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Source: The Journal of the Torrey Botanical Society, 133(4) : 626-647

Published By: Torrey Botanical Society

URL: [https://doi.org/10.3159/1095-5674\(2006\)133\[626:EAOOTC\]2.0.CO;2](https://doi.org/10.3159/1095-5674(2006)133[626:EAOOTC]2.0.CO;2)

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Evolution and origin of the Central Grassland of North America: climate, fire, and mammalian grazers¹

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ANDERSON, R.C. (Behavior, Ecology, Evolution and Systematics Section, 4120 Department of Biological Sciences, Illinois State University, Normal, IL 61790). Evolution and origin of the Central Grassland of North America: climate, fire, and mammalian grazers. *J. Torrey Bot. Soc.* 133: 626–647. 2006.—Grasslands are a widespread vegetation type that once comprised 42% of the plant cover on earth's surface. Features commonly shared among grasslands are climates with periodic droughts, landscapes that are level to gently rolling, high abundances of grazing animals, and frequent fires. World-wide expansion of grasslands occurred 8 to 6 MaBP and was associated with increasing abundance of grasses using the C4 photosynthetic pathway, a decline in woodlands, and coevolution of mammals adapted to grazing and open habitats. Beginning with Transeau's seminal paper on the prairie peninsula in 1935, North American ecologists debated the relative importance of fire and climate in determining the distribution of grasslands. In the 1960's, a major research interest was the response of prairies to fire, especially the productivity of burned and unburned grasslands. Understanding mechanisms for increased productivity on burned prairies began in the late 1960's and continued into the middle 1980's. During the past 20 to 25 years, grassland research has focused on the coevolution of grasses and mammalian grazers and fire-grazing interactions that affect habitat heterogeneity and diversity across trophic levels. While this paper does not follow a chronological development of our understanding of grasslands, all of these major research interests are considered.

Key words: bison, C4 grasses, Central Grassland, fire, grasslands, keystone species, mammalian grazers, prairie peninsula.

General Features of Grasslands. DISTRIBUTION AND STATUS. Grasslands occurred on all continents, comprised almost 42% of the world's plant cover, and once covered approximately 46 million km² 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 non-graminoid herbaceous species called forbs. Plant families most abundant as forbs are the sunflower (Asteraceae) and pea (Fabaceae) families (Curtis 1971, Risser et al. 1981). Extensive grasslands have been greatly altered by human activity especially those associated with their conversion to agricultural landscapes for growing crops or grazing livestock. Nevertheless, a recent estimate is that about 40 percent of the global land surface is grassland (excluding Greenland and Antarctica) (White

et al. 2000). This seemingly high estimate for extant grasslands, however, results from including not only "non-woody grasslands" but also savannas, woodlands, shrublands, and tundra in the definition of grasslands. This estimate of existing grassland is potentially misleading, because most ecologists would not include woodlands, shrublands, and tundra in a definition of grasslands. In addition, while this source recognizes that temperate grasslands have experienced heavy conversion to agriculture, it states that at least five percent of grasslands world-wide are "strongly to extremely denuded." This relatively low percentage possibly results from the inclusion of non-traditional landscapes in the definition of "grasslands." Applying a more widely used definition of grasslands, many of the world's temperate grassland ecosystems have been essentially destroyed by human activities. For the United States, Noss et al. 1995) lists grasslands as being critically endangered (i.e. have declined by more than 98%). For example, 99% of the tallgrass prairie lying east and north of the Missouri River has been completely destroyed (Chapman et al. 1990). In Illinois, of the 8,502,024 ha of original prairie (60% of the state), only 931 ha or 0.01 percent of high quality remnant prairie re-

¹ A substantial portion of this manuscript is reproduced with permission from a book on fuel management being published by the USDA Forest Service, entitled "Cumulative Watershed Effects of Fuel Management in the Eastern United States."

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Received for publication November 13, 2006, and in revised form December 5, 2006.

mains (Robertson et al. 1997). In this review, I summarize the results of more than fifty years of research studies of grassland ecosystems with a focus on the Central Grassland of North America. While these studies were conducted in a highly fragmented landscape, some on prairies that are ten hectares or less in size, they provide an overview of the structure and function of the historic grassland ecosystem, which none of the researchers experienced, and provide insight into how they might be restored.

One of the most marvelous sights of my whole life, unsurpassed in my travels in nearly all parts of the world, was that of the prairie in spring. Unfading are my memories of that waving rippling sea of lavender, when the wild sweet william, a species of phlox two or three feet in height was in full flower. It stretched away in the distance farther than the eye could reach...As the sea of phlox faded it was succeeded by another marvelous flower bed of nature's planting, and this in turn by others until mid-summer was reached...(Herre 1940).

CLIMATE. 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 annually, and in areas where mean annual temperatures vary from 0–30°C (Sauer 1950, Risser et al. 1981, Oesterheld et al. 1999). Grasslands are not necessarily treeless and they are transitional to savannas that are characterized by higher densities of drought-tolerant, fire-resistant trees than grasslands. The ratio of trees/grass increases as precipitation increases (Curtis 1971, Anderson and Bowles 1999, Oesterheld et al. 1999) and in landscapes receiving more than 650 mm of precipitation there is a trend for increasing cover of woody species with “long-term fire exclusion” (Sankaran et al. 2004). In areas of low precipitation, grasslands grade into desert communities. Common features found among grasslands include: climates with periodic droughts, frequent fires, occurrence on landscapes that are level to gently rolling, and an abundance of grazing animals (Sauer 1950, Risser et al. 1981, Anderson 1982, Anderson 1990).

DROUGHT, FIRE, AND GRAZING ANIMALS. Grassland plants evolved under the influence

of periodic droughts, frequent burning, and grazing animals and are adapted to all three (Gleason 1922, Anderson 1990). This adaptation for grasses is manifested in their ability to die down to underground organs and only expose dead tops above ground (Gleason 1922). Grasses can escape drought by having growing tips beneath soil that are not exposed to desiccation. Prairie fires have a narrow flame width and move relatively rapidly and, because the soil is a good insulator, there is little penetration of heat into the soil beyond a few mm below the surface (Anderson 1982). Consequently, the growing points of prairie plants below the ground surface are protected from the heat of the fire and also from grazing. Grazers can remove aboveground tissues, but new shoots can emerge from belowground once the grazing pressure is removed (Tainton and Mentis 1984).

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

The widespread expansion of grassland is associated with the appearance of the C4 photosynthetic pathway. The C4 photosynthetic pathway provides an advantage over the more common C3 pathway because it provides higher quantum yields for carbon dioxide uptake under conditions of high irradiance and temperature. The C4 photosynthesis is also favored over C3 photosynthesis when the concentration of atmospheric carbon dioxide is below 500 ppmV (Cerling et al. 1997, Ehleringer et al. 1997, 2002). During the Mesozoic, carbon dioxide concentrations were thought to be greater than 1000 ppmV. However, in the early Miocene or late Oligocene (Kellogg 1999), perhaps 20–25 MaBP, decline in atmospheric carbon dioxide

favored evolution of C4 plants in moist tropical and subtropical regions (Ehleringer et al. 1997). This photosynthetic pathway is found in less than 2% of all flowering plants but approximately one-half of the 10,000 species of grasses and sedges use this pathway. While C4 plants are a small percentage of flowering plants, they contribute 25% of total global productivity, largely due to monocots in grasslands (Ehleringer et al. 2002).

Accelerated development of C4 grasslands world-wide occurred during the Miocene-Pliocene transition (8–6 MaBP) when aridity increased world-wide associated with the expansion of the Antarctic Ice Sheet and atmospheric carbon dioxide was below 500 ppmV. During this period of time, the area occupied by forest and woodlands declined and there was an explosive evolution of grasses and forbs (Cerling et al. 1997, Ehleringer et al. 1997, 2002). However, Keeley and Rundel (2005) posit that the conversion of forest to C4 grassland four to seven MaBP was not directly due to a decline in atmospheric carbon dioxide or increased aridity, but rather to a climate change that encouraged fire. Under the new climatic conditions a warm moist growing season resulted in high biomass production that was converted into combustible fuels by a pronounced dry season. This monsoon climate likely would be accompanied by frequent lightning strikes at the end of the dry season. In the Keeley-Rundel (2005) model, fire would have been a primary driver, as it is today, in the conversion of forest to grasslands and the maintenance of grasslands.

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, there was an increase in mammalian fossils with high-crowned teeth (hypsodonty) adapted to grazing (Stebbins 1981, Axelrod 1985) and evolution of animals with more cursorial (running) and saltatorial (jumping) body forms.

The North American Grassland. Grasslands of North America constitute a diverse assemblage of vegetation types that occur under a wide range of climatic conditions and covered about 15% of the continent (Fig. 1). These grasslands are referred to as *prairies*, a French word meaning meadow or field, which was used by early French explorers to

describe the extensive grasslands of North America (Curtis 1971, Risser et al. 1981). Along a north-south gradient, grasslands extended from desert grasslands of southwestern United States and northern and central Mexico to mixedgrass prairies of the Canadian Provinces of Alberta, Saskatchewan, and Manitoba (Risser et al. 1981). Across this gradient mean annual temperatures vary from 2.8°C at Regina, Canada in the northern mixedgrass prairie to 22.6°C in Monterrey, Mexico at the edge of Chihuahuan Desert grasslands. From south to north along the eastern edge of grasslands lying east of the Rocky Mountains, precipitation varies from about 250 mm in southeast Texas to 750–1000 mm in Indiana (Risser et al. 1981).

Central Grassland of North America. GEOGRAPHIC VARIATION. This paper focuses on the Central Grassland of North America, which was a large triangular shaped grassland 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 (Outlined in Figure 1). 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. This area includes the grasslands of the twelve Great Plains states, and those grasslands described above lying east of the Mississippi River. Precipitation increases from west to east in this grassland from 260–1200 mm and across a north-south gradient annual temperature ranges from 3–22°C (Sala et al. 1988).

Ecologists traditionally have divided the grassland into three sectors based on height of the native grasses, which is a function of annual precipitation: a western shortgrass prairie (260–375 mm precipitation), the eastern tallgrass prairie or “True Prairie,” (625–1200 mm precipitation), and between the two the mid- or mixedgrass prairie (375–625 mm precipitation) (Fig. 1). Shortgrass prairie occupies an area dominated by grasses that are 0.3–0.5 m tall, which includes buffalo grass (*Buchloe dactyloides*), blue grama (*Bouteloua gracilis*), and side oats (*B. curtipendula*) and hairy (*B. hirsuta*) grama grasses. Big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), and little bluestem (*Schizachyrium scoparium*)

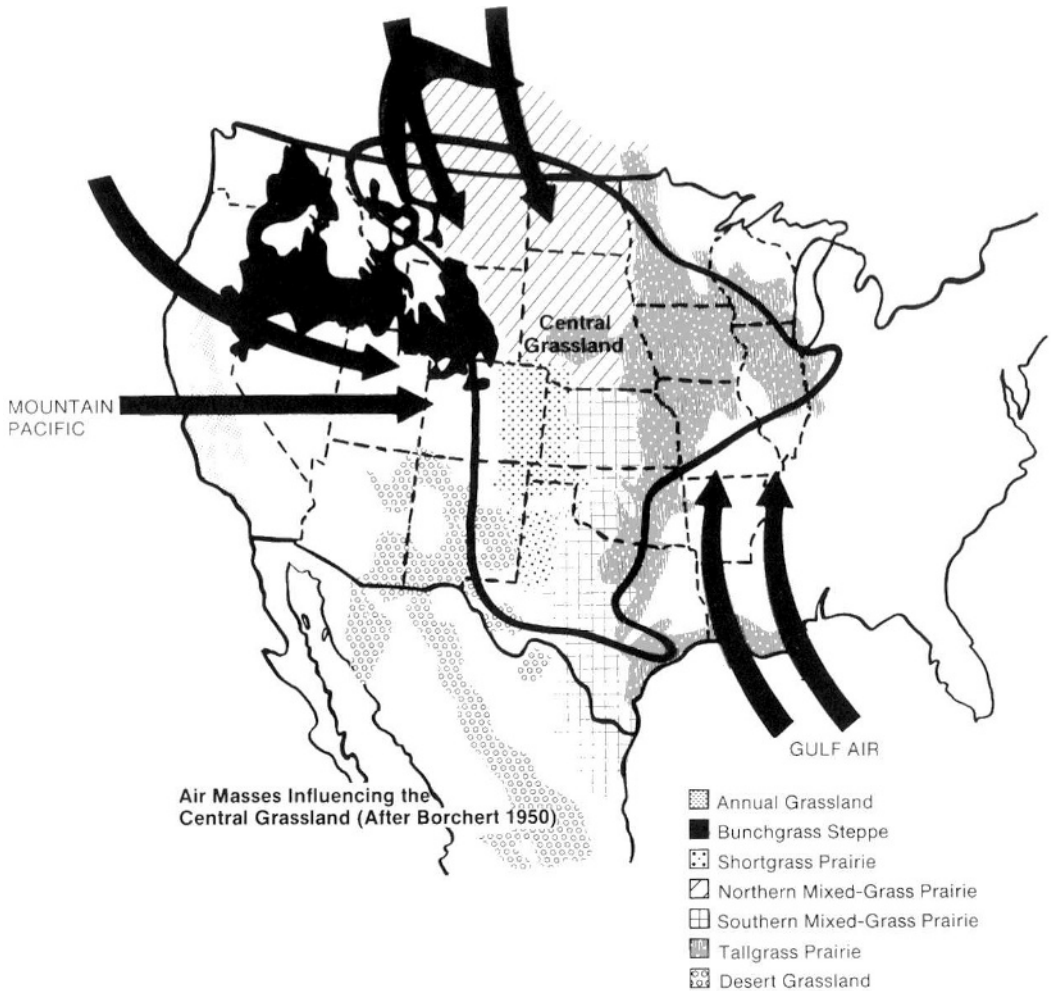


FIG. 1. The distribution of the major grasslands of North America and the air masses that influence the climate of the Central Grassland. The location of the Central Grassland is outlined. Adapted from Risser et al. 1981 and Anderson 1990. Reprinted from Anderson 1990 with permission of the University of Oklahoma Press.

are dominant species in the tallgrass prairie and reach heights of 1.8–2.4 m. The mixed-grass or midgrass prairie is dominated by species that are 0.8–1.2 m tall and includes little bluestem, western wheatgrass (*Pascopyrum smithii*), and green needle grass (*Nassella viridula*). In the mixedgrass prairie, tallgrass prairie species occur in depressed areas that are moister than upland sites resulting in a mixture of tall- and midgrass prairie species, which gives the midgrass prairie region its alternate designation of mixedgrass prairie. Across the Central Grassland, species composition and abundance varies continuously and there are no sharp

divisions between these arbitrarily designated grassland regions.

VARIATION WITHIN A GEOGRAPHICAL REGION. Within each of the major regions of the Central Grassland there are different types of prairie as a function of soil, aspect, slope position and other factors. A primary factor causing these varied vegetation patterns is availability of soil moisture as a function of variation in soils and topographic features (Curtis 1971, Nelson and Anderson 1983, Umbanhowar 1992, Corbett and Anderson 2006). For example, there are approximately 930 hectares of high quality remnant prairie in

Table 1. Leading species in six community types for species with mean (\pm SE) quadrat frequency at least 2.0%. Letters after species names indicate its modal community in Wisconsin (Curtis 1971), PD= dry prairie, PDM = dry mesic prairie, PM = mesic prairie, PWM = wet mesic prairie, PW = wet prairie, DUN = dune, OB = oak barren, CG = cedar glade, SB = sand barren, FN = fen, SS = southern sedge meadow, ND = Northern Dry Forest (Modified from Corbett and Anderson 2001, 2006).

Community type species	Dry sand	Gravel/sand	Hill prairie	Gravel/dry dolomite	Mesic/dry mesic	Wet/wet dolomite
<i>Schizachyrium scoparium</i> PD	16.9 \pm 1.5	17.3 \pm 2.9	15.4 \pm 0.7	11.6 \pm 1.4	3.6 \pm 0.4	
<i>Optunia humifusa</i> CG	8.4 \pm 1.8					
<i>Ambrosia psilostachya</i> SB	6.7 \pm 2.2					
<i>Calamovilfa longifolia</i> DUN	3.9 \pm 2.0					
<i>Panicum oligosanthos</i> PDM	3.3 \pm 1.7	2.4 \pm 1.6				
<i>Tephrosia virginiana</i> OB	3.3 \pm 1.7					
<i>Bouteloua hirsuta</i> CG	2.3 \pm 1.5					
<i>Stipa spartea</i> PDM	2.0 \pm 1.0	4.4 \pm 2.4		4.5 \pm 1.0		
<i>Euphorbia corollata</i> OB		5.4 \pm 2.0			3.6 \pm 0.4	
<i>Echinacea pallida</i> PM		3.1 \pm 2.0		3.4 \pm 0.6		
<i>Lithospermum carolinense</i> SB		2.7 \pm 2.2				
<i>Koeleria cristata</i> SB		2.5 \pm 2.0				
<i>Callirhoe triangulata</i> PDM		2.3 \pm 1.6				
<i>Bouteloua curtipendula</i> PD			9.1 \pm 0.8	3.8 \pm 0.8		
<i>Sorghastrum nutans</i> PDM			4.5 \pm 0.7	4.4 \pm 0.4		
<i>Dalea purpurea</i> DP		2.2 \pm 2.2	4.5 \pm 0.4			
<i>Euphorbia corollata</i> OB			4.1 \pm 0.4	4.6 \pm 0.7		
<i>Solidago nemoralis</i> DP			3.6 \pm 0.5			
<i>Psoralea tenuiflora</i>			2.8 \pm 0.4			
<i>Aster azureus</i> DMP			2.5 \pm 0.5			
<i>Amorpha canescens</i> DP			2.3 \pm 0.4	3.6 \pm 0.7		
<i>Sporobolus heterolepis</i> DP				3.0 \pm 0.6	3.0 \pm 0.4	
<i>Rosa caroliniana</i>				2.5 \pm 0.6	2.4 \pm 0.3	
<i>Aster ericoides</i> PDM				2.3 \pm 0.6	3.6 \pm 0.4	
<i>Andropogon gerardii</i> PM					5.0 \pm 0.5	2.5 \pm 0.7
<i>Fragaria virginiana</i> ND					2.2 \pm 0.3	2.7 \pm 0.8
<i>Carex</i> sp.						6.3 \pm 1.8
<i>Solidago gigantea</i> PW						4.3 \pm 0.9
<i>Pycnanthemum virginianum</i>						3.7 \pm 0.8
PWM						
<i>Calamagrostis canadensis</i> FN						3.5 \pm 1.5
<i>Spartina pectinata</i> PW						3.2 \pm 0.8
<i>Carex stricta</i> SS						2.2 \pm 2.1
<i>Helianthus grossesserratus</i>						2.7 \pm 1.1
PWM						
<i>Solidago riddellii</i> FN						2.7 \pm 0.9

Illinois representing diverse habitat types differing in topography and substrate. Dry prairies includes hill and bluff prairies that often occupy west or southwest facing slopes overlooking rivers with loess or glacial drift derived soils (Evers 1955). Dry prairies also occur on deep sand deposits or on dolomitic or gravel substrates with shallow stony soils. Additionally, there are wet-mesic to wet prairies on loess-derived, till-derived, or dolomite-containing substrates (Table 1). Historically, the most common prairie types were mesic and wet prairies covering as much as 55% of the state (Fehrenbacher et al. 1968), although most of these prairies have been converted to agricultural or urban uses.

CLIMATE OF THE CENTRAL GRASSLAND. *Major Air Mass Systems.* The climate of the Central Grassland is influenced by three primary air mass systems (Fig. 1): Polar, Gulf, and Mountain Pacific (Borchert 1950, Bryson and Hare 1974, Risser et al. 1981). The Polar Air Mass influence is reflected in part by the increased snow cover and decreasing temperatures from south to north within the Central Grassland (Risser et al. 1981) and the resultant north-south variations in vegetation patterns (Risser et al. 1982, Kebart and Anderson 1987, Diamond and Smeins 1988). Gulf and Mountain Pacific Air Masses are most important in determining the east-west variation in the Central Grassland. The Gulf Air Mass origi-

nates in the Gulf of Mexico. As the Gulf Mass moves northward into the eastern sector of the Central Grassland it brings humid air and often is associated with precipitation when it encounters cooler air or generates 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 mountains). As the air mass rises, it cools adiabatically, and gives up much of its moisture as orographic precipitation. The air mass is compressed by an increasing volume of atmosphere as it descends to lower elevations on the east side of the Rocky Mountains, causing the air mass 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 in the Central Grassland, the frequency of the Pacific Air Mass decreases and the frequency of the Gulf Air Mass increases. Associated with the change in air mass frequency, mean annual precipitation, periodic droughts, and periods of low humidity during summer decrease from west to east in the grassland (Transeau 1935, Borchert 1950, Bryson and Hare 1974, Risser et al. 1981). This west-east climatic variation causes the changes in vegetation from the foothills of the Rocky Mountains to the Midwestern United States that results in the short-, mixed- and tallgrass prairies. Annual net primary production is also affected by this climatic gradient and in years of average precipitation varies from 150–600 g m⁻² from west to east in the Central Grassland (Sala et al. 1988).

Pleistocene History. While grasslands may have been present on the North American continent for 20 million years (Weaver 1968, Risser et al. 1981, Axelrod 1985, Benedict et al. 1996), 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 or its replacement by other vegetation types. At the peak of Wisconsin glaciation (18,000 YBP), most of the Central Grassland was dominated by spruce and jack pine forest or covered with glacial ice. During the early Holocene, 10,000 YRBP, grasslands or oak savanna occurred in much of the current central grasslands, except for the eastern-most

extension into the Midwest that was oak-hickory forest (Delcourt and Delcourt 1981). In the eastern tallgrass prairie, prairie and savanna replaced oak-hickory forest during the warm, dry period of the Hypsithermal, which was accompanied by an increase in fire frequency, beginning about 8,000 YBP and ending 5,000–3,500 YBP depending upon location (Delcourt and Delcourt 1981, King 1981, Winkler et al. 1986, Winkler 1995, 1997, Baker et al. 1996, Anderson 1998). Using Illinois to illustrate changes in climate and vegetation during the Holocene, the drying trend of the Hypsithermal began about 8,700–7,900 YBP. A few hundred years later prairie was present in central Illinois. At the same time as prairie influx into central Illinois, mesic forest was replaced by oak-hickory forest in northern Illinois. At the peak of the Hypsithermal in Illinois (8,000–6,000 YBP) prairies occupied most of the state (King 1981). A similar pattern of vegetational change occurred in northeastern Iowa (Baker et al. 1996) and southern Wisconsin (Winkler et al. 1986, Winkler 1995, 1997), but the timing was somewhat different (Anderson 1998).

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, presence of few endemic plants (Wells 1970a) insects, (Ross 1970) or birds (Mengel 1970, Risser et al. 1981), the relict occurrence of a variety of tree species throughout the region, and the current invasion of woody plants into the grassland. Benedict et al. (1996) indicate that, among mammals, true grassland species comprise only 11.6% of those occurring on the central and northern plains and only 5.3% 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 southwest deserts or in mountain meadows (Gleason 1922, Risser et al. 1981).

The Prairie Peninsula. LOCATION AND ORIGIN. Near the Mississippi River and eastward in the Central Grassland the climate becomes increasingly favorable for trees. The wedge-like extension of the grassland into the Midwestern United States is called the prairie peninsula, because it is a peninsula of grass extending into a forested region (Fig. 2) (Transeau 1935). Annually, this region receives 750–

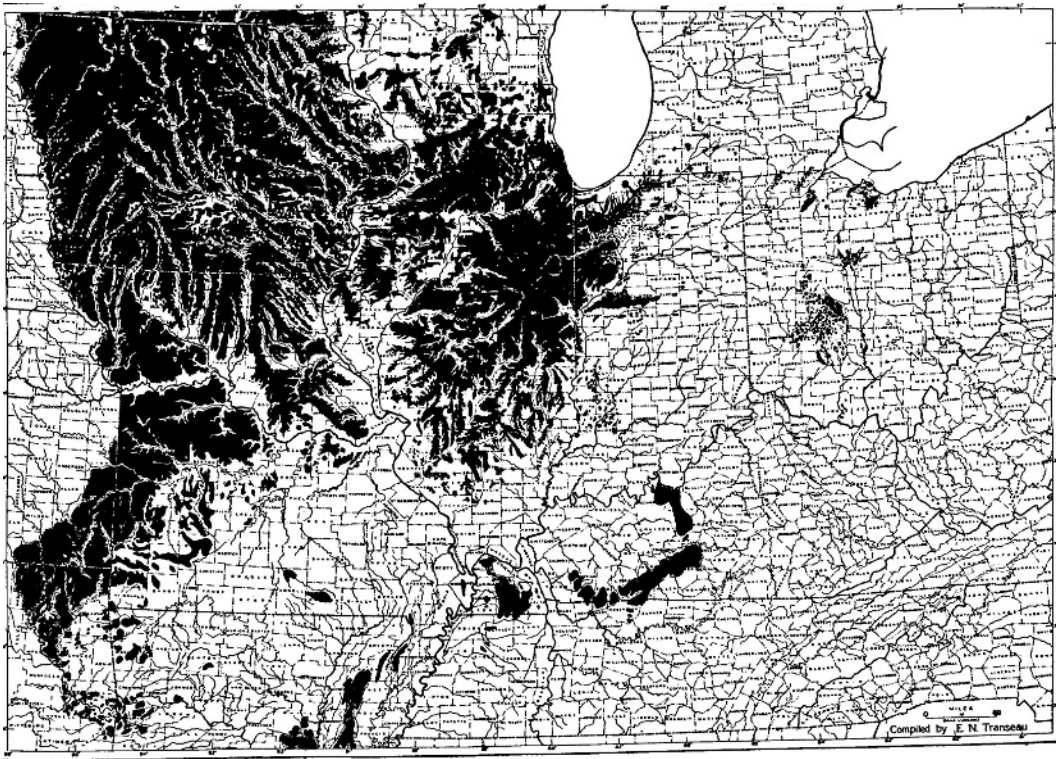


FIG. 2. The prairie peninsula from Transeau 1935 with permission from the Ecological Society of America.

1200 mm of precipitation, a climate capable of supporting forest. Historically, ecologists have debated why this area had grasslands rather than forest (Transeau 1935, Curtis 1971). Several general hypotheses emerged to explain this vegetational pattern. One hypothesis focused on the importance of climate as a primary determinate of vegetation patterns. The other hypotheses posited that fires set by Native Americans or soil conditions were responsible for absence of trees.

CLIMATE EFFECTS. Transeau (1935) reasoned that climatic extremes were more important than averages in determining the distribution of organisms. He demonstrated that the prairie peninsula has periodic droughts when there is essentially a shifting of the drier western climatic conditions eastward into the prairie peninsula. These periodic droughts would favor the prairie and set back the forest. Indeed, during the droughts of the 1930's, trees experienced high rates of mortality in the prairie peninsula (Albertson and Weaver 1945). Transeau (1935) noted that

there was a loss of trees from upland sites during the droughts of the 1930's and their retreat to sheltered locations adjacent to streams. Seedlings are strongly affected by drought and competition from grasses directly and indirectly through production of flammable, finely divided fuels that encourage the spread of fire (Anderson 1990, Sankaran et al. 2004).

DROUGHT AND ROOTING DEPTH. The differential effects of drought on prairie grasses and trees have been explained by the root growth forms of the two groups of plants. In tallgrass prairie in Missouri, 80% of the root mass occurred in the upper 25 cm of soil (Dahlman and Kucera 1965), and similar results were reported by other investigators (Zink and Weaver 1946, Old 1969, Bartos and Jameson 1974, Risser et al. 1981). Although prairie plants have most of their roots in the upper layers of the soil, many prairie plants have deep root penetration (Rooting Depth for 14 grasses and 15 forbs, Range = 0.5–7 m, mean \pm SE = 2.36 ± 0.24 m, original data from

Weaver 1954, recalculated by Risser et al. 1981). Scholes and Archer (1997) suggest that in habitats with grasses, available evidence suggests maximum rooting depth of trees is generally greater than that of grasses. They also note that trees and grasses have the maximum amount of their root mass in the upper soil layers. Nevertheless, grasses may be less dependent upon deep soil moisture than are trees (Schimper 1903, Walter 1971).

Britton and Messenger (1969) suggested that droughts that do not permit recharge of deep soil moisture are more detrimental to trees than grasses. Grasses can take advantage of light showers that recharge the soil surface layers because of their diffuse root system that is concentrated in the upper portions of the soil. 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 winter period of 1933–34 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.

GRASS ADAPTATIONS TO DROUGHT. *Morphological and Physiological Features.* There are many morphological and physiological features that allow grasses to tolerate high moisture stress including (1) the occurrence of bulliform cells in leaves that cause them to enroll when they lose water, thereby reducing leaf surface area for transpiration, (2) utilization of the C₄ or Hatch photosynthetic pathway that adapts plants to high temperatures, high levels of solar radiation, and periods of moisture stress. The C₄ plants have high water use efficiency, stomatal sensitivity to water loss, and photosynthetic rates, and the ability to grow under conditions of low soil-water potential (Ares 1976, Briske and Wilson 1978). While many of the dominant grasses in the Central Grassland are C₄ grasses, including Indian grass, big bluestem, switchgrass, little bluestem, sideoats and hairy grama grasses, there are many species of C₃ grasses that dominate some prairies. The C₃ plants only use the Calvin Cycle in dark fixation of carbon dioxide, maximize growth

under cool moist conditions and are known as “cool season grasses.” The C₃ grasses have lower water use efficiency, photosynthetic rates, and photosynthetic temperature optima and saturation levels for solar radiation, but higher rates of photorespiration and higher CO₂ compensation points than C₄ plants.

Seasonal separation of C₃ and C₄ grasses. In North America, the primary separation of C₄ and C₃ grass is related to temperature (Terri and Stowe 1976). Where daytime growing season temperatures are below 22°C, C₃ plants should dominate and where growing season temperatures are above 30°C, with adequate soil moisture, C₄ plants should predominate (Ehleringer et al. 1997). On a latitudinal gradient, C₄ plants should have a higher quantum yield for carbon dioxide fixation than C₃ plants at latitudes less than about 45° and C₃ plants should have higher quantum yield above that latitude (Ehleringer 1978). Where the two groups of grasses grow together in the Central Grassland, the C₃ grasses, e.g. wild rye, (*Elymus canadensis*), Western wheatgrass (*Pascopyrum smithii*), green needlegrass (*Nassella viridula*), porcupine grass (*Hesperostipa spartea*), and prairie Junegrass (*Koeleria macrantha*), grow in the spring and early summer, whereas the C₄ grasses (e.g., big bluestem, Indian grass, switchgrass, little bluestem, hairy and sideoats grama grasses) begin growth later than the C₃ grasses and maximize growth in mid-summer. Even though the C₄ grasses are more drought tolerant than C₃ grasses, during the drought of the 1930's western wheatgrass increased its abundance more than many C₄ grasses. During several years it was able to utilize moisture that was available in the early spring that was then unavailable to the later growing C₄ grasses (Weaver 1968, Monson et al. 1982).

FIRE AS A FACTOR. *Climate and fire in the Holocene.* Following the end of the Hypsithermal the prairie peninsula climate became cooler and moister and more favorable for trees. Following this climatic change, stabilization of the vegetation in the prairie peninsula is thought to be due to fires set by Native Americans and occasional lightning strikes in a climate that could support prairie, savanna, or forest (Curtis 1971, Anderson 1990, 1991a, 1998).

Again fire has killed the trees over wide areas on which grass was growing, exhibiting before our eyes nature's simple method of converting woodland into prairie. The reverse process is just as simple. When prairies are no longer swept over by fire, timber springs up, reconvert-ing prairie into woodland. Grass, with fire as its ally, can beat timber. Timber can beat grass when it has no fire to fight (Wight 1877).

Effect of fire on prairies and woody species.

Prairie fires can reach temperatures of 83 to 680°C on the soil surface (Wright 1973, Wright and Bunting 1975, Rice and Parenti 1978). Gibson et al. (1990) reported that on Konza Prairie in Kansas fire temperatures varied from 166 to 343°C as a function of habitat, 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 soil surface and there is little penetration of heat below the soil surface (Reichert and Reeder 1972, Anderson 1982). 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. Even if woody plants resprout, they lose several years of growth, which reduces their competitiveness against grasses. Anderson and Brown (1986) reported that after a single fire in a forest adjacent to sand prairie in central Illinois, 34.1% of blackjack oak (*Quercus marilandica*) and black hickory (*Carya texana*) trees greater than 9.0 cm (dbh) suffered mortality during the first year following the fire, and 4.9% and 8.5% in the second and third years after the burn, respectively. Frequent fire and periodic droughts may have interacted to effectively control woody plant invasion into grasslands, especially on sites supporting mesic species, such as sugar maple (*Acer saccharum*), ashes (*Fraxinus* spp.), elms (*Ulmus* spp.), and basswood (*Tilia americana*) that are more susceptible to fire and droughts than oaks. Even if the trees resprout, browsing by elk and deer may have kept woody species from dominating grasslands (Anderson 1982). Sankaran et al. (2004) suggested that through fuel reduction grazers favor trees but browsers encourage grass.

After the first frost, in the autumn of 1835, had killed the millions of tons of grass west of us, we began at Pike River, to see the rising smoke at a distance. The Indians probably had fired the prairies as early as they could for hunting purposes. It was sometime in the latter part of September. We began to see the advancing fire toward evening on the prairie, three miles west of us; and before twelve o'clock it became a serious affair. The wind was from the south-west, and pretty strong, and the fire progressed rapidly... The roaring terror came through the woods with awful grandeur. Large trees, as well as all smaller vegetation, quickly fell before the ruthless invader. (Lothrop 1856).

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, Howe 1994a,b, Bragg 1995). In Nebraska, in the western portion of the tallgrass prairie, lightning fires averaged 138 per year between 1971 and 1975 and the historic fire season was from spring through fall. 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, preventing the encroachment of woody species into grasslands, as a tool for hunting, controlling insect, easing travel, and for other reasons (Stewart 1956, Curtis 1971, Pyne 1983, 1997, Anderson 1990, 1997). Consequently, lightning and Native Americans were both responsible for igniting grassland fires. There may have been frequent summer fires in the Great Plains, because Native Americans and lightning set summer fires (Devoto 1963). In the northern Great Plains, 85% of lightning caused fires occurred in June, July and August, whereas Native American set fires occurred in almost every month, but a majority were set in autumn and late summer (Higgins 1986, Ewing and Engle 1988). Summer fires are smaller those set during the dormant season and lightning set fires are often extinguished by rains associated with the storm that generated the lightning strikes (Bragg 1995).

However, in the more humid eastern portion of the Central Grassland, where rainfall 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 a large proportion of the fires occurred in the autumn, during the period known as "Indian summer" (McClain and Elzinga 1994), a warm, dry period following killing frosts in the autumn, late October and early November. Howe (1995) suggested that North American grasslands evolved under a lightning caused summer fire regime since grasslands were on the continent millions of years before humans migrated to North America. He considers the dormant season fire regime that characterizes anthropogenic set fires not to be typical of the fire regime that shaped the North American Grasslands. Nevertheless, the post-Pleistocene grasslands of North America are of recent origin, as previously noted, and do not predate the arrival of humans on the continent and for the most part contain species that are not restricted to grassland (Gleason 1923, Axelrod 1985). Prescribed summer fires have been proposed as a way of increasing plant diversity in prairies because they set back the actively growing dominant C4 (warm season) grasses so they are less competitive against C3 plants, which are not actively growing. Many of the forbs are C3 plants and they contribute most of the species richness to the prairies (Ewing and Engle 1988, Howe 1994 a,b, 1995, Copeland et al. 2003). However, summer burns as a management practice are not widely applied at the present time (Anderson 1997).

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 fire frequency, which was strongly influenced by topographic features and distribution of waterways (Gleason 1913, 1922, Wells 1970a,b, Anderson 1983, Grimm 1984). In North American grasslands there can be sharp transitions to distinctly different vegetation types that are associated with topographic changes (Wells 1970a,b). The main affect of topography in determining vegetation patterns 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 their maintenance (Curtis 1971, Risser et al. 1981, Anderson 1982, 1990, 1991a). A regime of repeated fires might not be able to eliminate fire resistant woody species from grasslands but it can keep them in a reduced state and dependent upon recurring annual growth from roots for survival (Curtis 1971, Bragg and Hulbert 1976, Heisler et al. 2003). In dissected landscapes fires move rapidly up slopes, as the fire is carried upward by rising convection currents. However, as the fire moves down slope its movement is impeded by the upward flow of the convection currents. Steep slopes and ravines function as fire breaks and provide sheltered locations where forests can survive (Anderson 1998). Using a map of the historic 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 historic distribution of vegetation. About 60% of the state was tallgrass prairie (Anderson 1991a,b, Robertson et al. 1997). Most of the prairie (82.3%) occurred on landscapes with average slope range of 2–4%, whereas only 23% of the forest and savanna was associated with landscapes in this slope range category, mostly in flood plains. Seventy-seven percent of timber vegetation occurred on landscapes with average slope ranges greater than 4% (4–7% slope = 35.2% and >7% = 41.8%). Most of the timbered areas were associated with glacial moraines, highly dissected portions of the older Illinoian glacial till plain, non-glaciated 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 bodies of water support prairie but the east side supports forest (Gleason 1913). Clear skies and dry weather conditions favorable for fires are associated with high pressure systems. Highs have a clockwise flow of air and move from west to east. As a 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 body of water but vegetation on the east would be

sheltered from the fire. As the high pressure system passes, the winds originate from the back side of the system and shift to an easterly direction. Fires started under these conditions could be carried to the east of waterways. However, as the high pressure system passes, low pressure replaces it bringing in high humidity, an increased probability of precipitation, and a reduced likelihood of fire.

FIRE AFFECTS ON GRASSLANDS. *Factors influencing fires.* Golley and Golley (1972) noted that grasslands can produce 20% 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 can be varied depending upon a variety of factors, including the amount of precipitation an area receives, grazing, which reduces fuel loading, fire frequency, timing of the burn, climatic conditions (especially rainfall and temperature) before and after the burn, species composition, and fuel loading.

Climate and Fire Effects on Productivity. Oesterheld et al. (1999) summarized the effect of fire on productivity, which were both positive and negative across a wide precipitation gradient (439–1129 mm annually) that included sites from North America, Africa, and the Mediterranean area. Fire enhanced productivity by as much as 300% and reduced it by as much as 80% of unburned control sites. Positive effects of fire on productivity were associated with sites receiving more than about 700 mm of annual precipitation and negative effects of fire on productivity occurred where precipitation was less than 600 mm. In the eastern portion of the tallgrass prairie, burning enhances productivity (e.g., Hadley and Keickhefer 1963, Hulbert 1969, Kucera and Ehrenreich 1962, Old 1969, Vogl 1974, Peet et al. 1975, Rice and Parenti 1978). Exceptions to this generalization have been reported for burning xeric sites (Dix and Butler 1954, Zedler and Loucks 1969), although Dhillon and Anderson (1988) and Anderson et al. (1989) reported an increase in production 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 (Hopkins et al.

1948, Launchbaugh 1972, Wright 1969, 1972; Heirman and Wright 1973, Anderson 1976, Anderson 1982, Oesterheld et al. 1999).

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 production on native grass pastures. Burned sites had lower production than unburned sites following winter or early-spring burns but late-spring burns and non-burned areas had equal production. Decline of production on early burns compared to late-spring burns is due to litter being removed from the site for a longer period of time on the early burned than the late burned site, followed by early growth of the prairie on burned sites, 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 production (McMurphy and Anderson 1965, Owensby and Anderson 1967, Owensby and Smith 1972, Bragg and Hurlbert 1976, Anderson 1982, Knapp 1985, Svejcar 1990). Nevertheless, cattle grazing on forage on burned sites make faster weight gains than cattle grazing on unburned sites, because the forage on burned sites is more palatable and higher in protein than forage on unburned sites (Anderson 1976, Dyer et al. 1982, McNaughton et al. 1982, Knapp et al. 1999).

Litter Removal. The increased production on burned eastern tallgrass prairie is related to litter removal (Weaver and Roland 1952, Ehrenreich 1959, Kucera and Ehrenreich 1962, Hadley and Kieckhefer 1963, Hulbert 1969, Peet et al. 1975, Knapp 1984). Old (1969) reported that litter removal increased production whether it was removed by fire or by mechanical means. One of the mechanisms whereby litter removal enhances production is through the alteration of microclimatic conditions on the burned site to conditions more favorable for the growth of the dominant C4 grasses than on unburned sites.

Litter is a good insulating surface and it has high reflectance of solar radiation and low net radiation, the difference between incident and reflected solar radiation. Consequently, the soil warms up slowly in the spring (Peet et al. 1975). In contrast, on the burned surface 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, during daytime, soil temperatures at 3 mm were warmer on the burned site than the unburned site. During the night, the burned prairie has a good radiating surface and cools rapidly, whereas unburned site has the insulating litter cover that retains heat. Consequently, temperatures were cooler in the upper layers of soil on the burned site than the unburned site. However, at 25 cm depth in the soil the unburned site was constantly cooler than burned site. The differences in microclimate between burned and unburned sites decreased as a grass canopy developed on the unburned site (Brown 1967, Anderson 1972, Peet et al. 1975).

In the early spring, warmer soil temperatures during the day on the burned site resulted in plants beginning growth earlier on burned prairie than unburned prairie. Emergence of vegetation on the burned site can be 7–14 d or as much as 30 d later compared to the burned site (Knapp 1984). Peet et al. (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 University of Wisconsin-Madison Arboretum's Curtis Prairie. They reported no difference in maximum photosynthetic rates between plants of big bluestem on burned and unburned prairies. Higher production on burned prairies was attributed to the larger standing crop of green biomass earlier in the growing season on the burned prairie (Peet et al. 1975).

On the Konza Prairie, as leaves develop under standing dead biomass on unburned prairie they are shaded and acquire characteristics of shade leaves and have low light saturation values and photosynthetic rates. Standing dead litter reduces solar radiation and slows the wind speed (89% lower than above the canopy), which reduces convectional cooling. Leaf temperatures can rise above the optimum for photosynthesis for C4 plants (30–35°C, Black 1973) and depress photosynthesis (Knapp 1984). In contrast, on burned grasslands leaves develop in full sunlight as they emerge and have characteristics of sun leaves with high light saturation values and photosynthetic rates. Additionally, leaf temperatures on burned prairie are nearer the optimum for photosynthesis, because of greater convectional cooling as a result of the

absence of standing dead biomass and higher wind speeds (57% lower than above the canopy). For example on June 10, leaf temperatures for big bluestem were 41.5°C (7.9° above air temperature) and 39.4°C (4.0° above air temperature), for plants on unburned and burned sites, respectively, on the Konza Prairie. Because of active growth on the burned site early in the spring that reduced soil moisture, big bluestem plants on burned sites had greater water stress early in the growing season than plants on the unburned prairie (Knapp 1984).

In summary, key microclimatic differences between burned and unburned prairie that affect productivity and result in higher productivity on burned prairies than unburned prairies include: warmer spring temperatures on burned sites than unburned, greater availability of solar radiation and temperatures more favorable for optimum photosynthesis on burned sites than unburned sites (Peet et al. 1975, Knapp 1984). Differences in results between the Kansas and Wisconsin sites may be due to differences in standing dead biomass, which stood 42 cm tall in Kansas and 10 cm in Wisconsin (Peet et al. 1975, Knapp 1984). The more compacted litter on the Wisconsin site may have slowed soil warming more but reduced convectional cooling and radiation less than on the Kansas site.

Litter removal and 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 due to volatilization will reduce available nitrogen by about $1.0\text{--}4.0 \text{ g m}^{-2} \text{ yr}^{-1}$. This represents about two times as much nitrogen as the amount input by rainfall annually (Knapp and Seastedt 1986). Long-term there is a net loss of nitrogen from grasslands that are burned annually (Risser and Parton 1982, Ojima et al. 1990, Blair 1997), despite biogeochemical pathways to replenish nitrogen lost by burning.

In prairies, both living tissue and detritus absorb annual rainfall, with each absorbing about 20% of the annual deposition (Gilliam et al. 1987). Inorganic nitrogen in rainfall provides nitrogen equal to about 25–50% of that required by living foliage (Risser et al. 1981, Risser and Parton 1982). Nitrogen absorbed by microbes is converted to micro-

bial protoplasm and is unavailable to plants. As a consequence, more inorganic nitrogen in precipitation is available to plants on burned prairies than unburned prairies because there is no microbial sink for nitrogen in litter layers (Knapp and Seastedt 1986). Litter has high C/N and C/P ratios and microbes remove nutrients from the soil to carry out decomposition, which also reduces the availability of nitrogen to support plant growth (Seastedt 1988). The input of nitrogen into prairies from nitrogen fixation by free-living Cyanobacteria is higher on burned prairies than unburned prairies because more light reaches the soil surface on burned prairies than unburned prairies (Eisele et al. 1989). In addition, ignition of the litter releases phosphorus and an increase in available phosphorus enhances nitrogen fixation (Knapp and Seastedt 1986, Eisele et al. 1989).

Grasslands and Grazers. HISTORY OF NORTH AMERICAN GRAZERS. In North America, expansion of the grassland biome occurred in the Miocene-Pliocene transition 7–5 MaBP and was associated with a concomitant increase in animals adapted to grazing, as in other areas in the world (Axelrod 1985). Through the Pleistocene (1–3 Million MaBP) there was a diverse grazing megafauna on the continent, which included 32 genera and dozens of species of mammals such as camels, horses, rhinoceroses, antelopes, bison, and elephants. Near the end of the Pleistocene beginning about 25,000 YBP the number of grazing species sharply declined. This sharp decline has been attributed to the appearance of efficient human hunters and/or climatic change (Flores 1996, Ehleringer et al. 2002). The peak of the American-evolved megafaunal crash occurred about 10,000 YRP leaving only about a half dozen browsing and grazing forms. When Europeans entered the grasslands of North America the bison, elk, and other animals that characterized the grasslands were the remnants of the diverse fauna that had been present prior to the massive extinction at the end of the Pleistocene (Flores 1996).

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 productivity and diversity of grasslands. Golley and Golley (1972) suggested that the production of bio-

mass in excess of that which can be decomposed was a response to grazing. Grazing, like burning, accelerates the rates of mineralization of inorganic nutrients (Frank et al. 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 et al. 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 production (Frank et al. 1998). Some authors (McNaughton 1979, 1993, Owen 1981) have proposed a symbiotic relationship between grasses and grazers. Aboveground productivity of grasslands increases with moderate grazing (McNaughton 1979, Knapp et al. 1999), although other workers have questioned the beneficial effects of grazing (Belsky 1986, Painter and Belsky 1993). Additionally, increased shoot production occurs at the expense of belowground production and nitrogen and carbon are transferred from below ground to facilitate compensatory aboveground growth following grazing (Collins et al. 1998, Knapp et al. 1999) and excessive grazing will eventually cause a decline in productivity (Anderson 1982).

“What a thousand acres of *Silphiums* looked like when they tickled the bellies of the buffalo is a question never again to be answered, and perhaps not even asked.”

Aldo Leopold (1966)

BISON AS A KEYSTONE PRAIRIE SPECIES. *Grazing patterns and preferences.* Understanding the role of bison in tallgrass prairie has occurred only in the last two decades when reserve areas became available that were large enough to support a reasonable number of bison and to allow them to graze in a way that simulated historic conditions. Knapp et al. (1999) delineated a keystone role for bison in maintaining diversity of tallgrass prairie. On Konza Prairie bison fed primarily on grasses that constituted 90% of their diet and consumed only small quantities of forbs and essentially no woody vegetation (Fahnestock and Knapp 1993, Vinton et al. 1993, Hartnet et al. 1996, Damhoureyeh and Hartnett

1997, Steuter 1997, Knapp et al. 1999, Towne et al. 2005). While graminoids constituted the largest portion of the bison diet, the proportion of C3 and C4 grasses consumed varied seasonally.

Generally, mammalian herbivores prefer C3 grasses over C4 grass. The reason for this preference is not known, even though C3 grasses have higher digestibility and protein content but lower C/N than C4 grasses (Caswell 1973, Wilson and Hattersley 1989, Ehleringer et al. 2002). Nevertheless, while some studies have reported that C4 grasses have more fibers and higher silica concentration in their leaves than C3 grasses (Kepart and Baxton 1993, Kaiser 1998), other studies found no difference in the two traits between C3 and C4 grasses (Heidorn and Joern 1984, Scheirs et al. 2001). In South Dakota, C4 grasses constituted 33–44% of the bison diet from early June through August and then declined to 15% by September 30. Bison use of C3 graminoids (sedges and grasses) increased from 52–58% in mid-June to mid-August to greater than 80% after September 1 (Plumb and Dodd 1993). Similar patterns in seasonal shifts in consumption of C3 and C4 grasses were found on the Konza Prairie (Vinton et al. 1993).

Bison grazed in two patterns, which included creating distinctive grazing patches that were 20–50 m² in area and more extensive grazing lawns that were greater than 400 m². 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 compared to the ungrazed areas. Grazed areas initially experienced short-lived increased productivity following grazing, but productivity eventually declined as loss of aboveground tissues was compensated for by movement of carbon reserves from belowground. By repeatedly grazing the same areas, bison encouraged the growth of non-palatable species that are the forbs. This grazing pattern eventually encouraged shifting to other areas as forage quality declined. On average 6–7% of the grazing patches were abandoned annually (Knapp et al. 1999).

Enhancing grassland plant diversity. Bison grazing can offset negative effects of frequent burning on plant species diversity (Gibson and

Collins 1990, Knapp et al. 1999). Dormant season burns favors C4, warm season grasses and late flowering forbs. Periodic fires are necessary to maintain the species richness of tallgrass prairies (Leach and Givnish 1996). Nevertheless, frequent fires, especially annual burns, can encourage these grasses at the expense of C3 plants, which include many species of forbs (Kucera and Koelling 1964, Gibson and Collins 1990, Knapp et al. 1999). Importantly, forbs contribute most of the species richness to the prairie (Howe 1994a, Hartnett and Fay 1998). Bison graze on the C4 grasses and reduce their abundance, which favors unpalatable C3 forbs, which in turn enhances the plant diversity of the prairie.

Bison effects on animal diversity. Bison enhance spatial heterogeneity in the prairie through their grazing patterns that results in patches of lightly grazed to heavily grazed areas that have sparse grass cover and little litter (Knapp et al. 1999, Fuhlendorf and Engle 2001). This spatial heterogeneity is important for grassland bird diversity. In the eastern tallgrass prairie, some birds, such as the Killdeer and Upland Sand Piper require short vegetation across large areas. Other species, such as Eastern Meadow Lark and Bobolink, utilize medium height vegetation with moderate amounts of litter, whereas species such as Henslow's Sparrow and Marsh Wren occur where the vegetation is tall with heavy amounts of litter (Herkert et al. 1993). Endemic birds of western Great Plains also have characteristic distributions related to historic grassland types and grazing patterns (Knopf 1996).

Fire and bison grazing affect the diversity and density of grasshoppers. 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 (J) 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 (Vinton et al. 1993, Pfeiffer and Stuetter 1994, Pfeiffer and Hartnett 1995, Hartnett et al. 1996, Knapp et al. 1999, Fuhlendorf and Engle 2001). Conse-

quentially, fire and large mammalian grazing are crucial features for maintenance of grasshopper diversity.

Grassland small mammals. Microtine rodents also require a diversity of conditions with respect to vegetation and litter density. Even though there are species of small mammals that show positive (deer mice) and negative (western harvest mice and prairie voles) responses to burning, those showing negative responses to burning recover in two to three years after a burn (Schramm 1970, Schramm and Willcutts 1983, Kaufman et al. 1990, Matlack et al. 2001). Fires of varied intensity and completeness of fuel consumption should favor diversity of animals in grasslands. The mosaic of vegetation resulting from grazing creates uneven patterns of fire intensity as a result of having areas with fuel loadings that vary from sparsely grazed areas with heavy fuel loading to low fuel loading where areas were subjected to intensive grazing pressure.

Invertebrate Species Response to Prairie Fires. Even though grasshopper diversity is enhanced by a combination of bison grazing and burning, the response of invertebrates to burning is varied. A number of factors determine the response of the invertebrate species to fire, including where individuals are located at the time of the fire (Macfadyen 1952, Reichert and Reeder 1972, Seastedt 1984, Warren et al. 1987), microclimatic and vegetational structural changes after fire, and the ability of the invertebrate species to adapt to the changed environment following the burn (Anderson 1964, Evans 1984, 1988, Anderson et al. 1989). For example, species of spiders that were active on the soil surface at the time of a burn were eliminated, whereas other species survived in subsurface burrows, under rocks, or were protected in the bases of caespitose (clumped) grasses during a burn that had surface temperatures of 200°C (Riechert and Reeder 1972). Similarly, mixed responses of species to fire were reported for mites (Seastedt 1984), collembolans (Lussenhop 1976, Amburg et al. 1981), grasshoppers (Evans 1988), whereas butterflies (Swengel 1996, 1998, 2001), and leafhoppers decrease in abundance after fire (Panzer 1988). Grasshoppers that fed on forbs increased in frequency as fire frequency decreased; how-

ever, some grasshopper species increased after fire and/or showed rapid recovery following burning (Evans 1988, Anderson et al. 1989).

Thus, it is not possible to have a single burning regime that will be optimal for all insects, and an increasing number of entomologists are expressing concern that prairie insects are being harmed by current prescribed burning practices, that if continued, could result in a substantial number of species being lost (Pyle 1997, Schlicht and Orwig 1999, Swengel 1996, Swengel and Swengel 2001). However, Panzer and Schwartz (2000) concluded that the current rotational plan (burn about every 2–3 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 that involve burning fragmented remnant prairies or restorations nearly all or 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 50–70% as unburned “refugia” for fire sensitive species, which can reinvade the burned site after it regrows (Panzer 1988, Panzer and Schwartz 2000, Panzer 2003, Andrew and Leach 2006). 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 for insects (Panzer 1988).

White-Tailed Deer in Remnant Tallgrass Prairie. Historically, in much of the tallgrass prairie the bison was the most important large mammalian herbivore in nearly all of the Central Grassland, although its abundance may have been substantially lower in the eastern than in the western portion of the tallgrass prairies (Leach et al. 1999). However, currently the white-tailed deer is the large native mammal with the most impact on remnant and restored tallgrass prairies. While bison graze almost entirely on grass, forbs, which are little used by bison, are selectively browsed upon by white-tailed deer. Anderson et al. (2001) reported that deer browse very little on grasses or sedges during the late spring and summer. However, they browsed from

3.5–18.9% 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 could reduce the diversity of the prairie. Anderson et al. (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, Collins et al. 1995). However, the community quality of forbs, based on the degree to which species were associated with relatively undisturbed remnant prairies, declined as duration of intense deer browsing (disturbance) increased. Forb quality was highest after eight years of protection from browsing, suggesting a potential trade-off between maximizing diversity and maintaining quality of forb communities that land managers should consider (Anderson et al. 2006).

Conclusions. Since the 1950's, our understanding of grasslands has been greatly enriched by widening the scope of our research to include interactions among organisms in different trophic levels and examining the mechanisms that drive ecosystem processes. Fire has continued to be recognized as an important factor that determines the distribution and species composition of grasslands. For example, using simulation models Bond et al. (2005) concluded that without fire worldwide current closed forest would increase from 27–56% of vegetated cells mostly as the result of a reduction in cover of C4 plants. Without fires 52.3 percent of the cells with C4 grasses present would be converted to angiosperm forest. This conversion would occur in large areas of South America, Africa and smaller areas of Australia, especially in humid areas that have climates with the potential to support forests. In the Central Grasslands of North America, habitat fragmentation resulting from agriculture and urban development has reduced the potential for fires to be carried across landscapes and maintain the shifting mosaic of grasslands, forest, and savanna vegetation that characterized the prairie peninsula and the expansive area of mixed- and shortgrass prairie (Anderson and Bowles 1999). The effect of fire on these grasslands is complex, strongly influenced by climate, and

mitigated by large mammalian grazers. While burning separates fire-sensitive from fire-tolerant or fire-dependent species, this separation provides a simplistic view of the varied responses of grassland organisms to fire. For all major taxonomic groups of organisms, there is a continuum of responses to fire. To maintain the biological diversity of grasslands there must be areas large enough to support varied fire regimes and include or simulate the ecosystem functions provided by grazing, browsing, and burrowing animals (e.g., prairie dogs, pocket gophers, ground squirrels, and invertebrates), which play critical roles in developing and maintaining grasslands soils. Most of our remaining grasslands in the eastern portions of the Central Grassland are small remnant fragments, and in the mixed-grass and shortgrass prairies excessive grazing by cattle is an issue of concern. Maintaining or improving the quality of our remaining grasslands can be achieved through sound rangeland management, and restoration of prairies provides the means to ensure survival of prairie species. However, our efforts at prairie restoration are usually limited to establishing prairie plants with little attention given to other prairie organisms. Invertebrates provide the greatest species diversity of any group of grassland organisms. They carry out many important ecosystem functions such as pollination, decomposition, and are critical links in food chains. Invertebrate biomass exceeds that of most vertebrate groups combined (Risser 1996). Yet, it is rare for invertebrates to be included in prairie restorations (Taron 1997). While we know a great deal about prairies much of this information has not been adequately incorporated into our restoration practices. Nevertheless, our success in managing and preserving the remnant and restored prairies should be enhanced because of our realization that grasslands function because of the interactions that have evolved among the organisms within the system

If the land mechanism as a whole is good, then every part is good, whether we understand it or not. If the biota, in the course of eons, has built something we like but do not understand, then who but a fool would discard seemingly useless parts? To keep every cog and wheel is the first precaution of intelligent tinkering (Aldo Leopold 1966).

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