Cumulative Watershed Effects of Fuel Management in the Eastern United States

CHAPTER 9.

Ecology and Management of the Prairie Division

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General Features of Grasslands

Distribution and Climate

Grasslands occurred on all continents, comprised almost 42 percent of the world's plant cover, and once covered approximately 46 million km^2 of the Earth's surface. Grasslands contain few trees or shrubs, are dominated by grasses (members of the family Poaceae), and have a mixture of nongraminoid herbaceous species called forbs. Plant families most abundant as forbs are sunflower (*Asteraceae*) and pea (*Fabaceae*) families. No single climate characterizes grasslands and they occur in areas of the Earth that receive as little as 200 mm of precipitation annually to areas that receive 1300 mm, and in areas where average annual temperatures vary from 0 to 30 °C (Oesterheld and others 1999, Risser and others 1981, Sauer 1950). Grasslands are not necessarily treeless and they are transitional to savannas, which are characterized by higher densities of drought-tolerant, fire-resistant trees. The ratio of trees to grass increases as precipitation increases (Anderson and Bowles 1999, Curtis 1971, Oesterheld and others 1999); in landscapes receiving >650 mm of precipitation, the trend is for increasing cover of woody species with "long-term fire exclusion" (Sankaran and others 2004). In areas of low precipitation, grasslands grade into desert communities. Common features found among grasslands include: periodic droughts, frequent fires, landscapes that are level to gently rolling, and an abundance of grazing animals (Anderson 1982, 1990; Risser and others 1981, Sauer 1950).

Drought, Fire, and Grazing Animals

Grassland plants evolved under the influence of periodic droughts, frequent burning, and grazing animals; they are adapted to all three (Anderson 1990, Damhoureyeh and Hartnett 1997, Gleason 1922). This adaptation for grasses is manifested in their ability to die down to underground organs (rhizomes, root, and tillers); and only expose dead tops (Gleason 1922). Grasses grow tips beneath soil that are not exposed to desiccation—this allows them to escape drought. The leading edge of prairie fires can be long and historically they often extended many km in length; however, the flame depth is narrow in the range of 2 to 7 m. These fires move relatively rapidly and, because

the soil is a good insulator, heat penetration into the soil can be measured in millimeters (Anderson 1982). Consequently, the growing points of prairie plants are protected from the heat of the fire. Grazers can only remove aboveground tissues; once grazing pressure is removed, new shoots can emerge from belowground (Tainton and Mentis 1984).

The adaptation of grasses to fire, drought, and grazing animals may represent a preadaptation to one or more of these factors; however, grasses and herbivores likely coevolved based on other features of grasses. The post-Miocene expansion of grasslands and savannas worldwide was associated with the adaptive radiation of large grazing mammals (Anderson 1982, 1990; Axelrod 1985, McNaughton 1993, Oesterheld and others 1999, Stebbins 1981). Adaptive responses of grasses to herbivores that reflect a coevolutionary relationship include the presence of silica in epidermal cells, perennating organs below ground level, and aboveground productivity in excess of the amount of biomass which can decompose in a single year (Anderson 1982, 1990; Stebbins 1981).

The widespread expansion of grassland is associated with the appearance of the C_4 photosynthetic pathway (which initially produces a 4-carbon intermediary during fixation of carbon dioxide). The C_4 photosynthetic pathway provides an advantage over the more common C_3 pathway because it provides higher quantum yields for carbon dioxide uptake under high temperatures. The C_4 photosynthesis is also favored over C_3 photosynthesis when the concentration of atmospheric carbon dioxide is below 500 ppmV or parts per million by volume (Cerling and others 1997; Ehleringer and others 1997, 2002). During the Mesozoic, carbon dioxide concentrations were thought to be >1,000 ppmV. However, in the early Miocene or late Oligocene (Kellogg 1999), perhaps 20 to 25 million years ago, decline in atmospheric carbon dioxide favored evolution of C_4 plants in moist tropical and subtropical climates (Ehleringer and others 1997). This photosynthetic pathway is found in <2 percent of all flowering plants but approximately half of the 10,000 species of graminoid (grasses and sedges) use this pathway. Although C_4 plants are a small percentage of flowering plants, they contribute 25 percent of total global productivity, largely as monocotyledons in grasslands (Eherlinger and others 2002).

C_4 grasslands developed quickly worldwide during the Miocene-Pliocene transition (6 to 8 million years ago) with expansion of the Antarctic Ice Sheet, which some believe increased aridity, and reduced atmospheric carbon dioxide to <500 ppmV, causing declines in forest and woodlands accompanied by an explosive evolution of grasses and forbs (Cerling and others 1997; Ehleringer and others 1997, 2002). However, Keeley and Rundel (2005) posit that the conversion of forests to C_4 grasslands 4 to 7 million years ago was not directly attributable to a decline in atmospheric carbon dioxide or increased aridity but rather to new climatic conditions that encouraged fire: a warm moist growing season that increased biomass productivity and a pronounced dry season that created combustible fuels. This monsoon climate likely would be accompanied by frequent lightning strikes at the end of the dry season. In this model, fire would have been a primary driver in the conversion of forest to grasslands and the maintenance of grasslands as it is today.

Expansion of open grassland and savanna habitats was associated with increased fossilized silica bodies in the epidermis of grasses, which provide protection against grazing. Concomitantly, mammals with high-crowned teeth (hypsodonty) adapted to grazing (Axelrod 1985, Stebbins 1981) increased, and more cursorial (running) and saltational (jumping) body forms began to evolve.

Central Grassland of North America

Grasslands of North America are part of a diverse assemblage of vegetation types that occur under a wide range of climatic conditions and once covered about 15 percent of the continent. These grasslands are referred to as *prairies*, a word meaning meadow or field, which early French explorers used to describe the extensive grasslands they encountered (Curtis 1971, Risser and others 1981). Along a north-south gradient, grasslands extended from the deserts of Northern and Central Mexico to mixed-grass prairies of Alberta,

Saskatchewan, and Manitoba in Canada (Risser and others 1981). Across this gradient, average annual temperature varies from 2.8 °C in the northern mixed-grass prairie around Regina, SK to 22.6 °C in Monterrey at the edge of Chihuahuan Desert. In the desert grasslands of southwestern United States, annual precipitation averages 250–450 mm, whereas along the eastern edge of grasslands precipitation varies from about 2500 mm in southeast Texas to 750 to 1000 mm in Indiana (Risser and others 1981).

Geographic variation

The shape of the Central Grassland of North America resembled a large triangle whose base extended from the Canadian provinces of Alberta and Saskatchewan southward along the eastern foothills of the Rocky Mountains and then to southeastern Texas. The point of the triangle extended well into the Midwest in southwestern Wisconsin, Illinois, and western Indiana, with scattered outliers in Michigan, Ohio, and Kentucky (the Prairie Peninsula). This area includes the grasslands of the 12 Great Plains States, as well as the outliers east of the Mississippi River. Annual precipitation from the western Great Plains to the Prairie Peninsula increases from 260 to 1200 mm; across a north-south gradient, average annual temperature ranges from 3 to 22 °C (Sala and others 1988).

Ecologists have traditionally divided the grassland into three sectors based on annual precipitation: a western shortgrass prairie (260 to 375 mm precipitation), the eastern tallgrass prairie or "True Prairie," (625 to 1200 mm precipitation), and between the two the midgrass or mixed-grass prairie (375 to 625 mm precipitation) (fig. 1). Shortgrass prairie occupies an area dominated by grasses that are 0.3 to 0.5 m tall and include buffalo grass (*Buchloe dactyloides*), blue grama (*Bouteloua gracilis*), sideoats grama (*Bouteloua curtipendula*) and hairy grama (*Bouteloua hirsuta*). The tallgrass prairie is dominated by species that reach heights of 1.8 to 2.4 m and include big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), and little bluestem (*Schizachyrium scoparium*). The mixed-grass prairie is dominated by species that are 0.8 to 1.2 m tall and include little bluestem, western wheatgrass (*Pascopyrum smithii*), and green needlegrass (*Nassella viridula*). In the

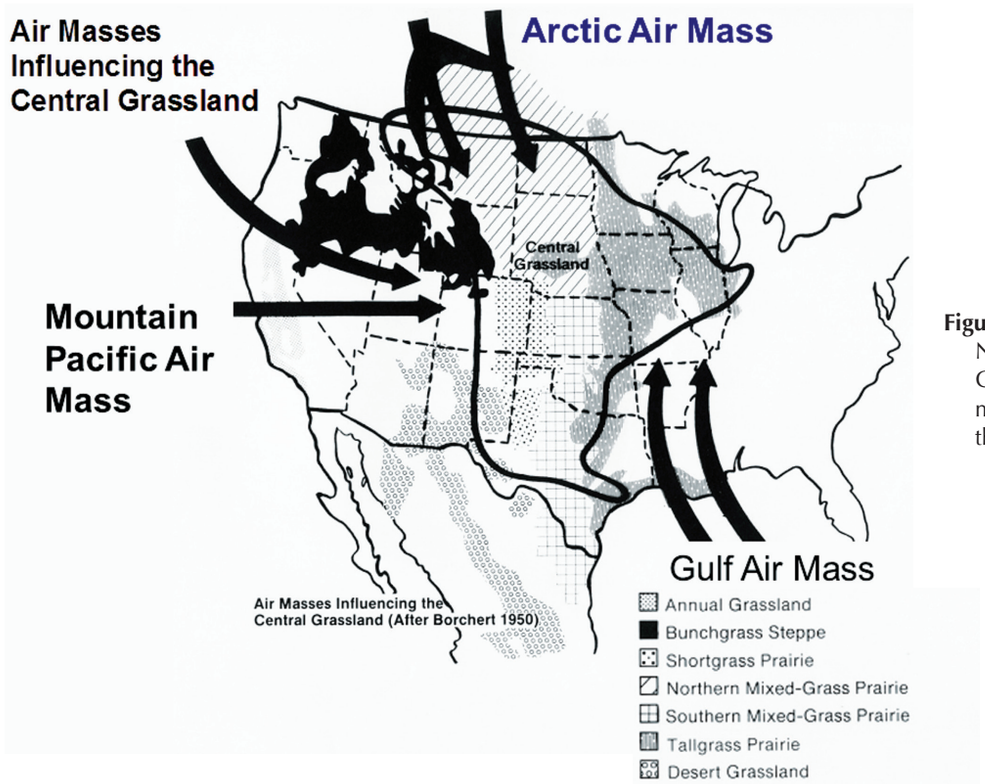

Figure 1. The Grassland of North America. The Central Grassland is outlined and the major area masses influencing the grassland are shown.

mixed-grass prairie, tallgrass prairie species occur in depressed areas that are moister than upland sites, and on drier sites short-grass prairie species can occur resulting in a mixture of tall-, short-, and mixed-grass prairie species. Across the Central Grassland, species composition and abundance varies continuously and with no sharp divisions among these arbitrarily designated grasslands.

Variation within a geographical area

Within each of the major areas of the Central Grassland differences among prairie types are the result of soil, aspect, slope position and other factors. At any location in the tallgrass prairie, the diversity of prairie types depends on soils and topographic features. A primary factor causing this varied vegetation patterns is availability of soil moisture (Corbett and Anderson 2006, Curtis 1971, Nelson and Anderson 1983, Umbanhowar 1992). For example, approximately 930 ha of high quality remnant prairie in Illinois consist of diverse habitat types with varying topography and substrate. They include dry hill and bluff prairies with loess or glacial drift derived soils that often occupy western or southwestern facing slopes overlooking rivers (Evers 1955). Dry prairies also occur on deep sand deposits or on dolomitic or gravel substrates with shallow stony soils. Additionally, wet-mesic to wet prairies occur on loess-derived, till-derived, or dolomite-containing substrates (Table 1). Historically, the most common Illinois prairie types were mesic and wet prairies covering as much as 55 percent of the State (Fehrenbacher and others 1967); most have been converted to agricultural or urban uses.

Climate

The climate of the Central Grassland is influenced by three primary air mass systems: Arctic, Gulf, and Mountain Pacific (Borchert 1950, Bryson and Hare 1974, Risser and others 1981). The Arctic air mass influence is reflected in part by the increased snow cover and decreasing temperatures from south to north (Risser and others 1981), as well as variations in vegetation (Diamond and Smeins 1988) and phenological patterns (Kebart and Anderson 1987, McMillan 1959). Gulf and Mountain Pacific air masses are most important in determining east-west variation. The Gulf air mass originates in the Gulf of Mexico. As it moves northward into the eastern part of the Central Grassland, it brings humid air and precipitation as it encounters cooler air or provides moisture for convectional storms. The Mountain Pacific air mass arrives on the west coast as a humid air mass. However, as it progresses eastward the air mass passes over several western mountain ranges (Coastal, Sierra, and Rocky). As the air mass rises, it cools adiabatically, and gives up much of its moisture and then is compressed by an increasing volume of atmosphere as it descends to lower elevations on the east side of the Rocky Mountains, causing it to become warmer and more arid as it spills out into the Great Plains. Thus, the Central Grassland occurs in the rain shadow of the western mountains.

From west to east, the influence of the Pacific air mass decreases and the influence of the Gulf air mass increases. Associated with these changes average annual precipitation increases, and periodic droughts, and periods of low humidity in summer decrease (Borchert 1950, Bryson and Hare 1974, Risser and others 1981). West-east climatic variation produces the changes in vegetation from the foothills of the Rocky Mountains to the Midwestern United States that results in the shortgrass, mixed-grass, and tallgrass prairies. Annual net primary productivity is also affected by this climatic gradient, which in years of average precipitation varies from 150 to 600 g/m^2.

Grass Adaptations to Drought

There are many morphological and physiological features that allow grasses to tolerate high moisture stress including: (1) the occurrence of bulliform cells in leaves, which cause them to enroll when they lose water, thereby reducing surface area for transpiration; and (2) utilization of the C_4 photosynthetic pathway, which adapts plants to high temperatures, high levels of solar radiation, and periods of moisture stress. The C_4

Table 1. Leading species (with average quadrat frequency of ≥2.0 percent, values are percent (± standard error) in six community types (modified from Corbett and Anderson (2001, 2006). The second column provides the native community of maximum presence (occurrence) in Wisconsin from Curtis (1971)

Species[a]	Community: Curtis 1971	Dry sand	Gravel/ sand	Hill prairie	Gravel/dry dolomite	Mesic/ dry mesic	Wet/wet dolomite
		percent (±standard error)					
Little bluestem	Dry prairie	16.9 (±1.5)	17.3 (±2.9)	15.4 (±0.7)	11.6 (±1.4)	3.6 (±0.4)	—
Devil's-tongue	Cedar glade	8.4 (±1.8)	—	—	—	—	—
Cuman ragweed	Sand barren	6.7 (±2.2)	—	—	—	—	—
Prairie sandreed	Dune	3.9 (±2.0)	—	—	—	—	—
Heller's rosette grass	Dry mesic prairie	3.3 (±1.7)	2.4 (±1.6)	—	—	—	—
Goat's rue	Oak barren	3.3 (±1.7)	—	—	—	—	—
Hairy grama	Cedar glade	2.3 (±1.5)	—	—	—	—	—
Porcupine grass	Dry mesic prairie	2.0 (±1.0)	4.4 (±2.4)	—	4.5 (±1.0)	—	—
Flowering spurge	Oak barren	—	5.4 (±2.0)	—	—	—	3.6 (±0.4)
Pale purple coneflower	Mesic prairie	—	3.1 (±2.0)	—	3.4 (±0.6)	—	—
Carolina puccoon	Sand barren	—	2.7 (±2.2)	—	—	—	—
Prairie June grass	Sand barren	—	2.5 (±2.0)	—	—	—	—
Gray clustered poppy mallow	Dry mesic prairie	—	2.3 (±1.6)	—	—	—	—
Sideoats grama	Dry prairie	—		9.1 (±0.8)	3.8 (±0.8)	—	—
Indian grass	Dry mesic prairie	—		4.5 (±0.7)	—	4.4 (±0.4)	—
Purple prairie clover	Dry prairie	—	2.2 (±2.2)	4.5 (±0.4)	—	—	—
Flowering spurge	Oak barren	—	—	4.1 (±0.4)	4.6 (±0.7)	—	—
Gray goldenrod	Dry prairie	—	—	3.6 (±0.5)	—	—	—
Scurfy pea	Not given	—	—	2.8 (±0.4)	—	—	—
Sky blue aster	Dry mesic prairie	—	—	2.5 (±0.5)	—	—	—
Pursh leadplant	Dry prairie	—	—	2.3 (±0.4)	3.6 (±0.7)	—	—
Gray prairie dropseed	Dry prairie	—	—	—	3.0 (±0.6)	3.0 (±0.4)	—
Carolina rose	Not given	—	—	—	2.5 (±0.6)	2.4 (±0.3)	—
Snow flurry	Dry mesic prairie	—	—	—	2.3 (±0.6)	3.6 (±0.4)	—
Big bluestem	Mesic prairie	—	—	—	—	5.0 (±0.5)	2.5 (±0.7)
Virginia strawberry	Northern dry forest	—	—	—	—	2.2 (±0.3)	2.7 (±0.8)
Sedge	Not given	—	—	—	—	—	6.3 (±1.8)
Giant goldenrod	Wet prairie	—	—	—	—	—	4.3 (±0.9)
Virginia mountain mint	Wet mesic prairie	—	—	—	—	—	3.7 (±0.8)
Bluejoint	Fen	—	—	—	—	—	3.5 (±1.5)
Prairie cordgrass	Wet prairie	—	—	—	—	—	3.2 (±0.8)
Upright sedge	Southern sedge meadow	—	—	—	—	—	2.2 (±2.1)
Sawtooth sunflower	Wet mesic prairie	—	—	—	—	—	2.7 (±1.1)
Riddell's goldenrod	Fen	—	—	—	—	—	2.7 (±0.9)

[a] Common names follow the USDA Plant database.
Source: Curtis (1971) modified from Corbett and Anderson (2001, 2006).

plants have high water use efficiency, photosynthetic rates, and stomatal sensitivity to water loss, and they can grow under conditions of low soil-water potential (Ares 1976, Briske and Wilson 1978). Although many dominant grasses in the Central Grassland are C_4 grasses—including Indian grass, big bluestem, switchgrass, little bluestem, sideoats and hairy grama grass—many species of C_3 grasses dominate some prairies. The C_3 plants maximize growth under cool moist conditions and are known as "cool season grasses." They have lower water use efficiency, photosynthetic rates, and photosynthetic temperature optima and saturation levels for solar radiation, but higher rates of photorespiration and higher carbon dioxide compensation points.

In North America, the primary separation of C_4 and C_3 grass is related to temperature (Terri and Stowe 1976). Where daytime growing season temperature are lower than 22 °C, C_3 plants should dominate and where growing season temperatures are above 30 °C and soil moisture is adequate, C_4 plants should predominate (Ehleringer and others 1997). C_4 plants have a higher quantum yield for carbon dioxide fixation at latitudes less than about 45° (Ehleringer and others 1978). Where the two groups of grasses grow together, the C_3 grasses—such as Canada wildrye, (*Elymus canadensis*), western wheatgrass, green needlegrass, porcupine grass (*Hesperostipa spartea*), and prairie Junegrass (*Koeleria macrantha*)—grow in the spring and early summer, whereas the C_4 grasses begin growth later and maximize growth in midsummer. Even though the C_4 grasses are more drought tolerant than C_3 grasses, western wheatgrass increased its abundance more than many C_4 grasses during the drought of the 1930s because it was able to use moisture that was only available in early spring—and not available to the later growing C_4 grasses (Monson and others 1982, Weaver 1968).

Pleistocene history

Although grasslands may have been present on the North American continent for 20 million years (Axelrod 1985, Benedict and others 1996, Risser and others 1981, Weaver 1968), the Central Grassland is of relatively recent origin. During the Pleistocene, climate change and the continental ice sheet caused destruction of the mid-continent grassland and other vegetation types that may have replacement it. At the peak of Wisconsinan glaciation (18,000 years ago), most of what now is the Central Grassland was dominated by spruce (*Picea* spp.) and jack pine (*Pinus banksiana)* forest or covered with glacial ice. During the early Holocene, 10,000 years ago, grasslands or oak (*Quercus* spp.) savanna occurred in much of the area, but forests occurred over most of the Prairie Peninsula (Delcourt and Delcourt 1981, Nelson and others 2006). In the eastern portion of the Prairie Peninsula, aridity increased between about 10,000 and 8,500 years ago and fire sensitive trees, such as elms (*Ulmus* spp.), ashes (*Fraxinus* spp.) ironwood (*Ostrya* sp.), and sugar maple (*Acer saccharum*), decreased in abundance and prairie species expanded. Between about 8,500 and 6,200 years ago aridity declined and prairie coexisted with fire-sensitive and fire tolerant tree taxa [e.g., oaks (*Quercus* spp.) and hickories (*Carya* spp.)]. After about 6200 years ago, prairie became dominant; however, the climate was less arid than it was around 8,500 years ago. Fires set by Native Americans and lightning are thought to the primary reasons tallgrass prairies persisted as the climate became less arid.

Information from several sources, however, suggests that changes in climatic patterns and vegetation in the area of the Prairie Peninsula varied spatially during the Holocene on millennial time scales (Baker et al. 1996, Nelson and others 2006, Nelson and Hu 2008, Winkler et al. 1986). For example, based on pollen records and charcoal deposits from Lake Mendota in southern Wisconsin, the climate was hotter and drier and fire frequency greater between 6,500 and 3,500 years ago than it was earlier in the Holocene and after 3,500 years ago the climate became cooler and more moist (Winkler 1995, 1997; Winkler and others 1986). In northeastern Iowa, forest dominated from about 8,000 to 5,100 years ago and then prairie replaced forest (Baker et al. 1996). The authors suggest that a climatic shift that increased the flow of arid Pacific air and increased frequency of fire probably caused the change in vegetation.

According to Axelrod (1985), the recent origin of the Central Grassland is indicated by the occurrence of most of its species in forest and woodlands; the presence of few endemic plants (Wells 1970a), insects (Ross 1970), or birds (Mengel 1970, Risser and others 1981); the relict occurrence of a variety of tree species throughout the area; and the current invasion of woody plants. Benedict and others (1996) indicate that, among mammals, true grassland species comprise only 11.6 percent of those occurring on the central and northern plains; and that only 5.3 percent of North American bird species evolved on prairies (Knopf 1996). Similarly, many of the grass species that occur in the Central Grassland evolved in eastern forest openings, the southwestern deserts, or mountain meadows (Gleason 1922, Risser and others 1981).

The Prairie Peninsula

Location and origin

Near the Mississippi River and eastward in the Central Grassland, the climate becomes increasingly favorable for the growth of trees. The wedge-like extension of the grassland into the Midwestern United States is called the Prairie Peninsula (fig. 2), because it is a peninsula of grass extending into forests (Transeau 1935). Annually, this area receives 750 to 1200 mm of precipitation, a climate capable of supporting forest. Historically, ecologists have debated why this area had grasslands rather than forest (Curtis 1971, Transeau 1935). Several general hypotheses emerged to explain this pattern. One hypothesis focused on the importance of climate as a primary determinate of vegetation patterns. The other posited that fires set by Native Americans or soil conditions were responsible for the absence of trees.

Climate effects

Transeau (1935) reasoned that climatic extremes are more important than averages in determining the distribution of organisms. He demonstrated that the Prairie Peninsula has periodic droughts when drier western climatic conditions shift eastward into the

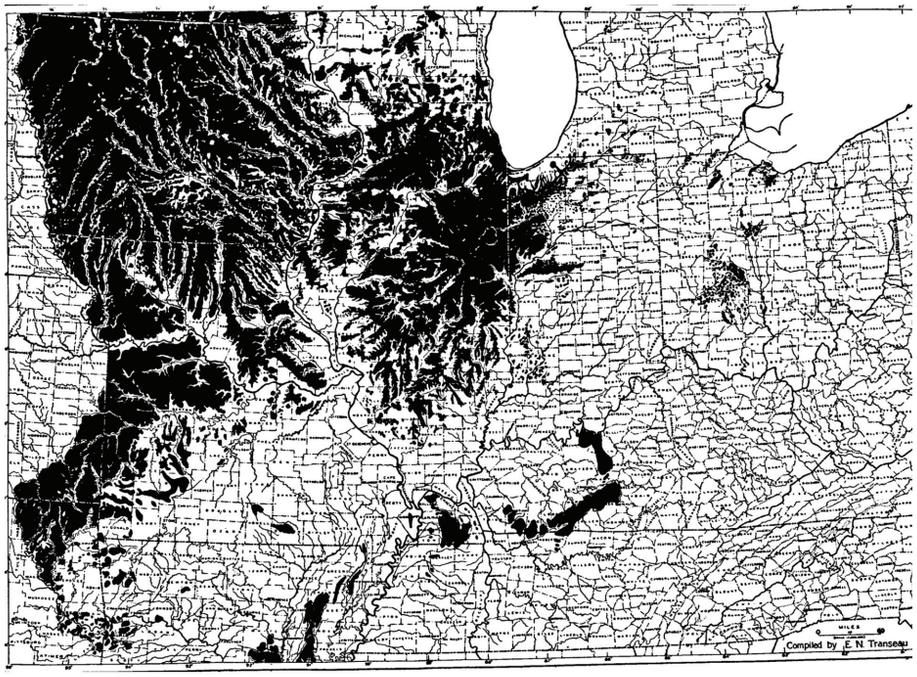

Figure 2. The Prairie Peninsula after Transeau (1935).

Prairie Peninsula. These periodic droughts would favor the prairie and set back the forest. Indeed, during the droughts of the 1930s trees experienced high rates of mortality in the Prairie Peninsula (Albertson and Weaver 1945). Transeau (1935) noted a loss of trees from upland sites during the droughts of the 1930s accompanied by a retreat to sheltered locations adjacent to streams. Seedlings are strongly affected by drought and by competition from grasses, both directly and indirectly—they produce flammable, finely divided fuels that encourage the spread of fire (Anderson 1990, Sankaran and others 2004).

Drought and rooting depth

The differential effects of drought on prairie grasses and trees have been explained by the root growth forms of these two groups. In Missouri tallgrass prairie, 80 percent of the root mass occurred in the upper 25 cm of soil (Dahlman and Kucera 1965), with similar results reported by others (Bartos and Jameson 1974, Old 1969, Risser and others 1981, and Zink and Weaver 1946). Although prairie plants have most of their roots in the upper layers of the soil, many also have deep root penetration; to illustrate, for 14 grasses and 15 forbs, the rooting depth range is 0.5 to 7.0 m; average ± SE is 2.36±0.24 m, according to original data from Weaver (1954), recalculated by Risser and others (1981). Scholes and Archer (1997) suggest that in habitats with grasses, maximum rooting depth of trees generally exceeds that of grasses. They also note that both trees and grasses have the maximum amount of their root mass in the upper soil layers. Nevertheless, grasses may be less dependent on deep soil moisture than trees (Schimper 1903, Walter 1971).

Britton and Messenger (1969) suggest that when droughts disrupt recharge of deep soil moisture, trees are more affected than grasses. Grasses use their diffuse root system to take advantage of light showers that recharge upper soil surface layers. In the Prairie Peninsula recharge of deep soil moisture usually occurs during the dormant season, because high rates of evapotranspiration during the growing season reduce the likelihood of deep soil moisture recharge. In the Midwest, areas that did not experience deep soil moisture recharge during the 1933–1934 winter corresponded to the location of the Prairie Peninsula (Britton and Messenger 1969). This finding supports the hypothesis that drought is an important factor in determining the occurrence of the Prairie Peninsula.

Fire as a factor

As previously noted, beginning about 6,000 to 3,000 years ago the Prairie Peninsula climate became cooler and moister and more favorable for trees. Following this change of climate to one that can support prairie, savanna, or forest, stabilization of the vegetation in the Prairie Peninsula is thought to be the result of fires set by Native Americans and occasional lightning strikes (Anderson 1990, 1991b, 1998; Curtis 1971).

Prairie fires can reach temperatures of 83 to 680 °C on the surface of the soil (Rice and Parenti 1978, Wright 1973). Gibson and others (1990) reported that on Konza Prairie in Kansas, fire temperatures ranged from 166 to 343 °C as a function of habitat, whether the fire occurred on an upland or lowland site, and time since last fire—all of which affected fuel loadings. As previously noted, prairie grasses are protected from fire because their growing points are located beneath the surface of soil and the penetration of heat below the soil surface is minimal (Anderson 1982, Reichert and Reeder 1972). Fire is detrimental to trees because their aboveground growing points, shoot apical meristems and vascular cambium, are exposed and vulnerable to fire. Woody species can be killed by fire or their shoots destroyed, and even if they resprout, growth is suppressed for several years, reducing their competitiveness against grasses. Anderson and Brown (1986) reported that after a single central Illinois fire in a forest adjacent to sand prairie, 34.1 percent of blackjack oak (*Q. marilandica*) and black hickory (*Carya texana*) trees >9.0 cm d.b.h. (diameter at breast height) suffered mortality in the first year following the fire, 4.9 percent in the second year, and 8.5 percent in the third years.

Frequent fire and periodic droughts may have interacted to effectively control woody plant invasion into grasslands, especially on sites supporting fire-sensitive-mesic species—such as sugar maple (*Acer saccharum*), ashes (*Fraxinus* spp.), elms (*Ulmus* spp.), and American basswood (*Tilia americana*)—that are more susceptible to fire and droughts than the oaks. Even if the trees resprout, browsing by elk (*Cervus canadensis*) and deer (*Odocoileus* spp.) may have kept woody species from dominating grasslands (Anderson 1982). Sankaran and others (2004) suggest that grazers reduce fuels and therefore favor trees, but conversely browsers favor grass.

The Vegetation Mosaic

Topography and fire spread

In the eastern portion of the Central Grassland, the occurrence of the three community types (prairie, savanna, and forest) in the vegetation mosaic was the result of climate and of fire frequency, which was strongly influenced by topographic features and distribution of waterways (Anderson 1983; Gleason 1913, 1922; Grimm 1984, Wells 1970b). In North American grasslands, sharp transitions to distinctly different vegetation types are associated with topographic changes (Wells 1970a, 1970b). The main effect of topography appears to be its control of fire frequency. Landscapes that are nearly level to slightly rolling can support the nearly annual fires that grasslands need for maintenance (Anderson 1982, 1990; Curtis 1971, Risser and others 1981). Fire might not be able to eliminate fire resistant woody species from grasslands, but it can keep them in a reduced state and dependent for survival on recurring annual growth from roots (Bragg and Hulbert 1976, Curtis 1971, Heisler and others 2003). In dissected landscapes, fire moves rapidly up slopes, as it is carried upward by rising convection currents. Conversely, as fire moves downslope, its movement is impeded by the upward flow of the convection currents; and steep slopes and ravines can function as firebreaks and provide sheltered locations were forests can survive (Anderson 1998). Using a map of the historical distribution of "timber" (forest/savanna) and prairie in Illinois (Anderson 1970) and distribution of average slope range in the State, Anderson (1991a) examined the relationship between topography and historical distribution of vegetation; about 60 percent of the State was tallgrass prairie (Anderson 1991a, 1991b; Robertson and others 1997). Most of the prairie (82.3 percent) occurred on landscapes with average slope ranging from of 2 to 4 percent, whereas only 23 percent of the forest and savanna was associated with landscapes in this slope range, mostly in flood plains. Seventy-seven percent of forest vegetation occurred on landscapes with average slope of >4 percent (4 to 7 percent slope = 35.2 percent; and >7 percent = 41.8 percent). Most of the forested areas were associated with glacial moraines, highly dissected portions of the older Illinoian glacial till plain, nonglaciated landscapes, and waterways.

Waterways and vegetation distribution

The distribution of waterways has a pronounced effect on the occurrence of prairie vegetation. Fires are generally swept from west to east so that areas to the west of waterways support prairie, but areas to the east support forest (Gleason 1913). Clear skies and dry weather conditions favorable for fires are associated with high-pressure systems, which have a clockwise flow of air and move from west to east. As the high-pressure system moves into an area, the leading edge of the front has wind in a westerly direction. Fire at this time would be carried to the west side of a waterway, but vegetation on the east would be sheltered. As the system passes, the winds originate from the back side and shift to an easterly direction. Fires started under these conditions would be carried to the east of waterways. However, as the system passes, low pressure replaces it and brings in high humidity and increased probability of precipitation, thereby reducing the likelihood of fire.

Fire affects on Grasslands

Factors Influencing Fires

Golley and Golley (1972) showed that grasslands can produce 20 percent more biomass than decomposes in a single growing season, and if the excess biomass is not removed by fire or grazing, the productivity of the grasslands declines. However, the response of grasslands to burning varies depending upon factors that include the amount of precipitation, grazing (which reduces fuel loading), fire frequency, timing of the fire, climatic conditions (especially rainfall and temperature) immediately before and after the burn, species composition, and fuel loading.

Oesterheld and others (1999) summarized the positive and negative effects of fire on productivity across a wide precipitation gradient (439 to 1129 mm annually) that included sites from North America, Africa, and the Mediterranean. Productivity increased by as much as 300 percent with fire and was reduced by as much as 80 percent in unburned control sites. The productivity increases were associated with sites receiving in the range of >700 mm of annual precipitation; conversely negative effects of fire on productivity occurred where precipitation was <600 mm. In the eastern portion of the tallgrass prairie, burning enhances productivity (Hadley and Kieckhefer 1963, Hulbert 1969, Kucera and Ehrenfield 1962, Old 1969, Peet and others 1975, Rice and Parenti 1978, Vogl 1974). Exceptions to this generalization have been reported for xeric sites (Dix and Butler 1954, Zedler and Loucks 1969), although Dhillion and Anderson (1994) and Anderson and others (1989) reported an increase in productivity following burning on a deep sand site in central Illinois. However, in the arid western portions of the North American Grassland, an increase in productivity does not always follow burning (Anderson 1976, 1982; Augustine and others 2010, Heirman and Wright 1973, Hopkins and others 1948, Launchbaugh 1972, Oesterheld and others 1999; Wright 1969, 1972).

Time of the Burn and Productivity

In the Flint Hills of Kansas, at the western edge of the tallgrass prairie, the time of the burn influences grass productivity on native grass pastures. Burned sites had lower productivity than unburned sites following winter or early-spring burns, but late-spring burns and nonburned areas had equal productivity. Decline of productivity on early burns compared to late-spring burns is attributed to litter being removed from the site for a longer period of time followed by early growth, which depletes soil moisture (Knapp 1985). Absence of litter increases runoff and evaporation of moisture from the soil surface. The resulting decline in soil moisture is the primary cause for a decline in productivity (Anderson 1982, Bragg and Hulbert 1976, Knapp 1985, McMurphy and Anderson 1965, Owensby and Anderson 1967, Owensby and Smith 1972, Svejcar 1990). Nevertheless, cattle (*Bos taurus*) grazing on forage on burned sites make faster weight gains than those grazing on unburned sites, because the forage on burned sites is more palatable and higher in protein (Anderson 1976, Dyer and others 1982, Knapp and others 1999, McNaughton and others 1982).

Ignition by Lightning and Humans

Lightning as an ignition source was important in the western portion of the Central Grassland and can cause prairie fires during the growing season if the vegetation is dry (Anderson 1982, Bragg 1995; Howe 1994a, 1994b). In the western portion of the tallgrass prairie, lightning fires in Nebraska averaged 138 per year from 1971 to 1975 and the historical fire season was from spring through autumn. Grasslands in the Great Plains originated during the Holocene and Native Americans have been on the continent for the past 30,000 years (Bragg 1995). They used fire as a vegetation management

tool for a variety of reasons—including encouraging the growth of the prairie and preventing the encroachment of woody species—and as a tool for hunting, controlling insect, and easing travel (Anderson 1990, 1997; Curtis 1971; Pyne 1983, 1997; Stewart 1956). Consequently, lightning and Native Americans both had important roles in igniting grassland fires, especially in the frequency of summer fires (Devoto 1963). Summer fires are smaller those set during the dormant season, and they are often extinguished by rains associated with the storm that generated the lightning strikes (Bragg 1995).

In the wetter eastern portion of the Central Grassland, where rainfall also usually accompanies lightning storms, most fires were apparently set by Native Americans (Curtis 1971, Pyne 2001). In the eastern tallgrass prairie, fires occurred most frequently during the dormant season. Historical evidence suggests that many fires occurred in autumn, during the period known as "Indian summer" (McClain and Elzinga 1994), a warm, dry period following killing frosts (late October and early November).

Litter Removal

Fire and litter removal

The increased productivity on burned eastern tallgrass prairie is related to litter removal (Ehrenreich 1959, Hadley and Kieckhefer 1963, Hulbert 1969, Knapp 1984, Kucera and Ehrenreich 1962, Peet and others 1975, Weaver and Roland 1952). Old (1969) reported that litter removal increased productivity whether it was removed by fire or by mechanical means. One of the mechanisms whereby litter removal enhances productivity is through the alteration of microclimatic conditions on the burned site to conditions more favorable for the growth of the dominant C_4 grasses.

Litter is a good insulating surface and it has high reflectance of solar radiation and low net radiation, which is the difference between incident (irradiance striking a surface) and reflected solar radiation. Consequently, the soil warms up slowly in the spring (Peet and others 1975). On the burned surface, however, the insulating and highly reflective litter layer and standing dead biomass is removed by burning and replaced by a darkened highly absorptive surface. At the Curtis Prairie in University of Wisconsin-Madison Arboretum, daytime soil temperatures at 3-mm depths were warmer on the burned site than the unburned site. At night, the burned prairie has a good radiating surface (a good absorbing surface is also a good radiating surface) and cools rapidly, compared to the unburned site whose insulating litter cover retains heat. Consequently, nighttime temperatures were cooler in the upper layers of soil on the burned site. However, at 25 cm depth, the unburned site was constantly cooler than the burned site. The differences in microclimate between burned and unburned sites decreased as a grass canopy developed on the unburned site (Anderson 1972b, Brown 1967, Peet and others 1975).

The warmer soil temperatures during the day in early spring resulted in plants beginning growth earlier on burned prairie than the unburned prairie. Emergence of vegetation on the unburned site can be 7 to 14 days or as much as 30 days later (Knapp 1984). Peet and others (1975) reported that a burned site established a larger standing crop of vegetation (43.6 g/m^2) than the unburned site (1.24 g/m^2) by May 31 at the Curtis Prairie. They reported no difference in maximum photosynthetic rates of big bluestem on burned and unburned prairies. The higher productivity on burned prairies was attributed to the larger standing crop of green biomass earlier in the growing season (Peet and others 1975).

As leaves develop underneath standing dead biomass on the Konza Prairie, they are shaded and acquire the shade-leaf characteristics of low light saturation and photosynthesis. Standing dead litter reduces solar radiation and slows wind speed (89 percent lower than above the canopy), which reduces convectional cooling. Leaf temperatures of 30 to 35 °C (Black 1973) can rise above the optimum for C_4 photosynthesis (Knapp 1984). On burned grasslands, however, leaves develop in full sunlight as they emerge and have characteristics of sun leaves with high light saturation and photosynthesis. Additionally, on burned prairie, leaf temperatures are near the optimum

for photosynthesis; the absence of standing dead biomass results in greater convectional cooling and higher wind speeds (57 percent lower than above the canopy). For example on June 10, leaf temperatures for big bluestem were 41.5 °C (7.9 °C above air temperature) on unburned sites and 39.4 °C (4.0 °C above air temperature), on burned sites (Knapp 1984). However, big bluestem plants on burned sites had greater water stress early in the growing season than plants on the unburned prairie (Knapp 1984). Microclimatic differences related to warmer spring temperatures on burned sites (Peet and others 1975), greater availability of solar radiation, and temperatures more favorable for optimum photosynthesis on burned sites are important factors in determining high productivity (Knapp 1984). Differences in results in photosynthetic rates of big bluestem on burned and unburned sites between the Kansas and Wisconsin may be due to differences in the height of standing dead tissue, which were 42 cm in Kansas and 10 cm in Wisconsin (Peet and others 1975, Knapp 1984). Leaves on unburned sites in Wisconsin should grow above of standing dead tissue more quickly than in Kansas and develop sun leaf characteristics resulting in similar photosynthetic rates between plants on burned and unburned sites. In contrast, in Kansas leaves would be shaded longer by standing dead tissues than in Wisconsin, retaining shade leaf characteristics and having lower rates of photosynthesis than plants on burned sites.

Inorganic nutrients

The presence of a litter layer reduces the availability of inorganic nutrients, especially nitrogen which is thought to be the most limiting nutrient in grasslands. Annual burning of litter on prairies will reduce available nitrogen by about 1.0 to 4.0 g/m^2/year, about twice as much as is input by rainfall (Knapp and Seastedt 1986). Although compensating mechanisms are available to replenish nitrogen lost by burning, grasslands that are burned annually are subject to a long-term net loss of nitrogen (Ojima and others 1990).

Grasslands and Grazers

In North America, expansion of the grassland biome occurred in the Miocene–Pliocene transition 5 to 7 million years ago and was associated with a concomitant increase in animals adapted to grazing, as was true for other areas (Axelrod 1985). Through the Pleistocene (1 to 3 million years ago), a diverse grazing megafauna (weight > 44 Kg) (Doughty, Wolf and Field 2010) on the continent included 32 genera and dozens of species of mammals such as camels (*Camelus* spp.), horses (*Equus caballus*), rhinoceroses (*Rhinoceros* spp.), antelopes (*Antilocapra* spp.), bison (*Bison bison*), and elephants (*Elephas maximus*). Near the end of the Pleistocene beginning about 25,000 years ago, the number of grazing species sharply declined. This sharp decline has been attributed to the appearance of efficient human hunters or climatic change or both (Ehleringer and others 2002, Flores 1996). The peak of the American-evolved megafaunal crash occurred about 14,800 to 13,700 years ago, and by 10,000 years ago only about a half dozen browsing and grazing forms remained. When Europeans arrived, the bison, elk, and other animals that characterized the grasslands were the remnants that survived the massive extinction at the end of the Pleistocene (Doughty, Wolf, and Field 2010, Flores 1996, Gill and others 2009).

Because of the long-term association of grazing animals and grasslands, it is not surprising that several lines of evidence suggest that grazers strongly influence the productivity and diversity of grasslands. Golley and Golley (1972) suggest that the productivity of biomass in excess of that which can be decomposed is a response to grazing. Grazing, like burning, accelerates the rates of mineralization of inorganic nutrients (Frank and others 1998). For example, grazers like bison are effective in changing some recalcitrant species of nitrogen to urea that is easily converted to ammonia, a plant-useable form of nitrogen. The increased availability of inorganic nutrients can enhance grassland productivity (Knapp and others 1999). Grazing removes the physiologically

older, less productive leaf tissue and these changes increase light and moisture for younger more photosynthetically active tissue, which enhances aboveground productivity (Frank and others 1998). Some authors (McNaughton 1979, 1993; Owen 1981) have proposed a symbiotic relationship between grasses and grazers. Aboveground productivity of grasslands has been said to increase with moderate grazing (Knapp and others 1999, McNaughton 1979), although others have questioned the beneficial effects of grazing (Belsky 1986, Painter and Belsky 1993). Additionally, evidence suggests that increased shoot productivity occurs at the expense of belowground productivity and nitrogen and carbon are transferred from below ground to facilitate compensatory aboveground growth following grazing (Collins and others 1998, Knapp and others 1999), meaning that excessive grazing will eventually cause a decline in productivity (Anderson 1982).

Bison as a Keystone Prairie Species

Grazing patterns and preferences

The role of bison in tallgrass prairie has not been understood until the last two decades, when reserve areas became available that were large enough to support reasonably sized populations and allow them to graze in a way that simulated historical conditions. Knapp and others (1999) delineated a keystone role for bison in maintaining diversity of tallgrass prairie. On Konza Prairie, bison fed primarily on grasses (90 percent) and consumed only small quantities of forbs and essentially no woody vegetation (Fahnestock and Knapp 1993, Hartnet and others 1996, Knapp and others 1999, Steuter 1997, Vinton and others 1993). Although grasses constituted the largest portion of the bison diet, the proportion of C_3 and C_4 grasses consumed varied seasonally.

Generally, mammalian herbivores prefer C_3 grasses, which have higher digestibility and protein content but lower carbon:nitrogen ratios than C_4 grasses (Ehleringer and others 2002). Nevertheless, while some studies reported that C_4 grasses have more fibers and higher silica concentration in their leaves than C_3 grasses (Kaiser 1998, Kepart and Buxton 1993), other studies found no difference in the two traits between C_3 and C_4 grasses (Heidorn and Joern 1984, Scheirs and others 2001). In South Dakota, C_4 grasses constituted 33 to 44 percent of the bison diet from early June through August and then declined to 15 percent by the end of September. Bison use of sedges and C_3 grasses increased from 52 to 58 percent in summer (mid-June to mid-August) to >80 percent after the beginning of September (Plumb and Dodd 1993). Similar patterns in seasonal consumption shifts were found on the Konza Prairie (Vinton and others 1993).

Bison grazed in two patterns, creating distinctive grazing patches that were 20 to 50 m^2 in area and more extensive patches that were >400 m^2. During the growing season, bison revisited previously grazed sites in preference to ungrazed locations. The grass that grew after grazing was higher in nitrogen, more palatable, and not intermixed with dead tissue. Grazed areas initially experienced short-lived productivity increases after grazing, but productivity eventually declined as movement of carbon reserves from belowground compensated for loss of aboveground tissues. By repeatedly grazing the same areas, bison encouraged the growth of non-palatable species that are the forbs. This grazing pattern eventually encouraged a shift to other areas as forage quality declined. On average, 6 to 7 percent of the grazing patches were abandoned annually (Knapp and others 1999).

Enhancing grassland plant diversity

Bison grazing can offset negative effects of frequent burning on plant species diversity (Gibson and Collins 1990, Knapp and others 1999). Burning favors C_4, warm season grasses and late flowering forbs. Frequent fires, especially annual burns, can encourage these grasses at the expense of C_3 plants, which include many species of forbs (Gibson and Collins 1990, Knapp and others 1999, Kucera and Koelling 1964). And forbs contribute most of the species richness to the prairie (Hartnett and Fay 1998,

Howe 1994a). Bison graze on the C_4 grasses and reduce their abundance, which favors unpalatable C_3 forbs, which enhances the plant diversity of the prairie.

Effects on animal diversity

Bison enhance spatial heterogeneity in the prairie through grazing patterns that result in patches of lightly grazed to heavily grazed areas with sparse grass cover and little litter (Fuhlendorf and Engle 2001, Knapp and others 1999). This spatial heterogeneity is important for grassland bird diversity. In the eastern tallgrass prairie, some birds, such as the killdeer (*Charadrius vociferus*) and upland sandpiper (*Bartramia longicauda*), require sparse vegetation across large areas. Other species, such as eastern meadowlark (*Sturnella magna*) and bobolink (*Dolichonyx oryzivorus*), utilize medium-height vegetation with moderate amounts of litter, whereas species, such as Henslow's sparrow (*Ammodramus henslowii*) and marsh wren (*Cistothorus palustris*), occur where the vegetation is tall and litter is abundant (Herkert and others 1993). Endemic birds of western Great Plains also have characteristic distributions related to historical grassland types and grazing patterns (Knopf 1996).

Fire and bison grazing affect the diversity and density of grasshoppers (suborder Caelifera) Joern (2005) found that upland or lowland topographic position and fire frequency had no significant affect on grasshopper species richness or diversity (Shannon Index) on the Konza Prairie. However, bison grazing increased species richness, diversity, and evenness of grasshoppers. Grasshopper species richness was positively related to plant species richness and heterogeneity in plant height. Joern (2005) concluded that fire influences grazing patterns, which effects structure and plant species richness in grasslands (Fuhlendorf and Engle 2001, Hartnett and others 1996, Knapp and others 1999, Pfeiffer and Hartnett 1995, Pfeiffer and Stueter 1994, Vinton and others 1993). Consequentially, fire and large mammalian grazing are crucial features for maintenance of grasshopper diversity.

Grassland small mammals (microtine rodents) also require a diversity of vegetation and litter density. Even though their responses to burning are mixed—positive for deer mice (*Peromyscus maniculatus*) and negative for western harvest mice (*Reithrodontomys megalotis*) and prairie voles (*Microtus ochrogaster*)—those responding negatively recover in 2 to 3 years after the burn (Kaufman and others 1990, Schramm 1970, Schramm and Willcutts 1983). Fires of varied intensity and completeness should favor diversity of animals in grasslands. The mosaic of vegetation resulting from grazing creates uneven patterns of fire intensity as a result of fuel loadings that vary from heavy fuel loading in sparsely grazed areas to low fuel loading in areas subjected to intensive grazing pressure.

White-tailed Deer in Remnant Tallgrass Prairie

Historically, the bison was the most important large mammalian herbivore in much of the Central Grassland tallgrass prairie; although its abundance may have been substantially lower in the eastern portion (Leach and others 1999). Today, the white-tailed deer (*O. virginianus*) is the large native mammal with the most impact on remnant and restored tallgrass prairies. Although bison graze almost entirely on grass, forbs (which are little used by bison) are favored by white-tailed deer. Anderson and others (2001) reported that deer browsed very little on grasses or sedges during the late spring and summer, but browsed from 3.5 to 18.9 percent of the standing crop of forb stems depending upon time of sampling. Because forbs contribute most of the diversity to the prairie (Howe 1994a) excessive white-tailed deer browsing can reduce the prairie diversity. Anderson and others (2005) demonstrated that diversity of prairie forbs was maximized at an intermediate level of deer browsing—supporting the intermediate disturbance hypothesis, which posits that diversity is maximized at intermediate levels of disturbance (Connell 1978). However, the community quality of forbs, based on the degree to which species were associated with relatively undisturbed remnant prairies, declined as the duration of intense deer browsing (disturbance) increased. Forb quality

was highest after 8 years of protection from browsing, suggesting a potential tradeoff between maximizing diversity and maintaining quality of forb communities (Anderson and others 2006).

Managing Tallgrass Prairie

Overview of Grassland Management

Successful prairie management requires knowledge about the ecology of individual prairie species, and how functional groups (such as C_4 grasses, C_3 grasses, early flowering forbs, and litter dwelling invertebrates) will respond to various management prescriptions. Fire is the most widely applied tool for managing tallgrass prairie and—because of rainfall being associated with lightning storms and habitat fragmentation, both of which limit the spread of fire—prescribed burning is necessary to maintain prairies and preserve plant species diversity (Leach and Givnish 1996). Nevertheless, the response of the whole community must be considered when fire or other management practices are applied. Compromises will have to be made in deciding on which practices to use when species or groups of species respond differently to management. This chapter does not provide a comprehensive management guide to prairie management as occurs in Packard and Mutel (1997). Rather it discusses some issues that are often of concern in the management of prairies.

Timing of the Burn

Prescribed fires most frequently occur in spring because the opportunity for burning is generally longer than in the autumn. Spring burns also have the advantage of retaining winter cover for wildlife. Nevertheless, autumn is apparently the time when most of the Native American set fires occurred; the effect of autumn vs. spring burns may be a yet unknown factor in community response to fire. Autumn burns occur when birds and mammals are not actively breeding. Large mammals readily move away from the fire and are rarely directly affected by burning. Direct small mammals losses in prescribed burns are usually small, even in head fires, but they do occur. Nevertheless, it is relatively common to burn cottontail rabbit (*Sylvilagus floridanus*) nests during spring burns, especially if the burn is delayed so that nonnative cool season plants like Kentucky bluegrass (*Poa pratensis*) and sweet clover (*Melilotus* spp.) are actively growing and can be set back by the burn (Curtis and Partch 1948; Kline 1986). Snakes can be active in the spring and suffer mortality in spring burns, although snakes seek shelter in holes and animal burrows during fires.

Summer burns have been proposed as a way of enhancing plant species diversity on prairies and also controlling invading woody species. Adams and others (1982) compared woody vegetation response to a summer burn (July) and a late-winter dormant season burn (March) in south central Oklahoma. The authors tested the hypothesis that summer burns would be more detrimental to woody species than dormant season burns, because the plants would have invested resources in building new leaves but would not have returned resources belowground to replace those used in the current year's growth. Unexpectedly, the late-winter burn was more detrimental than the summer burn to woody species, which they attributed to an unusually severe drought following the winter burn. Additionally, woody and herbaceous species can regrow in the same growing season in which a summer burn occurs; this may mitigate the affects of summer burns (Anderson 1972a).

The application of summer burns to enhance the diversity of prairie plants has been examined in several studies (Copeland and others 2002; Howe 1994a, 1994b). Burning in the summer when the dominant C_4 plants are actively growing should reduce their competitiveness against C_3 plants and reduce C_4 dominance. Copeland and others

(2002) reported a twofold increase in the species richness and average frequency of subdominant species in plots subjected to a late-summer fire, but these two measurements remained unchanged in plots subjected to early spring fires. Similarly, Abrams and Hulbert (1987) found that spring burning had no effect on plant species richness.

Although summer burns may have applicability, we should move cautiously on the use of summer burns, because information is lacking on animal responses and is insufficient on plant responses (Anderson 1997). In addition, under some conditions—for example, when green vegetation is dry enough to burn but still has high moisture content and is actively growing, with little dead biomass—summer burns can generate abundant smoke, which is substantially more irritating to respiratory systems than dormant season burns.

Fire Frequency

Vegetation response

For mesic tallgrass prairies, fires every 2 to 3 years will normally be appropriate. On dry prairies fire interval should be longer, perhaps in the range of 3 to 5 years. However, careful monitoring of the vegetation may indicate more or less frequent burning. Factors to be considered include the rate, at which litter accumulates, control of woody species, abundance of invasive weeds, and the relative abundance of forbs and C_4 grasses. Some biennial weeds, such as sweet clover (*Melilotus alba* and *M. officinalis*), may benefit from a burning schedule that occurs at intervals equal to or greater than two years and will require a varied burn schedule and/or mowing before seed set of sweet clover to achieve effective control (Kline 1986, Coles 2007).

Small mammals

Fire alters vegetation composition and structure, benefiting some small mammal species and causing others to have less favorable habitat conditions (Kaufman and others 1990). However, as previously noted species decreasing in abundance following fire recovered within 2 to 3 years. Burning sections of the prairie on a 2- or 3-year rotational basis should meet the habitats needs of most mammals.

Preserving invertebrates

The response of invertebrates to burning is varied and depends on a number of factors, including where the invertebrate is located at the time of the fire (Macfadyen 1952, Reichert and Reeder 1972, Seastedt 1984, Warren and others 1987), the microclimatic and vegetation structural changes after fire, and the ability of the invertebrate to adapt to the changed environment (Anderson 1964, Anderson and others 1989; Evans 1984, 1988). For example, during a burn that had surface temperatures of 200 °C, species of spiders that were active on the soil surface at the time of a burn were eliminated, whereas others survived in subsurface burrows, under rocks, or protected in the bases of caespitose (clumped) grasses (Riechert and Reeder 1972). Similarly, mixed responses of species to fire were reported for mites (Seastedt 1984), Collembola (springtails) (Lussenhop 1976, Van Amburg and others 1981), and grasshoppers (Anderson and others 1989, Evans 1988).

Deciding on appropriate grassland management methods to accommodate the needs of arthropods can be complicated. For example, some species of insects, such as butterflies and leafhoppers decrease in abundance after fire (Panzer 1988; Swengel 1996, 1998; Swengel and Swengel 2001). Grasshoppers that feed on forbs increased in frequency as fire frequency decreased; however, some grasshopper species increased or showed rapid recovery after fire (Anderson and others 1989, Evans 1988). For specialist butterfly species—those restricted to prairie, savanna, or barrens—occasional single wildfires were more favorable than rotational burning, and mechanical cutting more favorable than grazing. However, widely distributed butterflies were favored by more frequent management; mechanical cutting was not more favorable than grazing,

occasional wildfires, or rotational burning (Swengel 1998). Thus, it is not possible to have a single management prescription that will be optimal for all insects; an increasing number of entomologists are expressing concern that prairie insects are being harmed by current prescribed burning practices, and if continued, the outcome could be the loss of a substantial number of species (Pyle 1997, Schlicht and Orwig 1992). Swengel and Swengel (2007) recommend that permanent non-fire refugia be established to conserve Lepidoptera and these areas be managed with methods, such as brush cutting and mowing, if necessary. However, Panzer and Schwartz (2000) concluded that the current rotational plan (burn about every 2 to 3 years) in Illinois has been compatible with conservation of insect biodiversity.

Historically, some portions of extensive grasslands likely remained unburned each year and provided "refugia" for fire sensitive insects. However, under current conditions, which often involve burning fragmented remnant prairies or restorations, all or nearly all of the area is burned. Possible solutions to this management conundrum include burning only a portion of each site on a rotational basis, leaving 50 to 70 percent as unburned refugia so that fire sensitive species can reinvade the burned site after it regrows (Andrew and Leach 2006; Panzer 1988, Panzer 2003; Panzer and Schwartz 2000). Additionally, recommendations for burning practices to favor fire sensitive insects include leaving areas missed by the fire unburned, avoiding "hot fires" by burning early in the morning, and using spring burns to preserve clumps of grasses that are used as wintering sites (Panzer 1988).

Control of woody species

For a variety of reasons, fire does not always keep woody species under control or prevent their invasion into grasslands. Herbicide application is often necessary to achieve a reduction in woody vegetation (Solecki 1997).

Grazing and Fire Management

Patch-burn grazing

Grazing by bison has been shown to increase the plant diversity and spatial heterogeneity of grasslands; however, until recently, there were few studies (Fuhlendorf and Engel 2001, Steuter 1997) that examined the potential of grazing and burning combined as a grassland management tool. Nonetheless, "patch-burn grazing," which combines the two, may increase prairie diversity, especially in the western portion of the tallgrass prairie in Kansas and Oklahoma, where tallgrass prairie is used for cattle grazing. A common range management practice is annual spring burns followed by early cattle grazing and removal in mid- to late-summer, with double the cattle stock rates of year round grazing operations (Coppedge and others 2008, Powell 2006). This application of grazing and burning, called intensive early stocking (IES), results in low diversity grassland system with little habitat heterogeneity. Patch-burn grazing is an alternative to this management approach (Fuhlendorf and Engle 2001, Helzer and Steuter 2005, Steuter 1997, Towne and others 2005). Grazing animals (cattle or bison) are permitted to graze freely across the prescription area that has recently burned and unburned patches. Typically one-third to one-fourth of the area is burned annually on a rotational basis. The burning increases forage production and quality, and consequently, grazing pressure on the burned areas in the first year after the fire (Fuhlendorf and Engle 2001, Knapp 1999, Towne and others 2005). The combination of recently burned and heavily grazed sites and sites that have been unburned for 2 to 3 years, depending on rotation time, provides sites with varied structural features and plant species abundances. Recently burned sites have less cover of tallgrass, litter, and shorter vegetation height, but more bare ground than unburned sites (Fuhlendorf and others 2006). Birds are especially sensitive to these structural changes and species diversity of grassland bird species increases with patch-burn grazing as compared to annually burned grasslands (Coppedge and others 2008, Fuhlendorf and others 2006, Powell 2006).

Endangered species management

Although grazing can have positive and negative affects, it returns a historical function to grasslands that has the potential to increase diversity. For example, at the Midewin National Tallgrass Prairie in northeastern Illinois, cattle grazing on cool season domesticated grasses has provided habitat for the State's largest nesting population of upland sandpipers, "prairie plover," an endangered species in Illinois (Meyer 2002). We need to know if native grazers or their surrogates can produce similar habitats, short grass with bare ground, on restored native tallgrass prairie. Heavy grazing before and during the breeding season—with periods of cessation so the native grasses can recover—and rotating the portions of the grassland that are grazed annually might provide breeding habitat for the upland sandpiper and retain plant species diversity.

Prairie restoration

The intense grazing on the patch-burn areas creates openings and reduces competition from the C_4 grasses that are preferred and encourages the growth of ruderals and cool-season plants including less palatable forbs, which increase in abundance in the year after the burn (Fuhlendorf and Engle 2001, Towne and others 2005). On restored prairies, the heavily grazed patch-burn areas could be sown with forb seeds to enhance species richness. This procedure may be especially useful to increase forb diversity on restorations that have a heavy dominance of C_4 grasses and low diversity of forbs. Stocking rates may have to be modified for each specific site to prevent overgrazing.

Management decisions

Grazing is not an option on all prairies because of size limitations and other factors. Leach and others (1999) have proposed that the eastern portions of the tallgrass prairie supports plant species that are sensitive to grazing; historically, bison were not abundant on these prairies so a strong interaction between grazers and prairies did not develop. This concern remains an unresolved issue (Henderson 1999, Howe 1999). Moreover, the effect of patch-burn grazing on the diversity of prairie forbs is not as well documented as the effect grassland on birds, and further studies are need in this area. Moreover, in the highly fragmented grasslands of the eastern portions of the tallgrass prairie in Iowa and Missouri, no treatment effects were observed for bird species richness, grassland obligate bird species richness, or diversity for patch-burn grazing, burn only and grazed-and-burned treatments. Differentiation of community structure was most strongly correlated with visual obstruction and wooded edge density, to which birds are responsive, and are well developed in fragmented habitats (Pillsbury 2011).

The choice of whether to use bison or cattle for grassland management depends on a number of factors. Their grazing patterns differ somewhat, with cattle consuming more forbs and browse. Economic returns are greater from cattle than bison and space needs and facility and management costs are greater with bison, but bison provide better management for natural areas (Plumb and Dodd 1993).

Conclusions

Managing vegetation requires an understanding of the major ecosystem functions that originally maintained the system and how these functions can be reestablished or manipulated to ensure stability and health. The practice of adaptive management can be applied and the health of the ecosystem monitored to determine if management goals are achieved. Management prescriptions should be continued, modified, or abandoned (with alternate procedures adopted) to achieve desired goals. Records should be kept of the management practices applied and their effectiveness. This information would be valuable to others managing prairies. Additionally, more research on prairie management practices is needed—if the management is designed appropriately it can serve as an experiment to test options.

The Central Grasslands are of recent origin, and have depended on human intervention, through fire management, at least for the past 6,000 years or longer. Persistence of this ecosystem will require continued fire management or appropriate surrogate practices. The most effective management will have goals that are holistic in their scope and will attempt to preserve the diversity and stability of all trophic levels. Large mammalian grazers and browsers have keystone roles in grasslands and, to the extent that it is possible, their effects on this ecosystem should be included in management practices and goals.

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