

**EFFECTS OF PRESCRIBED FIRE ON
HABITAT STRUCTURE OF SAND
SHINNERY COMMUNITIES**

By

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CHAPTER I

INTRODUCTION

This thesis is composed of 4 manuscripts formatted for submission to scientific journals: Journal of Range Management (Chapter II), Wildlife Society Bulletin (Chapter III) Southwestern Naturalist (Chapter IV), and Rangelands (Chapter V).

CHAPTER II

Effects of prescribed fire on habitat structure and composition of sand shinnery communities

Abstract

Sand shinnery communities are a threatened shrubland ecosystem of the southern Great Plains and extend from northern Texas and western Oklahoma southward into the Chihuahuan Desert. They are dominated by sand shinnery oak (*Quercus havardii* Rydb.), a member of the white oak group. Habitat structure and composition of sand shinnery communities in relation to natural disturbances, such as fire, have not been adequately investigated. Objectives were to determine the influence of fire on shrub composition and habitat structure of sand shinnery communities, and to determine the persistence of structural and compositional changes. Data were collected from native deep sand savanna and sandy prairie range sites on Black Kettle National Grasslands (BKNG) in western Oklahoma during the growing seasons of 1998 and 1999. Habitat measurements including line transects, visual obstructions, heights, cone of vulnerabilities, shrub patch sizes, and shrub patch densities were used to estimate plant functional group cover, shrub composition, and habitat structure of sand shinnery communities. Fire in sand shinnery communities had the most effect on vegetation structure the first year following fire. After four years, structure in burned communities was similar to unburned sand shinnery communities. We found no differences in composition of shrub species between burned and unburned sites. Multiple fire events had less influence on habitat structure than the initial fire event. Sand shinnery communities appear to be highly resilient to periodic fire

events. Prescribed fire is an effective tool for short-term alteration (< 1 year) of sand shinnery structure; however, rapid recovery following fire suggests that fire may have minimal long-term influences on habitat structure and composition.

Introduction

Sand shinnery communities occupy 2 to 3 million hectares of rangeland in the southern Great Plains (Peterson and Boyd 1998). These communities extend from northern Texas and western Oklahoma southward into the Chihuahuan Desert and are dominated by sand shinnery oak, a member of the white oak group. Sand shinnery communities are one of the few shrub-dominated vegetation types in the Southern Great Plains and have been documented as threatened (Bailey and Painter 1994, Dhillion et al. 1994). Shrub-dominated communities are important to conservation and management of many wildlife species, because they provide food and critical cover (Dhillion et al. 1994). Loss of area and changes in structure of sand shinnery communities have been associated with declines in abundance and distribution of sensitive species such as lesser prairie-chickens (*Tympanuchus pallidicinctus*) (Taylor and Guthery 1980).

Historical accounts of sand shinnery oak rangelands in western Oklahoma document a dense growth of dwarf oak vegetation about 45 cm high which seemed to have attained full maturity (Marcy 1854). Currently, sand shinnery oak appears to be taller and denser on some range sites than many historical accounts describe. Fire has been important in maintaining grasslands of the Great Plains (Collins 1987); however, its historical importance in sand shinnery communities is unknown. It has been suggested that sand shinnery communities were once dominated by tallgrasses, but the increase of livestock grazing and the decrease in fire has allowed sand shinnery oak to gain structural

dominance and reduce the cover of tallgrasses (Peterson and Boyd 1998). Based on this assumption, many land managers have attempted to control sand shinnery oak to improve forage quantity for livestock production. This has reduced and fragmented sand shinnery communities over their entire range through extensive brush control efforts and cultivation (Peterson and Boyd 1998). Control efforts with herbicide may stem from early classifications of sand shinnery oak as an invader by the Natural Resource Conservation Service (NRCS) and others because of lack of fire and overgrazing (Conner et al. 1974, Hodson et al. 1980, Peterson and Boyd 1998). Lack of extensive reproduction by seed for sand shinnery oak and reconstruction of composition in the pollen record characterizing a stable existence for hundreds of years question the invasive classification of this species (Beckett 1976, Gross and Dick-Peddie 1979).

It is surmised that alterations in fire and grazing regimes since European settlement may have increased density, cover, and altered spatial arrangement of sand shinnery communities. However; some reports suggest that shrub abundance is not drastically altered by natural disturbances such as fire (McIlvain and Armstrong 1966), suggesting that sand shinnery communities are stable and resilient. Little is known of the effects of fire on habitat structure of sand shinnery communities. Therefore, our objectives were to evaluate sites within sand shinnery communities that vary in time since fire and number of recent fires specifically to 1) quantify structural and compositional influences of fire, 2) determine the rate of recovery following single fire events, and 3) determine the interactive effects of time since fire and the number of recent fires on habitat structure.

Study Area and Methods

Our study sites were selected in sand shinnery communities on the Black Kettle National Grasslands (BKNG) in Roger Mills County, Oklahoma (35° 37', 100° 40'). BKNG were formed in 1953 after the Forest Service was granted authority over 13,476 ha (Burgess et al. 1963). Currently, BKNG are used for recreational activities such as camping and hunting, as well as leased grazing. The climate of the region is semiarid, with mean August and January temperatures of 28.0°C and 2.7°C, respectively (Burgess et al. 1963, Dhillon and Mills 1999). The area has an average growing season of 209 days, with a mean rainfall of 65 cm (Burgess et al. 1963). Precipitation is highly variable with a bimodal distribution of rainfall with peaks in May-June and August-September. Topography of the area consists of rolling hills, with variable altitudes ranging from 518 to 793 m above sea level.

Sites were located on sand shinnery oak communities within deep sand savannah and sandy prairie range sites (Burgess et al. 1963). Sand shinnery oak dominates these sites with sand sage (*Artemisia filifolia* Torr.) codominating (Peterson and Boyd 1998). Common grasses include sand bluestem (*Andropogon gerardii* var. *paucipilus* Nash), little bluestem (*Schizachyrium scoparium* Nash), and sideoats grama (*Bouteloua cirtipendula* Torr.). Nomenclature follows Hatch et al. (1990). Preliminary data analysis indicated that both range sites were similar in regards to vegetation structure, composition, and response to fire; thus, further analyses combined both range sites into a single ecological type. All sites sampled were grazed by cattle at light to moderate rates (ca. 1.5 ha/AUM) relative to NRCS recommendations.

Sites sampled varied with time since fire and number of fires including single event fires that occurred 1 (n=4), 2 (n=4) and 4 (n=2) growing seasons prior to sampling, two event fires that occurred 1, 3 (n=2) and 2, 4 (n=2) growing seasons prior to sampling, and unburned sites that served as controls (n=4). All fires were conducted during the spring. Vegetation was sampled during the late growing season of 1998 and 1999. Four, 100-m line transects per experimental unit (18 units \times 4 transects = 72 line transects) were used to measure relative plant functional group dominance at a 10-cm interval (Bonham 1989). The fine sampling resolution was used so that small-scale changes in habitat structure that may be important to some wildlife species could be detected. Plant functional groups sampled along each line included canopy cover of shrubs, herbaceous vegetation, and litter. Precedence was given to shrubs because of their dominance, so other functional groups were only recorded if shrubs were absent. Shrub patch density and average size of shrub patches were considered measures of habitat structure and were determined from the line transect data by summing the number of distinct shrub patches and averaging their linear lengths. Frequency of each shrub species was determined by dividing number of occurrences of a given shrub species by the total number of shrub patches for each transect.

Habitat structure was measured along the transects by vegetation height, visual obstruction, and cone of vulnerability. Measurements of vegetation height were taken at a point every 1 m along the transect. We estimated visual obstruction every 10 m along the transect using a profile board as described by Nudds (1977) and modified for sand shinnery communities by Guthery et al. (1981). The 6.8-cm wide profile board had 12

strata, with each stratum being 10 cm tall. Estimates were taken perpendicular to the line transect at a distance of 7 m, with the observer kneeling at a height of 1.5 m over the transect. Percent visual obstruction was estimated for each stratum. We measured cone of vulnerability (Kopp et al. 1998) every 10 m along the transects. The cone of vulnerability is a 3-dimensional view of visual obstruction and has been identified as a measure that quantifies habitat structure important for northern bobwhites (*Colinus virginianus*) (Kopp et al. 1998). A larger cone of vulnerability equates to a structurally more open habitat. We measured cone of vulnerability by measuring 8 angles around a point 10 cm above ground level to the top of the nearest obstructing vegetation. We then calculated the volume of the air space included within the cone formed by the angles (Kopp et al. 1998).

We used a completely randomized design to evaluate the effects of fire and recovery time from fire on habitat structure in sand shinnery communities. Sites in which single event fires occurred, including sites burned 1, 2, and 4 years prior to sampling and unburned sites were considered treatments. Statistical differences in time since fire for percent cover (shrub, herbaceous, and litter), vegetation height, average visual obstruction, cone of vulnerability, shrub patch size, and shrub patch density were assessed using one-way analysis of variance (PROC MIXED, SAS Institute Inc. 1988). The mixed procedure with Satterthwaith's approximation for degrees of freedom was utilized. Differences between means at varying time since fire were determined using least square means ($P < 0.05$). We used multivariate analysis of variance methods (MANOVA, Wilk's Lambda statistic) to test for differences in shrub species composition among treatments (Stroup and Stubbendieck 1983).

We used a 2×2 factorial arrangement of treatments using paired factors of time since fire and number of times burned (PROC MIXED, SAS Institute Inc. 1988) to determine the interactive effects of time since fire and the number of recent fires on habitat structure within sand shinnery communities. Sites that were included in the analysis consisted of single event fires, 1 and 2 years prior to sampling and 2 event fires, 1, 3 and 2, 4 years prior to sampling. This analysis focused on the interaction between the main effects of time since fire and number of times burned.

We employed repeated measures using MANOVA (PROC GLM, SAS Institute Inc. 1988) to analyze visual obstruction of individual strata (1-12) along our density board. Visual obstruction of each stratum was not an independent observation, but was dependent on the visual obstruction of other strata, hence strata were repeated measures in this analysis. All possible time since fire combinations were used to test for significant interactions with strata in the analysis of visual obstruction.

Results

Fire effects and rate of recovery

Sand shinnery oak was the dominant cover type on all sites (Table 1). Other shrub species that occurred included sandsage, skunkbush (*Rhus aromatica* Ait.), sand plum (*Prunus spp.* L.), soapweed yucca (*Yucca glauca* Nutt.), netleaf hackberry (*Celtis reticulata* Torr.), leadplant (*Amorpha canescens* Nutt.), honey mesquite (*Prosopis glandulosa* Torr.), and catclaw mimosa (*Mimosa biuncifera* Benth.). We found no differences ($P = 0.55$) in composition of shrub species between burned and unburned sites.

Analysis for differences among time since fire (1, 2, 4 years since fire and unburned) indicated differences ($P < 0.01$) for all three plant functional groups (shrub, herbaceous, litter) (Table 2). Shrub cover decreased the first year after fire ($P < 0.01$), yet was comparable to that of unburned sites by 2 years ($P = 0.26$) and 4 years ($P = 0.33$) after a fire. Litter cover decreased the first year ($P < 0.01$) and second year ($P < 0.01$) following burning, but was similar to unburned sites after four years ($P = 0.09$). Herbaceous cover was higher on sites burned one year ($P < 0.01$) and 2 years prior ($P = 0.05$) than on unburned sites, but was similar to unburned areas four years after a single fire ($P = 0.07$).

Measures of habitat structure (height, cone of vulnerability, shrub patch density, shrub patch size, and visual obstruction) in sand shinnery communities indicated that fire changed structure ($P < 0.05$), but the effect was short lived (< 4 years) (Table 2). Average height of vegetation differed among time since fire treatments ($P < 0.01$). Fire decreased vegetation height for 1 year ($P < 0.01$) and 2 years ($P = 0.04$) post burn, but vegetation height after 4 years did not differ from unburned sites ($P = 0.82$). The cone of vulnerability increased 1 year following fire ($P < 0.01$), but was similar to unburned sites by the second ($P = 0.81$) growing season following fire.

One year following fire, shrub patch density averaged 92/100 m, but was higher 2 years following a fire ($P < 0.01$) (Table 2). Two years following fire, shrub patch density averaged 110 /100 m, but decreased 4 years after a fire to 93/100 m ($P = 0.03$). Shrub patch density in unburned control sites averaged 103/100 m, which was similar to that found in all burned sites. Shrub patch size was smallest (41 cm) 1 year after fire, and greatest (62 cm) 4 years after fire ($P < 0.01$) (Table 2).

A single fire lowered average visual obstruction values 1 year ($P < 0.01$) and 2 years ($P < 0.01$) post burn, but visual obstruction after 4 years was comparable to unburned sites ($P = 0.81$). Visual obstruction estimates were significantly different for the strata by treatment interaction ($P < 0.01$). Individually, strata 2-10 (20-100 cm) were different among treatments ($P < 0.05$) (Fig. 1). After 4 years, visual obstruction of sand shinnery communities was similar to unburned sites for all strata (Fig. 1).

Number of fires and time since fire interaction

We tested the interaction of time since fire and number of burns in determining the influence of fire in sand shinnery communities, and main effects ($P < 0.05$) were detected for all of the variables analyzed (Table 3). An interaction between number of fires and time since fire occurred for cone of vulnerability ($P = 0.04$) (Table 3), shrub patch density ($P < 0.01$) (Table 3) and shrub patch size ($P < 0.01$) (Table 3).

Shrub cover did not have an interaction ($P = 0.95$); however, both main effects, number of fires ($P < 0.01$) and time since fire ($P < 0.01$) were significant. Shrub cover increased with time since fire and after more than a single fire (Table 3). Shrub cover was greater (62%) on sites burned twice than on those burned only once (47%). Height did not have an interaction ($P=0.92$), but increased with time since fire ($P < 0.01$) and number of fires ($P < 0.01$) (Table 3). Average vegetation height for sites burned twice was 40.4 cm, while sites burned once averaged 31 cm. The cone of vulnerability had a significant interaction ($P = 0.04$) (Table 3). Cone of vulnerability was greater (more open structurally) following a single fire than after two fires ($P < 0.01$). Decrease in the cone of vulnerability following 2 fires was more rapid than after a single fire (Table 3). Patch density had an interaction ($P < 0.01$). For single fires, shrub patch density was

positively associated with increasing time since fire, but was associated negatively with time since fire on twice burned sites (Table 3). Shrub patch size also had an interaction ($P < 0.01$). Shrub patch size increased at a greater rate after the second fire compared with single event fires (Table 3).

Discussion

In the Great Plains, as well as other rangelands, many changes in vegetation structure and composition are caused by altered fire regimes (Hanes 1971, Collins et al. 1987). The importance of time since fire and number of fires on habitat structure of sand shinnery communities is largely unknown, but rapid resprouting following fire has been recognized (McIlvain and Armstrong 1966, Peterson and Boyd 1998). Similar oak communities, such as Madrean oak trees (*Quercus emoryi*) in Mexico have rapidly recovered following fire (Ffolliott and Bennett 1996). However, other shrubland ecosystems have not exhibited this high capacity for recovery from periodic disturbance. Composition and structure of the chaparral communities in southern California were altered after fire, with subsequent changes lasting < 3 decades (Hanes 1971, Zedler et al. 1983, Riggan et al. 1988). Our data indicated that fire influenced structure of sand shinnery communities by reducing the stature, visual obstruction, and canopy coverage of shrubs. Habitat structure of sand shinnery communities was highly resilient, recovering in 2--4 years after a fire. Shrub species composition was unaffected by fires. Two fires, 2 years apart, had less effect on habitat structure than the initial fire.

Response to disturbance of shrubland and forest communities may be determined by variable life history traits of dominant species (Noble and Slayter 1980). Species utilizing vegetative regrowth after fire regenerate more rapidly than those that reproduce

primarily by seed (Hobbs et al. 1984). Typically, species that have the ability to propagate through vegetative means allocate large amounts of resources to root systems to survive and resprout following fire damage, while species that reproduce primarily by seed rely on immediate post-fire dispersal, germination, and seedling growth to recover from disturbances (Hodgkinson 1998). Shrub communities in which reproduction by seed plays a large role in recruitment may be susceptible to long-term compositional and structural changes following a disturbance due to variable species response to disturbance (Tyler 1996). Extensive shifts in species composition cause secondary succession to proceed slowly. For example, the California chaparral, a shrub community in which seed germination is important, exhibits long-term changes in species composition following fire (Hanes 1971). Conversely, secondary succession advances rapidly in communities dominated by resprouting shrubs, permitting only short term changes in habitat structure and composition to occur.

Clonal species, such as sand shinnery oak, reproduce largely through vegetative means with sprouts arising from underground rhizomes, and rarely expend extra energy to produce seed (Cook 1985, Peterson and Boyd 1998). Germination of sand shinnery oak has not been reported under field conditions, but occasionally crops of acorns are produced (Dhillion et al. 1994, Peterson and Boyd 1998). The aboveground sprouts are resilient to disturbance, often resprouting rapidly after fire (McIlvain and Armstrong 1966). At a height of 0.3--1.5 m and consisting of clones as old as several thousand years, shinnery oak has the greatest ratio of underground to aboveground tissues of all American shrubs with estimates from 10:1 to 16:1 (Pettit 1986). The capacity of sand

shinnery oak to recover rapidly following a fire is expected because of its ability to resprout from a massive underground root system.

Our data suggested that recovery of sand shinnery oak habitat structure is more rapid after 2 burns than after a single fire. This is contrary to what was expected, considering past literature suggested that multiple fires may create more open habitat in shrubland communities (Scifres and Hamilton 1993). This may have resulted from a lack of adequate fine fuel available for a successful fire at the time of the second burn, resulting in lower fire intensity and lower woody plant mortality (Savage and Swetnam 1990, Fuhlendorf and Smeins 1997). Oak leaf litter is often the primary fine fuel available for successful fires in sand shinnery communities (Boyd and Peterson 1998), and our data indicated that at least 4 years is needed for accumulation of litter to attain preburn levels. Recovery of habitat structure was rapid (< 2 yrs), and subsequent fires were implemented at 2-year intervals. According to our data, creation of stable or long-term open habitat structure in sand shinnery communities through the use of prescribed fire would be difficult, requiring frequent fires and diligent grazing management to maintain adequate fine fuel loads.

Management Implications

Many rangelands throughout the world have been described as inherently unstable with marked fluctuations in species composition in response to many different disturbances and climatic variability (Walker 1993, Allen et al. 1995, Westoby et al. 1997). Sand shinnery communities, however, appear to be stable in respect to habitat structure and composition, even following fire. Lack of knowledge concerning the ecology of dominant species in this community and their response to disturbance has led

to haphazard management. Past research has focused on management to reduce sand shinnery oak, the dominant plant in these communities, through the use of herbicides (Peterson and Boyd 1998).

Federal agencies, such as Natural Resource Conservation Service and Bureau of Land Management, have identified sand shinnery oak as an invasive plant within sand shinnery communities. Undoubtedly, this classification has played a role in the broad-scale conversion of many shrubland communities to grasslands through herbicide applications, which can permanently change ecosystem structure and function (Peterson and Boyd 1998). Ecological consequences of herbicide use on sand shinnery communities include enduring changes in community structure and composition, wind erosion, and potential concomitant effects on sensitive wildlife species. Pettit (1979) stated, "These lands are perhaps the most fragile of all ecosystems on the southern High Plains of Texas and the landowner cannot afford to abuse them." As a short-term management tool, fire can alter habitat structure of sand shinnery communities, minimizing permanent effects associated with herbicides. Management schemes that avoid crossing permanent thresholds recognize the unique ecological values of sand shinnery communities and their importance in providing critical wildlife habitat.

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Table 1. Frequency of occurrence (%) and standard error (SE) of shrub species in sand shinnery communities of Black Kettle National Grassland, Oklahoma following prescribed fire, 1998-1999.

Shrub species	Time since fire (year)			
	1 (SE)	2 (SE)	4 (SE)	Control (SE)
Sand Shinnery-Oak (<i>Quercus havardii</i>)	94 (1.3)	98 (0.79)	96 (0.08)	96 (1.14)
sandsage (<i>Artemisia filifolia</i>)	9.4 (3.3)	4.5 (1.08)	7.9 (1.73)	8.0 (2.16)
skunkbush (<i>Rhus aromatica</i>)	2.6 (1.88)	2.1 (0.84)	0.40 (0.40)	2.0 (1.40)
sand plum (<i>Prunus spp.</i>)	1.1 (0.91)	0.92 (0.66)	0.27 (0.27)	1.66 (1.58)
soapweed yucca (<i>Yucca glauca</i>)	0.41 (0.08)	0.12 (0.12)	0.40 (0.40)	0.82 (0.40)
netleaf hackberry (<i>Celtis reticulata</i>)	0 (0)	0 (0)	0.40 (0.40)	0.07 (0.07)
leadplant (<i>Amorpha canescens</i>)	0 (0)	1.83 (1.83)	0 (0)	0.42 (0.42)
catclaw mimosa (<i>Mimosa biuncifera</i>)	0.25 (0.25)	0 (0)	0 (0)	0.07 (0.07)
honey mesquite (<i>Prosopis glandulosa</i>)	0.06 (0.06)	0 (0)	0 (0)	0(0)

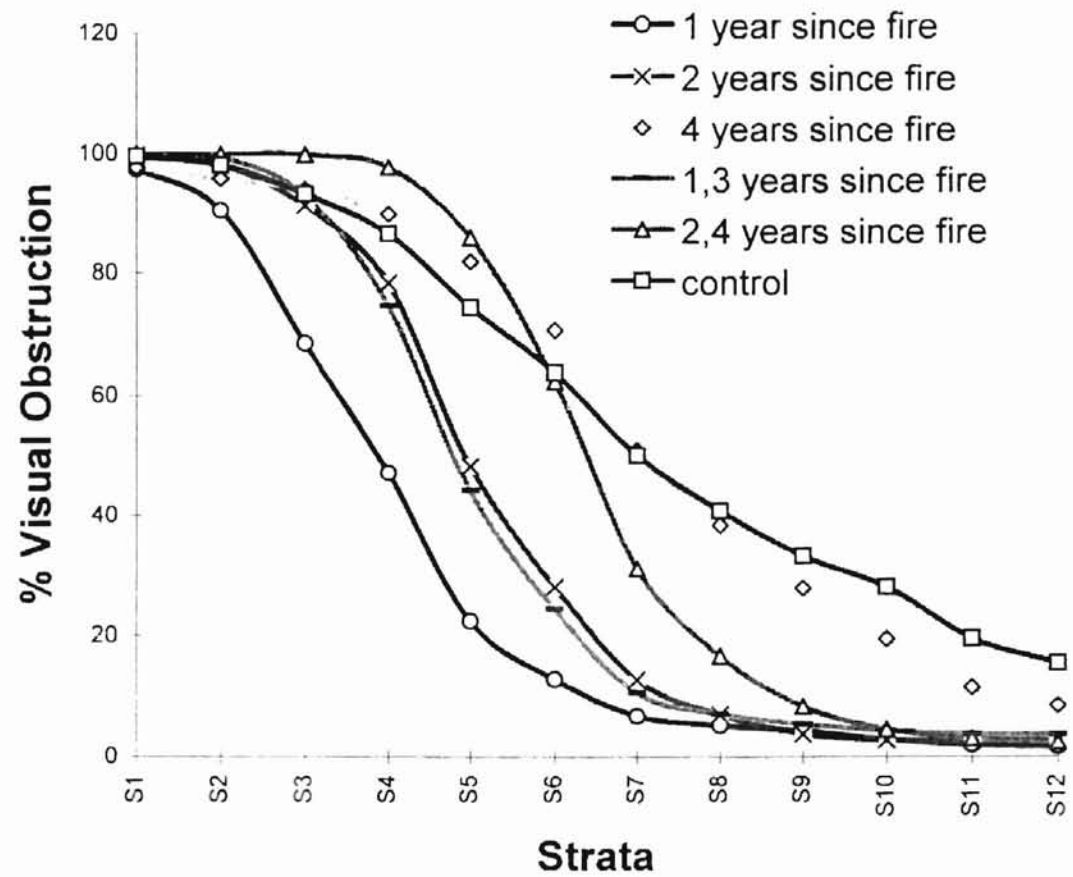
Table 2. The effect of time since fire on structural and compositional responses of sand shinnery communities following prescribed fire at Black Kettle National Grassland, Oklahoma (1998-1999). Means in rows followed by the same letters are similar ($P = 0.05$) by least significant means test.

Habitat Variable	Time since fire (years)			
	1	2	4	Control
Cone of Vulnerability ($m^3 \times 10^{-3}$)	1105.0a	492.0b	445.0b	514.0b
Height (cm)	26.2a	35.3b	42.4bc	43.9c
Shrub (%)	38.0a	56.0b	56.0b	51.0b
Litter (%)	22.0a	21.0a	34.0b	34.0b
Herb (%)	37.0a	21.0bc	7.0d	14.0cd
Shrub Patch size (cm)	41.2a	51.0ab	62.1b	51.9ab
Shrub Patch density (no. /100 m)	92.0a	110.0b	93.0a	103.0ab
Visual Obstruction (%)	30.0a	40.0b	57.0c	59.0c

Table 3. The effect of time since fire (TSF) and number of fires (NF) interaction on structural responses of sand shinnery communities following prescribed fire at Black Kettle National Grassland, Oklahoma (1998-1999). Significant interactions ($P < 0.05$) are indicated by $TSF \times NF$, and significant main effects ($P < 0.05$) are indicated by TSF, NF.

Habitat Variable	1 year since fire		2 years since fire		Significant effect
	1 fire	2 fires	1 fire	2 fires	
Cone of Vulnerability ($m^3 \times 10^{-3}$)	1105.0	632.0	492.0	198.0	$TSF \times NF$
Height (cm)	26.2	36.1	35.3	44.7	TSF, NF
Shrub (%)	38.0	53.0	56.0	71.0	TSF, NF
Shrub patch size (cm)	41.2	38.9	51.0	77.1	$TSF \times NF$
Shrub patch density (no./ 100 m)	92	137	110	93	$TSF \times NF$

Figure 1. Visual obstruction profiles in sand shinnery communities following prescribed fire at Black Kettle National Grasslands, Oklahoma 1998-1999. S1-S12 represents increasing height from ground-level (S1) to 120 cm (S12). Legend indicates the visual obstruction curves for time since fire treatments ($P < 0.05$, Wilk's Lambda statistic).



CHAPTER III

Evaluation of habitat structural measures in sand shinnery communities

Abstract: Habitat structure often determines wildlife responses to various habitat management practices, but little information is known concerning exactly what dimension, vertical or horizontal, is measured with a given technique. The general goal of this study was to quantify relationships among several techniques that are commonly used to measure habitat structure. Objectives of the study were to evaluate relationships between measures of habitat structure in sand shinnery communities, determine which measures correlate with structural variation explained in the vertical and horizontal dimensions, and evaluate the usefulness of several techniques in merging structural heterogeneity in 3 dimensions.

Visual obstruction estimates, using a profile board, adequately measured variability in the vertical dimension of structure as indicated by its association with height in a principal components analysis. Many of our variables related to vertical structure, and hence, were redundant with each other. Shrub patch density was orthogonal to height (vertical structure) and was the only variable that directly measured variability in the horizontal dimension of structure. The cone of vulnerability and angle of obstruction provided useful, single indices to measure both dimensions of habitat structure. Knowledge of the relationships among structural measures and the dimension of habitat

structure measured enables managers and researchers to choose efficient and meaningful techniques.

Key Words: cone of vulnerability, gallinaceous bird, habitat, vegetation structure, sand shinnery, visual obstruction

Introduction

Quantifying habitat structure is crucial to identifying wildlife habitat (Rotenberry and Weins 1980, Schulte and Niemi 1998, Sutter and Brigham 1998). Vegetation structure has been identified as a key habitat feature for gamebirds in particular (Guthery 1996). Species composition and abundance of mammals, birds, reptiles, and insects are affected by habitat structure directly through mechanical effects such as providing nesting cover and indirectly through changes in microclimate (Bell et al. 1991). However, concrete definitions of habitat structure are difficult to obtain. Past literature dealing with habitat structure often avoids definitions entirely because of the apparent confusion (Verner et al. 1986). Other definitions simply use juxtaposition of vegetation features to explain habitat structure (Bookhout 1994). Guthery (1996:63) stated that "structure refers to the height, density, biomass, and dispersion of herbaceous and woody vegetation." Rotenberry and Weins (1980) defined habitat structure as the physical configuration of a terrestrial environment provided by vegetation. Some attempts to define habitat structure describe 2 dimensions, vertical and horizontal, which dictate this physical configuration of vegetation in space (Smith 1986). However, past explanations of the relationships between horizontal and vertical dimensions of habitat structure have been imprecise, and

there is little information evaluating the appropriateness of individual measurement techniques in consolidating these dimensions (Rotenberry and Weins 1980).

Techniques used to monitor habitat structure are diverse, and minimal descriptions of relationships between different techniques often result in poorly designed habitat evaluations. Traditional techniques to measure vegetation structure such as plot sampling and line-intercept methods often focus on estimates of cover provided by various plant functional groups, which are often correlated well with structure (Bonham 1989). Tools such as profile boards and Robel poles can provide measures of structure in different vegetation communities by estimating visual obstruction (Guthery et al. 1981). Recently, a 3-dimensional technique, the cone of vulnerability (Kopp et al. 1998), was developed in an attempt to collapse infinitely diverse structural features into a single index of structure (F. S. Guthery, personnel communication). Coefficients of variation of the aforementioned techniques are often touted as a way to measure horizontal heterogeneity (Roth 1976, Madden et al. 1999). Other approaches to measuring horizontal heterogeneity, such as landscape level investigations, focus on variably scaled spatial patterns in communities (McGarigal and McComb 1995). All of these techniques vary as to the dimension and proportion of variation in habitat structure that they explain, yet few studies have evaluated the relationships between different approaches. Furthermore, it is important to search for measurements that optimize variation in 3 dimensions into an index of habitat structure (Rotenberry and Weins 1980). Our objectives were to (1) evaluate relationships between measures of habitat structure in sand shinnery communities to determine which measures correlate with structural

variation explained in the vertical and horizontal planes, and (2) evaluate the usefulness of several techniques in merging structural heterogeneity in 3 dimensions.

Study area

Study sites were sand shinnery communities on the Black Kettle National Grasslands (BKNG) in Roger Mills County, Oklahoma and adjacent private land in Hemphill County, Texas. Sand shinnery communities are the largest of the oak forest communities found in the United States, occupying about 2--3 million ha in the southern Great Plains (Peterson and Boyd 1998). These oak communities are only 0.25-1.5 m tall, and are classified as shrublands. Sand shinnery oak (*Quercus havardii*) is the dominant species, with sand sagebrush (*Artemisia filifolia*) and a variety of grasses often codominating.

Sand shinnery communities support a wide variety of wildlife species including mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), pronghorn antelope (*Antilocapra americana*), peccary (*Dicotyles tajacu*), lesser prairie-chickens (*Tympanuchus pallidicinctus*), northern bobwhites (*Colinus virginianus*), Rio Grande turkeys (*Melagris gallopavo*), mourning doves (*Zenaida macroura*), various species of songbirds, lagomorphs, rodents, reptiles, and invertebrates (Peterson and Boyd 1998). Of these species, lesser prairie-chickens are most closely associated with sand shinnery communities. Historically, lesser prairie-chickens were found on the BKNG, but are apparently absent now (Biodiversity Legal Foundation 1998).

Black Kettle National Grasslands were formed in 1953 after the U. S. Forest Service was granted authority over 13,476 hectares (Burgess et al. 1963). Currently, BKNG are used for recreational activities such as camping and hunting, as well as leased

grazing. All sites sampled were grazed by cattle at light to moderate rates (ca. 1.5 ha/AUM) relative to Natural Resource Conservation Service (NRCS) recommendations. The BKNG is not contiguous, but consists of a series of land fragments ranging in size from 10 to 500 ha (Burgess et al. 1963). The climate of the region is semiarid, with mean August and January temperatures of 28.0°C and 2.7°C, respectively. The area has an average growing season of 209 days, with a mean rainfall of 65 cm (Burgess et al. 1963). Precipitation is highly variable with a bimodal distribution of rainfall with peaks in May-June and August-September. Topography of the area consists of rolling hills, with variable altitudes ranging from 518 to 793 m above sea level.

Methods

Site Selection

We randomly chose sample sites within available sand shinnery communities on the BKNG and adjacent private land. We classified each site as deep sand savannah or sandy prairie sites according to county soil maps (Burgess et al. 1963). Sites on BKNG had various prescribed fire histories ranging from unburned to burned as recently as 1 growing season prior to sampling. Private land had a past history of herbicide applications to reduce shrub cover. Preliminary analysis indicated that this variable management history led to a wide range of structural variation among sites.

Measures of habitat structure

We measured habitat structure during the growing seasons of 1998 and 1999. Eighty-four 100-m line transects were used to measure relative canopy cover of the dominant plant functional groups (shrub and herbaceous; Bonham 1989). Shrub cover was considered dominant if both plant functional groups were present and total cover on a

line added to 100%. Average size of shrub patches and shrub patch density were determined from the line-transect data by summing the number of distinct shrub patches and averaging their linear lengths. Minimum resolution used to define plant functional group cover along the transect was 10 cm. Height measurements of vegetation were taken at a point every 1 m along the transect.

We estimated visual obstruction every 10 m along the transect using a profile board as described by Nudds (1977) and modified for sand shinnery communities by Guthery et al. (1981). The 6.8-cm-wide profile board had 12 strata, with each stratum being 10 cm tall. Estimates were taken perpendicular to the line transect at a distance of 7 m, with the observer kneeling at a height of 1.5 m over the transect. Percent visual obstruction was estimated for each stratum.

We measured the cone of vulnerability (Kopp et al. 1998) every 10 m along the transects. The cone of vulnerability is a 3-dimensional view of visual obstruction and has been identified as a measure that quantifies habitat structure important northern bobwhites (Kopp et al. 1998). We assessed the cone of vulnerability by measuring angles in 8 directions (N, NE, E, SE, S, SW, W, NW) from a point located 10 cm above the ground to the top of the nearest obstructing vegetation. We considered the average of the 8 angles for each point the angle of obstruction. We then used the angle of obstruction to calculate the volume of the air space included within a cone (Kopp et al. 1998). A larger cone of vulnerability equates to a structurally more open habitat, that is less visual obstruction. The angle of obstruction used in determining the cone of vulnerability is formed by 2 basic components, height of nearest obstructing plant and distance from the

point of measure to the plant (Fig. 1). These components suggest the potential of this measure to integrate the vertical and horizontal dimensions of habitat structure.

Data Analysis

We conducted a principal components analysis (PCA) on 84 transects using CANOCO software (ter Braak and Smilauer 1998) to assess the relationships among the structural measures, identify structural variables that were redundant, and determine the percent of structural variation explained by various dimensions of habitat structure. The variables for each transect included in the PCA were shrub cover, herbaceous cover, mean cone of vulnerability, mean angle of obstruction, mean shrub patch size, shrub patch density, mean vegetation height, percent visual obstruction of stratum 1 through stratum 12, the mean of all visual obstruction values, and coefficient of variation (CV) for the cone of vulnerability, angle of obstruction, height, and visual obstruction. We analyzed the cone of vulnerability and angle of obstruction separately to determine if the transformation from an angle to a volume had an effect on their relationship to other measures. Matrix scaling in the PCA focused on inter-variable correlations, with all variables centered and standardized. Correlations using linear and second order polynomials were used to further explore relationships of several meaningful variables, verify our PCA, and obtain probability values (SAS Institute Inc. 1988). We determined the best fit line by choosing the model that maximized the r^2 and minimized MSE.

Results

The spectrum of habitat structural conditions that would typically be encountered in shrubland communities with diverse management histories were present in our data. Shrub cover ranged from 4 to 86% with a mean of 50%. Average height of vegetation

along each transect ranged from 13 to 88 cm with a mean of 38 cm. Shrub patch density ranged from 13 to 166/100 m with a mean of 95/100 m. The cone of vulnerability ranged from $19 \text{ m}^3 \times 10^{-3}$ to $1,782 \text{ m}^3 \times 10^{-3}$ with a mean of $667 \text{ m}^3 \times 10^{-3}$.

Variation in structure explained by axis 1 and axis 2 of the PCA were 0.579 and 0.174, resulting in a cumulative total of 75.3%. Axis 3 and 4 of the PCA did not contribute substantial variation using the variables that we measured. Axis 1 and 2 of the PCA were related to measures of variation in the vertical and horizontal dimensions of habitat structure, respectively (Fig. 2). Measures typically associated with vertical structure, such as mean visual obstruction and mean vegetation height, were strongly correlated with axis 1 of the PCA, but were not correlated with axis 2 (Table 1). Other variables that were associated with axis 1 included mean cone of vulnerability, cone of vulnerability CV, mean angle of obstruction, angle of obstruction CV, mean shrub patch size, shrub cover, herbaceous cover, and strata 3--11 of the profile board (Table 1, Fig. 2). Most of these structural measures were highly correlated with each other (Table 1).

Shrub cover had high positive correlations with mean shrub patch size, mean vegetation height, cone of vulnerability CV, mean angle of obstruction, and strata 3--5 of the profile board (Table 1). Mean cone of vulnerability, angle of obstruction CV, and herbaceous cover had high negative correlations with shrub cover (Table 1). CVs for angle of obstruction and cone of vulnerability had a strong negative correlation ($r = -0.737, P < 0.01, r = -0.837, P < 0.01$), indicating that CVs for these techniques are in disagreement with each other as to the variability within this community.

Shrub patch density had the highest component score on axis 2 of the PCA (Table 1) and low linear correlations with the other variables in our analysis (Table 2). When a

second order polynomial regression was applied, shrub patch density had a quadratic relationship with shrub cover (Fig. 3). Shrub cover, herbaceous cover, angle of obstruction, cone of vulnerability, and strata 7--11 of the profile board had relatively high component scores for both axes, indicating that these variables were correlated with both the vertical and horizontal dimensions of habitat structure (Table 1, Fig. 2).

Discussion

Past studies often either fail to quantify the dimension (vertical or horizontal) of vegetation structure measured or measure structure in a single dimension (Haensly et al. 1987, Goguen and Mathews 1998, McKee et al. 1998). Our results were similar to Rotenberry and Weins (1980) findings, suggesting that vertical and horizontal structural components are not strongly correlated. Furthermore, our data suggested that many commonly used measures of habitat structure are redundant measures of vertical structure, and few adequately measure variability in the horizontal dimension. A few quantitative measures from our data, cone of vulnerability and angle of obstruction, integrated variation in both dimensions, and may be critical in the development of a simple index of habitat structure.

Horizontal structure is often defined in terms of habitat patchiness or porosity (Forman and Godron 1986, Bell et al. 1991). Patchiness is a more accurate predictor of bird species diversity than vertical variability (MacArthur et al. 1962, Roth 1976). Shrub patch density was the only variable in the PCA that directly related to variation in the horizontal dimension of structure, explaining the most variation on axis 2. Physical characteristics of vegetation, such as shrub patch density, that measure horizontal

structure are often measured at the landscape level, (Forman and Godron 1986, McGarigal and McComb 1995) but rarely at a habitat-patch level.

Past literature has used the coefficient of variation for height or visual obstruction as a measure of horizontal patchiness of a structural attribute (Roth 1976, Madden et al. 1999). Coefficient of variation only measures variation around a mean, whereas shrub patch density measures spatially explicit horizontal variation. The PCA suggested that the mean vegetation height and mean visual obstruction measured vertical structure, and their CVs measured attributes more closely related to horizontal variability. However, the PCA also indicated that CVs for angle of obstruction and cone of vulnerability were strictly a function of their respective means, and do not provide meaningful, independent data. In fact, the cone of vulnerability CV suggests that the greatest amount of horizontal variability occurred at high levels of shrub cover, while the angle of obstruction CV indicated that the highest horizontal variability was at low levels of shrub cover. Though angle of obstruction CV is likely more appropriate than the cone of vulnerability CV because angle of obstruction data have not been transformed, neither agreed with other measures of horizontal variability. Relationships of shrub patch density with shrub cover, as well as landscape-level models, suggest that the greatest amount of horizontal variability occurs at intermediate levels of shrub cover (Fig. 3; Hargis et al. 1997).

Estimating visual obstruction using density or profile boards with multiple strata has been employed as a method to quantify structural density of vegetation (Nudds 1977, Guthery et al. 1981, DeFazio et al. 1988). Our data suggested that average visual obstruction is redundant with height; and therefore, primarily measures vertical structure of vegetation. However, examining the 12 individual strata of the profile board

independently gave a wide range of information, including horizontal and vertical structure, that was not gained from any other single measure. The greatest challenge in quantifying vegetation structure using visual obstruction is associated with data analysis. To analyze data from a density board without violating statistical assumptions of independence, each stratum should be considered dependent on the lower strata. This results in a complex vector of interdependent variables instead of a single index.

The angle of obstruction and cone of vulnerability are recently developed techniques that have potential to integrate multiple dimensions of habitat structure. Cone of vulnerability is calculated from the angle of obstruction (A), which is a function of the height (v) of a plant and the ground distance (h) of the plant from a point in space, indicating that it is a direct mathematical integration of vertical and horizontal dimensions of habitat structure (Fig. 1). The PCA supported this, suggesting that the cone of vulnerability and the angle of obstruction are an integration of vertical and horizontal structure. A recent model suggests that an ideal landscape for northern bobwhites would be comprised of an average cone of vulnerability of $691 \text{ m}^3 \times 10^{-3}$, shrub cover of 53%, and relatively high variability ($CVs > 50\%$) (Kopp et al. 1998). A technique, such as the cone of vulnerability or angle of obstruction, that integrates the horizontal and vertical components of habitat structure could be used as a measure of overall structural heterogeneity in shrubland communities.

All of the sites were considered shrublands. Consequently, management that alters shrub composition or arrangement can change overall habitat structure drastically in these communities. At a high level of shrub dominance, alterations in habitat management practices, such as grazing, that primarily change herbaceous structure and composition

may not change the overall habitat structure appreciably (Guthery 1996, Goguen and Mathews 1998). Conversely, habitat management practices, such as herbicide applications, that reduce shrub dominance alter habitat structure dramatically (Guthery 1996). As shrub cover decreases in a community, practices such as grazing that change herbaceous vegetation structure and composition begin to have a larger role in dictating overall habitat structure (Guthery 1996). Habitat structure dictated by herbaceous vegetation may result in greater variability and short term fluctuations in response to local management and year-to-year weather changes.

Conclusions

Various habitat management practices influence both the vertical and horizontal dimensions of vegetation structure differently, yet often studies only measure a single dimension of structure. Choosing multiple techniques that measure distinct dimensions of habitat structure or a single measure that integrates multiple dimensions is crucial in the design of efficient field studies. The cone of vulnerability and angle of obstruction performed well at integrating the vertical and horizontal dimensions of habitat structure in sand shinnery communities. Incorporation of the cone of vulnerability or angle of obstruction in future research may lead to a better understanding of the relationship of this technique to the response of wildlife to changes in structure following habitat management practices such as fire and herbicide use. Individual strata along a profile board also provided information about multiple structural dimensions. Shrub patch density provided more information about horizontal variability than did the coefficient of variation for height and visual obstruction. These data suggested that more effort should focus on defining appropriate techniques to monitor habitat structure.

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Table 1. Component scores and correlation coefficients of habitat structural variables for sand shinner communities in Oklahoma and Texas, 1998-1999. Component scores reflect degree of correlation with vertical (axis 1) and horizontal (axis 2) habitat structure represented by 2 orthogonal axes of a principal component analysis.

Habitat Variable	PCA Axis 1 Scores	PCA Axis 2 Scores	Shrub Cover (%)	Shrub Patch Density
Shrub cover	0.840**	-0.340**		0.391**
Herbaceous cover	-0.765**	0.245*	-0.838**	-0.510**
Height	0.886**	0.112	0.732**	-0.0356
Height (CV)	-0.312**	0.449**	-0.410**	-0.103
Cone of vulnerability	-0.864**	0.387**	-0.896**	-0.402**
Cone of vulnerability (CV)	0.822**	-0.167	0.765**	0.072
Angle of obstruction	0.881**	-0.351**	0.883**	0.335**
Angle of obstruction (CV)	-0.679**	0.390**	-0.742**	-0.387**
Visual obstruction	0.955**	0.252*	0.675**	-0.026
Visual obstruction (CV)	-0.516**	0.478**	-0.552**	-0.222*
Stratum 1	0.441**	-0.468**	0.386**	0.290**
Stratum 2	0.612**	-0.478**	0.540**	0.288**
Stratum 3	0.810**	-0.407**	0.739**	0.359**
Stratum 4	0.892**	-0.297**	0.809**	0.301**
Stratum 5	0.921**	-0.062	0.752**	0.115
Stratum 6	0.918**	0.1701	0.672**	-0.025
Stratum 7	0.862**	0.398**	0.556**	-0.154
Stratum 8	0.822**	0.507**	0.487**	-0.202
Stratum 9	0.784**	0.582**	0.438**	-0.211
Stratum 10	0.739**	0.611**	0.390**	-0.203
Stratum 11	0.709**	0.605**	0.394**	-0.200
Stratum 12	0.676**	0.584**	0.394**	-0.191
Shrub patch size	0.790**	0.189	0.730**	-0.282**
Shrub patch density	0.1250	-0.655**	0.391**	

** $P < 0.01$, * $P < 0.05$

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Fig. 1. Depiction of measurement components to determine cone of vulnerability (an integration of vertical and horizontal dimensions of habitat structure) where: v = height of obstruction (vertical structure), h = distance from random point to base of obstruction (horizontal structure), c = line used to determine angle of obstruction, A = angle of obstruction ($\arcsin h/c$). Adapted from Kopp et al. (1998).

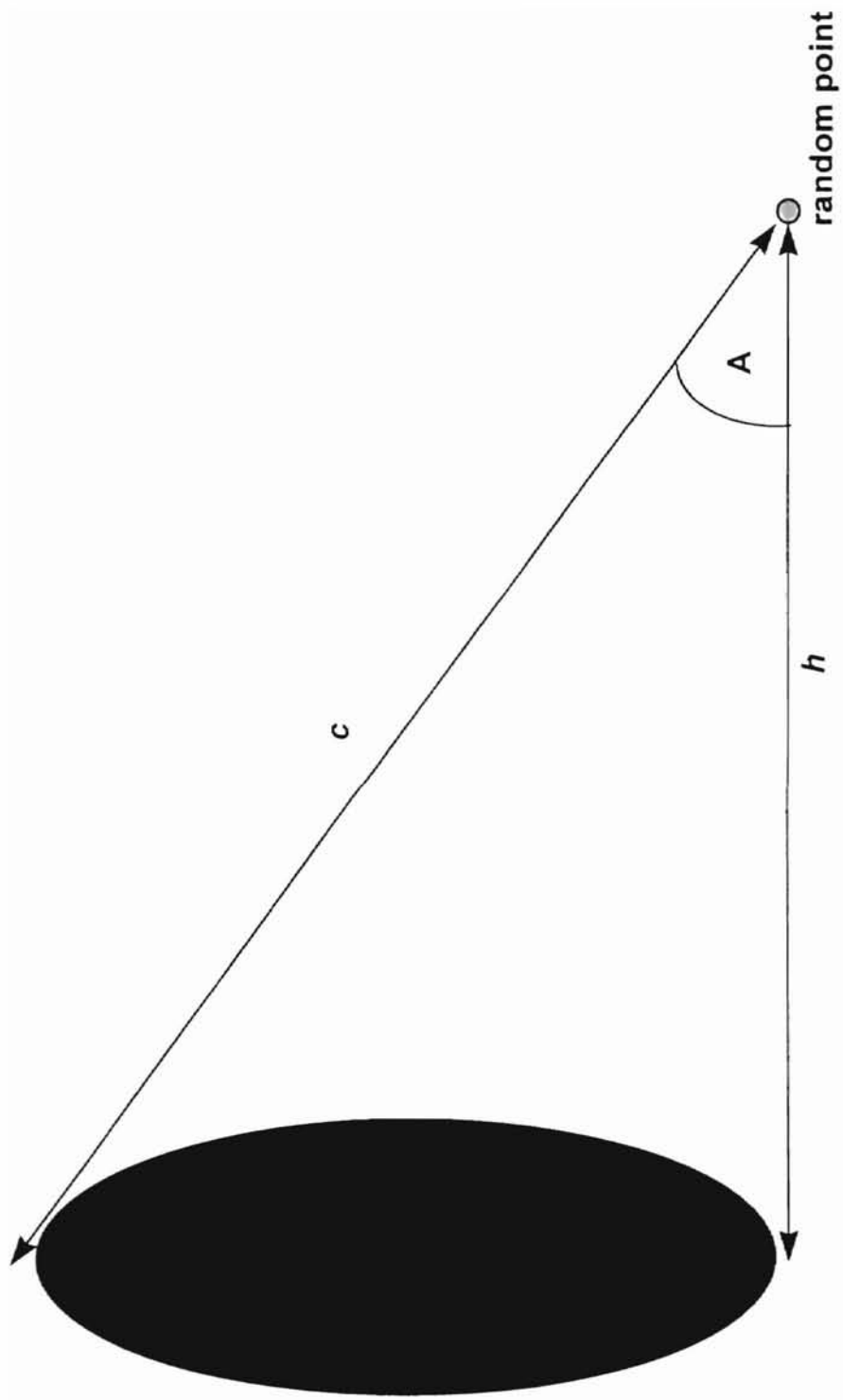


Fig. 2. Principal components analysis of vertical and horizontal structural relationships among habitat variables for sand shinnery communities in Oklahoma and Texas, 1998-1999. Arrows pointing opposite of one another depict negative relationships, arrows pointing in the same direction depict positive relationships, and arrows at right angle depict orthogonality. Strata 1--12 (S1--S12) represent individual strata along a density board from ground level to 120 cm at 10-cm intervals.

Oklahoma Sand Shinnery Communities, 1998-1999

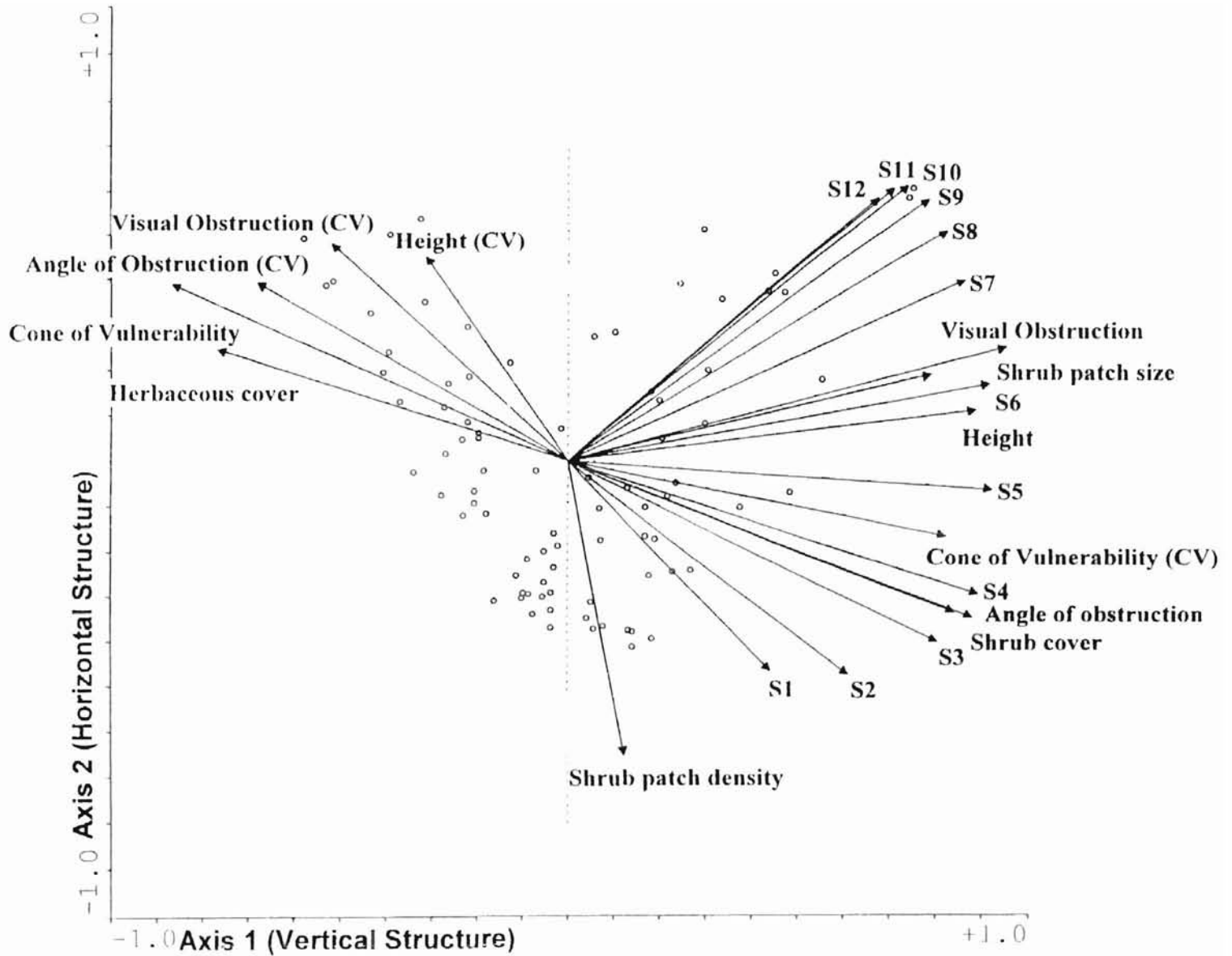
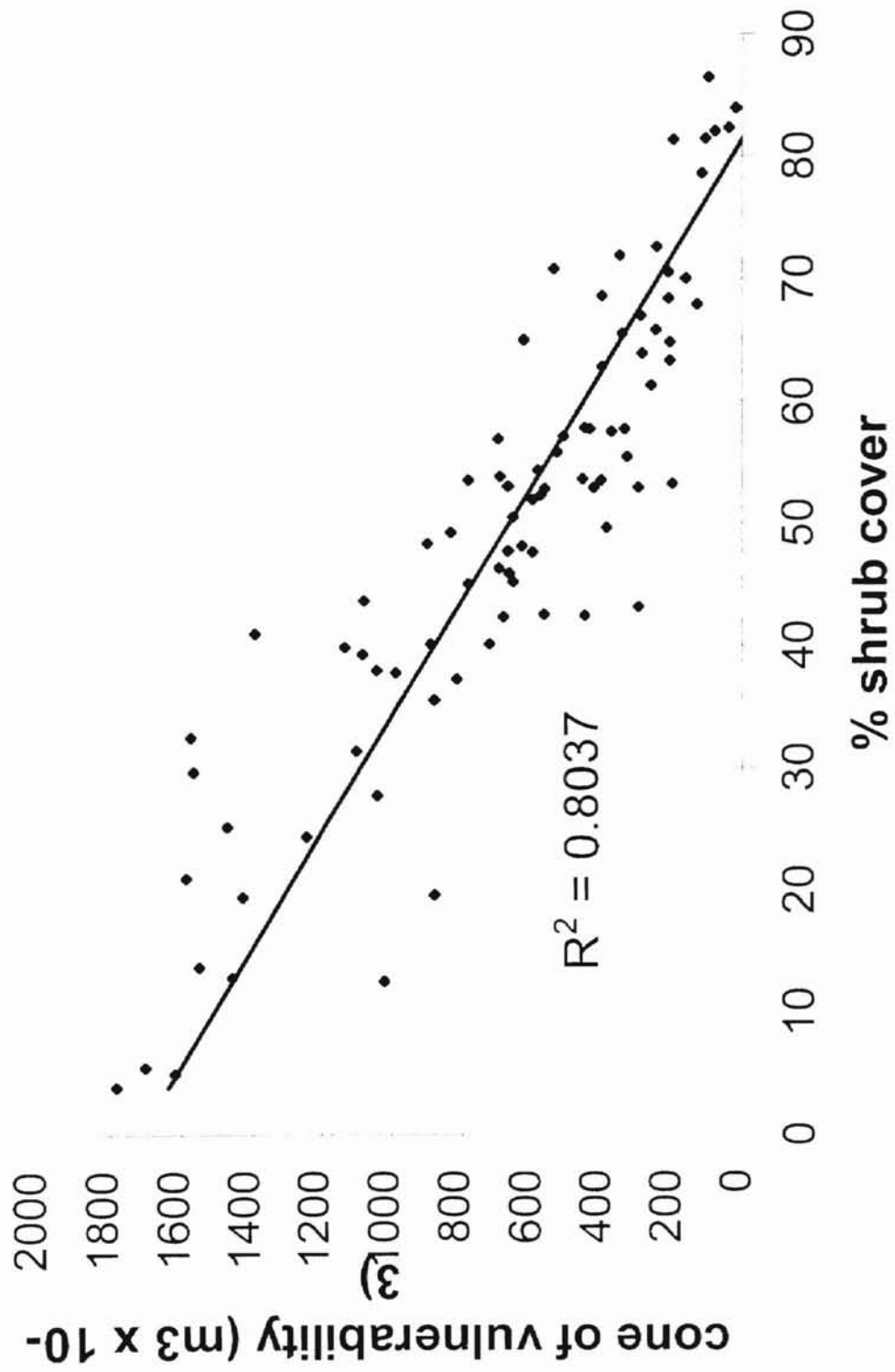


Fig. 3. Quadratic relationship between shrub patch density and percent shrub cover from 84 line transects in sand shinnery communities of Oklahoma and Texas, 1998-1999. Shrub patch density and shrub cover were taken at 10-cm intervals along 100-m line transects.

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CHAPTER IV

Historical changes in woody plant dominance of sand shinnery communities

Abstract

Differences in historical accounts and current landscape compositions suggest that density and cover plants as well as spatial arrangement of woody plants in sand shinnery communities have changed over time. We used stable carbon isotope analysis to determine if relative proportions of woody plants and grasses differed between historic and current sand shinnery communities. Increasing $\delta^{13}\text{C}$ with depth in the soil profile indicated that historically, these rangelands had lower relative dominance of woody plants than recent landscapes. Furthermore, greater CV of $\delta^{13}\text{C}$ beneath the soil surface indicated that spatial arrangement of vegetation was historically more heterogeneous than that of current sand shinnery communities. Extensive studies are needed that use carbon dating to identify when these community compositional changes took place, and to further examine proximate causes for the increase of woody plants within sand shinnery communities.

Introduction

Sand shinnery communities occupy 2--3 million ha of rangeland in the southwestern United States (Peterson and Boyd 1998). These communities extend from northern Texas and western Oklahoma southward into the Chihuahuan Desert and are dominated by sand shinnery oak (*Quercus havardii* Rydb.), a member of the white oak group. Sand shinnery communities are one of the few shrub-dominated vegetation types

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in the southwestern United States that have been documented as threatened (Dhillon et al. 1994, Bailey and Painter 1994). Historical accounts of sand shinnery communities in western Oklahoma document a dense growth of dwarf oak vegetation about 45 cm high which seemed to have attained full maturity (Marcy 1854). Currently the dominant shrub of these communities, sand shinnery oak, appears to be taller and denser on some rangelands than many historical accounts describe. Alterations in fire and grazing regimes since European settlement may have increased density and cover of woody plants and altered spatial arrangement of sand shinnery communities (Peterson and Boyd 1998). This assumption has been used by the Natural Resource Conservation Service (NRCS) and Bureau of Land Management (BLM), as partial justification for the broad-scale conversion of these shrubland communities to grasslands through herbicide applications. However, most reports suggest that shrub abundance is not drastically altered by natural disturbances such as fire (McIlvain and Armstrong 1966), indicating that sand shinnery communities are stable and resilient. Lack of extensive reproduction by seed for sand shinnery oak and reconstruction of composition in the pollen record characterizing a stable existence for hundreds of years also questions the historical fire-driven dynamics of sand shinnery communities (Beckett 1976, Gross and Dick-Peddie 1979).

Stable carbon isotope ($\delta^{13}\text{C}$) analysis has been used to assess the stability of woody-herbaceous interactions (Tieszen and Archer 1990, Boutton et al. 1998). The majority of carbon in natural systems is in the isotopic form carbon-12, while only a small percentage (1.11%) is in the form of carbon-13. These 2 forms fractionate and result in samples of carbon that are enriched or depleted in the relative proportion of

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carbon-13. Mass balance of both carbon forms is always maintained, so 1 compartment in organic carbon samples is depleted in carbon-13, while another is enriched, resulting in variable ratios of carbon-13/carbon-12. This ratio can be measured in vegetation and soil organic matter using a ratio isotope mass spectrometer. In the southwestern United States, most grasses utilize a C4 carbon pathway, while woody plants utilize a C3 carbon pathway. C4 plants are depleted slightly more than bulk atmospheric air (around $-12.5 \delta^{13}\text{C}$ vs. $-7 \delta^{13}\text{C}$), and C3 plants are depleted more strongly (around $-26.5 \delta^{13}\text{C}$). Differences in carbon discrimination persist in organic carbon within the soil. Isotopic ratios can thus be used as tracers for quantitative and qualitative ecological change in communities that represent fluctuations in the relative dominance of C3 plants (mostly woody) and C4 plants (grasses). Historic changes in ratios of woody plants to grasses can be described as soil is sampled at an increasing depth.

For this study, the ability of isotopic ratios to distinguish carbon sources (C3 or C4 plants) and quantitatively estimate their relative contributions to community composition was of major interest. Isotopic ratios have been used in other areas of North America ranging from prairie to woodland landscapes (Boutton et al. 1998), and has the potential to identify differences between the historical dominance of woody plants and the current ratio of woody plants and grasses within communities. Our objective was to determine if relative proportions of woody plants and grasses differed between historic and current sand shinnery communities using stable carbon isotope analysis.

Study Area

Study sites were in sand shinnery communities on the Black Kettle National Grasslands (BKNG) in Roger Mills County, Oklahoma (35° 37', 100° 40'). The Black Kettle National Grasslands were formed in 1953 after the Forest Service was granted authority over 13,476 ha (Burgess et al. 1963). Currently, BKNG are used for recreational activities such as camping and hunting, as well as leased grazing. The climate of the region is semiarid, with mean August and January temperatures of 28.0°C and 2.7°C, respectively (Burgess et al. 1963, Dhillion and Mills 1999). The area has an average growing season of 209 days, with a mean rainfall of 65 cm (Burgess et al. 1963). Precipitation is highly variable with a bimodal distribution of rainfall with peaks in May-June and August-September. Topography of the area consists of rolling hills, with variable altitudes ranging from 518 to 793 m above sea level.

Sand shinnery communities are usually found on fine sands characterized by moderate to high permeability, low water erosion, high susceptibility to wind erosion, and low nutrient and organic matter levels (Pettit 1986, Peterson and Boyd 1998). The high root/shoot ratio of sand shinnery oak and the erosiveness of the sites where sand shinnery is found indicate the importance of its structure to site stability. A typical soil series associated with sand shinnery oak, such as Brownfield, has a surface horizon of 92% sand, is 25 to 100 cm thick, and is highly permeable. Underlying the sand is a sandy-clay-loam subsoil up to 160 cm deep and moderately permeable (Dittemore and Hyde 1964, Pettit and Deering 1974, Zobeck et al. 1989). Some sand shinnery soils lack any clay layer. In general, as the clay content increases, sand shinnery oak cover decreases

(Pettit 1986). The Brownfield series and other associated sandy soils were influenced by formations of the Pliocene, Pleistocene, and recent epochs of the Tertiary and Quaternary ages (Burgess et al. 1963). Most deep sands essential to the persistence of sand shinnery communities were formed during the post-Pleistocene drying of the Southern Great Plains (Weaver and Clements 1938, Huffington and Albritton 1941).

Methods

Soils were collected from sand shinnery communities on the BKNG. Cores were collected with a hand-held soil auger from 16 random locations. Soil cores (5 cm x 150 cm) collected for analysis were divided into 6 depths (0-15 cm, 16-30 cm, 31-60 cm, 61-90 cm, 91-120 cm, and 121-150 cm) and coarse roots removed by hand. Stable carbon isotope analysis of soils followed descriptions by Boutton et al. (1998). Samples were dried at 60°C, ground to pass through a 2-mm screen, and fine roots removed from the soil by flotation in saturated NaCl solutions. Soils found free of particulate organic matter were treated with 1 N HCl at 25°C for 3 days to remove carbonate carbon, washed to neutrality with distilled water, dried, and pulverized. Particles of separate size were then dried, pulverized, and saved for isotopic analysis. Analysis of soil cores included total carbon, total nitrogen, and CaCO₃ carbon equivalent. Carbon signatures for C3 and C4 plants were analyzed throughout the soil profile. We used a completely randomized design to evaluate differences in $\delta^{13}\text{C}$ levels at various soil depths. Statistical differences in $\delta^{13}\text{C}$ were assessed using one-way analysis of variance (PROC MIXED, SAS Institute Inc. 1988). Differences between means at varying soil depths were determined using least square means ($P < 0.05$).

Results and Discussion

All soils sampled contained no CaCO_3 layer in the first 15 cm of the soil profile. A CaCO_3 layer occurred in 9 of 16 samples at varying depth from 16 to 120 cm. Overall organic carbon and total nitrogen were low throughout the soil profile, and decreased with increasing depth (Table 1). $\delta^{13}\text{C}$ for C3 plant material (*Quercus havardii* Rydb.) was -28.03, while $\delta^{13}\text{C}$ for C4 plant material (*Schizachyrium scoparium* Michx.) was -13.39. In general, $\delta^{13}\text{C}$ was most negative in the 0-15 cm layer of the soil, and increased with depth up to 90 cm (Table 2). From 91 to 150 cm, $\delta^{13}\text{C}$ again increased to levels similar to those at the initial depth layer (Table 2). Increasing $\delta^{13}\text{C}$ with depth in the soil profile indicated that historically, these rangelands had lower relative dominance of woody plants than recent landscapes. Currently, landscapes are composed of continuous shrublands dominated by sand shinnery oak, with canopy cover of shrubs averaging 50% and a relative dominance of as much as 86% (Chapter III).

Numerous studies throughout the southwest have reported a similar increase in the relative dominance of woody plants over the past 100--300 years (Archer 1994, Fuhlendorf et al. 1996, McClaran and Umlauf 2000). Causes for this regional shift in woody plant dominance include climatic fluctuations (Conley et al. 1992, Boutton et al. 1998), increased atmospheric CO_2 concentrations (Archer et al. 1995, Polley et al. 1997), reductions of naturally occurring fire (Fuhlendorf et al. 1996, Archer 1989), and introduction and confinement of domestic livestock (Walker et al. 1981, Belsky and Blumenthal 1996). Changes observed with depth in soil profiles were correlative with

changes in atmospheric CO₂ and climate. Studies have demonstrated that removal of grazing and reintroduction of fire are not sufficient to lead to a reduced dominance of woody plants (Archer 1989, Chapter II). This suggests that this landscape has either crossed an ecological threshold limiting the return to grassland dominance or changes in climate and atmospheric CO₂ have contributed to increased woody plant dominance.

In addition to changes in the relative dominance of woody plants, it is likely that there have been shifts in variability across the landscape. Rangelands throughout the southwestern U. S. have been described as inherently heterogeneous such that species dominance is highly variable and dependent upon topo-edaphic features and spatially explicit disturbances (Patten and Ellis 1995, Fuhlendorf and Smeins 1998). Increasing CV of $\delta^{13}\text{C}$ with soil depth suggested that spatial arrangement of vegetation was historically more heterogeneous than that of current sand shinnery communities. Coefficient of variation was lowest at the 0—15-cm layer, and increased to a maximum at the 31—60-cm layer (Table 2). This increased variability is consistent with historical reports that describe the landscape as predominantly a grassland with spatially variable woody plant dominance (Marcy 1854, Smeins et al. 1997).

In conclusion, the results suggested that woody plants were historically less dominant and more spatially variable across the landscape than in current sand shinnery communities. Studies of sand shinnery oak describe a complete dependence of this plant on vegetative reproduction and dramatic resistance to natural disturbances (Cook 1985, Peterson and Boyd 1998, Chapter II). This demonstrates the difficulty in determining the causal mechanisms of increased woody plant dominance of sand shinnery oak in this

community. Additional research that considers the dynamics of these communities at a greater resolution and supplemented with carbon-14 dating could better relate these changes to causal factors such as climatic shifts.

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Table 1. Percent organic carbon and total nitrogen values from soil samples at various depths collected on Black Kettle National Grasslands (BKNG) in Roger Mills Co., Oklahoma, 1999. Each depth interval contains 16 samples.

Soil Depth (cm)	Organic Carbon (%)		Total Nitrogen (%)	
	\bar{x}	<i>SE</i>	\bar{x}	<i>SE</i>
0-15	0.98	0.07	0.08	0.01
16-30	0.58	0.06	0.05	0.01
31-60	0.35	0.04	0.04	0.01
61-90	0.28	0.04	0.03	0.01
91-120	0.16	0.03	0.02	0.01
121-150	0.12	0.02	0.02	0.01

Table 2. $\delta^{13}\text{C}$ ratios (mean, minimum, maximum, standard error, and coefficient of variation) from soil samples collected on Black Kettle National Grasslands (BKNG) in Roger Mills Co., Oklahoma (1999). $\delta^{13}\text{C}$ at increasing soil depth indicates relative vegetation composition of historic plant community over time. Increasing $\delta^{13}\text{C}$ indicate greater community composition of warm season grasses. C4 plants (warm season grasses) have a $\delta^{13}\text{C}$ of -13.39 and C3 plants (cool season plants) have a $\delta^{13}\text{C}$ of -28.03. Means in rows followed by the same letters are not significantly different ($\alpha=0.05$) by least significant means test. Each depth interval contains 16 samples.

Soil Depth (cm)	$\delta^{13}\text{C}$				
		Min.	Max.	SE	CV
0-15	-19.01 a	-20.84	-16.48	0.30	-6.39
16-30	-16.73 bc	-19.19	-14.82	0.35	-8.37
31-60	-16.05 b	-20.64	-13.84	0.42	-10.49
61-90	-16.19 b	-18.70	-14.38	0.33	-8.12
91-120	-17.31 c	-20.26	-15.93	0.32	-7.32
121-150	-18.35 a	-21.68	-16.69	0.41	-8.89

CHAPTER V

Evaluation of the Lesser Prairie-chicken Interstate Working Group's Habitat Recommendations

Introduction

Shrub-dominated communities provide food and cover for many wildlife species within the Great Plains. For example, lesser prairie-chickens (LPC) (*Tympanuchus pallidicinctus*) depend on sand shinnery oak (*Quercus havardii*)-bluestem (*Andropogon spp.*) and sand sagebrush (*Artemisia filifolia*) communities for several important life functions (Copelin 1963, Jackson and DeArment 1963, Jones 1963, Riley et al. 1993). Sand shinnery oak provides food and cover for lesser prairie-chickens, including green foliage, mast, and habitat for insect populations (Crawford and Bolen 1976, Taylor and Guthery 1980). Larger mottes provide thermal cover, while scattered, smaller plants provide nesting cover and brood habitat (Riley and Davis 1993). Sand shinnery oak acorns provide a seasonal food source critical during fall and winter (Davis et al. 1979). Sand shinnery communities have been reduced and fragmented by cultivation and extensive brush control to maximize livestock production and are now considered a threatened community type (Dhillion et al. 1994, Peterson and Boyd 1998).

The LPC has the most restricted distribution and smallest population size of all North American prairie grouse species with the exception of Attwater's prairie-chicken (*Tympanuchus cupido*), which is near extinction (Aldrich 1963, Johnsgard 1973, Giesen 1998). Since the 1800's, LPC have declined 97%, with a 92% reduction their range (Crawford 1980, Taylor and Guthery 1980). Alterations and loss of sand shinnery habitat

are at least partially associated with declines in abundance and distribution of LPC (Taylor and Guthery 1980). Declines of the LPC and their habitat have prompted a petition to list the species as threatened under the Federal Endangered Species Act (BLF 1995). In response to declining populations and species listing, the 5 state agencies within the current LPC range formed the lesser prairie-chicken interstate working group (LPCIWG) and drafted a regional LPC conservation plan with specific recommendations concerning habitat management (LPCIWG 1998). These recommendations include (1) shrub coverage of 25--30% of the community, (2) forb coverage of 15%, (3) grass coverage of 60%, and (4) at least 10% of the community having visual obstruction readings > 30 cm.

Some disagreement exists as to the amount of sand shinnery oak optimal for lesser prairie-chicken populations (Jackson and DeArment 1963, Donaldson 1966, Olawsky and Smith 1991). Recommendations for the optimal percent cover of shrubs in these communities range from 10 to 60%. The most beneficial sand shinnery oak management creates a mosaic of small blocks of vegetation (Davis et. al 1979, Sell 1979, Taylor and Guthery 1980), but it is clear that broad-scale eradication of sand shinnery oak negatively affects prairie-chickens (Olawsky and Smith 1991, Riley et al. 1993).

Objectives of this study were to compare habitat recommendations of the LPCIWG to current habitat conditions on a site with a stable population of LPC, and evaluate the effectiveness of prescribed fire as a habitat management tool in meeting LPCIWG recommendations.

Study area and methods

Study sites were located in sand shinnery communities on the Black Kettle National Grasslands (BKNG) in Roger Mills County, Oklahoma, and adjacent private land in Hemphill County, Texas (LPC site). Sand shinnery communities are the largest of the oak forest communities found in the United States, occupying approximately 2--3 million ha in the southern Great Plains (Peterson and Boyd 1998). These oak communities are 0.25--1.5 m tall and are classified as shrublands. Sand shinnery oak is the dominant species, with sand sagebrush and a variety of grasses often codominating.

The Black Kettle National Grasslands were formed in 1953 after the U.S. Forest Service was granted authority over 13,476 hectares (Burgess et al. 1963). Currently, BKNG are used for recreational activities such as camping and hunting, as well as leased grazing. The BKNG are not contiguous, but consist of a series of land fragments ranging in size from 10 to 500 ha (Burgess et al. 1963). The climate of the region is subhumid, with mean August and January temperatures of 28.0°C and 2.7°C, respectively. The area has an average growing season of 209 days, with a mean rainfall of 65 cm (Burgess et al. 1963). Precipitation is highly variable with a bimodal distribution of rainfall with peaks in May-June and August-September. Topography of the area consists of rolling hills, with altitudes ranging from 518 to 793 m above sea level.

We randomly chose sample sites within available native sand shinnery communities on the BKNG and adjacent private land. Historically, LPC's were found on the BKNG, but are apparently absent now (Biodiversity Legal Foundation 1998). Adjacent private land in Hemphill County, Texas had a population of LPC, and was

located < 5 km from sites on BKNG. Sites on BKNG had various prescribed fire history ranging from unburned to burned as recently as 1 growing season prior to sampling. Private land sites had a past history of herbicide applications to reduce shrub cover. All sites had been grazed by cattle at light to moderate rates (1.7-0.9 ha/AUM).

We measured habitat structure during the growing season of 1998 and 1999. Line transects were used to measure canopy cover of the dominant functional groups: shrub, grass, forb, and litter (Bonham 1989). Shrub cover was considered dominant if present (total cover on a line always added to 100%). Shrub patch density was determined from the line transect data by summing the number of distinct shrub patches. Shrub patch density is a measure of horizontal structure (Chapter III) and gives an estimate of habitat patchiness that is often not measured with traditional techniques. Minimum resolution used to define vegetation along the transect was 10 cm.

We estimated visual obstruction every 10 m along the transect using a profile board (Nudds 1977) modified for sand shinnery communities (Guthery et al. 1981). The 6.8-cm-wide profile board had 12 strata, with each stratum being 10 cm tall. Estimates were taken perpendicular to the line transect at a distance of 7 m, with the observer kneeling at a height of 1.5 m over the transect. Percent visual obstruction was estimated for each stratum.

We measured cone of vulnerability every 10 m along the transects by measuring 8 angles around a point 10 cm above ground level to the top of the nearest obstructing vegetation (Kopp et al. 1998). We then calculated the volume of the air space included within the cone formed by the angles. A larger cone of vulnerability equates to a structurally more open habitat, with less visual obstruction. Cone of vulnerability is

highly correlated with shrub cover and is an efficient and accurate way to access shrub dominance and overall habitat structure in sand shinnery communities (Chapter III). This measure has been used to estimate habitat suitability for northern bobwhite (*Colinus virginianus*) (Kopp et al. 1998).

Results

Most habitat conditions on the LPC site were comparable to recommendations of the LPCIWG (Table 1). In general, habitat conditions sampled on BKNG were not within the LPCIWG recommendations, regardless of fire history (Table 1). Compared to the LPCIWG recommendations, shrub cover was lower on the LPC site and higher on the BKNG (Table 1). Grass cover on both the LPC site and BKNG sites was lower than recommended by the LPCIWG (Table 1). Forb cover on BKNG sites was closest to the LPCIWG recommendations 1 year after fire (Table 1), while forb cover on the LPC site was near the LPCIWG recommended value. Visual obstruction was within LPCIWG recommendations on all sites sampled regardless of land management history. Variables not considered by the LPCIWG: such as litter, cone of vulnerability, and shrub patch density, differed between BKNG sites and the LPC site. Litter cover was higher on unburned BKNG sites than on all other sites (Table 1). Cone of vulnerability was highest on the LPC site and after 1 year since fire on BKNG (Table 1). Shrub patch density was considerably lower on the LPC site than any BKNG sites (Table 1).

Discussion

Many of our habitat measurements were taken with methods that were not described by the LPCIWG and should be considered accordingly. For example, estimates

of visual obstruction may be misleading, since our data were collected during the growing season, while the LPCIWG recommends taking visual obstruction estimates in the fall--winter after sand shinnery oak leaf drop. Thus, visual obstruction as described by the LPCIWG recommendations is based primarily upon grass obstruction, but it is often impossible to separate grass visual obstruction from shrub visual obstruction. All of our functional group estimates (shrub, grass, forb, litter) were measured as relative canopy cover using the line intercept method, while LPCIWG recommends step-point methodology.

The LPC site closely resembled the recommendations of the LPCIWG and sustains a stable LPC populations, indicating that the LPCIWG recommendations are useful in determining useable LPC habitat. However, relationships between measurements suggest that LPCIWG recommendations should be elaborated on and thoroughly examined. For example, data suggested that measuring shrub cover of 25-30%, grass cover of 60%, and forb cover of 15% may be impossible to achieve with the methods we used. Estimates of litter were not considered in the LPCIWG recommendations, yet are important in determining the relative cover of plant functional groups. Furthermore, the recommendations do not include a quantitative measure of the spatial pattern or heterogeneity, such as shrub patch density, that may be critical for LPC populations. A simple index of habitat structure, such as the cone of vulnerability, that integrates vertical and horizontal variability may also be useful in evaluating LPC habitat (Chapter III).

The use of fire as a management tool on the BKNG, a site with no currently known LPC populations, appeared to have only short term effects (<2 years) on habitat

conditions (Chapter II) and was not effective in achieving LPCIWG recommendations. Undoubtedly, past herbicide applications have contributed to the current habitat conditions found on the LPC site. However, economic and ecological cost limit the usefulness of herbicides. Land managers should consider the long-term risks of herbicides in sand shinnery communities, such as wind erosion and permanent changes to ecosystem structure and function, when contemplating their use (Pettit 1979, Peterson and Boyd 1998).

Another important factor that is often overlooked is the landscape context of these habitat types. Local changes in habitat conditions of shrublands may have less importance to long-term LPC conservation than landscape level changes such as the conversion of native rangeland into agricultural cropland (Doerr and Guthery 1980, Olawsky and Smith 1991). Landscape analysis has suggested >63% of home ranges should be dominated by native rangeland, indicating critical levels of quality native habitat must be present for viable LPC populations (Crawford and Bolen 1976). Large scale differences in land use and habitat patch size may account for why the LPC site had a stable population of LPC's, while the BKNG did not have any known LPC populations. The LPC site in Texas was a large, continuous tract of native rangeland that was used primarily for livestock production. Habitat management at a patch level may only be effective for LPC conservation if the landscape is composed of sufficient amounts of continuous native rangeland.

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Table 1. Lesser prairie-chicken interstate working group (LPCIWG) recommendations for lesser prairie-chicken (*Tympanuchus pallidicinctus*) (LPC) habitat vs. habitat conditions found on private land in Hemphill County, Texas; (stable LPC population 1998-1999) and on Black Kettle National Grassland in Roger Mills County, Oklahoma; (no known LPC population 1998-1999)

Habitat Variables	LPCIWG	Hemphill County, Texas	1 year since fire, BKNG	2 years since fire, BKNG	Unburned sites, BKNG
Shrub cover (%)	25.0-30.0	13.0	38.0	56.0	51.0
Grass cover (%)	60.0	46.0	27.0	13.0	9.0
Forb cover (%)	15.0	17.0	10.0	8.0	5.0
Litter cover (%)	N/A	22.0	22.0	21.0	34.0
visual obstructions <30 cm (%)	≥10.0	95.0	90.0	97.0	98.0
cone of vulnerability (m ³ x 10 ⁻³)	N/A	1469.0	1105.0	492.0	514.0
shrub patch density (per 100 m)	N/A	31.0	92.0	110.0	103.0

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