Ecology of fire in shortgrass prairie of the southern Great Plains

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Abstract.—The ecology of fire in shortgrass prairie of the southern Great Plains includes a complex interaction between the shortgrass prairie ecosystem and its inhabitants, all inextricably linked to land-use patterns. The history of the relationship between man and fire has been filled with ambivalence and mistrust, along with an appreciation of the power of fire as a management tool. Fire is now used as a management tool on at least a limited scale in all areas of North America, and perhaps nowhere is the role of fire in community organization more widely acknowledged than in grassland ecosystems. Numerous studies have indicated that plant, arthropod, bird, and mammal populations and communities respond differentially to disturbance by fire, due in part to the fact that fire can have both direct and indirect effects. Therefore, grassland fires may directly or indirectly elicit major or minor changes in population or community structure depending upon the vagility, life history and trophic level of the organisms, degree of modification of habitat, and the timing, extent, and frequency of the fire. Interpretation and application of the results of previous studies of fire effects are constrained by the descriptive nature of these studies. Field-based experimental research is needed to help resource managers predict community responses to fire.

INTRODUCTION

"The effect of fire must be regarded as having been always operative in the Great Plains region. Fires are started by lightning during almost every thunderstorm, and the advent of man, has, if anything, tended to check rather than to increase their ravages."

(Shantz 1911)

"Fire is rightly comparable to a two-edged sword. While it may be used to good advantage at times to obtain definite desired results, its abuse, or careless uncontrolled use, may be productive of great harm."

(Stoddard 1931)

The history of the relationship between man and fire has been filled with ambivalence and mistrust, along with an appreciation of the power of fire as a management tool. Native Americans frequently started grassland fires to modify habitat and to aid in hunting activities by both driving and attracting wild game (Bahre 1985; Pyne 1982). Early non-native attitudes regarding fire were colored by the European philosophy of fire suppression as being tantamount to fire management. In the past 50 years attitudes have changed significantly regarding the use of fire. Fire as a management tool was reintroduced into North America first in the southeastern U.S. (1930s), following research by scientists, including Chapman (1926, 1932, 1936), the first scientist to provide a scientific basis for prescribed burning. Further support for burning in the 1930s was provided by the works of Green (1931), Heyward (1936, 1937, 1939) and Stoddard

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(1931), who published on the effects of fire on forest structure, soil, and wildlife, respectively (Wright and Bailey 1982). Yet, from 1940 to the early 1960s there were still many followers of the European philosophy who feared fire would be misused (Wright and Bailey 1982).

Biologists began taking a more benign view of fire in North America starting in the early 1960s with the release of the Leopold Report. The report enlightened the general public about negative effects of total fire suppression in plant communities, including excessive fuel loading, declining wildlife species diversity, and encroachment of shrubs and trees into grasslands. Fire is now used as a management tool on at least a limited scale in all areas of North America (Leopold et al. 1963; Wright and Bailey 1982). And perhaps nowhere is the role of fire in community organization and development more widely acknowledged than in grassland ecosystems (McPherson 1995).

The origin of the North American grasslands can be traced to the Miocene-Pliocene transition, perhaps 7-5 million years before present (YBP), associated with the beginning of a drying trend. The increased aridity resulted from the chilling of the ocean as the Antarctic ice sheet spread and from the Miocene uplift of the Rocky Mountains, which served as a partial barrier to moist Pacific air masses. Grasses are generally better adapted to drought than most tree species, and the spread of the grasslands occurred at the expense of forest vegetation (Axelrod 1985; Anderson 1990). Fire interacts with other factors including topography, soil, insects, herbivores (rodents, lagomorphs), and herbaceous plants to restrict woody plant establishment in grasslands (Grover and Musick 1990; McPherson 1995; Wright and Bailey 1982). Currently, there is general agreement that fire is necessary (though usually not sufficient) to control the abundance of woody plants and maintain most grasslands. In the absence of periodic fires, grasslands usually give way to dominance by woody plants (McPherson 1995). However, the question of how fire affects rangelands still needs to be fully addressed (McPherson 1995; Steuter and McPherson 1995). This literature review is intended to discuss the possible role of fire in structuring plant and animal communities in shortgrass prairie of the southern Great Plains.

HISTORY

Reliable historical records of fire frequencies in prairie of the southern Great Plains are not available because there are no trees to carry fire scars from which to estimate fire frequency. However, the recent fire history of the northern Great Plains was reconstructed by examining charcoal fragments taken from lake sediment cores (Umbanhowar 1996). The same method could be used in lakes and playas to reconstruct the fire history of the southern Great Plains. Results of Umbanhowar's research indicated that post-settlement patterns of charcoal deposition were highly variable but generally much lower than pre-settlement intervals, suggesting settlement resulted in a decrease in the number of fires due to active fire suppression. This conclusion is similar to that of Bahre (1991), who with the use of historical accounts, concluded fire size and frequency have diminished greatly in desert grasslands since the 1880s. Removal of available fuel by livestock overgrazing most likely also contributed to the post-settlement decline in fire frequency.

Historical accounts of fires by early settlers in the southern Great Plains do exist. However, such accounts are often anecdotal and biased toward documenting particularly large or destructive fires (McPherson 1995; Wright and Bailey 1982). Historical records of disturbance by fire may not be crucial for present-day land management concerns. Disturbances that caused past vegetation change (e.g., heavy cattle grazing, decreased fire frequency, specific timing of precipitation) may fail to produce similar responses today, because of profound changes in physical and biological environments over the last century. These changes include increased concentrations of atmospheric greenhouse gases (i.e., CO_2, methane), increased abundance of native (i.e., woody perennial), and non-native plants (i.e., lovegrasses, buffelgrass, *Cenchrus ciliarus* several herbaceous dicots), and decreased abundance of some plant and animal species (McPherson (in press); Weltzin and McPherson 1995). Furthermore, changes in economic, social, and political conditions have also had an impact on land use practices.

Consider the many factors influencing the extreme vegetation change in the Great Plains 100 years ago. The large migration of settlers into the

Plains and the expansion of cultivated and heavily grazed areas occurred during comparatively wet periods following the end of the Civil war in 1865 (Rasmussen 1975; Washington D.C. 1936). From 1864 through 1891, El Niño[3] activity was unusually strong and frequent (Quinn et al. 1987) producing wetter than average spring and fall seasons in the Southwest. The succession of wet years and good harvests may have acted to accelerate settlement, when farmers and ranchers mistook a prolonged El Nino event for the permanent climate. In 1934 and again in 1936 drought conditions in the Great Plains area of the United States, including the southern Great Plains, became so severe that it was necessary for the Federal Government to take emergency intervention (Rasmussen 1975). To this effect, the government created the Great Plains Drought Area Committee in the 1936. The following is an excerpt from *The Future of the Great Plains* (Washington, 1936). This report from the U.S. Great Plains Committee, analyzed the factors causing the severe "dust bowl" changes in vegetation in the Great Plains:

> *The present situation in the Great Plains area is the result of human modification of natural conditions. Prior to the coming of the white man, and to a large extent prior to about 1866, man did not greatly alter conditions on the Plains. The Indians did two things: they killed buffalo and they sometimes set fire to the grass. They do not seem to have reduced the number of buffalo seriously, and though their fires may have influenced the nature of the vegetation they did not destroy primitive grass cover. There is no evidence that in historic times there was ever a severe enough drought to destroy the grass roots and cause wind erosion comparable with that which took place in 1934 and 1936; that phenomenon is chargeable to the plowing and over cropping of comparatively recent years.*

The report goes on to state that the Great Plains are estimated to have been nearly 100 percent overstocked with cattle in 1935. And with the advent of tractors, combines, and other powerful machinery, farmers were able to plant and harvest a much larger acreage than before. Therefore, soil not previously plowed was exposed to the wind with no cover crop to protect it between seasons. The effects of wind erosion were more disastrous in the southern Great Plains than further north, but the exposed and friable soils almost everywhere were washed or blown to some extent. Many itinerant farmers put in crops, but because of low prices, did not return to harvest what they had sown, leaving the soil partially exposed to the drying and eroding winds.

The report further stated that there were approximately 24,000 crop farms, covering a total of 15 million acres (37,065,000 ha), which should no longer be plowed. It recommended that the Federal Government continue the policy of purchasing scattered crop farms and other appropriate lands in areas devoted largely to grazing, the formation of cooperative grazing associations, and the creation of erosion control districts (Rasmussen 1975).

Other federal programs designed in part to protect the environment, and that directly affected the Great Plains, include: the Bankhead-Jones Farm Tenant Act of 1937, that included a directive to retire submarginal land, and under which most national grasslands administered by the United States Forest Service were acquired; The Taylor Grazing Act of 1934, which gave the Department of the Interior authority to regulate grazing on the public domain to stop injury to public grazing lands by preventing overgrazing and soil deterioration; and establishment of the Soil Conservation Service in 1935 which was to provide technical range management assistance to private landowners.

Southern Great Plains: Shortgrass Prairie

Natural History

The southern Great Plains includes the eastern third of New Mexico, the northern two-thirds of Texas, and most of Oklahoma. The region can be divided into shortgrass, mixed, and tallgrass prairie categories (fig. 1). Within the area, the shortgrass prairie lies west of the 100 meridian

[3] El Niño-Southern Oscillation (ENSO) events are global-scale climatic anomalies that recur at intervals of 2 to 10 years and at varying intensities (Philander 1983), with weak tradewinds and high sea-surface temperatures off the western coast of the Americas. Southern Oscillation is measured as the normalized differences in monthly mean pressure anomalies between Tahiti, French Polynesia and Darwin, Australia. El Niño and Southern Oscillation are linked in a global climate complex of changing ocean currents, ocean temperatures, atmospheric pressure and temperature gradients. Climatic effects of ENSO are highly variable, sometimes leading to droughts in some regions and flooding in others (Swetnam 1990). In the southwestern United States, ENSO events are most consistently related to wetter than average spring and fall seasons (Andrade and Sellers 1988).

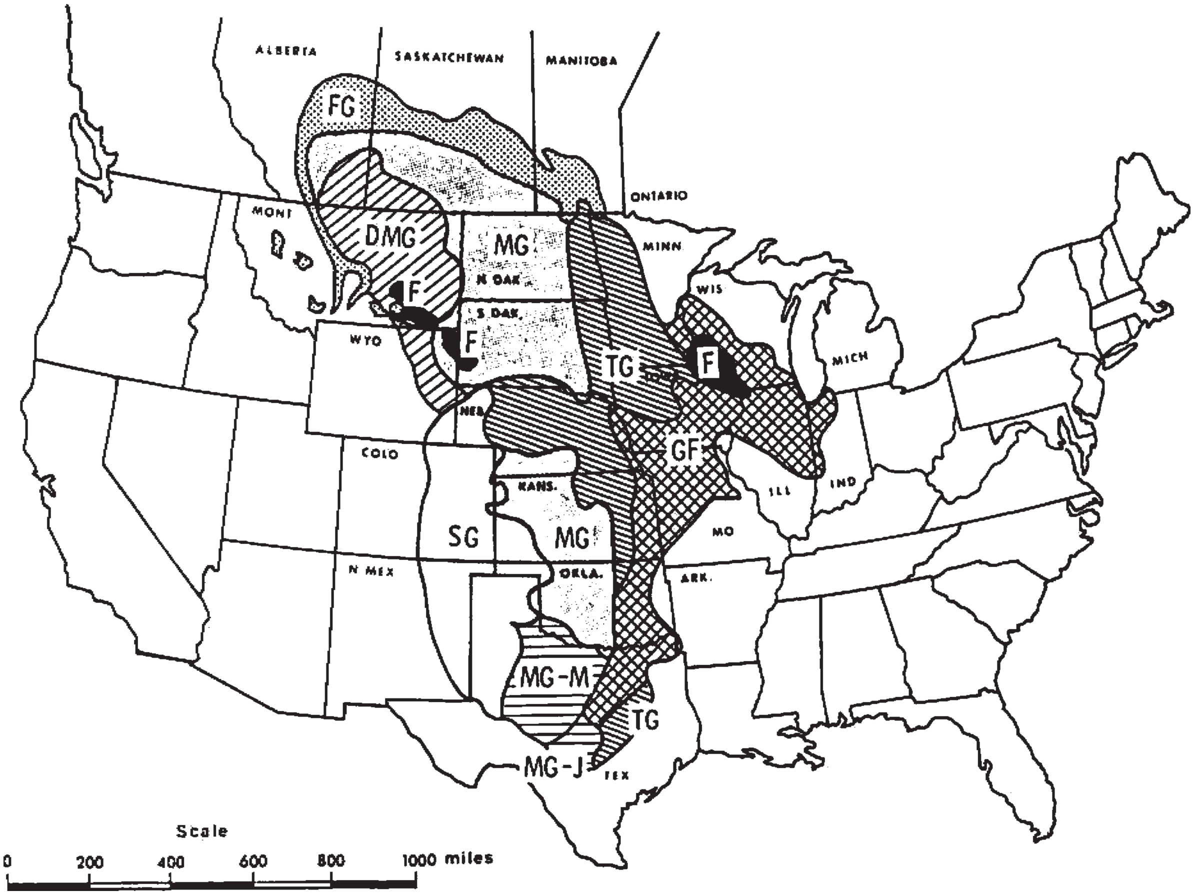

Figure 1. Natural vegetation of Great Plains grasslands (Wright and Bailey 1980). Modified from Kuchler (1965) and Rowe (1972). DMG, Dry mixed grassland; F, Forest; FG, Fescue grassland; GF, Grassland forest; MG, Mixed grassland; MG–J, Mixed grassland–juniper–oak; MG–M, Mixed grassland-mesquite; SG, Short grassland; TG, Tall grassland.

(Wright and Bailey 1982). It is estimated that less than 23% of true shortgrass prairie still exists in native vegetation (NGMR 1995). The grassland is semi-arid; annual precipitation in shortgrass prairie ranges between 15 and 20 inches (38 to 51 cm). Except for sandy soils in southeastern New Mexico and the Canadian River country in northern Texas and western Oklahoma, soils are primarily clay loams, silt loams, and sandy loams. A caliche layer is frequently present at 20 to 36 inches (51 to 91 cm) in the fine-textured soils. Most of the area is tableland that is 4,000 to 6,000 ft (1,200 to 1,829 m) in elevation (south to north) on the western edge, and slopes eastward to 3,000 ft (915 m) on the edge of Llano Estacado in Texas. Dominant grasses are buffalograss (*Buchloe dactyloides*) and blue grama (*Bouteloua gracilis*), with varying amounts of threeawns (*Aristida* spp.), lovegrass (*Eragrostis* spp.), tridens (*Tridens* spp.), sand dropseed (*Sporobolus cryptandrus*), sideoats grama (*Bouteloua curtipendula*), tobosagrass (*Hilaria mutica*), galleta (*H. jamesii*), vine-mesquite (*Panicum obtusum*), bush muhly (*Muhlenbergia porteri*), and Arizona cottontop, *Digitaria californica* (Bailey 1995; Wright and Bailey 1982).

Forbs can be abundant during wet years, but they are seldom a major component of the shortgrass prairie. Common forbs include annual broomweed (*Xanthocephalum dracunculoides*), false mesquite (*Hoffmanseggia densiflora*), western ragweed (*Ambrosia psilostachya*), horsetail conyza (*Conyza candensis*), warty euphorbia (*Euphorbia spathulata*), silver-leaf night shade (*Solanum elaeagnifolium*), manystem evax (*Evax multicaulis*), woolly plantago (*Plantago purshii*), dozedaisy (*Aphanostephus* spp.), goosefoot (*Chenopodium* spp.), croton (*Croton* spp.), summercypress (*Kochia scoparia*), and globemallow (*Sphaeralcea* spp.) (Wright and Bailey 1982).

Dominant woody plants are honey mesquite, sand shinnery oak (*Quercus havardii*), sand sagebrush (*Artemisia filifolia*), perennial broomweed (*Gutierrezia sarothrae*), yucca (*Yucca* spp.), and fourwing saltbush (*Atriplex canescens*). Cactus (*Opuntia* spp.) can also be abundant. The prevalent species include pricklypear (*Opuntia polyacantha*), brownspine pricklypear (*O. phaeacantha*), walkingstick cholla (*O. imbricata*), and tasajillo (*O. leptocaulis*) (Wright and Bailey 1982).

VEGETATION RESPONSES TO FIRE

All previous research on vegetation responses to fire in shortgrass prairie of the southern Great Plains is based on single-fire or burned vs. unburned (i.e., non-experimental) research. Most of this research was conducted before 1980, and was primarily interested in the use of fire as a tool to increase forage value of vegetation. Results of these studies are hampered by weak inference (Platt 1964), and therefore must be interpreted cautiously. A more reliable approach would be to use experiments designed specifically to test hypotheses about vegetation responses to fire.

One such example of this type of research is a study in progress by Brockway (1995) on the effects of restoring fire to shortgrass prairie on the Kiowa National Grasslands in northeastern New Mexico. The study employs a completely randomized experimental design, with seven treatments and five replicates, to analyze how grassland nutrient cycling, plant productivity, and community structure are affected by fire frequency and season of burn. Research on the effects of fire on tallgrass prairie and desert grassland by Long-Term Ecological Research Programs at the Konza Prairie Research Natural Area in Kansas, and the Sevilleta National Wildlife Refuge in New Mexico, respectively, also use the experimental method to answer questions concerning vegetation response to fire. More of these types of studies are needed in the southern Great Plains to develop an accurate picture of how fire affects the shortgrass prairie ecosystem.

EARLY RESEARCH

Considerable research was conducted to address fire effects in shortgrass prairie before 1980. In general, these studies indicate that fire leads to decreased herbaceous production for 1-3 years, and herbaceous response is influenced strongly by precipitation. Fires also contribute to reductions in woody plant cover and increases in density and diversity of herbaceous dicots.

Following a spring wildfire in shortgrass prairie, when the soil was dry, Launchbaugh (1964) concluded that fire caused short-term declines in plant biomass. It took three growing seasons for a burned buffalograss-blue grama community to return to a level comparable to that of unburned areas. Similar results of burning in prairie were reported in west-central Kansas (Hopkins et al. 1948). Following a wildfire in New Mexico when the moisture balance was more favorable, Dwyer and Pieper (1967) found that biomass production of blue grama was reduced only by 30 percent during the first year growing season following the burn. Blue grama biomass returned to pre-burn status with above-average precipitation the second year after burning.

Results from prescribed burns in Texas during years with above-normal winter and spring precipitation showed that buffalograss and blue grama tolerated fire with no loss in herbage yield at the end of the first growing season (Trlica and Schuster 1969; Heirman and Wright 1973; Wright 1974; Wright and Bailey 1980). The tolerance of most grass species to fire in the shortgrass prairie, under different moisture regimes, appears to be similar to that of buffalograss and blue grama (Wright and Bailey 1982).

In the southern Great Plains, patches of sandy soil are common among the heavy clay soils that are dominated by buffalograss and blue grama. The sandy soils are dominated by sand bluestem (*Andropogon hallii*), little bluestem (*A. scoparius*), switch grass (*Panicum virgatum*), and sand shinnery oak. Burning generally increased production of sand bluestem and switchgrass about 300 lb/acre (337 kg/ha) and, decreased production of little bluestem, with a net increase in total forage of 20 percent (McIlvain and Armstrong 1968; Wright and Bailey 1982).

ANIMAL RESPONSE TO FIRE

Arthropods, birds, and mammals all play important roles in ecosystem functioning of shortgrass prairie, serving as decomposers, pollinators, herbivores, predators or prey. They cycle nutrients and form valuable links among trophic levels. Numerous studies have indicated animal species, populations and communities respond differentially to disturbance by fire, due in part to the fact that fire can have both direct and indirect effects. Direct effects are acute but ephemeral i.e., fire induced mortality. Indirect effects (i.e., alterations in habitat) are long-lasting and usually more important. Therefore, grassland fires may directly or indirectly elicit major or minor population or community structure changes depending upon the vagility, life history and trophic level of the animal, and the timing, extent and intensity of the fire.

Arthropods

Little is known about the diversity of arthropods on southwestern rangelands. Available data indicate that species diversity for most groups of rangeland arthropods is higher in the Southwest than in other parts of the country (Parmenter et al. 1994). Our surveys have already yielded close to 100 species of arthropods [4] (table 1). Data collection took place during autumn 1995 on the Kiowa National Grasslands proposed Research Natural Area (RNA) in Union County, New Mexico. The RNA consists of approximately 400 acres (160 ha) of relatively flat, homogeneous shortgrass prairie that has never been plowed, though it was grazed until approximately six years ago. Collection of arthropods took place on 15, 2 ha plots spaced in a checkerboard pattern across the RNA. Average temperatures ranged from a low of 35 °F (2 °C) to a high of 70 °F (21 °C) throughout the collection dates. Post-treatment, and spring and summer collections are expected to yield even more species of arthropods.

Arthropods common to shortgrass prairie include species considered to be beneficial (i.e., pollinators, parasites, predators), as well as others that are known to cause extensive damage to grasslands. For example, more than 1,200 insect species representing 11 taxonomic orders feed on grasses in Arizona, New Mexico, Utah, Nevada and Colorado (Thomas and Werner 1981). Grasshoppers alone regularly consume 21-23% of the annual available forage on rangelands in the western United States (Hewitt and Onsager 1983) and, in some cases, remove as much plant biomass as do domestic livestock (Swain 1943; Haws 1978). Not surprisingly, insects of southwestern rangelands are often thought of as agricultural pests because of the economically costly forage consumption by some species; however, most arthropod species are not agricultural pests, and many are beneficial components of rangeland ecosystems. In addition to serving as pollinators, arthropods are detritivores and have important roles in the decomposition of dead plant material and nutrient cycling. Furthermore, plant-feeding arthropods may even beneficially affect nutrient cycling rates (Lightfoot and Whitford 1990; Parmenter et al. 1994). Arthropods also serve as an important prey base for small mammals and birds.

Grassland burning elicits a diverse array of responses by arthropods. The degree of modification of arthropod populations by fire, the direction of change, and whether the effects are acute or chronic vary with several factors including fire characteristics, arthropod species, timing of the burn relative to phenological stage of arthropod development, influence of the fire on predator/prey and parasite/host ratios, post-burn weather, and the direction and degree of habitat restructuring (Warren et al. 1987).

One example of such interactions is the response of centipedes to fire. Centipedes feed primarily on other arthropods, and generally seek seclusion in the soil or under bark, stones or crevices of rotting logs. Although their immediate response to burning is probably minimal due to their choice of habitat, they may be affected during the recovery phase because of their dependence on other arthropods as food (Warren et al. 1987).

Preliminary results of experimental research on fire effects on predator groups of arthropods (spiders, carabid beetles, centipedes, scorpions, and solpugids) by Brantley and Parmenter (unpublished data) [5] indicate that there was no response to

[4] *Voucher specimens are deposited with the Museum of Southwestern Biology, Division of Arthropods, University of New Mexico, Albuquerque.*

[5] *Data on file with Sevilleta LTER, New Mexico.*

Table 1. Arthropods of the Proposed Research Natural Area on the Kiowa National Grasslands, Union County, New Mexico, fall 1995.

Family	Common name	Species	Authority[a]
Acrididae	Grasshoppers	*Ageneotettix deorum*	(Scudder)
		Amphitornus coloradus	(Thomas)
		Arphia conspersa	(Scudder)
		Arphia pseudonietana	(Thomas)
		Aulocara femoratum	(Scudder)
		Cordillacris crenulata	(Bruner)
		Dactylotum b. bicolor	(Thomas)
		Encoptolophus sordidus	(Burmeister)
		Hadrotettix magnificus	(Rehn)
		Hesperotettix viridis	(Scudder)
		Hypochlora alba	Dodge
		Melanoplus arizonae	(Scudder)
		Melanoplus gladstoni	Scudder
		Melanoplus occidentalis	(Thomas)
		Melanoplus packardii	Scudder
		Mermiria bivattata	(Serville)
		Metator pardalinus	(Saussure)
		Opeia obscura	(Thomas)
		Phlibostroma quadrimaculatum	(Thomas)
		Phoetaliotes nebracensis	(Thomas)
		Spharagemon equale	(Say)
		Syrbula admirabilis	(Uhler)
		Trachyrhachys aspera	Scudder
		Trimerotropis pistrinaria	Saussure
		Tropidolophus formosus	(Say)
Gryllidae	Crickets	*Cycloptilum comprehendens*	Hebard
		Gryllus pennsylvanicus	
		Gryllus undesc.	
Mantidae	Mantids	*Litaneutra minor*	(Scudder)
Rhaphidophoridae	Camel Crickets	*Ceuthophilus nodulosus*	Bruner
		Ceuthophilus pallidus	Thomas
Romaleidae	Lubber Grasshoppers	*Brachystola magna*	(Girard)
Tettigoniidae	Katydids	*Pediodectes stevensonii*	(Thomas)
Agelenidae	Funnel Web Spiders	*Agelenopsis longistylus*	(Banks)
		Agelenopsis spatula	Chamberlin & Ivie
		Hololena hola	(Chamberlin & Gertsch)
Gnaphosidae	Ground Spiders	*Drassodes gosiuta*	Chamberlin
		Drassyllus sp.	
		Zelotes anglo	Gertsch & Reichert
Hahniidae		*Neoantistea mulaiki*	Gertsch
Lycosidae	Wolf Spiders	*Hogna sp*.	
		Pardosa sp.	
		Rabidosa santrita	(Chamberlin & Ivie)
		Schizocosa mccooki	(Montgomery)
		Trochosa terricola	Thorell
Salticidae	Jumping Spiders	*Habronattus sp.*	
		Pellenes limatus	Peckham & Peckham
		Phidippus sp.	in revision
Philodromidae		*Thantus sp.*	

Table 1. Cont'd.

Family	Common name	Species	Authority[a]
Theridiidae	Black Widows/Comb-footed Spiders	*Latrodectus hesperus*	Chamberlin & Ivie
		Steatoda sp.	
Thomisidae		*Xysticus gulosus*	Keyserling
Carabidae	Ground Beetles	*Pasimachus californicus*	Chaudoir
		Pasimachus elongatus	(LeConte)
		Pasimachus obsoletus	(LeConte)
		Cyclotrachelus substriatus	(LeConte)
		Cyclotrachelus constrictus	(Say)
		Dyschirius globulosus	Say
		Amara (near) *idahoana*	
		Harpalus amputatus	Say
		Harpalus caliginosus	Fabricius
		Harpalus pennsylvanicus	DeGeer
Tenebrionidae	Darkling Beetles	*Asidopsis polita*	Say
		Stenomorpha consors	(Casey)
		Stenomorpha convexicollis	(LeConte)
		Bothrotes plumbeus	
		Eleodes extricatus	Say
		Eleodes fusiformis	LeConte
		Eleodes hispilabris	Say
		Eleodes obscurus	Say
		Eleodes obsoletus	(Say)
		Eleodes opacus	Say
		Eleodes suturalis	Say
		Embaphion muricatum	Say
		Glyptasida sordida	(LeConte)
		Eusattus convexus	LeConte
		Metopoloba pruinosa	Casey
Scarabaeidae	Scarab Beetles	*Euphoria inda*	(Linnaeus)
		Eucanthus sp.	
		Paracoltalpa puncticollis	LeConte
		Cremastocheilus (near) *nitens*	
Chrysomelidae		*Galeruca sp*.	
Cicindelidae	Tiger Beetles	*Cicindela scutellaria*	
		Amblycheila cylindriformis	Say
Nitidulidae	Sap Beetles	*Carpophilus lugubris*	Murray
Melyridae	Soft-winged Flower Beetles	*Collops quadrimaculatus*	Fabricius
Cleridae	Checkered Beetles	*Phyllobaenus sp*	
Anthicidae	Ant-like Flower Beetles	*Baulius tenuis*	Casey
Melandryidae	False Darkling Beetles	*Anaspis rufa*	Say
Formicidae	Ants	*Crematogaster sp*.	
		Pheidole sp.	
		Camponotus sp.	
		Pogonomyrmex occidentalis	(Cresson)

[a] *Names in parenthesis indicate that the generic name changed since description. No parenthesis indicate original name as author described.*

fire treatment. The research was conducted on the Sevilleta LTER in New Mexico. The site is a desert grassland containing many components of shortgrass prairie, including blue grama and black grama. Treatment was a light burn in July 1993, with four replicates in burn treatment and control. Most of the species were able to move out of the path of the fire and recolonize the area quickly. Stronger patterns were seen in response to seasonal change than to the fire.

Other research on fire and arthropods in a prairie ecosystem include the following: fire results in increases in macroarthropod herbivores, such as white grubs and root xylem-sucking cicada nymphs (Seastedt 1984a; Seastedt et al. 1986). Only microarthropod fauna that live and feed on surface litter in tallgrass prairie exhibit declines in densities following fire (Seastedt 1984b). This response probably results more from the loss of habitat than from direct mortality (Seastedt and Ramundo 1990). True soil-dwelling microarthropods have been reported to increase in densities in response to frequent prairie fires. Higher microarthropod densities occurred in prairie areas that were more productive but had less organic matter than adjacent areas (Lussenhop 1976).

Prescribed burning may be a viable management tool against pest species of arthropods when their phenology and habits have been identified (Warren et al. 1987). For example, short-horned grasshoppers (Acrididae), the most serious grassland pests, are excellent flyers. Most short-horned grasshoppers can escape flames and quickly populate burned areas, a process that selectively favors species that are adults during the dry season when most fires occur (Gillon 1972). Spring burning in Kansas effectively controlled a few species of short-horned grasshoppers that overwinter as nymphs, but the majority of species overwinter as eggs in the soil and were not reduced when burning occurred prior to the emergence of nymphs, even after 17 consecutive annual burns (Campbell et al. 1974; Knutson and Campbell 1976). In addition, elevated post-burn soil temperatures allowed nymphs to emerge earlier than usual, which, coupled with the more nutritious vegetative regrowth, progressively increased the grasshopper population. Burning after a greater proportion of grasshopper nymphs had emerged improved control (Warren et al. 1987).

Birds

Shortgrass prairie of the southern Great Plains is used by hundreds of bird species. Many are migrants, while others breed in the Great Plains, or can be classified as summer, winter, or yearlong residents. According to newly published Breeding Bird Survey accounts, several migratory bird species that breed or winter in the southern Great Plains have declined over a 30-year period. Because birds are highly mobile, fires rarely kill birds directly, but rather affect population levels indirectly by altering habitat structure, abundance of competing species, and food levels (Bock and Bock 1990; Dickson 1981; Rotenberry et al. 1995). Some birds react to fire itself. Birds of prey in particular are attracted to fire and smoke. This positive response to fire appears to be related to vulnerability and ease of capture of prey species that are forced to flee before the flames. Several other species are attracted to recently-burned grasslands (Clark 1935; Handley 1969; Komarek 1969; Kramp et al. 1983; Lyon and Marzluff 1984; Tombak 1986). Increased forb composition and seed availability after fire is beneficial to avian herbivores and seed eaters (Bock and Bock 1990; Brock et al. 1976; Lawrence 1966; Wirtz 1977).

Other effects of fire include increased habitat heterogeneity. In shrub-grass complexes, bird diversity and abundance are enhanced if shrub cover and nesting sites are interspersed with open grassy areas maintained by fire (Baldwin 1968; Kramp et al. 1983; Pulliam and Mills 1977). Fire has also been suggested to have a cleansing effect on bird populations by lowering the numbers of parasites that affect health and vigor of individuals (Kramp et al. 1983; Lyon et al. 1978).

Many bird species that inhabit grasslands have been documented to increase habitat use in shrublands or grasslands after fire. They are reportedly attracted to smoke and flames of fire, and to recently-burned grasslands because of increased insect availability and small mammal prey vulnerability (table 2). Far fewer bird species are reported to be negatively affected by fire. These species are generally closely associated with shrubby habitat, and more abundant in unburned areas. Shrubs are required for nesting and perching, but nests are destroyed by fire, potentially reducing productivity of birds (table 2). For ex-

Table 2. Positive, negative, and mixed responses of birds of the southern Great Plains to fire events and burns based on counts, monitoring records, and anecdotal observations reported in the literature.

Species	Common Name	Response	Reference
Corvus brachyrhynos	American Crow	Positive	Komarek 1969
Falco sparverius	American Kestrel	Positive	Bock and Lynch 1970; Lawrence 1966; Marshall 1963; Stoddard 1963
Turdus migratorius	American Robin	Positive	Bock and Lynch 1970; Komarek 1969; Marshall 1963; Michael and Thornburgh 1971; Roppe and Hein 1978; Stoddard 1963
Ammodramus bairdii	Baird's Sparrow	Positive	Madden 1995; Winter 1995
Pica pica	Black-billed Magpie	Positive	Komarek 1969
Guiraca caerulea	Blue Grosbeak	Positive	Komarek 1969
Toxostoma rufum	Brown Thrasher	Positive	Komarek 1969
Molothrus ater	Brown-headed Cowbird	Positive	Bock and Lynch 1970; Komarek 1969; Lowe et al. 1978
Branta canadensis	Canada Goose	Positive	Komarek 1969
Corvus corax	Common Raven	Positive	Lawrence 1966
Gallinago gallinago	Common Snipe	Positive	Komarek 1969
Accipiter cooperii	Coopers's Hawk	Positive	Komarek 1969; Lawrence 1966
Tyrannus tyrannus	Eastern Kingbird	Positive	Komarek 1969
Sturnella neglecta	Western Meadowlark	Positive	Komarek 1969; Lawrence 1966
Sturnus vulgaris	European Starling	Positive	Komarek 1969
Ardea herodias	Great Blue Heron	Positive	Komarek 1969
Bubo virginianus	Great Horned Owl	Positive	Bock and Lynch 1970; Komarek 1969
Geococcyx californianus	Greater Roadrunner	Positive	Marshall 1963
Picoides villosus	Hairy Woodpecker	Positive	Bock and Lynch 1970; Koplin 1969; Lowe et al. 1978; Taylor 1976; Taylor and Barmore 1980
Eremophila alpestris	Horned Lark	Positive	Komarek 1969
Troglodytes aedon	House Wren	Positive	Bock and Lynch 1970; Franzreb 1977; Gruell 1980; Komarek 1969
Charadrius vociferus	Killdeer	Positive	Komarek 1969
Calamospiza melanocorys	Lark Bunting	Positive	Komarek 1969
Ammospiza leconteii	LeConte's Sparrow	Positive	Madden 1995
Lanius ludovicianus	Loggerheaded Shrike	Positive	Komarek 1969
Zenaida macoura	Mourning Dove	Positive	Brock 1976; Bock and Lynch 1970; Komarek 1969; Lawrence 1966; Lowe et al. 1978; Soutiere and Bolen 1973; Stoddard 1963; Wirtz 1977
Mimus polyglottos	Northern Mockingbird	Positive	Komarek 1969
Icterus spurius	Orchard Oriole	Positive	Komarek 1969
Buteo jamaicensis	Red-Tailed Hawk	Positive	Baker 1974; Bock and Lynch 1970; Franzreb 1977; Komarek 1969; Lawrence 1966; Stoddard 1963
Agelaius phoeniceus	Red-winged Blackbird	Positive	Komarek 1969
Passerculus sandwichensis	Savannah Sparrow	Positive	Brown 1978; Daubenmire 1968; Komarek 1969; Pulliam and Mills 1977
Callipepla squamata	Scaled Quail	Positive	Brown 1978; Komarek 1969
Anthus spragueii	Sprague's Pipit	Positive	Madden 1995
Tachycineta bicolor	Tree Swallow	Positive	Bock and Lynch 1970; Gruell 1980; Komarek 1969; Taylor 1976; Taylor and Barmore 1980

Table 2. Cont'd.

Species	Common Name	Response	Reference
Cathartes aura	Turkey Vulture	Positive	Bock and Lynch 1970; Komarek 1969
Sialia mexicana	Western Bluebird	Positive	Franzreb 1977; Lowe et al. 1978; Marshall 1963; Szaro and Balda 1979
Tyrannus verticalis	Western Kingbird	Positive	Lawrence 1966
Contopus sordidulus	Western Wood-pewee	Positive	Bock and Lynch 1970; Komarek 1969; Lowe et al. 1978
Thryomanes bewickii	Bewicks's Wren	Negative	Lawrence 1966; Wirtz 1977
Pipilo fuscus	Brown Towhee	Negative	Lawrence 1966; Marshall 1963; Pulliam and Mills 1977; Wirtz 1977
Psaltriparus minimus	Bushtit	Negative	Buttery and Shields 1975; Wirtz 1977
Geothlypis trichas	Common Yellowthroat	Negative	Madden 1995
Ammodramus henslowii	Henslow's Sparrow	Negative	Herkert and Glass 1995
Ammodramus savannarum	Grasshopper Sparrow	Mixed	Bock and Lynch 1970; Pulliam and Mills 1977; Madden 1995
Colinus virginianus	Northern Bobwhite	Mixed	Komarek 1969; Renwald et al. 1978; Thomas 1979; Wolfe 1973
Sturnella magna	Eastern meadowlark	Mixed	Brock et al. 1976; Komarek 1969
Zonotrichia leucophrys	White-crowned Sparrow	Mixed	Pulliam and Mills 1977; Taylor and Barmore 1980

ample, the shrub-associated common yellowthroat, *Geothlypis trichas*, was found to reach highest abundance on unburned areas in mixed-grass prairie, where prescribed fire has been used as a management tool for the past 20 years (Madden 1995).

Several bird species exhibit a mixed response to fire. The northern bobwhite, *Colinus virginianus*, is reportedly attracted to recently-burned grasslands and is most productive in grass-forb habitat. However, it requires scattered woody plants for cover, and populations decrease in shrub-dominated stands (Brown 1978; Komarek 1969; Kramp et al. 1983; Renwald et al. 1978; Wolfe 1973). The eastern meadowlark, *Sturnella magna*, may be attracted to recent burns, but fires that destroy all shrub cover may be detrimental (Brock et al. 1976; Komarek 1969; Kramp et al. 1983). The white-crowned sparrow, *Zonotrichia leucophrys*, depends on shrub cover, and may decrease habitat use on some burns. But it also aggregates in large groups to feed in open burns (Kramp et al. 1983; Taylor and Barmore 1980). The lark sparrow, *Chondestes grammacus*, reportedly benefits from litter removal in grasslands and reduction but not complete removal of shrubs (Lawrence 1966; Renwald et al. 1978; Wirtz 1977).

Fire or the lack of fire may also indirectly affect birds. Several bird species, including the federally listed Species of Concern, Baird's sparrow, *Ammodramus bairdii*, grasshopper sparrow, *A. savannarum*, LeConte's sparrow, *Ammospiza leconteii*, Sprague's pipit, *Anthus spragueii*, and western meadowlark, *Sturnella neglecta*, were the most common, and abundant birds, overall, in mixed-grass prairie, where fire has been used as a habitat management tool since the 1970s, but were all completely absent from unburned prairie (Madden 1995). Baird's sparrow was found to reach high densities in areas that had been frequently burned. The areas were characterized by low litter and high cover variability of forbs and bunchgrass (Winter 1995). The decline of Montezuma quail, *Cyrtonyx montezumae*, has been linked with widespread replacement of grassland with shrubland in the last 150 years. It may benefit from fires that decrease shrub cover (Brown 1978; Kramp et al. 1983). Populations of the burrowing owl, *Athene cumicularia*, have reportedly declined on grasslands with increases in litter cover. This suggests that the use of fire to reduce litter cover may be beneficial to this species (Komarek 1969; Kramp et al. 1983). The lesser prairie-chicken, *Tympanuchus pallidicinctus*, is also a grassland species reported to be declining in the Southwest because of decreased grassland habitat due to suppression of rangeland fires (Brown 1978). Regrowth of grasses, reduced litter, and decreased shrub cover in grasslands following fire is beneficial for the Sandhill crane, *Grus canadensis*, a common grassland migrant (Kirsh and Kruse 1973; Kramp et al. 1983).

Herpetofauna

There is a general paucity of data on the response of reptiles and amphibians to fire in grasslands. See Scott (this volume) for a discussion of herpetofauna and fire in grasslands.

Mammals

The reaction of mammals to fire is a function of size and vagility. Deer and elk easily avoid injury during fire (Boeker et al. 1972; McCulloch 1969; Dills 1970; Hallisey and Wood 1976), although young ungulates are frequently killed by large fires (Daubenmire 1968; Kramp et al. 1983). Most small mammals escape fires by hiding in burrows or rock crevices (Howard et al. 1959; Heinselman 1973). Komarek (1969) observed that mature cotton rats successfully moved themselves and their young to safe refuge areas. Thus, even small mammals of limited mobility are capable of avoiding fire (Kramp et al. 1983).

The most common cause of death for small mammals during fire is a combination of heat effects and asphyxiation. However, studies cited by Bendell (1974) indicate that soil provides insulation from fire for burrowing animals (Kramp et al. 1983). Other causes of death include physiological stress as mammals overexert themselves to escape, trampling as large mammals stampede, and predation as small mammals flee from fire (Kaufman et al. 1990).

Grassland fires that temporarily remove food and cover (litter and standing dead vegetation) may be detrimental to small rodents immediately after fire (Daubenmire 1968; Kaufman et al. 1990). However, repopulation of such areas is reported to be nearly complete within 6 months (Cook 1959). Mice and rodent populations often increase after fire in response to increased availability of forb seeds and insects (Lyon et al. 1978). In addition, burned areas often support more diverse animal populations than comparable unburned sites due to increased habitat diversity(Beck and Vogl 1972; Wirtz 1977). Omnivores and carnivores are attracted to burns by increased plant diversity and associated small mammal populations (Gruell 1980). Levels of animal parasites are often lower in burned habitats (Bendell 1974).

Kaufman et al. (1990) suggest that most effects of fire on small mammals in grasslands are not neutral, but are instead either fire-positive or fire-negative responses. Fire-negative mammals include species that forage on invertebrates in the litter layer, species that live in relatively dense vegetation and eat plant foliage, and species that use, at least partially, aboveground nests of plant debris. Examples in the southern Great Plains include the cotton rat, *Sigmodon hispidus*, Bailey's pocket mouse, *Perognathus baileyi*, the pinyon mouse, *Peromyscus truei*, the white-tailed antelope ground squirrel, *Ammospermophilus leucurus*, the southern red-backed vole, *Clethrionomys gapperi*, the white-throated woodrat, *Neotoma albigula*, the western harvest mouse, *Reithrodontomys megalotis*, and the meadow vole, *Microtus pennsylvanicus* (Beck and Vogl 1972; Bock and Bock 1978; Brock et al, 1976; Bradley and Mauer 1973; Geier and Best 1980; Hanson 1978; Kaufman et al. 1990; Komarek 1969; Kramp et al. 1983; Lawrence 1966; Lowe et al. 1978; Mazurek 1981; Rowe and Scotter 1973; Taylor 1969).

Fire-positive mammals include species that use ambulatory locomotion in microhabitats with a relatively open herbaceous layer and feed on seeds and/or insects and that use saltatorial locomotion (Kaufman et al. 1990). They exhibit an increase in populations and habitat use after fire because of an increased availability of forb seeds, insects, newly greening vegetation, the creation of open areas in otherwise dense habitat, and eventually an increase in forb cover. Increases may occur immediately, or gradually as the areas begin to revegetate and habitat diversity increases. The small mammals include the deer mouse, *Peromyscus maniculatus*, the white-footed mouse, *Peromyscus leucopus*, the eastern cottontail, *Sylvilagus* *floridanus*, Merriam's kangaroo rat, *Dipodomys merriami*, (*Dipodomys ordii* occurs in the southern Great Plains), the southern grasshopper mouse, *Onychomys torridus*, (*Onychomys leucogaster* occurs in the southern Great Plains), Nuttall's cottontail, *Sylvilagus nuttallii*, the thirteen-lined ground squirrel, *Spermophilus tridecemlineatus*, and the hispid pocket mouse, *Chaetodipus hispidus* (Beck and Vogl 1972; Bradley and Mauer 1973; Cable 1967; Cook 1959; Daubenmire 1968; Heinselman 1973; Kaufman et al. 1990; Komarek 1969; Kramp et al. 1983; Lawrence 1966; Lowe et al. 1978; Roppe and Hein 1978; Thomas 1979; Williams 1955).

Carnivores that occur in the southern Great Plains include badger, *Taxidea taxus*, bobcat, *Felis rufus*, red fox, *Vulpes vulpes*, and coyote, *Canis latrans*. These species may increase habitat use in response to fire-enhanced rodent populations (prey) (Gruell 1980; Kramp et al. 1983; Wirtz 1977).

Most native ungulates, including buffalo, *Bison bison*, white-tailed deer, *Odocoileus virginianus*, elk, *Cervus elaphus*, and pronghorn, *Antilocapra americana*, increase in population and habitat use after fire. The response is due to an increase in forage quality and quantity in newly burned areas. Deer have also been observed eating ash after a fire, possibly for the concentrated mineral content (Baldwin 1968; Basile 1979; Boeker et al. 1972; Carpenter et al. 1979; Davis 1977; Dills 1970; Ffolliott et al. 1977; Gruell 1980; Hallisey and Wood 1976; Hendricks 1968; Keay and Peck 1980; Kirsh and Kruse 1973; Kittams 1973; Komarek 1969; Kramp et al. 1983; Kruse 1972; Leege and Hickey 1971; Leege 1968; Leopold 1923; Lowe et al. 1978; McCulloch 1969; Miller 1963; Nelson 1974; Pederson and Harper 1978; Reynolds 1969; Roppe and Hein 1978; Rowe and Scotter 1973; Short 1977; Short et al. 1977; Wallmo et al. 1977).

TIMING AND FREQUENCY OF FIRE

Grassland communities are likely to be influenced by seasonality and frequency of fire due to their evolutionary adaptations to particular habitat features and conditions. In many areas, however, effects of different fire regimes remain poorly understood and, where important conservation or management issues are involved, controversial (Glitzenstein et al. 1995).

Summer fires can stimulate seed yields of native grasses more than fires in winter or early spring (Biswell and Lemon 1943; Patton et al 1988). Variability in the population dynamics of some plant species appear to be related largely to variation in fire behavior (intensity, percent of area burned, fuel consumption), regardless of the season of burning, while other plant species are least vulnerable to dormant-season burning and most vulnerable to burning early in the growing season (Glitzenstein et al. 1995). In general, plant species in semi-arid grasslands are more strongly influenced by fire season and frequency than behavior (Steuter and McPherson 1995). Responses of arthropods to season and frequency of fire also appear to vary by species (Warren et al. 1987).

Birds, in general, are most vulnerable to fire during nesting and fledging periods. Fires can be devastating to ground-nesting birds because they destroy existing nests, remove protective cover and eliminate insect food resources (Daubenmire 1968) that may be associated with ground litter and vegetation. Therefore timing of prescribed burns should be a major consideration to resource managers concerned with declining populations that breed in the southern Great Plains. The effects of seasonal prescribed burns in Florida prairies on the federally endangered Florida grasshopper sparrow, *Ammodramus savannarum floridanus*, and Bachman's sparrow, *Aimophila aestivalis*, were experimentally examined. Even though endangered species management for the Florida grasshopper sparrow was focused on the concept of winter season burns, both species were found to respond favorably to summer burns (Shriver and Vickery 1995).

No studies have focused on the issue of seasonal effects of fire on small mammals. Since most of the effects of season on population responses will undoubtedly be more subtle than general fire-negative and fire-positive responses, studies of differences in effects of grassland fires on small mammal populations will require intensive, replicated studies (Kaufman et al. 1990). Numerous studies have examined the response of small mammals in spring and autumn or spring and winter burn plots (Bock and Bock 1978, 1983; Bock et al. 1976; Tester and Marshall 1961); however, due to lack of replicates, no effects of season were evident, and these analyses focused on only the general effects of fire on small mammals (Kaufman et al. 1990).

CONCLUSION

The effects of fire on animal community structure in grasslands are related to trophic relationships and plant community structure (i.e., amount of litter, shrub, and grass cover). Conceivably, the effects of fire on arthropods will carry over to birds and small rodents that rely on arthropods as their prey base. This in turn will affect larger mammals and raptors. These relationships change rapidly as vegetation establishes and grows in recently-burned areas. Thus, community structure is likely to be temporally dynamic. Change is the normal course of events for most ecological systems (Connell and Sousa 1983). Management of ecosystems is challenging in part because we seek to understand and manage areas that change (ESA 1995).

Knowledge of plant and animal response to fire timing and frequency should allow scientists and resource managers to predict the effects of prescribed burns on ecosystems. For example, prescribed fire in prairie in Illinois eliminated the federally listed Species of Concern, Henslow's sparrow (*Ammodramus henslowii*) from burned areas. Data suggest that Henslow's sparrows relocate to adjacent unburned areas of prairie when their preferred areas were burned. Because of the species sensitivity to prescribed fire, it was recommended by the Illinois Endangered Species Protection Board that managers of prairies where this species occurs use a rotational system of burning in which no more than 20-30% of the site is burned in any year (Herkert and Glass 1995).

Research Needs

Most previous research on the effects of fire on plant and animal communities in shortgrass prairie has not employed the experimental approach, but has instead relied on study designs that are largely descriptive in nature. Descriptive research is suitable for identifying patterns, but is considerably less useful for determining underlying mechanisms. This type of research has limited predictive power, and consequently, limited utility to managers. Thus, although descriptive research has generated many hypotheses about ecological phenomena, few of these hypotheses have actually been tested (Weltzin and McPherson 1995). Manipulative field-based experimental research will help disentangle important driving variables because of strong correlations between factors under investigation (Gurevitch and Collins 1994). Identification of underlying mechanisms of change in community structure will enable us to predict community response to changes in driving variables (e.g., climate change, or fire) with a level of certainty useful to management. Some examples of research needs that can be addressed with experiments are the evaluation of the population responses of arthropods and vertebrates to prairie restoration using prescribed fire; identification of plant and animal species that are fire-dependent, neutral, or exhibit positive or negative responses to fire; evaluation of length of time after fire before positive or negative responses are produced; evaluation of the use of prescribed fire to benefit sensitive, threatened, or endangered plant and animal species; and, determination of whether fire suppression, or differences in season and frequency of prescribed burns will continue to contribute to population declines of some species.

Some important questions can be addressed only at spatial scales may be incompatible with experimentation. These include the assessment of prescribed fire to create desirable landscape patterns for managing populations of plant and animal species, such as game animals, endangered species, neotropical migratory birds, and other featured species; landscape and regional analysis of patterns of species endangerment and abundance in relation to quantity and configuration of vegetation type and structure; and modeling of fire use to reverse undesirable trends in sizes of populations and habitats.

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