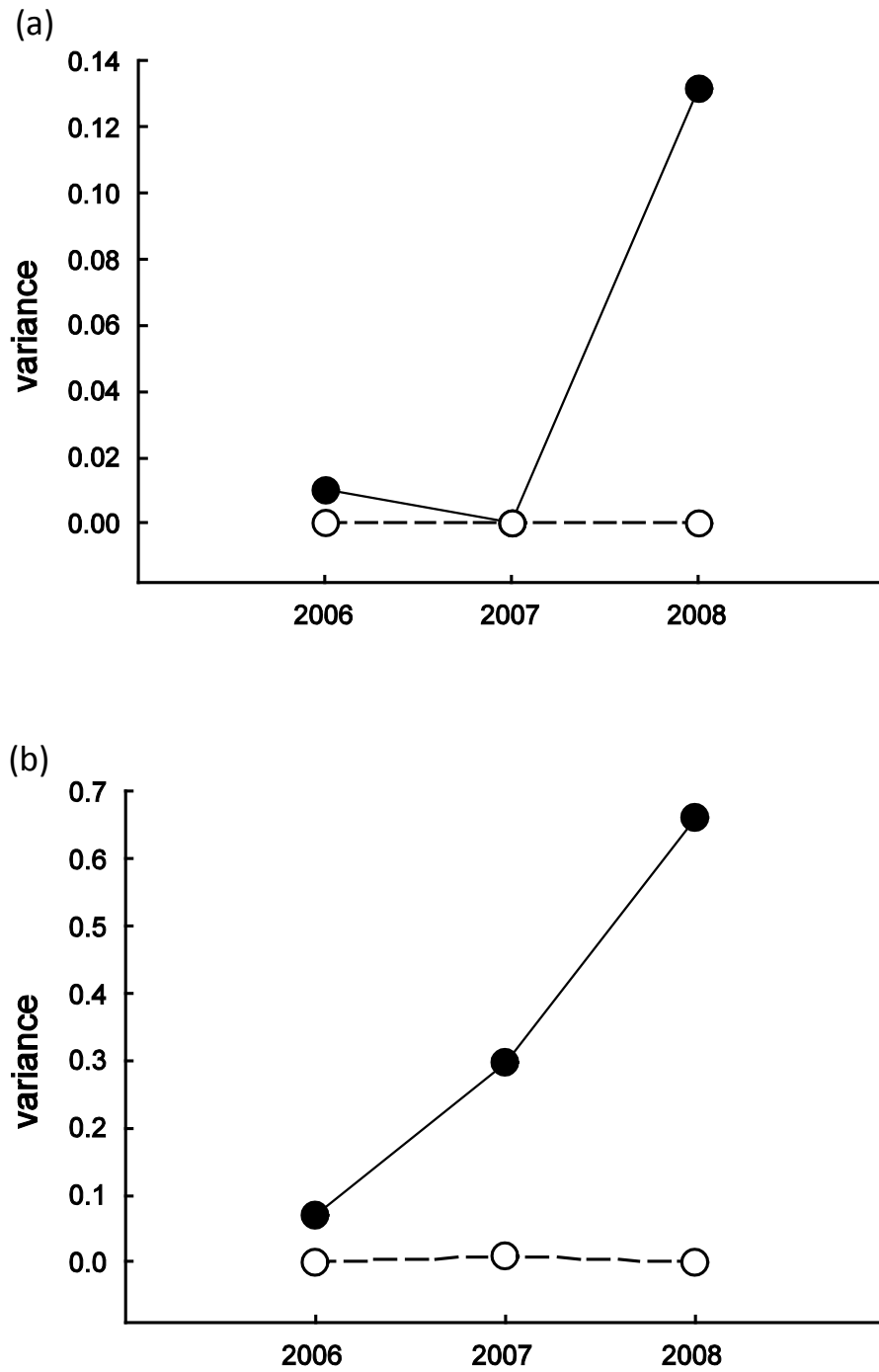


Fig. 4. Patch-scale variation (derived from restricted maximum likelihood variance estimates) in (a) percent cover live vegetation and (b) percent cover dead vegetation for treatment pastures (closed circles) and control pastures (open circles) during each year of the study at Cooper Wildlife Management Area, Oklahoma, USA.

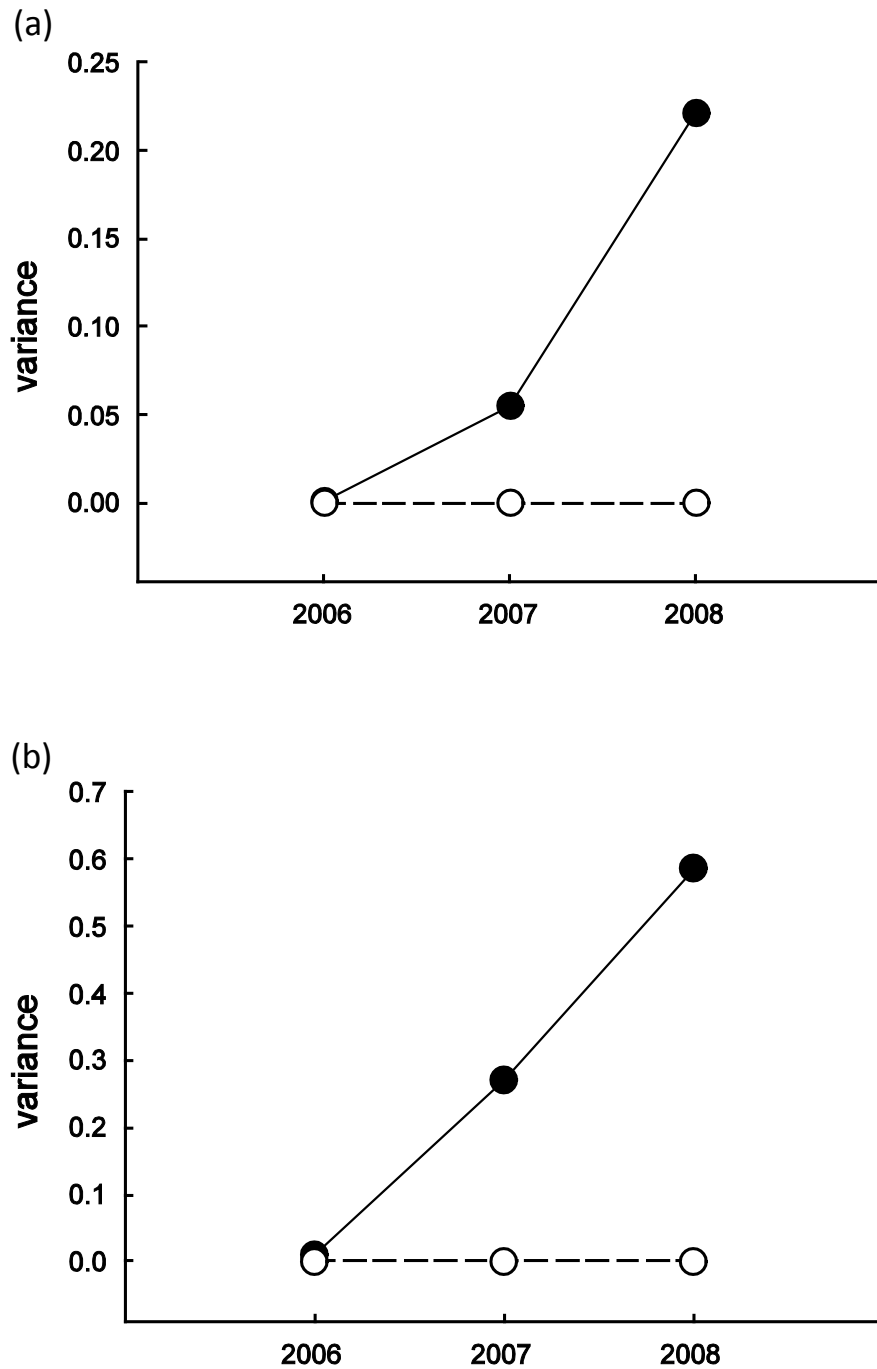


Fig. 5. Patch-scale variation (derived from restricted maximum likelihood variance estimates) in (a) percent cover live grass and (b) percent cover dead grass for treatment pastures (closed circles) and control pastures (open circles) during each year of the study at Cooper Wildlife Management Area, Oklahoma, USA.

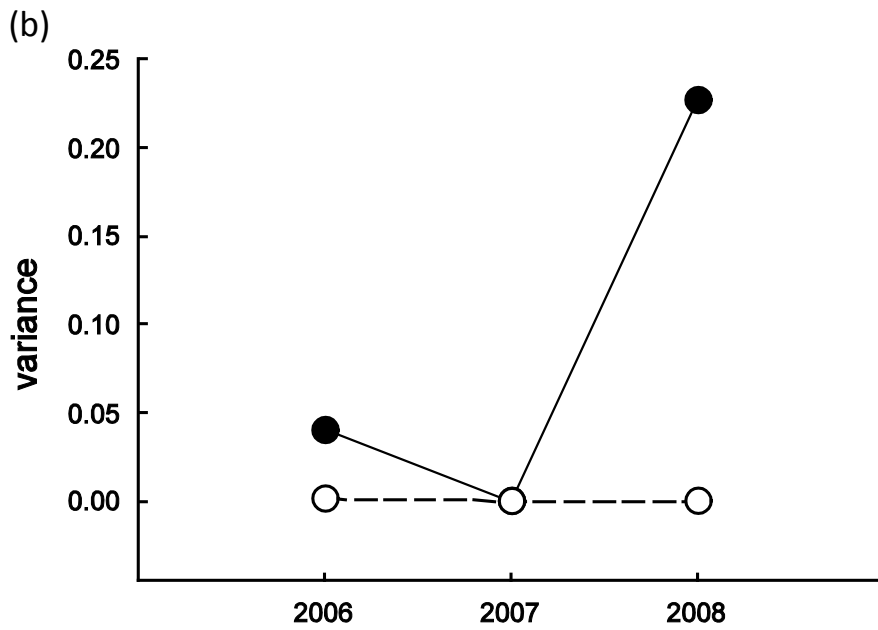
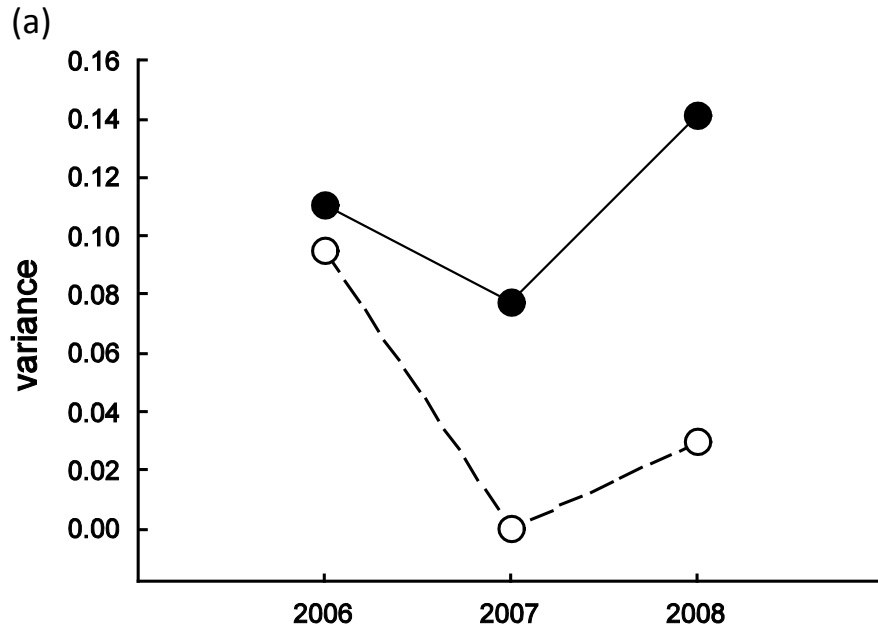


Fig. 6. Patch-scale variation (derived from restricted maximum likelihood variance estimates) in (a) percent live forbs and (b) percent cover dead forbs for treatment pastures (closed circles) and control pastures (open circles) during each year of the study at Cooper Wildlife Management Area, Oklahoma, USA.

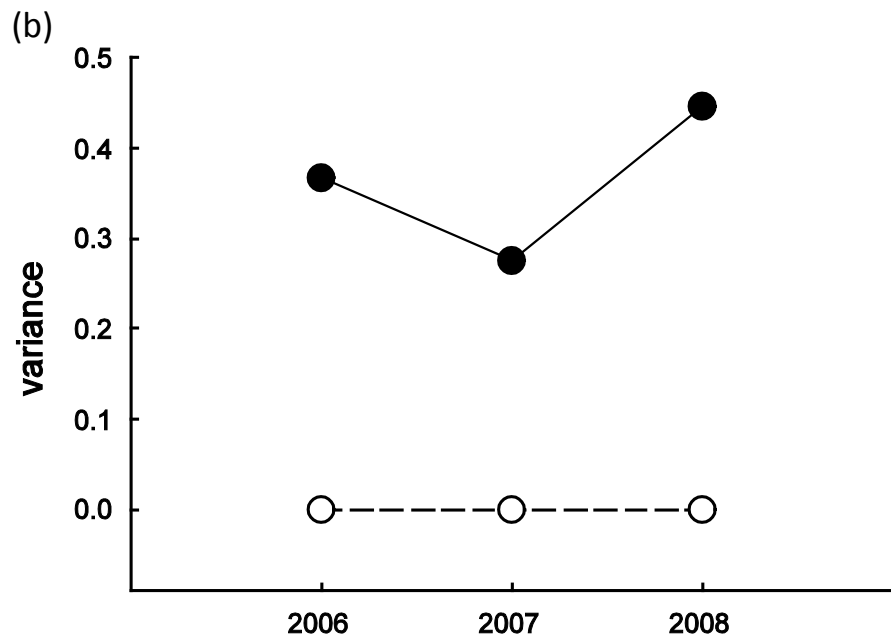
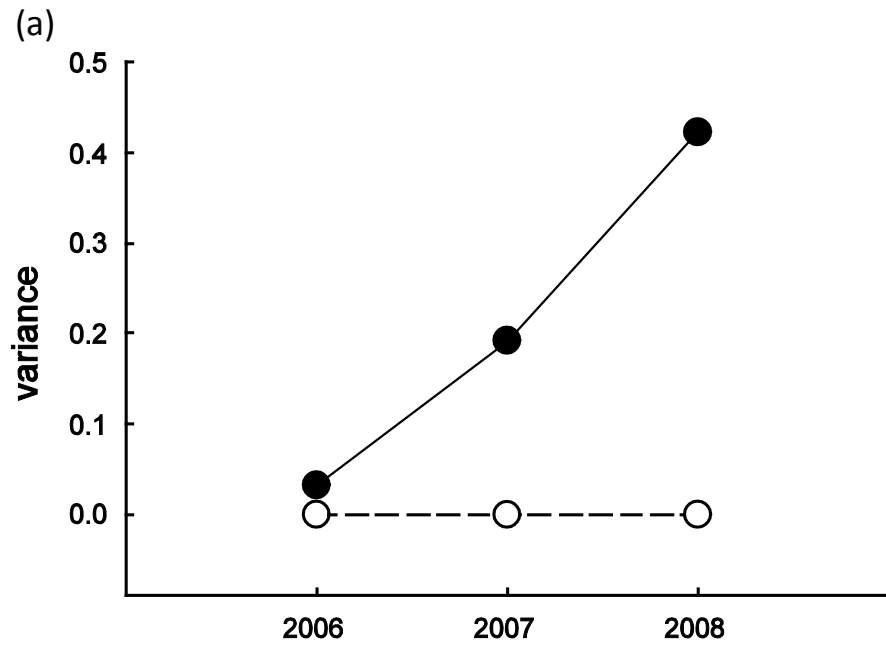


Fig. 7. Patch-scale variation (derived from restricted maximum likelihood variance estimates) in (a) percent cover live shrubs and (b) percent cover dead shrubs for treatment pastures (closed circles) and control pastures (open circles) during each year of the study at Cooper Wildlife Management Area, Oklahoma, USA.

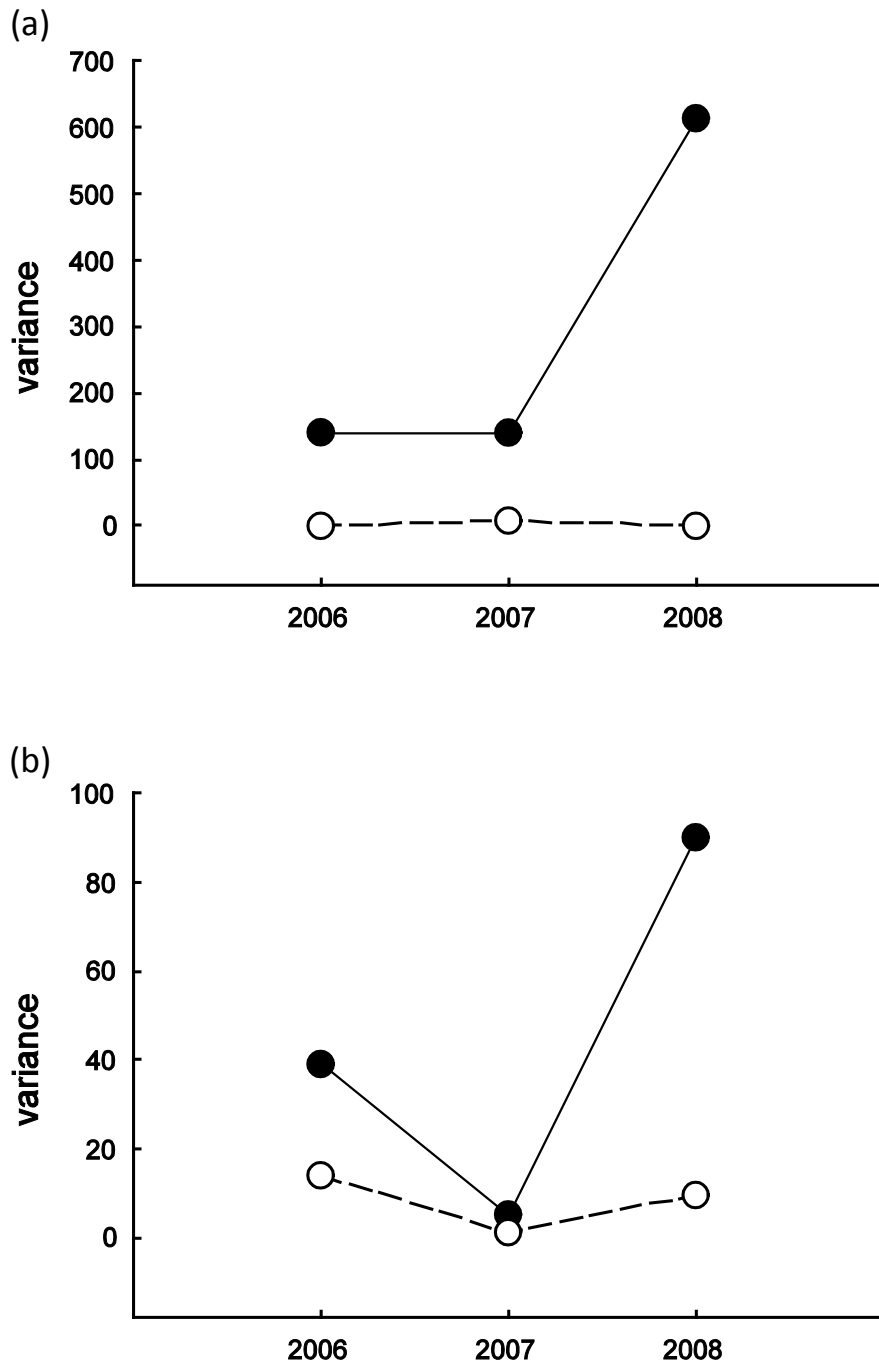


Fig. 8. Patch-scale variation in (a) vegetation height (derived from restricted maximum likelihood variance estimates) and (b) vegetation visual obstruction (derived from residual pseudo likelihood variance estimates) for treatment pastures (closed circles) and control pastures (open circles) during each year of the study at Cooper Wildlife Management Area, Oklahoma, USA.

CHAPTER III

TOPOEDAPHIC VARIABILITY AND PYRIC-HERBIVORY: EFFECTS OF INHERENT VS. IMPOSED HETEROGENEITY ON VEGETATION STRUCTURE

Topoedaphic Variability and Pyric-Herbivory: Effects of Inherent vs. Imposed Heterogeneity on Vegetation Structure

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Abstract Pyric-herbivory is the interaction of fire and grazing across multiple spatial and temporal scales resulting in a shifting landscape mosaic of patches that differ in the amount and intensity of disturbance. We examined effects of pyric-herbivory on vegetation structure and animal distribution across contrasting topographical sites in *Artemisia filifolia* shrubland of the southern Great Plains in North America. Our results indicate that landscapes at our study site were characterized by an inherent amount of heterogeneity in vegetation structure due to variability in topoedaphic sites while the pyric-herbivory treatment superimposed an additional layer of heterogeneity that was constrained by topoedaphic characteristics. We were unable to detect an effect of topoedaphic site or the pyric-herbivory treatment on animal distribution, but our results suggest this was due to insufficient replication of study sites.

Key Words disturbance ecology · fire-grazing interaction · heterogeneity · habitat · patchiness

Introduction

Fire has a profound influence on large herbivore distribution by concentrating grazing on recently-burned areas while areas that have not been recently burned receive light to no grazing impact (Archibald et al. 2005; Fuhlendorf & Engle 2004; Murphy & Bowman 2007; Sensenig et al. 2010). The phenomena of grazing driven by fire has been termed “pyric-herbivory,” and it is an expression of the evolutionary interaction of fires, forage quantity and quality, and foraging herbivores (Fuhlendorf et al. 2009). With pyric-herbivory, areas that receive high and low animal impact shift through time in a landscape; the ensuing habitat patchiness, or heterogeneity, that results from cycles of disturbance and rest are likely crucial for the maintenance of biodiversity in these systems (Fuhlendorf et al. 2009). What has not been determined, however, is how effects of pyric-herbivory on landscape heterogeneity may or may not be distinct from other sources of heterogeneity that could be inherent to a landscape in the absence of pyric-

herbivory. One source of inherent heterogeneity in landscapes is the variation in topographic and edaphic (hereafter topoedaphic) features that can influence vegetation structure and composition (Davies et al. 2007; Dodd et al. 2002; Parker 1991; Reed et al. 2009; Shumar & Anderson 1986). In previous studies of pyric-herbivory involving cattle (*Bos taurus*), the heterogeneity of topoedaphic features across landscapes was inherently minimal or was minimized through study design (Coppedge et al. 2008; Fuhlendorf & Engle 2004; Vermeire et al. 2004). To better understand the interaction of topoedaphic variability with fire and grazing, we conducted our study of pyric-herbivory in a landscape characterized by contrasting topoedaphic features. Our objective was to quantify the unique effects of pyric-herbivory and topoedaphic variability on measurements of vegetation structure and cattle distribution in North American *Artemisia filifolia* shrubland.

Methods

Study Location The study site was the Hal and Fern Cooper Wildlife Management Area (Cooper WMA) in Woodward County, Oklahoma, USA (99°30'05"W, 36°32'10"N). The long-term (1940–2008) average annual precipitation at the National Oceanic and Atmospheric Administration Fort Supply weather station was 59.9 cm (www.ncdc.noaa.gov). The annual total precipitation and percent deviation from the long-term average for 2005 and 2006 was 72.5 cm (121%) and 40.5 cm (68%), respectively. Two contrasting topoedaphic sites occurred at Cooper WMA whose soil composition and associated vegetation differed substantially: the Eda-Tivoli soil complex and the Carwile-Eda soil complex. Eda-Tivoli loamy fine sands and fine sands are rapidly permeable, mixed, thermic Lamellic (Eda part) and Typic (Tivoli part) Ustipsamments which occur as undulating to rolling dunes with slopes of 3–12% (USDA-NRCS 2009a). Carwile-Eda loamy and loamy fine sands are slowly permeable, fine, mixed, superactive, thermic Typic Argiaquolls (Carwile part) which occur as level to nearly level areas between dunes with slopes of 0-5% (USDA-NRCS 2009a). At the study site, Eda-Tivoli soils were the most

prevalent soil-type, representing about 65% of all soils while Carwile-Eda soils were less common, representing about 9% of all soils (USDA-NRCS 2009b).

Vegetation of the study region was considered an *Artemisia* shrubland with the dominant species being the shrub *A. filifolia* (Collins et al. 1987; Gillen & Sims 2004). At the Cooper WMA study site, plant species associated with Eda-Tivoli soils were *A. filifolia*; the perennial tall grasses *Andropogon hallii* and *Panicum virgatum*; the perennial mid-height grasses *Schizachyrium scoparium*, *Eragrostis trichodes*, *Poa arachnifera* and *Sporobolus cryptandrus*; the perennial short grasses *Paspalum setaceum* and *Bouteloua gracilis*; and a variety of perennial and annual forbs including *Ambrosia psilostachya*, *Eriogonum annuum*, *Commelina erecta*, *Croton texensis* and *Conyza canadensis*. *Artemisia filifolia* canopy cover on Eda-Tivoli soils can range from 20–50% (Gillen & Sims 2006; Vermeire et al. 2004). Plant species associated with Carwile-Eda soils included the perennial mid-height grasses *P. arachnifera*, *Pascopyrum smithii* and *Panicum obtusum*; the perennial short grasses *Bouteloua gracilis* and *Bouteloua dactyloides*; and a variety of forbs including *Plantago patagonica*, *Gaillardia pulchella*, *A. psilostachya* and *C. texensis*. *Artemisia filifolia* was sparse to absent in Carwile-Eda soils. All study pastures at Cooper WMA were annually grazed by yearling cattle from 1 April to 15 September. Stocking level in all pastures was approximately 6.85 ha per animal unit (1 animal unit = 0.6 yearling steer).

Study Design At Cooper WMA, four pastures (North, South, Middle and East pastures, Appendix Fig. 1) were sampled and pasture size was 769–848 ha (mean = 658 ha). Each pasture was divided into three patches, resulting in a total of 12 patches of 101–415 ha (Appendix Fig. 3, Appendix Table 1). In two of the pastures (treatment pastures), one patch representing about one-third of each pasture had been treated with prescribed fire during a previous year (2004 in one treatment pasture and 2005 in the other treatment pasture). Cattle had free access to all areas of the treatment pastures during all grazing seasons following prescribed fires. In the remaining two study pastures (control pastures), grazing occurred on an annual basis as previously described but no large-scale burning had occurred. Twelve 4-ha burns were conducted in the study pastures in 1999–2001 (Vermeire et al. 2004; Appendix Fig. 2, Appendix Table 3)

but we avoided these areas during our sampling activities. Prior to the prescribed fires conducted during 1999–2001 and those described for this study, no fires had occurred in the study pastures at least since the property was purchased by the State of Oklahoma in 1992.

Sampling We randomly established 12, 100-m transects in each of the four pastures and stratified them by topoedaphic site; six transects were located on sand dune sides and tops characterized by Eda-Tivoli soils (Appendix Fig. 1, Appendix Table 2) and six transects were located on level areas characterized by Carwile-Eda soils (Appendix Fig. 5, Appendix Table 2). Transects were distributed within pastures so that four transects, stratified by topoedaphic site (two in Eda-Tivoli soils, two in Carwile-Eda soils), were present in each one-third portion of each pasture. Thus, each control pasture contained 12 transects, stratified by topoedaphic site, distributed across the pasture. Within the treatment pastures, the two unburned patches contained eight transects, stratified by topoedaphic site, and each burned patch contained four transects, stratified by topoedaphic site.

During July 2006, percent bare ground, percent cover of litter, percent canopy cover of vegetation structural groups (live and dead vegetation, live and dead grass, live and dead forbs, live and dead shrubs), and the height of the tallest grass, forb and shrub were quantified within 0.10-m² rectangular (0.20 x 0.50 m) plots placed at 2-m intervals along each transect ($n = 50$ plots/transect). Vegetation height data were collected incorrectly along four transects in a control pasture and four transects in an unburned patch of a treatment pasture so height data from those transects were excluded from analyses. To assess cattle distribution, frequency of cattle dung and frequency of grass defoliation were quantified within the 0.10-m² plots. Frequency of grass defoliation was determined by presence or absence of at least one blade of grass within a plot that had been clipped at a right angle to the long axis of the blade. Our method of quantifying grass defoliation by cattle was similar to the approach of Dwyer (1961) for determining grazing preferences of cows in tallgrass prairie, and deposition of cattle dung is commonly used to infer cattle distribution (Bailey & Welling 1999; Senft et al. 1983).

Analysis We treated all vegetation structural measurements (percent bare ground; percent cover of litter, live and dead vegetation, live and dead grass, live and dead forbs, live and dead shrubs; tallest grass, forb and shrub) and measurements of cattle distribution (frequency of cattle dung and frequency of grazing) as response variables and calculated their mean transect values. We treated topoedaphic site (Carwile-Eda soils and Eda-Tivoli soils) and treatment category (control unburned, treatment burned, treatment unburned) as main effects and conducted significance tests of main effects and the interaction of main effects using the GLIMMIX procedure in SAS (SAS Institute 2007). When necessary, multiple comparisons were conducted using the Tukey-Kramer method (Kramer 1956).

Multivariate analyses were conducted utilizing CANOCO for Windows, version 4.5 (ter Braak & Šmilauer 2002) and percent cover vegetation structure measurements (bare ground, litter, live and dead grass, live and dead forbs, live and dead shrubs) were treated as response variables. We used variance partitioning to determine the amount of variation in the response variables that could be specifically attributed to topoedaphic site or treatment category (Borcard et al. 1992). A redundancy analysis (RDA) was conducted in which the two topoedaphic sites (Carwile-Eda soils and Eda-Tivoli soils) and three treatment categories (control unburned, treatment burned, treatment unburned) were treated as distinct environmental variables, generating a sum of all canonical eigenvalues representing the total amount of variation in the data. This was followed by two partial redundancy analyses (pRDA) in which topoedaphic site and treatment category were alternately treated as an environmental variable and a covariable; the sum of all canonical eigenvalues generated in each pRDA accounts for the amount of variation contributed by an environmental variable when the variation due to the covariable is factored out. Finally, to describe the effect of a topoedaphic site-treatment category interaction on the response variables, an RDA was conducted in which six interaction dummy variables (control unburned on Carwile-Eda soils; control unburned on Eda-Tivoli soils; treatment burned on Carwile-Eda soils; treatment burned on Eda-Tivoli soils; treatment unburned on Carwile-Eda soils, treatment unburned on Eda-Tivoli soils) were created and treated as environmental variables. In all ordination analyses, Monte

Carlo tests, utilizing 9,999 iterations, were conducted to assess the significance ($\alpha = 0.05$) of relationships between response variables and canonical axes, whereas all other CANOCO settings were maintained at their default settings.

Results

The pyric-herbivory treatment, topoedaphic patterns, and the interaction of treatment and topoedaphic site all influenced vegetation structure and grazing animal distribution. Topoedaphic site was significant as a main effect for percent bare ground, percent cover litter, percent cover live and dead shrubs, tallest forb and tallest shrub, which were all higher ($P < 0.001$) on Eda-Tivoli soils than on Carwile-Eda soils (Table 1). Treatment was significant as a main effect for percent bare ground which was higher ($P = 0.010$) in the burned patches of treatment pastures than in the unburned patches of treatment pastures (Table 2).

The interaction of pyric-herbivory and topoedaphic site had a significant effect on the values of percent cover dead vegetation, percent cover live grass and tallest grass ($P \leq 0.022$). For percent cover of dead vegetation, there was an effect of topoedaphic site in the burned patches of the treatment pastures where percent cover of dead vegetation was higher ($P \leq 0.001$) on Carwile-Eda soils than on the Eda-Tivoli soils. An effect of treatment category on percent cover of dead vegetation was found only on the Eda-Tivoli soils where values were lower ($P = 0.015$) in the burned patches of the treatment pastures than in the unburned patches of the treatment pastures (Table 3). There was an effect of topoedaphic site on percent cover of live grass in all treatment categories where values were higher ($P < 0.001$) on Carwile-Eda soils than on Eda-Tivoli soils and there was an effect of treatment category only on the Eda-Tivoli soils where values were lower ($P = 0.024$) in the burned patches of the treatment pastures than in the unburned patches of the treatment pastures and the control pastures (Table 3). There was an effect of topoedaphic site on the height of the tallest grass within the unburned patches of the treatment pastures and the control pastures where values on the Carwile-Eda soils were lower ($P \leq 0.001$) than on the Eda-

Tivoli soils and there was an effect of treatment category only on the Eda-Tivoli soils where values in the burned patches of the treatment pastures were lower ($P \leq 0.002$) than in the unburned patches of the treatment pastures and the control pastures (Table 3).

When topoedaphic site and treatment category were treated as distinct environmental variables in RDA, there was a significant ($P < 0.001$) effect of the environmental variables on the distribution of response variables in ordination space. The sum of all canonical eigenvalues was 0.654 and eigenvalues for the first, second, third and fourth axes were 0.604, 0.042, 0.008 and 0.209, respectively. When topoedaphic site was treated as a covariable in pRDA, treatment category was also identified as a significant effect ($P = 0.006$). The sum of all canonical eigenvalues was 0.068 and eigenvalues for the first, second, third and fourth axes were 0.056, 0.012, 0.209 and 0.051, respectively. When treatment category was treated as a covariable, pRDA identified a significant effect of topoedaphic site ($P < 0.001$). The sum of all canonical eigenvalues was 0.585 and eigenvalues for the first, second, third and fourth axes were 0.585, 0.209, 0.051 and 0.032, respectively. Variance partitioning showed that treatment category explained 6.8% of the variation in the data, topoedaphic site explained 58.5% of the variation, the intersection of treatment category and topoedaphic site explained 0.1% of the variation, and 34.6% of the variation in the data was left unexplained.

The RDA using topoedaphic site-treatment category interaction dummy variables identified the interaction of topoedaphic site and treatment category as a significant ($P < 0.001$) effect on the distribution of response variables in ordination space. The sum of all canonical eigenvalues was 0.691 and the eigenvalues of the first, second, third and fourth axes were 0.613, 0.064, 0.010 and 0.003, respectively. An ordination biplot (Fig. 1) of the RDA utilizing interaction dummy variables identified a gradient associated with topoedaphic site along axis 1. Along the topoedaphic site gradient of axis 1, percent cover of live and dead grass are associated with Carwile-Eda soils while percent bare ground, percent cover litter, and percent cover of live and dead shrubs are associated with Eda-Tivoli soils. Axis 2 is characterized by a gradient of differing levels of disturbance created by the fire-grazing interaction on

Eda-Tivoli soils: unburned patches of the treatment pastures occupy the lower portions of the gradient, control pastures occupy the middle portions, and burned patches of the treatment pastures occupy the upper portions of the gradient along axis 2. Relative to Eda-Tivoli soils, Carwile-Eda soils were relatively unresponsive to this gradient of disturbance driven by the fire-grazing interaction.

Discussion

Our study differed from previous pyric-herbivory research involving cattle (Coppedge et al. 2008; Fuhlendorf & Engle 2004; Fuhlendorf et al. 2006; Vermeire et al. 2004) because it examined the fire-grazing interaction across contrasting topoedaphic sites. While the research of Vermeire et al. (2004) also took place at Cooper WMA, that study controlled for soil heterogeneity by limiting data collection to areas characterized by the Eda and Tivoli soil series. In our study, we collected data from topoedaphic sites with contrasting characteristic soil particle sizes, slopes and vegetation communities with the intent of determining the influence of pyric-herbivory on vegetation structure in complex landscapes.

Our results indicated that topoedaphic site had a substantial influence on the vegetation structure of *A. filifolia* shrubland at our study site. There was a main effect of topoedaphic site on six variables (bare ground, litter, live shrubs, dead shrubs, tallest forb and tallest shrub), with values of those variables consistently higher on the Eda-Tivoli sites (Table 1). The contrast of vegetation structure between the two topoedaphic sites reflected the contrast in species composition between the sites. Carwile-Eda sites were characterized by sod-forming mid-height and shortgrasses with *A. filifolia* being scarce to absent. Eda-Tivoli sites, conversely, were characterized by a diverse mixture of tall and mid-height grasses with the bunch-forming growth habit being particularly common. Additionally, *A. filifolia* was the dominant species on Eda-Tivoli sites. Differences in plant species composition between the two topoedaphic sites are likely explained by soil-plant water relationships. In Sandhills mixed-grass prairie of the northern Great Plains, differences in water-use efficiencies of various grass species resulted in their segregation

along a topographic gradient of coarse sands on a dune slope to the fine-textured soils of an adjacent lowland (Barnes & Harrison 1982). Soil-plant water relations have been shown to vary with soil texture and landscape position in North American tallgrass prairie (Knapp et al. 1993) and Great Basin desert (Rosenthal et al. 2005). An inverse relationship between soil texture and plant productivity has been described whereby plant productivity is greater on coarse-textured soils than fine-textured soils in arid and semi-arid regions whereas plant productivity is greater on fine-textured soils than on coarse-textured soils in humid climates (Noy-Meir 1973). Various analyses across the North American Great Plains have demonstrated the relationship between plant productivity and soil texture (Epstein et al. 1998) and have provided support for the inverse-texture hypothesis when examining plant productivity (Epstein et al. 1997; Sala et al. 1988), vegetation structure (Dodd et al. 2002), and community composition (Lane et al. 1998).

In our study, vegetation structure was altered by the pyric-herbivory treatment on Eda-Tivoli sites while vegetation structure on Carwile-Eda sites was relatively unresponsive to the effects of pyric-herbivory (Tables 2 and 3; Fig. 1). Differential effects of disturbance on vegetation communities in different topographical positions has been demonstrated in tallgrass prairie where productivity in lowlands responded positively to fire whereas productivity in uplands did not (Abrams et al. 1986; Briggs & Knapp 1995). When tallgrass prairie was unburned or burned every four years, species composition of uplands was distinct compared with lowlands, but annual burning resulted in the two topographical positions having similar species composition (Gibson & Hulbert 1987). Topography, fire and grazing have been shown to have multiple interactive effects on species composition in tallgrass prairie: the effect of grazing on the abundance of dominant warm season tall grasses was greater on uplands in annually-burned watersheds but greater on lowlands in watersheds burned every four years; the effect of grazing on species richness was greatest on lowland sites within annually-burned watersheds; and grazing had a significant effect on community heterogeneity (% dissimilarity in species composition) on uplands and

lowlands of annually-burned watersheds but only on uplands in watersheds burned every four years (Hartnett et al. 1996).

Topography is considered to have a strong influence on cattle distribution with individuals preferring to graze in areas characterized by low slope values (Bailey et al. 1996). We, however, did not find a significant effect of topoedaphic site or the pyric-herbivory treatment on the measurements of animal distribution we quantified – frequency of cattle dung and frequency of grazed grass plants. However, our data suggested that greater replication of study pastures would result in the detection of a statistically significant effect for one or both of these factors. Mean frequency of cattle dung was 16x higher on Carwile-Eda soils than on Eda-Tivoli soils (Table 1) and was 10x higher within burned patches of the treatment pastures than within unburned patches of the same pastures (Table 2). When the measurements of animal distribution are broken down by topoedaphic site within treatment categories (Table 3), it suggested that in the unburned control pastures cattle prefer Carwile-Eda soils over Eda-Tivoli soils whereas in the treatment pastures cattle prefer burned patches over unburned patches, regardless of topoedaphic site. Fire has been shown to override the effect of ecological site on bison (*Bison bison* L.) distribution in tallgrass prairie (Biondini et al. 1999; Steuter et al. 1995), and it is likely that similar results would be found with cattle in *A. filifolia* shrublands with additional research.

Landscape heterogeneity has been deemed important to the persistence of populations and communities (Fryxell et al. 2005; Fuhlendorf et al. 2006; Godfree et al. 2010), and the link between species diversity and the heterogeneity of abiotic features, such as topoedaphic site, has been of continuing interest to researchers (Burnett et al. 1998; Lundholm 2009; Nichols et al. 1998; Parks & Mulligan 2010). Additionally, the role of disturbances in altering ecological patterns of heterogeneity is receiving increased attention (Fraterrigo & Rusak 2008). Our results indicated that landscapes are characterized by an inherent amount of heterogeneity in vegetation structure due to variability in topoedaphic features. Furthermore, variance partitioning determined that topoedaphic site explained 58.5% of the variation in our vegetation structure data. These results suggest that the primary determinant

of heterogeneity at our study sites was due to topoedaphic site while the effects due to pyric-herbivory were secondary. However, our results require careful interpretation because we used a balanced sampling design in which equal amounts of data were collected from each topoedaphic site. In actuality, the majority (65%) of the landscape at our study site is characterized by Eda-Tivoli soils while Carwile-Eda soils comprise less than 10% of the landscape. Thus, if we would have allocated data collection within each topoedaphic site in a manner that was proportional to the area represented by each topoedaphic site, it is likely the effect of the pyric-herbivory treatment on vegetation structure would have been more pronounced. Nonetheless, at our study site in *A. filifolia* shrubland, an inherent level of heterogeneity in vegetation structure was present as a result of contrasting topoedaphic sites, while the pyric-herbivory treatment superimposed an additional layer of heterogeneity that was constrained by topoedaphic characteristics.

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Table 1. Mean \pm SE vegetation structure and cattle distribution measurements on contrasting topoedaphic sites at Cooper Wildlife Management Area, Oklahoma, U.S.A. Superscripts with different letters within a row indicate significant differences at the $\alpha = 0.05$ level.

Response variable	Carwile-Eda sites	Eda-Tivoli sites
bare ground	8.06 \pm 1.08^a	18.12 \pm 1.68^b
litter	22.02 \pm 1.33^a	32.57 \pm 1.60^b
live vegetation	39.33 \pm 1.50 ^a	36.94 \pm 1.49 ^a
dead grass	59.32 \pm 2.65 ^a	31.30 \pm 2.52 ^a
live forbs	5.42 \pm 0.91 ^a	6.71 \pm 0.98 ^a
dead forbs	5.53 \pm 0.30 ^a	5.88 \pm 0.31 ^a
live shrubs	0.14 \pm 0.08^a	18.63 \pm 1.95^b
dead shrubs	0.16 \pm 0.08^a	15.93 \pm 1.19^b
tallest forb	8.64 \pm 1.20^a	17.01 \pm 1.48^b
tallest shrub	0.41 \pm 0.18^a	36.83 \pm 1.95^b
cattle dung frequency	0.16 \pm 0.03 ^a	0.01 \pm 0.01 ^a
grazing frequency	0.47 \pm 0.06 ^a	0.38 \pm 0.06 ^a

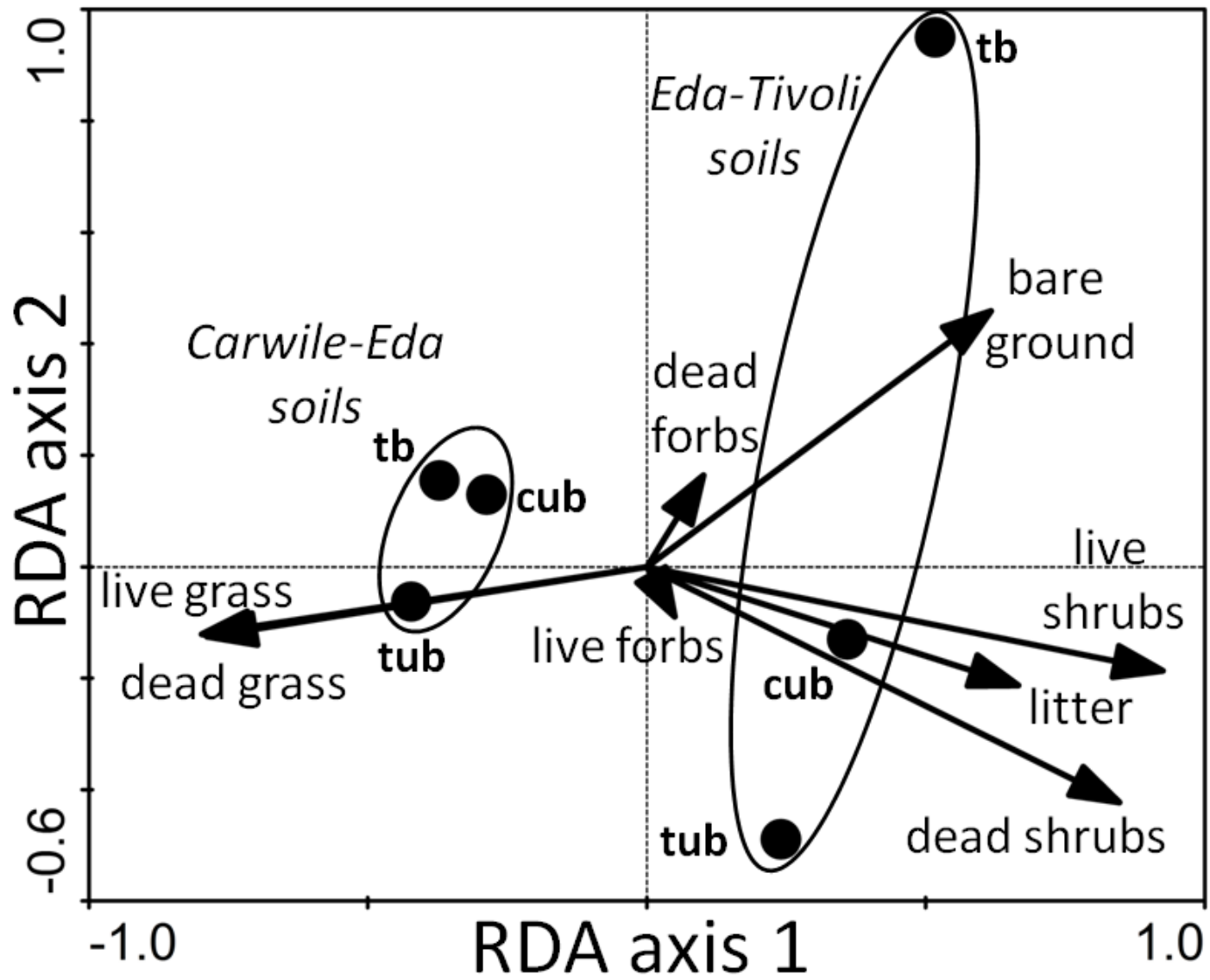
Table 2. Mean \pm SE vegetation structure and cattle distribution measurements within treatment categories at Cooper Wildlife Management Area, Oklahoma, U.S.A. Superscripts with different letters within a row indicate significant differences at the $\alpha = 0.05$ level.

Response variable	Control unburned	Treatment burned	Treatment unburned
bare ground	12.03 \pm 1.38^{a b}	19.04 \pm 3.17^a	7.75 \pm 1.29^b
litter	28.62 \pm 1.69 ^a	25.32 \pm 2.74 ^a	27.04 \pm 2.01 ^a
live vegetation	40.42 \pm 1.61 ^a	33.97 \pm 2.64 ^a	40.13 \pm 2.00 ^a
dead grass	42.55 \pm 2.83 ^a	40.22 \pm 5.01 ^a	52.07 \pm 3.54 ^a
live forbs	6.88 \pm 1.09 ^a	4.46 \pm 1.38 ^a	7.12 \pm 1.37 ^a
dead forbs	5.41 \pm 0.31 ^a	6.05 \pm 0.58 ^a	5.66 \pm 0.39 ^a
live shrubs	2.51 \pm 0.78 ^a	1.44 \pm 1.04 ^a	1.49 \pm 0.79 ^a
dead shrubs	1.96 \pm 0.63 ^a	1.25 \pm 0.70 ^a	2.11 \pm 0.76 ^a
tallest forb	13.62 \pm 1.26 ^a	11.07 \pm 2.00 ^a	13.78 \pm 1.63 ^a
tallest shrub	20.66 \pm 1.29 ^a	14.66 \pm 2.04 ^a	20.55 \pm 1.67 ^a
cattle dung frequency	0.05 \pm 0.02 ^a	0.10 \pm 0.04 ^a	0.01 \pm 0.01 ^a
grazing frequency	0.46 \pm 0.07 ^a	0.54 \pm 0.12 ^a	0.29 \pm 0.07 ^a

Table 3. Mean \pm SE vegetation structure and cattle distribution measurements on contrasting topoedaphic sites within treatment categories at Cooper Wildlife Management Area, Oklahoma, U.S.A. Superscripts with different letters within a row indicate significant differences at the $\alpha = 0.05$ level as determined from tests for interactive effects.

Response variable	Control		Treatment		Treatment	
	unburned		burned		unburned	
	Carwile-Eda sites	Eda-Tivoli sites	Carwile-Eda sites	Eda-Tivoli sites	Carwile-Eda sites	Eda-Tivoli sites
bare ground	8.21 ± 1.42	17.27 ± 2.08	10.65 ± 2.81	31.70 ± 2.81	5.94 ± 1.46	10.06 ± 1.93
litter	24.77 ± 1.80	32.82 ± 2.05	20.51 ± 2.82	30.82 ± 3.45	20.95 ± 2.02	34.12 ± 2.54
live vegetation	40.28 ± 1.93	40.57 ± 1.93	37.17 ± 3.27	30.91 ± 3.07	40.58 ± 2.36	39.68 ± 2.35
dead vegetation	53.97 ± 3.01^{a b}	47.27 ± 3.02^{b c}	61.40 ± 5.04^{a b}	31.47 ± 4.71^c	64.12 ± 3.49^a	53.76 ± 3.69^{a b}
live grass	37.51 ± 2.11^a	22.96 ± 1.77^b	36.67 ± 3.64^a	12.47 ± 2.29^c	37.76 ± 2.59^a	24.21 ± 2.21^b
dead grass	53.10 ± 3.45	32.64 ± 3.18	61.08 ± 5.79	22.39 ± 4.71	63.57 ± 4.03	40.34 ± 4.13
live forbs	6.71 ± 1.24	7.05 ± 1.29	3.14 ± 1.31	6.30 ± 2.07	7.46 ± 1.64	6.79 ± 1.54
dead forbs	5.43 ± 0.38	5.40 ± 0.38	5.55 ± 0.66	6.60 ± 0.74	5.60 ± 0.47	5.71 ± 0.48
live shrubs	0.28 ± 0.15	19.03 ± 3.28	0.10 ± 0.14	18.21 ± 3.50	0.10 ± 0.10	18.67 ± 3.32
dead shrubs	0.16 ± 0.10	20.19 ± 1.94	0.15 ± 0.16	9.74 ± 1.73	0.19 ± 0.13	19.94 ± 2.16
cattle dung frequency	0.16 ± 0.04	0.01 ± 0.01	0.21 ± 0.08	0.04 ± 0.03	0.11 ± 0.04	0.00 ± 0.00
grazing frequency	0.58 ± 0.08	0.33 ± 0.07	0.55 ± 0.13	0.53 ± 0.13	0.29 ± 0.08	0.29 ± 0.08
tallest grass	15.35 ± 2.04^b	28.40 ± 1.97^a	10.15 ± 2.75^b	13.74 ± 2.64^b	17.39 ± 2.44^b	32.77 ± 2.35^a
tallest forb	8.95 ± 1.59	18.30 ± 1.95	6.98 ± 2.51	15.16 ± 3.09	9.98 ± 2.05	17.57 ± 2.52
tallest shrub	0.65 ± 0.24	40.67 ± 2.57	0.29 ± 0.37	29.02 ± 4.06	0.29 ± 0.30	40.82 ± 3.32

Fig. 1. Redundancy analysis (RDA) biplot of vegetation structure measurements, using topoedaphic site-treatment category interaction dummy variables, from Cooper Wildlife Management Area, Oklahoma, U.S.A. Treatment categories were control unburned (cub), treatment burned (tb) and treatment unburned (tub). Interaction dummy variables segregated out along axis 1 by soils type as indicated by ellipses. Axis 2 reflects a gradient of disturbance intensity.



APPENDICES

Appendix Table 1. Pastures, patch sizes and burn dates at Cooper Wildlife Management Area.

Pasture	Patch	Patch Size (ha)	Burn Date
Bodwell	A	167	03-21-2003
Bodwell	B	144	03-16-2004
Bodwell	C	95	04-02-2008
East	A	83	05-08-2008
East	B	415	03-08-2007, 03-14-2007 ¹
East	C	350	03-18-2004
Middle	A	101	03-19-2008
Middle	B	198	03-14-2007
Middle	C	204	03-24-2005
North	A	160	NA
North	B	198	NA
North	C	156	NA
South	A	301	NA
South	B	211	NA
South	C	257	NA

¹ The East B patch was originally-planned to be a 352 ha burn conducted on 03-08-2007. On 03-14-2007, the burn conducted in the adjacent Middle B patch escaped and burned a 106-ha portion of the originally-planned East A patch. Thus, East B consists of the total acreage burned in 2007.

Appendix Table 2. Geographic coordinates of all sampling points at Cooper Wildlife Management Area.

Pasture	Patch	Point ID	Latitude Decimal Degrees ¹	Longitude Decimal Degrees ¹	UTM Northing 2	UTM Easting 2	Soil ³	Chapter 1	Chapter 2	Chapter 3
Bodwell	A	053 Bodwell A	36.521376	-99.487016	4041890	456397	Pt	2006–2008	2006–2008	
Bodwell	A	056 Bodwell A	36.532733	-99.492021	4043152	455955	Pt	2006–2008	2006–2008	
Bodwell	A	057 Bodwell A	36.527706	-99.495428	4042596	455647	Pt	2006–2008	2006–2008	
Bodwell	A	058 Bodwell A	36.520969	-99.493759	4041847	455793	Pt	2006–2008	2006–2008	
Bodwell	B	027 Bodwell B	36.526880	-99.483916	4042499	456678	Pt	2006–2008	2006–2008	
Bodwell	B	028 Bodwell B	36.531199	-99.483567	4042978	456711	Pt	2006–2008	2006–2008	
Bodwell	B	029 Bodwell B	36.523350	-99.481046	4042106	456933	Pt	2006–2008	2006–2008	
Bodwell	B	055 Bodwell B	36.516210	-99.481062	4041314	456927	Pt	2006–2008	2006–2008	
Bodwell	C	054 Bodwell C	36.516076	-99.486845	4041302	456409	Pt	2006–2008	2006–2008	
Bodwell	C	059 Bodwell C	36.515846	-99.492606	4041279	455893	Pt	2006–2008	2006–2008	
Bodwell	C	060 Bodwell C	36.512557	-99.491560	4040913	455985	Pt	2006–2008	2006–2008	
Bodwell	C	061 Bodwell C	36.512439	-99.485166	4040897	456558	Pt	2006–2008	2006–2008	
East ⁴	A	025 East A	36.549609	-99.497858	4045026	455443	Pt	2006	2006	2006
East ⁴	A	026 East A	36.553493	-99.496710	4045457	455547	Pt	2006	2006	2006
East	A	035 East A	36.562935	-99.497809	4046504	455454	Pt	2006–2008	2006–2008	
East ⁴	A	036 East A	36.557785	-99.497954	4045933	455439	Pt	2006	2006	
East ⁴	A	098 East A	36.563867	-99.499857	4046608	455273	Pt	2007, 2008	2007, 2008	

Appendix Table 2. Continued.

Pasture	Patch	Point ID	Latitude Decimal Degrees ¹	Longitude Decimal Degrees ¹	UTM Northing 2	UTM Easting 2	Soil ³	Chapter 1	Chapter 2	Chapter 3
East	B	033 East B	36.558927	-99.482778	4046053	456797	Pt	2006–2008	2006–2008	2006
East	B	034 East B	36.566539	-99.483277	4046898	456757	Pt	2006–2008	2006–2008	
East	B	037 East B	36.560569	-99.488314	4046238	456303	Pt	2006–2008	2006–2008	2006
East	B	052 East B	36.572934	-99.488041	4047609	456334	Pt	2006–2008	2006–2008	
East	C	030 East C	36.538510	-99.486619	4043790	456442	Pt	2006–2008	2006–2008	2006
East	C	031 East C	36.547630	-99.488926	4044803	456241	Pt	2006–2008	2006–2008	2006
East	C	032 East C	36.551562	-99.482306	4045236	456835	Pt	2006–2008	2006–2008	
East	C	038 East C	36.543086	-99.495374	4044302	455661	Pt	2006–2008	2006–2008	
Middle	A	013 Middle A	36.553654	-99.513109	4045482	454080	Pt	2006–2008	2006–2008	
Middle	A	040 Middle A	36.559560	-99.513661	4046138	454034	Pt	2006–2008	2006–2008	2006
Middle	A	041 Middle A	36.564860	-99.511773	4046725	454206	Pt	2006–2008	2006–2008	2006
Middle	A	043 Middle A	36.566556	-99.513039	4046913	454094	Pt	2006–2008	2006–2008	
Middle	B	020 Middle B	36.551363	-99.509236	4045226	454425	Pt	2006–2008	2006–2008	2006
Middle	B	024 Middle B	36.553332	-99.503083	4045442	454977	Pt	2006–2008	2006–2008	
Middle	B	039 Middle B	36.556497	-99.505620	4045794	454752	Pt	2006–2008	2006–2008	2006
Middle	B	042 Middle B	36.562023	-99.502326	4046405	455050	Pt	2006–2008	2006–2008	
Middle	C	004 Middle C	36.540817	-99.509547	4044056	454391	Pt	2006–2008	2006–2008	

Appendix Table 2. Continued.

Pasture	Patch	Point ID	Latitude Decimal Degrees ¹	Longitude Decimal Degrees ¹	UTM Northing ₂	UTM Easting ₂	Soil ³	Chapter 1	Chapter 2	Chapter 3
Middle	C	021 Middle C	36.544572	-99.512170	4044474	454159	Pt	2006–2008	2006–2008	2006
Middle	C	022 Middle C	36.543456	-99.503909	4044347	454897	Pt	2006–2008	2006–2008	
Middle ⁵	C	023 Middle C	36.539079	-99.504005	4043861	454886	Pt	2006	2006	
Middle ⁵	C	099 Middle C	36.536896	-99.503807	4043619	454903	Pt	2007, 2008	2007, 2008	2006
North	A	014 North A	36.557575	-99.519358	4045920	453523	Pt	2006–2008	2006–2008	2006
North	A	015 North A	36.559383	-99.522915	4046122	453206	Pt	2006–2008	2006–2008	
North	A	016 North A	36.562344	-99.524181	4046451	453094	Pt	2006–2008	2006–2008	2006
North	A	017 North A	36.561459	-99.529572	4046356	452611	Pt	2006–2008	2006–2008	
North	B	010 North B	36.547109	-99.522958	4044761	453195	Pt	2006–2008	2006–2008	2006
North	B	011 North B	36.550752	-99.520249	4045164	453439	Pt	2006–2008	2006–2008	
North	B	012 North B	36.552699	-99.524304	4045382	453077	Pt	2006–2008	2006–2008	2006
North	B	019 North B	36.548601	-99.529551	4044930	452605	Pt	2006–2008	2006–2008	
North	C	007 North C	36.536209	-99.523548	4043552	453135	Pt	2006–2008	2006–2008	
North	C	008 North C	36.540903	-99.517524	4044070	453677	Pt	2006–2008	2006–2008	2006
North	C	009 North C	36.538913	-99.523763	4043852	453118	Pt	2006–2008	2006–2008	
North	C	018 North C	36.542882	-99.528043	4044294	452737	Pt	2006–2008	2006–2008	2006
South	A	001 South A	36.527519	-99.514992	4042584	453896	Pt	2006–2008	2006–2008	2006

Appendix Table 2. Continued.

Pasture	Patch	Point ID	Latitude Decimal Degrees ¹	Longitude Decimal Degrees ¹	UTM Northing ₂	UTM Easting ₂	Soil ³	Chapter 1	Chapter 2	Chapter 3
South	A	002 South A	36.524450	-99.506891	4042240	454619	Pt	2006–2008	2006–2008	2006
South	A	003 South A	36.529976	-99.507637	4042853	454556	Pt	2006–2008	2006–2008	
South	A	005 South A	36.528152	-99.500105	4042647	455229	Pt	2006–2008	2006–2008	
South	B	044 South B	36.519520	-99.514713	4041697	453916	Pt	2006–2008	2006–2008	2006
South	B	045 South B	36.519274	-99.504520	4041664	454829	Pt	2006–2008	2006–2008	
South	B	046 South B	36.513357	-99.510335	4041011	454304	Pt	2006–2008	2006–2008	
South	B	048 South B	36.513115	-99.497809	4040978	455426	Pt	2006–2008	2006–2008	2006
South	C	047 South C	36.507279	-99.498738	4040331	455339	Pt	2006–2008	2006–2008	
South	C	049 South C	36.509097	-99.506221	4040536	454670	Pt	2006–2008	2006–2008	2006
South	C	050 South C	36.502574	-99.497058	4039808	455487	Pt	2006–2008	2006–2008	2006
South	C	051 South C	36.500648	-99.504333	4039598	454835	Pt	2006–2008	2006–2008	
East	A	118 East A	36.559029	-99.494762	4046070	455725	Cp			2006
East	A	119 East A	36.546675	-99.497933	4044701	455434	Cp			2006
East	A	124 East A	36.562503	-99.499052	4046456	455344	Cp			
East	A	125 East A	36.566784	-99.495559	4046930	455659	Cp			
East	B	120 East B	36.562366	-99.485386	4046436	456566	Cp			2006
East	B	121 East B	36.576560	-99.480976	4048008	456968	Cp			2006

Appendix Table 2. Continued.

Pasture	Patch	Point ID	Latitude Decimal Degrees ¹	Longitude Decimal Degrees ¹	UTM Northing ₂	UTM Easting ₂	Soil ³	Chapter 1	Chapter 2	Chapter 3
East	C	122 East C	36.537695	-99.498952	4043705	455338	Cp			2006
East	C	123 East C	36.544277	-99.486271	4044429	456477	Cp			2006
Middle	A	112 Middle A	36.563879	-99.508726	4046614	454478	Cp			2006
Middle	A	113 Middle A	36.562146	-99.511322	4046423	454245	Cp			2006
Middle	B	114 Middle B	36.558133	-99.506146	4045976	454706	Cp			2006
Middle	B	115 Middle B	36.556438	-99.507954	4045788	454543	Cp			2006
Middle	C	116 Middle C	36.546654	-99.504558	4044701	454841	Cp			2006
Middle	C	117 Middle C	36.547678	-99.515201	4044820	453889	Cp			2006
North ⁶	A	110 North A	36.563117	-99.526938	4046538	452848	Cp			2006
North	A	111 North A	36.555693	-99.520952	4045712	453379	Cp			2006
North ⁶	A	126 North A	36.559023	-99.521817	4046081	453305	Cp			
North	B	108 North B	36.548091	-99.517711	4044867	453665	Cp			2006
North	B	109 North B	36.545382	-99.518843	4044567	453562	Cp			2006
North	C	106 North C	36.534728	-99.516628	4043384	453754	Cp			2006
North	C	107 North C	36.541391	-99.521509	4044126	453321	Cp			2006
South	A	100 South A	36.531048	-99.502203	4042969	455043	Cp			2006
South	A	101 South A	36.523082	-99.511537	4042090	454203	Cp			2006

Appendix Table 2. Continued.

Pasture	Patch	Point ID	Latitude Decimal Degrees ¹	Longitude Decimal Degrees ¹	UTM Northing ₂	UTM Easting ₂	Soil ³	Chapter 1	Chapter 2	Chapter 3
South	B	102 South B	36.517691	-99.509236	4041491	454405	Cp			2006
South	B	103 South B	36.512659	-99.500014	4040929	455228	Cp			2006
South	C	104 South C	36.507402	-99.501640	4040346	455080	Cp			2006
South	C	105 South C	36.508582	-99.505604	4040479	454725	Cp			2006

¹ North American Datum 1983.

² North American Datum 1983; UTM zone 14N.

³ Pt = Eda-Tivoli soils; Cp = Carwile-Eda soils.

⁴ Three sampling locations (25 East A, 26 East A, 36 East A) that were sampled in 2006 and subsequently burned in a wildfire in 2007 and not used during 2007 and 2008; one replacement sampling location (98 East A) that was established after the wildfire of 2007.

⁵ One sampling location (23 Middle C) that was deemed unsuitable for use after soil disturbance in 2006 and one sampling location (99 Middle C) that was established to replace it.

⁶ One sampling location (110 North A) that was destroyed by petroleum development after the 2006 field season and replaced by another sampling point (126 North A). Data collected at 126 North A in 2007 and 2008 were not used in the analyses described in this dissertation but will be used in subsequent analyses and publications.

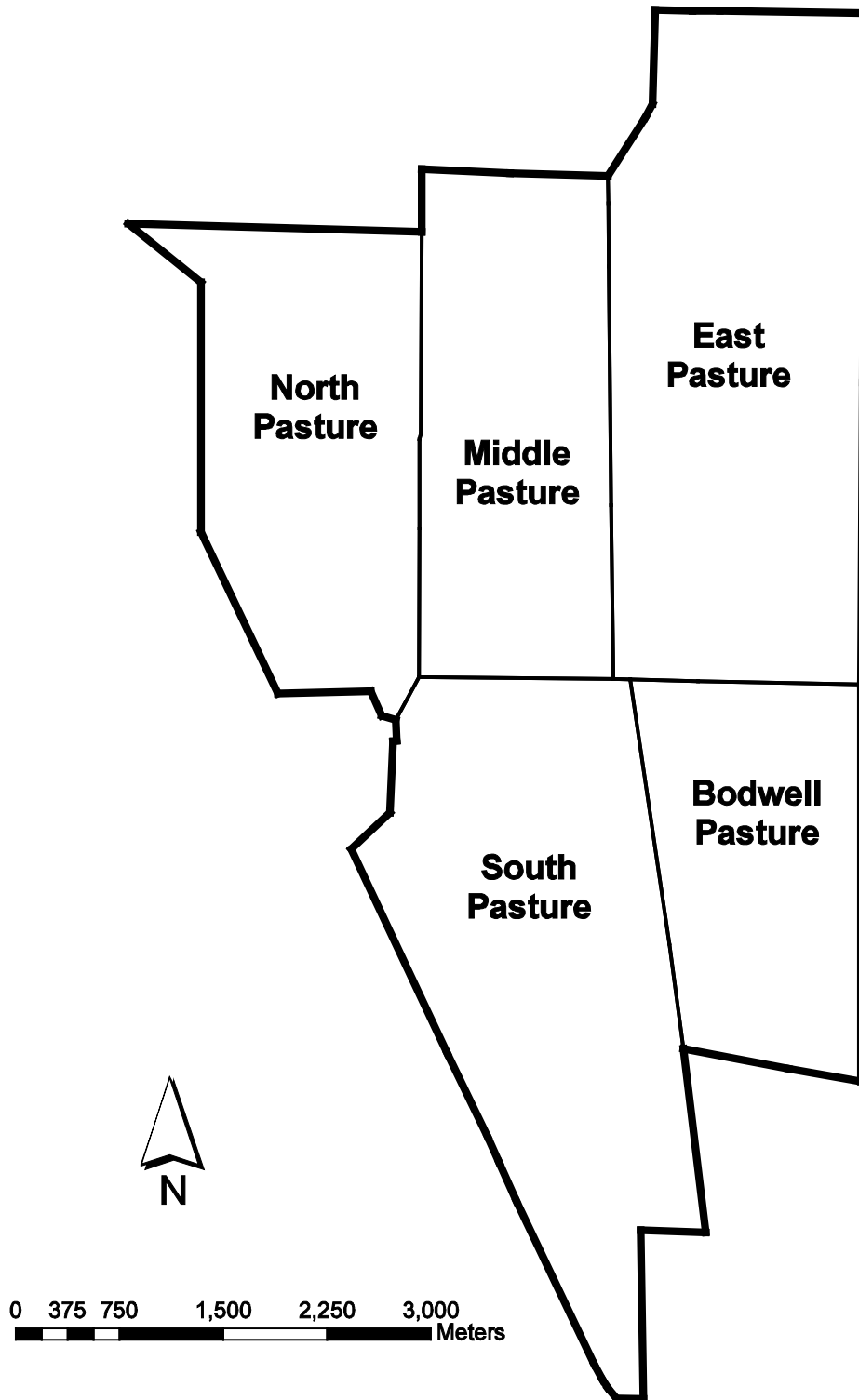
Appendix Table 3. Geographic coordinates of 4-ha plot centroids originally burned in 1999-2001 by Vermeire (2000) and sampled in 2008 at Cooper Wildlife Management Area.

Pasture	Patch	Point ID	Latitude Decimal Degrees¹	Longitude Decimal Degrees¹	UTM Northing²	UTM Easting²	Soil³	Chapter 1	Original Burn Date
Bodwell	A	010 Vermeire	36.532434	-99.495642	4043120	455631	Pt	2008	11-1999
Bodwell	C	012 Vermeire	36.516643	-99.492571	4041367	455897	Pt	2008	04-2000
East	A	007 Vermeire	36.548729	-99.498796	4044929	455358	Pt	2008	04-2000
East	B	005 Vermeire	36.567473	-99.485282	4047002	456578	Pt	2008	04-2000
East	C	006 Vermeire	36.551461	-99.483260	4045225	456750	Pt	2008	11-1999
East	C	009 Vermeire	36.536393	-99.497455	4043560	455471	Pt	2008	11-1999
Middle	A	024 Vermeire	36.552130	-99.513065	4045313	454083	Pt	2008	11-2000
Middle	B	023 Vermeire	36.566710	-99.504030	4046926	454900	Pt	2008	04-2001
North	A	022 Vermeire	36.559715	-99.516445	4046156	453785	Pt		04-2001
North	C	020 Vermeire	36.536815	-99.521007	4043618	453363	Pt		11-2000
South	A	017 Vermeire	36.533157	-99.499568	4043202	455280	Pt		11-2000
South	B	016 Vermeire	36.516226	-99.508148	4041328	454502	Pt		04-2001
South	C	014 Vermeire	36.492386	-99.498435	4038679	455358	Pt		04-2001
South	C	015 Vermeire	36.501253	-99.501484	4039664	455090	Pt		11-2000
river		001 Vermeire	36.568813	-99.509632	4047162	454400			11-1999
river		002 Vermeire	36.578706	-99.500375	4048255	455234			04-2000

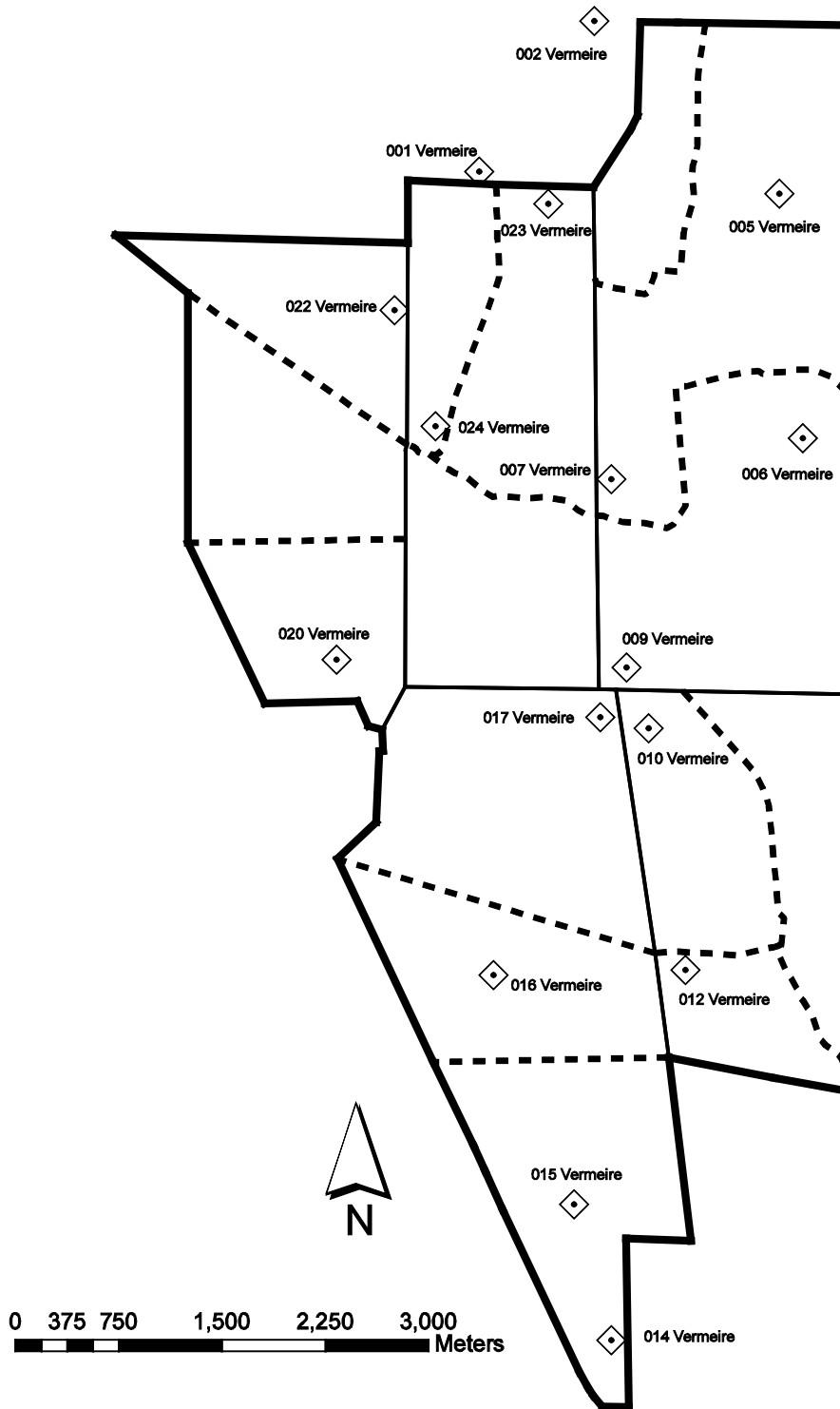
¹ North American Datum 1983; ² North American Datum 1983; UTM zone 14N.

³ Pt = Eda-Tivoli soils

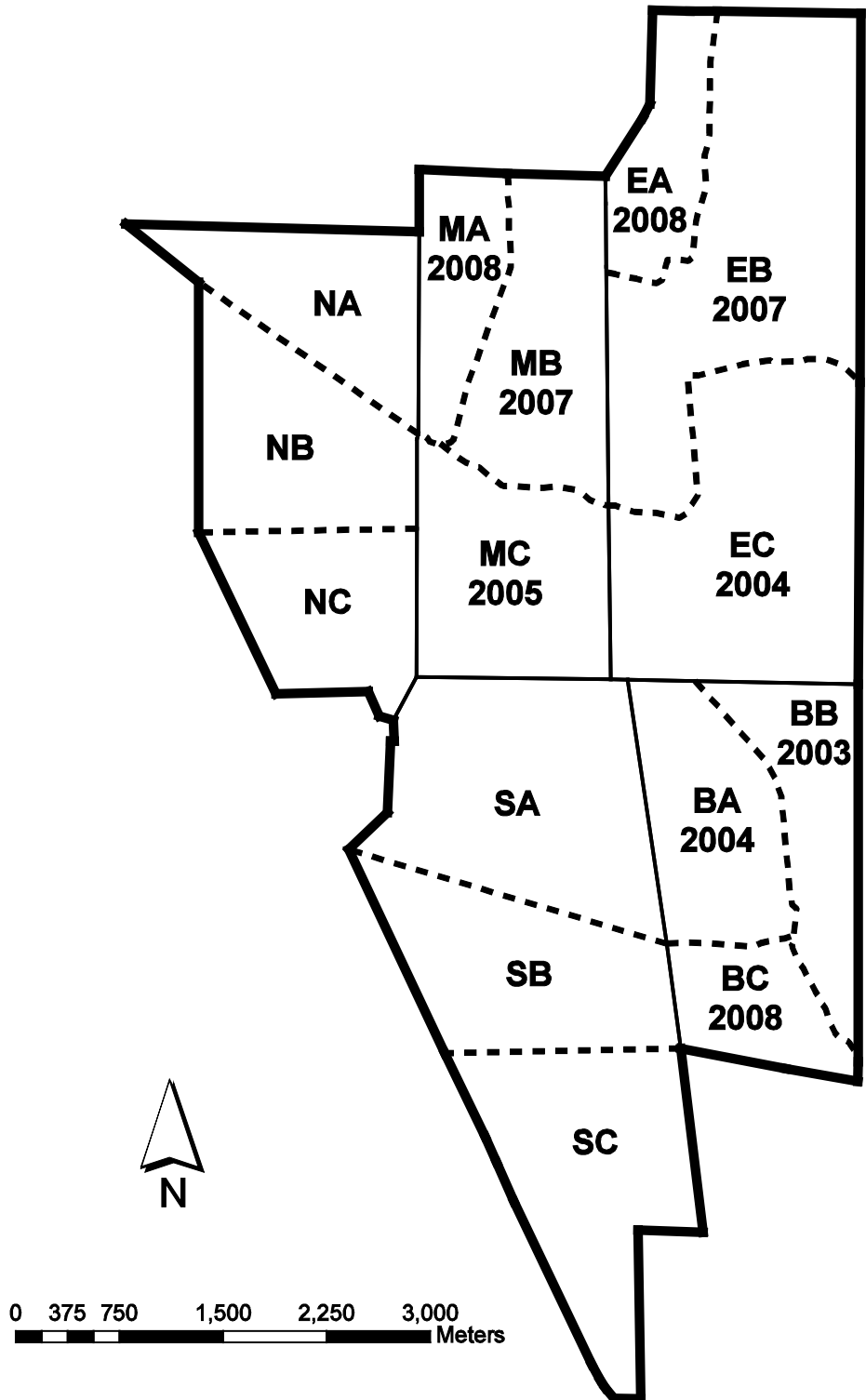
Appendix Figure 1. Study pastures at Cooper Wildlife Management Area.



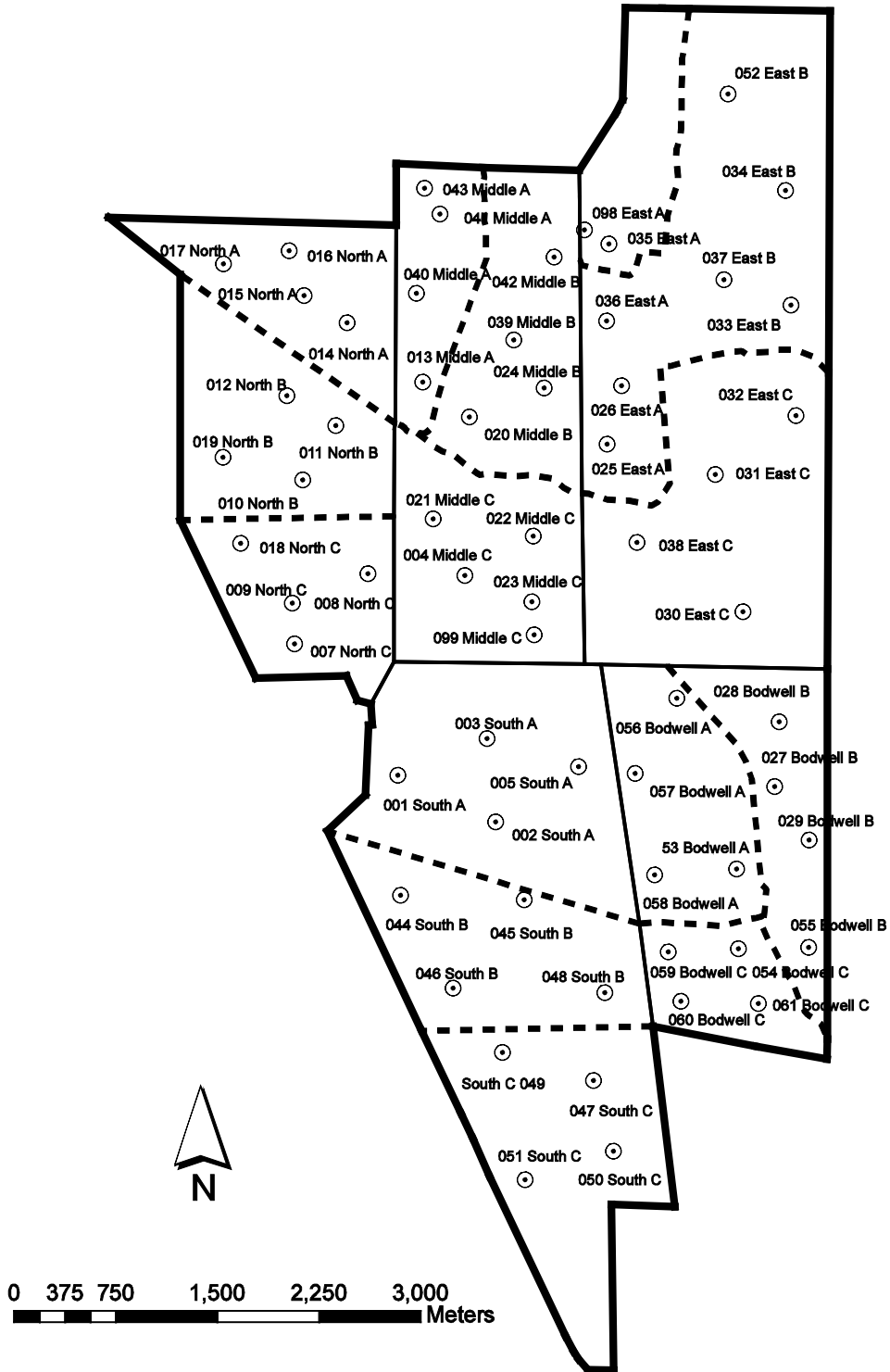
Appendix Figure 2. Patch boundaries and 4-ha plot centroids (diamond symbols) originally burned in 1999-2001 by Vermeire (2000) at Cooper Wildlife Management Area. The 4-ha plot centroids sampled in 2008 (Chapter 1) are identified in Appendix Table 2.



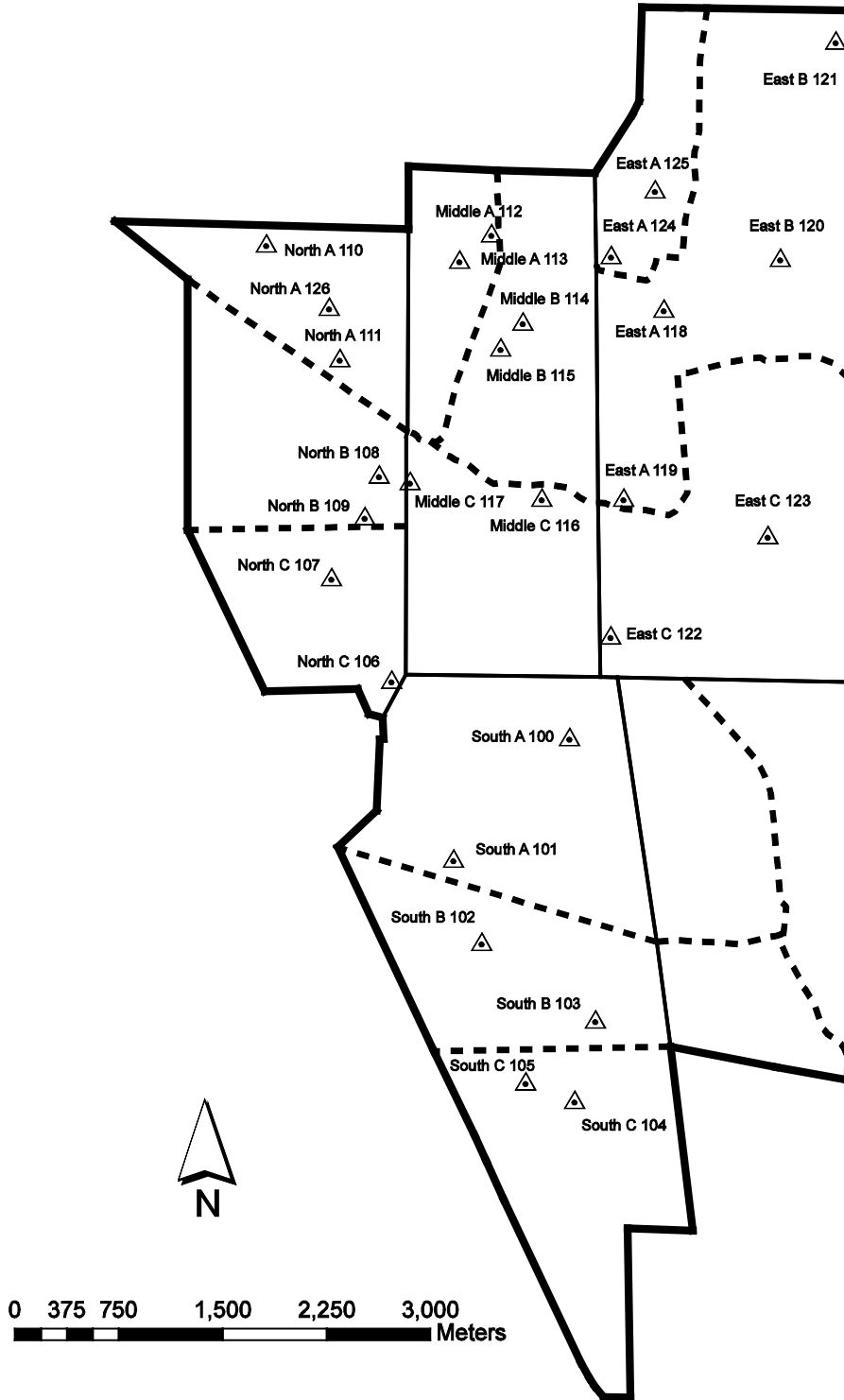
Appendix Figure 3. Patch boundaries and burn histories within study pastures at Cooper Wildlife Management Area.



Appendix Figure 4. Patch boundaries and sampling locations (circle symbols represent the midpoint of 100-m transects) on Eda-Tivoli soils within study pastures at Cooper Wildlife Management Area.



Appendix Figure 5. Patch boundaries and sampling locations (triangle symbols represent the midpoint of 100-m transects) on Carwile-Eda soils within study pastures at Cooper Wildlife Management Area.



VITA

Stephen L. Winter

Candidate for the Degree of

Doctor of Philosophy

Dissertation: THE INTERACTION OF FIRE AND GRAZING IN OKLAHOMA *ARTEMISIA
FILIFOLIA* SHRUBLAND

Major Field: Natural Resource Ecology and Management; Rangeland Ecology and Management
Option

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Pages in Study: 105

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Major Field: Natural Resource Ecology and Management; Rangeland Ecology and Management Option

Scope and Method of Study: We conducted research in *Artemisia filifolia* shrublands located in Woodward County, Oklahoma to determine the effect of restoring the fire-grazing interaction on vegetation structure. Data were collected for three years (2006, 2007 and 2008) in replicated pastures grazed by cattle (*Bos taurus*) where the fire-grazing interaction had been restored (treatment pastures) and in pastures that were grazed but remained unburned (control pastures).

Findings and Conclusions: Vegetation structure in *Artemisia filifolia* shrublands of our study site was readily altered by the fire-grazing interaction but also demonstrated substantial resilience to these effects. Most measurements of vegetation structure returned to levels characteristic of unburned sites within one to four years after being burned. The fire-grazing interaction changed the total amount of heterogeneity characterizing this system, the scale at which heterogeneity in this system was expressed and the amount of heterogeneity expressed through time. Landscapes at our study site were characterized by an inherent amount of heterogeneity in vegetation structure due to variability in topographic sites while the fire-grazing interaction superimposed an additional layer of heterogeneity.

ADVISER'S APPROVAL: Dr. Sam Fuhlendorf