

ECOLOGY AND MANAGEMENT OF THE PRAIRIE DIVISION ROGER C. ANDERSON

Roger C. Anderson
Distinguished Professor of Plant Ecology
4120 Department of Biology
Illinois State University
Normal, Illinois 61790-4120

ABSTRACT. Grasslands are a widespread vegetation type that once comprised 42% of the plant cover on earth's surface. World-wide expansion of grasslands occurred 8 to 6 million YBP and was associated with increasing abundance of plants using the C4 photosynthetic pathway, a decline in woodlands, and coevolution of mammals adapted to grazing and open habitats. In North America, the largest grassland (Central Grassland) occurred east of the Rocky Mountains and is of recent origin (post Pleistocene). This grassland changed in plant species' composition and structure in response to a precipitation gradient that increased from west to east. The Prairie Division occupies the eastern portion of this grassland where the climate can support forests or grasslands and fire is necessary for its maintenance. During the past two decades, grassland research has focused on fire-grazing interactions that affect habitat heterogeneity and diversity across trophic levels. Managing grassland requires understanding and manipulating these interactions.

GENERAL FEATURES OF GRASSLANDS

Distribution and Climate

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. 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 to 30 °C (Sauer 1950, Risser and others 1981, Oesterheld and others 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 and others 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 and others 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 and others 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 and others 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 can decompose in a single year (Stebbins 1981, Anderson 1982, 1990).

The wide spread 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 and others 1997, Ehleringer and others 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 million YBP, decline in atmospheric carbon dioxide favored evolution of C4 plants in moist tropical and subtropical regions (Ehleringer and others 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 and others 2002).

Accelerated development of C4 grasslands world-wide occurred during the Miocene-Pliocene transition (8-6 million YBP) 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 and others 1997, Ehleringer and others, 1997, 2002). However, Keeley and Rundel (2005) posit that the conversion of forest to C4 grassland four to seven million YBP was not directly, due to a decline in atmospheric carbon dioxide or increased aridity directly but rather to a climate change that encouraged fire. Under the new climatic conditions high biomass production resulted from a warm moist growing season 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 the Keeley-Rundel (2005) 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, 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 Central 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. 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 and others 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 and others 1981). Across this gradient mean annual temperature varies 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 to 1000 mm in Indiana (Risser and others 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. 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 to 1200 mm and across a north-south gradient 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 (260-375 mm precipitation), the eastern tallgrass prairie or "True Prairie," (625-1200 mm

precipitation), and between the two the mid- or mixed grass prairie (375-625 mm precipitation) (Figure 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 grama (*Bouteloua hirsuta*) grasses. Big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), and little bluestem (*Schizachyrium scoparium*) are dominant species in the tallgrass prairie and reach heights of 1.8-2.4 m. The mixedgrass or midgrass prairie is dominated by species that are 0.8 to 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 mid-grass 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. At any location in the tallgrass prairie there can be a diversity of prairie types as a function of soils and topographic features. A primary factor causing this varied vegetation patterns is availability of soil moisture (Curtis 1971, Nelson and Anderson 1971, Umbanhowar 1992, Corbett and Anderson 2006). For example, there are approximately 930 hectares of high quality remnant prairie in Illinois representing diverse habitat types differing in topography and substrate. These prairies includes dry 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 and others 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: Polar, Gulf, and Mountain Pacific (Borchert 1950, Bryson and Hare 1974, Risser and others 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 and others 1981). There are also north-south variations in vegetation patterns (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 originates 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 as 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 decrease from west to east in the grassland (Borchert 1950, Bryson and Hare 1974, Risser and others 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 to 600 g/m² from west to east in the Central Grassland.

Pleistocene History--While grasslands may have been present on the North American continent for 20 million years (Weaver 1968, Risser and others 1981, Axelrod 1985, Benedict and others 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 Wisconsinan 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 central grasslands

but oak-hickory forest covered most of the prairie peninsula (Delcourt and Delcourt 1981). In the eastern tallgrass prairie, prairie and savanna replaced oak-hickory forest during the warm, dry period of the Hypsithermal, that was accompanied by an increase in fire frequency, beginning about 8,000 YBP and ended 5,000 – 3,500 YBP depending upon location (Delcourt and Delcourt 1981, King 1981, Winkler and others 1986, Winkler 1995, 1997, Baker and others 1996, Anderson 1998). Using Illinois to illustrate changes in climate and vegetation during the Holocene, the drying trend of the Hypothermal 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 and others 1996) and southern Wisconsin (Winkler and others 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 and others 1981), the relict occurrence of a variety of tree species throughout the region, and the current invasion of woody plants into the grassland. Benedict and others (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 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, because it is a peninsula of grass extending into a forested region (Figure 2) (Transeau 1935). Annually, this region receives 750-1200 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 soils 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 and grasses indirectly by producing 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 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 and others 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 \pm 0.24 m, original data from Weaver 1954, recalculated by Risser and others 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 (1970) 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 1970). 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 grass, 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 temperature are below than 22 °C, C3 plants should dominate and where growing season temperatures are above 30 °C, with adequate soil moisture, C4 plants should predominate (Ehleringer and others 1997). On a latitudinal gradient C4 plants have a higher quantum yield for carbon dioxide fixation at latitudes less than about 45 ° (Ehleringer 1978). Where the two groups of grasses grow together, 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 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 because 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 and others 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).

Effect of fire on prairies and woody species--Prairie fires can reach temperatures of 83 to 680 °C on the surface of the soil (Wright 1973, Rice and Parenti 1978). Gibson and others (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 surface of soil and there is little penetration of heat below the soil surface (Reichert and Reeder 1971, 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 and others (2004) suggested that through fuel reduction grazers favor trees but browsers encourage grass.

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 1990, 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). 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).

However, in the more humid eastern portion of the Central Grassland, where rainfall usually accompanies lightning storms, most of the 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.

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 influence by topographic features and distribution of waterways (Gleason 1913, 1922, Wells 1970b, 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 appears to be its control of fire frequency. Landscapes that are nearly level to slightly rolling can support the nearly annuals fires that grasslands need for their maintenance (Curtis 1971, Risser and others 1981, Anderson 1982, 1990). 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 and others 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 the movement of the fire is impeded by the upward flow of the convection currents, and 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 1979, 1991a,b, Robertson and others 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 and brings in high humidity and increased probability of precipitation and reduces the likelihood of fire.

Fire effects 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--Oosterheld and others (1999) summarized the effect of fire on productivity, which were both positive and negative across a wide precipitation gradient (439 to 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. Partch and Curtis 1949, Hadley and Keickhefer 1963, Hulbert 1969, Kucera and Ehrenfeld 1962, Old 1969, Vogl 1974, Peet and others 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 Dhillion and Anderson (1988) and Anderson and others (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 and others 1948, Launchbaugh 1972, Heirman and Wright 1973, Wright 1969, 1972, Anderson 1976, Anderson 1982, Oosterheld and others 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 1963, Owensby and Anderson 1967, Owensby and Smith 1973, 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 and others 1982, McNaughton and others 1982, Knapp and others 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 and others 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 and others 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 (a good absorbing surface is also a good radiator) and cools rapidly. The 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 and others 1975).

The warmer soil temperatures during the day on the burned site in early spring resulted in plants beginning growth earlier on burned prairie than unburned prairie. Emergence of vegetation on the burned site can be 7-14 days or as

much as 30 days later compared to the burned site (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 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. The 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 and others 1975).

On the Konza Prairie, as leaves develop under standing dead biomass 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 convective cooling. Leaf temperatures can rise above the optimum for photosynthesis for C4 (30-35 °C, Black 1973) plants (Knapp 1984) and depress photosynthesis. 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, on burned prairie leaf temperatures are near the optimum for photosynthesis, because of greater convective 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 $41.5 \text{ }^\circ\text{C}$ (7.9° above air temperature) and $39.4 \text{ }^\circ\text{C}$ (4.0° above air temperature), for plants on unburned and burned sites, respectively. Kansas. 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 than unburned sites in Wisconsin (Peet and others 1975), greater availability of solar radiation and temperatures more favorable for optimum photosynthesis on burned sites than unburned sites are important factors in determining high production on burned prairies than unburned prairies (Knapp 1984). Differences in results between the Kansas and Wisconsin sites may be due to differences in standing dead, which was 42 cm in Kansas and 10 cm in Wisconsin (Peet and others 1975, Knapp 1984).

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 $1.0\text{-}4.0 \text{ g/m}^2/\text{yr}$. This represents about two times as much nitrogen as the amount input by rainfall annually (Knapp and Seastedt 1986). There are compensating mechanisms to replenish nitrogen lost by burning. Nevertheless, long-term there is a net loss of nitrogen from grasslands that are burned annually (Ojima and others 1990). The effects of litter removal on inorganic nutrient availability are given in chapter (.) of this volume.

Grasslands and Grazers

In North America, expansion of the grassland biome occurred in the Miocene-Pliocene transition 7-5 million years before present (YBP) 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 YBP) 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 and others 2002). The peak of the American-evolved megafaunal crash occurred about 10,000 YBP 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 biomass 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 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 production (Frank and others 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 and others 1999), although other workers have questioned the beneficial effects of grazing (Belsky 1979, Painter and Belsky 1993). Additionally, evidence suggests that 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 and others 1998, Knapp and others 1999) and excessive grazing will eventually cause a decline in productivity (Anderson 1982).

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 and others (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 and others 1993, Hartnet and others 1996, Steuter 1997, Knapp and others 1999). 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 (Ehleringer and others 2002). The C4 grasses have more fibers and higher silica concentration in their leaves than C3 grasses (). In South Dakota, C4 grasses constituted 33% to 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% from mid-June to mid-August and 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 and others 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 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 C4, warm season grasses and late flowering forbs. 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). And forbs contribute most of the species richness to the prairie (Howe 1994, Hartnett and Fay 1998). Bison graze on the C4 grasses and reduce their abundance, which favors unpalatable C3 forbs, which 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 sparse 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 and others 1993). Endemic birds of western Great Plains also have characteristic distribution 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 and others 1993, Pfeiffer and Stuetter 1994, Pfeiffer and Hartnett 1995, Hartnett and others 1996, Knapp and others 1999, Fuhlendorf and Engle 2001). Consequentially, 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 1973, Kaufman and others 1990). 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.

White-tailed deer in remnant tallgrass prairie

Historically, in much of the tallgrass prairie the bison was the most important large mammalian herbivore in most 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 and others 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 and others (2001) reported that deer browse very little on grasses or sedges during the late spring and summer. However, they browsed from 3.5% to 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 1994), excessive white-tailed deer browsing could reduce the diversity of the prairie. 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 degrees 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 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 (e.g. C4 grasses, C3 grasses, early flowering forbs, litter dwelling invertebrates, etc.) will respond to various management prescriptions. Fire is the most widely applied tool in managing tallgrass prairie and, because of rainfall being associated with lightning storms and habitat fragmentation, which limits spread of fire, prescribed burning is necessary to maintain prairies, including 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. In some cases, compromises will have to be made in deciding on which management practices should be used when species or groups of species respond differently to management. This section does not provide a comprehensive management guide to prairie management. Rather it discusses some issues that are often of concern in the management of prairies. Comprehensive discussions of prairie management are provided in Packard and Mutel (1997).

Timing of the Burn

Prescribed fires most frequently occur in spring because the opportunity for burning is generally longer in the spring than in the fall. Spring burns also have the advantage of retaining winter cover for wildlife. Nevertheless, fall is apparently the time of year that most of the Native American set fires occurred and this may be a yet unknown factor in community response to fire. Fall burns occur when birds and mammals are not actively breeding as they can be at the time of spring burns. Large mammals readily move away from the fire and are rarely directly affected by burning. Direct small mammal losses in prescribed burns are usually small, even in head fires, but they do occur. Nevertheless, it is relatively common to burn cottontail rabbit nests during spring burns, especially if the burn is delayed so that exotic cool season plants like Kentucky bluegrass and sweet clover are actively growing and can be

set back by the burn. 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 (March, dormant season burn) in south central Oklahoma. The authors tested the hypothesis that summer burns would be more detrimental to woody species than dormant season burns, because 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 usually pronounced drought following the winter burn. Additionally, woody and herbaceous species can regrow in the same growing season in which a summer burn occurs, and this may mitigate the affects of summer burns (Anderson 1972).

The application of summer burns to enhance the diversity of prairie plants has been examined in several studies (Howe 1994a,b, Copeland and others 2000). Burning in the summer when the dominant C4 plants are actively growing should reduce their competitiveness against C3 plants and reduce the dominance of the C4 plant. Copeland and others (2000) reported a twofold increase in the species richness and mean frequency of subdominant species in plots subject to a late-summer fire, but these two measurements remained unchanged in plots subjects to early spring fires. Similarly, Abrams and Hulbert (1987) found that spring burning had no effect on plant species richness.

While summer burns may have applicability we should move slowly on the use of summer burns, because we have no information available on response of animals to summer burns and only limited data on plant response (Anderson 1997). In addition, under some conditions, e.g. green vegetation that 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 at 2-3 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 C4 grasses.

Small mammals-- Fire alters vegetation composition and structure so that some small mammal species benefit from the changes and others have less favorable habitat conditions following burning (Kaufman and others 1990). However, as previously noted species decreasing in abundance following fire recovered within two or three years without burning. By burning sections of the prairie on a two or three year rotational basis the habitats needs of the mammal species should be met.

Preserving Invertebrates. The response of invertebrates to burning is varied and is dependent upon 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), microclimatic and vegetational structural changes after fire, and the ability of the invertebrate to adapt to the changed environment following the burn (Anderson 1964, Evans 1984, 1988, Anderson and others 1989). For example, species of spiders that were active on the soil surface at the time of a burn were eliminated, whereas species survived in subsurface burrows, under rocks, or 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 and others 1981) and grasshoppers (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 1998). Grasshoppers that fed on forbs increased in frequency as fire frequency decreased; however, some grasshopper species increased after fire and/or showed rapid recovery following burning (Evans 1988, Anderson and others 1989). For specialist species of butterflies, those restricted to prairie, savanna and/or barrens, occasional single wildfires were more favorable than rotational burning, and mechanical cutting more favorable than grazing. However, widely distributed grassland butterflies were favored by more frequent management and 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, and an increasing number of entomologists are expressing concern that prairie insects are being harmed by current prescribed burning practices, and if continued, they could result in a substantial number of species being lost (Pyle 1997, Schlicht and Orwig 1999). 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...”

Possible solutions to this management conundrum include burning only a portion of each site on a rotational basis leaving 50 to 70% as unburned “refugia” for fire sensitive species, which can invade the burned site after it regrows (Panzer 1988, Panzer and Schwartz 2000, Panzer 2003). 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).

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 in some cases to achieve a reduction in woody vegetation. Procedures for controlling woody species using herbicide are provided by Solecki (1997).

Grazing and Fire Management

Grazing by bison has been shown to increase the plant diversity and spatial heterogeneity of grasslands. However, the use of grazing as a grassland management tool has been little applied, especially in the eastern portions of the tallgrass prairie. Nonetheless, “patch-burn grazing” appears to be a practice that has good potential for maintaining prairie diversity (Helzer and Steuter 2005). In this management practice, grazing animals (cattle or bison) are permitted to graze freely across the prescription area that has recently burned and unburned patches. The burning increases the grazing pressure on the burned areas in the first year after the fire. The intense grazing in the burned area creates openings and reduces competition from the C4 grasses that are preferred forage for both bison and cattle and encourages the growth of the unpalatable forbs (Towne and others 2005). On restored prairies, the heavily grazed 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 C4 grasses and low diversity of forbs. Information on stocking rates for bison and cattle are provided by Steuter (1999), Helzer and Steuter (2005), and Towne and others (2005). Stocking rates may have to be modified for each specific site to ensure that overgrazing of the grasslands does not occur.

The choice of whether to use bison or cattle for grassland management is dependent upon a number of factors. The grazing pattern of the two ungulates is somewhat different with cattle consuming more forbs and browse than bison. Economic returns are greater from cattle than bison, space needs and facility and management costs are greater with bison, but bison provide better management for natural areas (Plumb and Dodd 1993).

Grazing is not an option on all prairies because of size limitations and other factors. Leach and others (1999) have proposed that in the eastern portions of the tallgrass prairie there are plant species sensitive to grazing; historically bison were not abundant on these prairies so a strong interaction between these grazers and prairies did not develop. This concern remains an unresolved issue. Grazing can have positive and negative effects on grasslands; nevertheless, grazing returns a historical function to grassland 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 provided habitat for the largest nesting population of Upland Sand Pipers in Illinois. We need to know if native grazers or their surrogates can utilize native prairie plants and produce similar habitats. Heavy grazing before and during the period of breeding with removal of grazing so the native grasses can recover, and rotating the portions of the grassland that are grazed annually, might provide breeding habitat for the SandPiper.

Mowing as a management tool

Mowing can be substituted for burning, although the effects of the two management procedures will be different (Curtis and Partch 1949, Old 1969, Anderson 1976, Gibson and others 1993, Collin and others 1998). For example, both burning and mowing with removal of cut materials can stimulate biomass production. However, burning stimulates the flowering of the dominant grasses but early spring mowing and removal of biomass does not (Old 1969). Mowing can be used alone or following fire to reduce the competitiveness of woody species. The response of

C4 grasses and forbs to burning, mowing or a combination of the two can be different (Gibson, Seastedt, and Briggs 1993, Collins and others 1998).

Tallgrass prairie normally should not be mowed more than once a year. Two alternative mowing times would be acceptable: late summer or early fall (mid-September to early October) when most of the prairie plants are undergoing senescence or are dormant, or near the middle of the growing season (late-June to early July) so the prairie could regrow before the growing season ends. Biomass should be removed following mowing. Early spring mowing with removal of biomass should produce results similar to spring burns. If the biomass is removed during the growing season it could be used for hay. Late harvested prairie hay could be used for seeding prairie on restoration sites, especially if was “chopped” into smaller fragments. Relatively little research is available on mowing as a natural area management practice. However, if burning is not an option mowing may be the most feasible alternative management prescription.

CONCLUSIONS

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

The grasslands of the Prairie Division are of recent origin, and have been dependent upon human intervention, through fire management, at least since the end of the hypsithermal. Persistence of this ecosystem will require continued fire management or appropriate surrogate practices. The management should have goals that are holistic in their scope and 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 affects on this ecosystem should be included in management practices and goals.

ACKNOWLEDGEMENTS

Most of this information in this paper, exclusive of the information in the management section, is published in a review article in Journal of Torrey Botanical Society with the permission of the Editor-in-Chief of the Journal.

Figure Captions

See Power Point

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

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

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 (Modified from Corbett and Anderson 2001, 2006).

Community Type	Dry Sand	Gravel/Sand	Hill Prairie	Gravel/Dry
Mesic/Dry				
Wet/Wet				
Mesic				Dolomite
Dolomite				
Species				
<i>Schizachyrium scoparium</i> PD 3.6 \pm 0.4	16.9 \pm 1.5	17.3 \pm 2.9	15.4 \pm 0.7	11.6 \pm 1.4
<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 oligosanthes</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 3.6 \pm 0.4		5.4 \pm 2.0		
<i>Echinacea pallida</i> PM		3.1 \pm 2.0		3.4 \pm 0.6
<i>Lithospermum caroliniense</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 0.4				3.0 \pm 0.6
<i>Rosa caroliniana</i> 2.4 \pm 0.3				2.5 \pm 0.6
<i>Aster ericoides</i> PDM 3.6 \pm 0.4				2.3 \pm 0.6
<i>Andropogon gerardii</i> PM 5.0 \pm 0.5				
<i>Fragaria virginiana</i> ND 2.2 \pm 0.3				
<i>Carex</i> sp. 6.3 \pm 1.8				
<i>Solidago gigantea</i> PW 4.3 \pm 0.9				
<i>Pycnanthemum virginianum</i> PWM 3.7 \pm 0.8				
<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				

Helianthus grosseserratus PWM

2.7±1.1

Solidago riddellii FN

2.7±0.9

Literature Cited

- Abrams, M. D. and L. C. Hulbert. 1987. Effect of topographic position and fire on species composition in tallgrass prairie in northeast Kansas. *American Midland Naturalist*. 117:442-445.
- Adams, D., R. Anderson, and S. Collins. 1982. Differential response of woody and herbaceous species to summer and winter burning in an Oklahoma grassland. *Southwestern Naturalist*. 27:56-61.
- Ares, J. Dynamics of the root systems of blue grama. *Journal of Range Management*. 29:209-213.
- Albertson, F. W. and J. E. Weaver. 1945. Injury and death or recovery of trees in prairie climate. *Ecological Monographs*. 15:393-433.
- Anderson, R. C. 1970. Prairies in the prairie state. *Transaction of the Illinois State Academy of Science*. 63:214-221.
- Anderson, Roger C. 1972. Prairie history, management and restoration in southern Illinois. In: Zimmerman, J., ed. Madison, WI: Proceedings of the Second Midwest Prairie Conference: 15-21.
- Anderson, Roger C. 1972a. The use of fire as a management tool on the Curtis Prairie. Tallahassee, FL: Proceedings Annual Tall Timbers Fire Ecology Conference. No. 12.:23-25.
- Anderson, Roger C. 1976b. Role of fire in grassland management. In: J. Estes and R. Tylr., eds. The grasses and grasslands of Oklahoma. *Annals of the Oklahoma Academy of Science*. No. 6:27-44.
- Anderson, R.C. 1982. An evolutionary model summarizing the roles of fire, climate and grazing animals in the origin and maintenance of grasslands: An end paper. In: Estes J., Tylr, R., and Brunken, eds. Grasses and Grasslands: Systematics and Ecology. Norman, OK: University of Oklahoma Press: 297-308.
- Anderson, Roger C. 1983. The eastern prairie transition -- an overview. In: Brewer, R., ed. Proceedings 8th North American Prairie Conference. Kalamzoo, MI: Western Michigan University:86-92.
- Anderson, R. C., T. Leahy, and S. S. Dhillion. 1989. Numbers and biomass of selected insect groups on burned and unburned sand prairie. *American Midland Naturalist*. 122(1):151-162.
- Anderson, R. C. 1990b. The historic role of fire in the North American Grassland. In: Wallace, L. and Collins, S., eds. Fire in tallgrass prairie ecosystem. Norman, OK: University. of Oklahoma Press:8-18.
- Anderson, R. C. 1991a. Presettlement forest of Illinois. In: Burger, G. V., Ebinger, J. E., and Wilhelm, G. S., eds. Proceedings of the oak woods management workshop. Charleston, IL: Eastern Illinois University:9-19.
- Anderson, R. C. 1991b. Illinois prairies: a historical prospective. In: L. M. Page, L. M. and M. R. Jeffords., eds. Our living heritage. Illinois Natural History Survey. Champaign, IL: Survey Bulletin 34(4):384- 391.
- Anderson, Roger C. 1997. Response of the midwestern tallgrass prairies to summer burns. In: S. Packard, S and C. Mutel C., eds. *The Tallgrass Restoration Handbook*, Washington, D. C.: Island Press:245-249.
- Anderson, R. C. 1998. Overview of Midwestern Oak Savanna. *Transactions of the Wisconsin Academy of Sciences, Arts and Letters* 86:1-18.
- Anderson, Roger C. and Marlin L. Bowles. 1999. Deep-soil savannas and barrens of the Midwestern United States. In: Anderson, R., Fralish, J, and Baskin, J. eds., *Savannas, barrens, and rock outcrop plant communities of North America*. New York, NY: Cambridge University Press:155-170.
- Anderson, R. C., E. A. Corbett, M. R. Anderson, and others. 2001. High White-tailed Deer Density has Negative Impact on Tallgrass Prairie Forbs. *Journal of the Torrey Botanical, Society*. 128:381-392.
- Anderson, R. C., D. Nelson, M. R. Anderson, M. A. Rickey. 2005. White-tailed deer browsing effects on tallgrass prairie forbs: diversity and species abundances. *Natural Areas Journal*. 25:19-25.
- Anderson, R. C., Debora Nelson, M. Rebecca Anderson, and Marcia Rickey. 2006. White-tailed deer (*Odocoileus virginianus* Zimmermann) browsing effects on quality of tallgrass prairie community forbs. In: Egan, D. and J. Harrington, J. eds. Madison, WI: Proceedings of the 19th North American Prairie Conference: The Conservation Legacy Lives On:63-68.
- Amburg, G. L. van, J. A. Swaby, R. H. Pemble. 1981. Response of arthropods to a spring burn of a tallgrass prairie in northwestern Minnesota. In: Stuckey, R. L. and Reese, K. J., eds. *The prairie peninsula in the "shadow of Transeau: Proceeding of the sixth North American prairie conference*. Columbus, OH: Ohio Biological Survey Biological Notes No. 15. Ohio State University:240-243.
- Axelrod, D.I. 1985. Rise of the grassland biome, central North America. *Botanical Review*. 51:163-202.
- Baker, R. G., L. J. Maher, Jr., C. A. Chumbley, and K. L. Van Zant. 1992. Patterns of Holocene environmental change in the midwestern United States. *Quaternary Research*. 37:379-389.
- Baker, R. G., E. A. Bettis III, D. P. Schwert, D. G. Horton, C. A. Chumbley, L. A. Gonzalez, and M. K. Regan. 1996. Patterns of Holocene paleoenvironments of northeast Iowa *Ecological Monographs*. 66:203-234.
- Bartos, D. L. and D. A. Jameson. 1974. A dynamic root model. *The American Midland Naturalist*. 91(2):499-504.
- Belsky, A. J. 1986. Does herbivory benefit plants? A review of the evidence. *The American Naturalist*. 127(6):870-892.

- Benedict, A. B., P. W. Freeman, H. H. Genoway. 1996. Prairie Legacies-Mammals. In: Sampson and Knopf., eds. Prairie Conservation, Washington, D. C.:Island Press:149-166.
- Black, C. C. 1973. Photosynthetic carbon fixation in relation to net CO₂ uptake. Annual Review of Plant Physiology. 24:253-286.
- Borchert, J. R. 1950. The climate of the central North American Grassland. Annals of the Association of American Geographers. 40:1-29.
- Bragg, T.B. and Hulbert, L.C. 1976. Woody plant invasion of unburned Kansas bluestem prairie. Journal of Range Management 29: 19-29.
- Bragg, T. B. 1995. The physical environment of Great Plains Grassland. In: A. Joem, A. and K. Keeler, K. eds. The changing prairie North America grassland. New York, NY: Oxford University Press:49-81.
- Britton, W. and A. Messenger. 1969. Computed soil moisture patters in and around the prairie peninsula during the great drought of 1933-34. Transactions of the Illinois State Academy of Science. 62:181-187.
- Briske, D.D. and A.M. Wilson. 1978. Moisture and temperature requirements for adventitious root development in blue grama seedlings. J. Range Manage. 31: 174-178.
- Brown, C. T. 1967. Growth and energy relationships on burned and unburned prairie in southern Wisconsin. Madison, WI: University of Wisconsin, Madison. 51p. M.S. Thesis.
- Bryson, R. A. and F. K. Hare (eds.) 1974. World Survey of Climatology. Vol. 11. New York: Climates of North America. Elsevier.420 p.
- Cerling, T. E., J. M. Harris, B. J. MacFadden, Meave G. Leakey, and others . 1997. Global vegetation change through the Miocene/Pliocene boundary. Nature. 389:153-158.
- Collins, S.L., S.M. Glenn, and D.J. Gibson. 1995. Experimental analysis of intermediate disturbance and initial floristic composition: Decoupling cause and effect. Ecology. 76:486-492.
- Collins, S., A. Knapp, J. Briggs, and E. Steinauer. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. Science 280:745-747.
- Connell, J.H. 1978. Diversity in tropical rainforests and coral reefs. Science 199:1302-1310.
- Copeland, T. E., W. Sluis, and H. F. Howe. 2003. Fire season and dominance in an Illinois tallgrass prairie restoration. Restoration Ecology10:315-323.
- Corbett, E. A. and Roger C. Anderson. 2006. Landscape analysis of Illinois and Wisconsin remnant prairies. The Journal of the Torrey Botanical Society. 133:267-279.
- Curtis, J. T. and M. L. Partch. 1948. Effect of fire on the competition between blue grass and certain prairie plants. American Midland Naturalist 39(2):437-443.
- Curtis, J.T. and M.L. Partch. 1950. Some factors affecting flower production in *Andropogon gerardi*. Ecology. 31(3):488-489.
- Curtis, J. T. 1971. The Vegetation of Wisconsin. Madison, WI: University of Wisconsin Press.657 p.
- Dahlman, R. C. and C. L. Kucera. 1965. Root productivity and turnover in native prairie. Ecology. 46:(1/2)84-89.
- Damhoureyeh, S. A., and D. C. Hartnett. 1997. Effects of bison and cattle on growth, reproduction, and abundances of five tallgrass prairie forbs. American Journal of Botany. 84:1719-1728.
- Delourt, P. and H. A. Delcourt. 1981. Vegetation maps for eastern North America: 40,000 BP to present. In: Roman, R., Geobotany II. New YK. Plenum:123-165.
- Devoto, B. 1963, The journals of Lewis and Clark. Boston, MA: Houghton Mifflin.504p.
- Dhillion, S. S. and R. C. Anderson. 1994. Production on burned and unburned sand prairies during drought and non-drought years. Vegetatio. 115:51-59.
- Diamond, D. D. and F. E. Smeins. 1988. Gradient analysis of remnant True and Coastal Prairie grasslands of North America. Canadian Journal of Botany. 66: 2152-2161.
- Dix, R. L. and J. E. Butler. 1954. The effects of fire on a dry, thin soil prairie in Wisconsin. Journal of Range management. 7:265-268.
- Dyer, M. I., J. K. Deltung, D. C. Coleman, and D. W. Hilbert. 1982. The role of herbivores in grasslands. In: Estes, J., Tyrl, R and Brunken, J., eds. Grasses and Grasslands: Systematics and Ecology. Norman, OK: University of Oklahoma Press:255-295.
- Ehleringer, J. R. 1978. Implications of quantum yield differences to the distribution of C3 and C4 grasses. Oecologia. 31:255-267.
- Ehleringer, J. R. T. E. Cerling, and B. R. Helliker. 1997. C4 photosynthesis, atmospheric CO₂, and climate. Oecologica. 112:285-299.
- Ehleringer, J. A., Cerling, T. E. and M. D. Dearing 2002. Atmospheric CO₂ as global change driver influencing plant-animal interactions. Integrative and Comprehensive Biology. 42:424-430.

- Ehrenreich, J. H. 1959. Effect of burning and clipping on growth of native prairie in Iowa. *Journal Range Management* 12:133-137.
- Evans, E. W. 1984. Fire as a natural disturbance to grasshopper assemblages of tallgrass prairie. *Oikos* 43:9-16.
- Evans, E. W. 1988. Grasshopper (Insects: Orthoptera: Acrididae) assemblages of tallgrass prairie; influences of fire frequency, topography, and vegetation. *Canadian Journal of Zoology*. 66: 1495-1501.
- Evers, R. A. 1955. Hill prairies of Illinois. *Bulletin of the Illinois Natural History Survey*. 26: 367-466.
- Ewing, A. L. and D. M. Engle. 1988. Effects of late summer fires on tallgrass prairie microclimate and community composition. *American Midland Naturalist*. 120(1):212-223.
- Fahnestock, J.T., and A.K. Knapp. 1993. Water relations and growth of tallgrass prairie forbs in response to selective herbivory by bison. *International Journal of Plant Science*. 154:432-440.
- Fahnestock, J.T., and A.K. Knapp. 1994. Plant responses to selective grazing by bison - interactions between light, herbivory and water stress. *Vegetation*. 115(2): 123-131.
- Fehrenbacher, J. B., G. O. Walker, and H. L. Wascher. 1967. Soils of Illinois. Bulletin 725 of the College of Agriculture of the University of Illinois at Urbana-Champaign, Agricultural Experiment Station, in Association with the Soil Conservation Service of the United States Department of Agriculture.
- Flores, D. 1996. A long love affair with an uncommon country: environmental history and the Great Plains. In: Samson, F. and Knopf, F., eds. *Prairie Conservation: preserving North America's most endangered ecosystem*. Washington, D. C., Island Press:3-17.
- Frank, D. A., S. J. McNaughton, and B. F. Tracy. 1998. The ecology of the earth's grazing ecosystems. *BioScience*. 48(7):513-512.
- Fuhlendorf, S. D. and D. M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. *BioScience*. 51(8):625-632.
- Gibson, D. J., D. C. Hartnett, and G. L. S. Merrill. 1990. Fire temperature heterogeneity in contrasting fire prone habitats: Kansas tallgrass prairie and Florida sandhill. *Bulletin of the Torrey Botanical Club*. 117(4):349-356.
- Gibson, D. and S. Collins. 1990. Effect of fire on community structure in tallgrass and mixed-grass prairie. In: Collins, S. and Wallace, L., eds.. *Fire in North American tallgrass prairie*. Norman, OK: University of Oklahoma Press:81-98.
- Gibson, D. J., T. R. Seastedt, and J. M. Briggs. 1993. Management practices in tallgrass prairie: large and small-scale experimental effects on species composition. *Journal of Applied Ecology*. 30:247-255.
- Gilliam F.S, T. R Seastedt, and A.K Knapp. 1987. Canopy rainfall interception and throughfall in burned and unburned tallgrass prairie. *The Southwestern Naturalist*. 32:267-271
- Gleason, H. A. 1913. The relation of forest distribution and prairie fires in the middle west. *Torreya*.13:173-181.
- Gleason, H. A. 1922. Vegetational history of the Middlewest. *Annals of the American Association of Geographers*. 12:39-86.
- Golley, P. M. and F. B. Golley, editors. 1972. *Papers from a symposium on tropical ecology with emphasis on organic productivity*. Athens Ga.: Institute of Ecology, University of Georgia.
- Grimm, E. 1984. Fire and other factors controlling the Big Woods vegetation of Minnesota in the mid-nineteenth century. *Ecological Monographs* 54:291-311.
- Hadley, E. B. and B. J. Kieckhefer. 1963. Productivity of two prairie grasses in relation to fire frequency. *Ecology* 44 (2):389-395.
- Hartnett, D. C. and P. A. Fay. 1998. Plant populations; patterns and processes. In: Knapp, A. K. Knapp, Briggs, J. M., Hartnett, D. C and Collins, S. L., eds. *Grassland Dynamics: long-term ecological research in tallgrass prairie*. New York, NY: Oxford University Press:81-100.
- Hartnett, D. C., K. R. Hickman, and L. E. F. Walter. 1996. Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. *Journal of Range Management*. 49: 413-420.
- Heirman, A. L. and H. A. Wright. 1973. Fire in medium fuels of west Texas. *Journal of Range Management*. 26:331-335.
- Heisler, J. L., J. M. Briggs, and A. K. Knapp. 2003. Long-term pattern of shrub expansion in a C4- dominated grassland: fire frequency and the dynamics of shrub cover and abundance. *American Journal of Botany*. 90:423-423.
- Helzer, C. J. and A. A. Steuter. 2005. Preliminary effects of patch-burn grazing on a high diversity prairie restoration. *Ecological Restoration*. 23(3):167-171.
- Herkert, J. R., R. E. Szafoni, V. M. Kleen, and J. E. Schwegman. 1992. *Habitat establishment, enhancement and management for forest and grassland birds in Illinois*. Division of Natural Heritage, Illinois Department of Conservation, Springfield, Illinois. Natural Heritage Technical Publication #1.

- Hopkins, H. F., F. W. Albertson, and A. Riegel. 1948. Some effects of burning upon a prairie in west-central Kansas. *Transactions of Kansas State Academy of Science*. 51:131-141.
- Howe, H. F. 1994a. Managing species diversity in tallgrass prairie: assumptions and implications. *Conservation Biology*. 8:691-704.
- Howe, H. F. 1994b. Response of early- and late-flowering plants to fire season in experimental prairies. *Ecological Applications*. 4:121-133.
- Howe, H. F. 1995. Succession and fire season n experimental prairie plantings. *Ecology*. (6):1917-1925.
- Hulbert, L. C. 1969. Fire and litter effects in undisturbed bluestem prairie in Kansas. *Ecology*. 50(5):874-877.
- Joern, A. 2005. Disturbance by fire frequency and bison grazing modulate grasshopper assemblages in tallgrass prairie. *Ecology*. 86:861-873
- Kaufman, D. W., E. J. Finck, and G. A. Kaufman. 1990. Small mammals and grasslands fires. L. Wallace, L. and S. Collins, S., eds. *Fire in tallgrass prairie ecosystem*. Norman, OK: University of Oklahoma Press:46-80..
- Kebart, Karen K. and Roger C. Anderson. 1987. Phenological and climatic patterns in three tallgrass prairies. *Southwestern Naturalist*. 39:29-37.
- Keeley, J. E. and P. W. Rundel. 2005. Fire and the Miocene expansion of C4 grasslands. *Ecology Letters*. 8:683-690.
- Kellogg, E. A. 1999. Phylogenetic aspects of the evolution of C4 photosynthesis. In: Sage, R. F. and Monson, R. K., ed. *C4 Plant Biology*. Diego, CA: Academic Press:411-414.
- King, J. 1981. Late quaternary vegetational history of Illinois. *Ecological Monographs*. 51:43-62.
- Knapp, A. K. 1984. Post-burn differences in solar radiation, leaf temperature and water stress influencing production in a lowland prairie. *American Journal of Botany*. 71:220-227.
- Knapp, A. K. 1985. Effect of fire and drought on the ecophysiology of *Andropogon gerardii* and *Panicum virgatum* in a tallgrass prairie. *Ecology*. 66:1309-1320.
- Knapp, A. K. and F. S. Gilliam. 1985. Response of *Andropogon gerardii* (Poaceae) to fire-induced high vs. low irradiance environments in tallgrass prairie: leaf structure and photosynthetic pigments. *American Journal of Botany* 72(11):1668-1671.
- Knapp, A. K. and T. R. Seastedt. 1986. Detritus accumulation limits productivity of tallgrass prairie. *BioScience*. 36(10):662-668.
- Knapp, A., J. Blair, J. Briggs, S. Collins, D. Hartnett, L. Johnson, and E. Towne. 1999. The keystone role of bison in North American tallgrass prairie. *BioScience* 49(1):39-50.
- Knopf, F. L. 1996. Prairie legacies-birds. In: Sampson, F. B. Knopf, F. L. Knopf., eds., *Prairie Conservation*, Washington, D. C.: Island Press, California: 135-148.
- Kucera, C. L. and J. H. Ehrenreich. 1962. Some effects of burning on central Missouri prairie. *Ecology*. 43:334-336.
- Kucera, C. L. and M. Koelling. 1964. The influence of fire on composition of central Missouri prairie. *American Midland Naturalist*. 72:142-147.
- Launchbaugh, J. L. 1972. Effect of fire on short and mixed prairie species. Tallahassee, FL: Proceedings of the Tall Timbers Fire Ecology Conference. No 12:129-151.
- Leach, M. K. and T. J. Gvinish. 1996. Ecological determinant of species loss in remnant prairies. *Science*. 273:1555-1558.
- Leach, M. K., R. A. Henderson, and T. J. Gvinish. 1999. A caution against grazing. *BioScience*. 49(8):599-600.
- Lussenhop, J. 1976. Soil arthropod response to prairie burning. *Ecology*. 57(1):88-98.
- Matlack, R. S., D. W. Kaufman, G. A. Kaufman. 2001. Influence of grazing by bison and cattle on deer mice in burned tallgrass prairie. *American Midland Naturalist*. 146(2):361-368.
- McClain, W. E. and S. L. Elzinga. 1994. The occurrence of prairie and forest fires in Illinois and other Midwestern states, 1679-1853. *Erigenia*. 13:79-90.
- McMurphy, W. E. and K.L. Anderson. 1965. Burning flint Hills range. *Journal of Range Management*. 18:265-269.
- McNaughton, S. J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. *The American Naturalist*. 113:691-703.
- McNaughton, S. J, M. B. Coughenour, and L. L. Wallace. 1982. Interactive processes in grassland ecosystems. In: L. Wallace, L. and S. Collins, S. eds., *Fire in tallgrass prairie ecosystem*. Norman, OK: University of Oklahoma Press:167-193.
- McNaughton, S. J. 1993. Grasses and grazers, science and management. *Ecological Applications*. 3:17-20.
- McNaughton, S. J., R. Ruess, and S. Seagle. 1988. Large mammals and process dynamics in African ecosystems. *Bioscience*. 38:794-800.

- Mengel, R. M. 1970. The North American Central Plains as an isolating agent in bird specialization. In: Dort, Jr. W. and Jones, J. K. Jr. eds. Pleistocene and Recent Environments of the Central Great Plains. Lawrence, KA: University of Kansas Press: 279-340
- Monson, R. K., M. A. Stidham, G. J. Williams III, and others . 1982. Temperature dependence of photosynthesis in *Agropyron smithii* Rydb. Plant Physiology. 69:921-928.
- Nelson, D. C., and R. C. Anderson. 1983. Factors influencing the distribution of prairie plants along a moisture gradient. American Midland Naturalist. 109:367-375.
- Nelson, E. N. 1916. The prairie peninsula. Ecology. 16(3):423-437.
- Oesterheld, M., J. Loreti, M. Semmartin, and J. M. Paruelo. 1999. Grazing, fire, and climate effects on primary productivity of grasslands and savanna. In: L. R. Walker, L. R. (ed.), Ecosystems of the World 16 Ecosystems of Disturbed Ground. , New York, NY: Elsevier.:287-306.
- Ojima, D. S., W. J. Parton, D. S. Schimel, and C. E. Owensby. 1990. Simulated impacts of annual burning on prairie ecosystems. Fire in tallgrass prairie ecosystem. Norman, OK: University of Oklahoma Press: 118-132 167-193.
- Old, S. 1969. Microclimate, fire and plant production in an Illinois prairie. Ecological Monographs. 39(4):355-384.
- Owen, D. F. 1981. Mutualism between grasses and grazers: an evolutionary hypothesis. Oikos. 36:376-378.
- Owensby, C. E. and K. L. Anderson. 1967. Yield response to time of burning in the Kansas Flint Hills. Journal of Range Management. 20:12-16.
- Owensby, C. E. and E. F. Smith. 1972. Burning the true prairie. In: Hurlbert, L. C., ed.: Third Prairie Conference Proceedings. Manhattan, KA: Kansas State University:1-14.
- Packard, S. and C. F. Mutel. 1997. The tallgrass restoration handbook., Washington, D. C: Island Press.
- Painter, E. and A. J. Belsky. 1993. Application of herbivore optimization to rangelands of the western United States. Ecological Applications. 3:2-9.
- Panzer, R. 1988. Managing prairie remnants for insect conservation. Natural Areas Journal. 8(2):83-90.
- Panzer, R. 2003. Importance of in situ survival, recolonization, and habitats gaps in the postfire recovery of fire-sensitive prairie insects. Natural Areas Journal. 23 (1):14-21.
- Panzer, R. and M. Schwartz. 2000. Effects of management burning on prairie insect species richness with a systems of small, highly fragmented reserves. Biological Conservation. 96:363-369.
- Peet, M., R. Anderson, and M. S. Adams. 1975. Effect of fire on big bluestem production. American Midland Naturalist. 94:15-26.
- Pfeiffer, K. E. and A. A. Steuter. 1994. Preliminary response of Sandhills prairie to fire and bison grazing. Journal of Range Management. 47: 395-397
- Pfeiffer, K. E. and D. C. Hartnett. 1995. Bison selectivity and grazing response of little bluestem in tallgrass prairie. Journal of Range Management. 48: 26-31
- Plumb, G. E. and J. L. Dodd. 1993. Foraging ecology of bison and cattle and a mixed prairie: implications for natural area management. Ecological Applications. 3(4):631-643.
- Pyle, R. M. Burning Bridges. Wings. 20:22-23.
- Pyne, S. J. 1983. Indian fires. Natural History. 2:6-11.
- Pyne, S. 1997. Fire in America: A cultural history of wildland and rural fire. Seattle, WA: University of Washington Press.
- Pyne, S. J. 2001. The fires, this time and next. Science. 294(5544):1005-1006.
- Rice, E. I. and R. L. Parenti. 1978. Causes of decreases in productivity in undisturbed tall grass prairie. American Journal of Botany. 65:1091-1097.
- Riechert, S. E. and W. C. Reeder. 1972. Effect of fire on spider distribution in southwestern Wisconsin prairies. In: Zimmerman, J., ed. Madison, WI: Proceedings of the Second Midwest Prairie Conference: 73-90.
- Risser, P.G., E. C. Birney, H. D. Blocker, S. W. May, J. F. Parton, and J. A. Weins. 1981. The True Prairie Ecosystem., Stroudsburg, PA: Hutchinson-Ross Publishing Company.
- Robertson, K. R., R. C. Anderson, and M. Schwartz. 1997. The tallgrass prairie mosaic. pp. 55-87. In Mark Schwartz (ed.), Conservation in highly fragmented landscapes., New York, NY: Chapman and Hall, New York.
- Ross, H. H. 1970. The ecological history of the Great Plains: evidence from grassland insects. In: Dort, W. and Jones, D. K. Jr., eds. Pleistocene and recent environments of the central Great Plains., Lawrence, KA: Special Publication of the University of Kansas Department of Geology. 3:225-240.
- Sage, R. f. and A. D. McKown. 2006. Is C4 photosynthesis less phenotypically plastic than C3 photosynthesis? Journal of Experimental Botany 57(2):303-317.
- Sala, O. E., W. Parton, L. A. Joyce, and W. K. Lauenroth. 1988. Primary production of the central grassland region of the United States. Ecology. 69(1):40-45.

- Sankaran, M., J. Ratnam, and N. P. Hanan. 2004. Tree grass coexistence in savannas revisited-insight from an examination of assumptions and mechanisms invoked in existing models, *Ecology Letters*. 7:480-490.
- Saur, C. 1950. Grassland climax, fire and man. *Journal of Range Management*. 3:16-20.
- Schlicht, D. W. and T. T. Orwig. 1992. Sequential use of niche by prairie obligate skipper butterflies (Lepidoptera: Hesperiiidae) with implications for management. In: Smith, D and Jacob, C. A., eds. *Proceedings of the twelfth North American Prairie Conference: Recapturing a vanishing heritage*, Cedar Falls, Iowa: University of Northern Iowa:137-139.
- Schimper, AFW. 1903. *Plant Geography on a Physiological Basis*. Clarendon, UK: Oxford University Press.
- Scholes, R. J. and S. R. Archer. 1997. Tree-grass interactions in savannas. *Annual Reviews in Ecology and Systematics*. 28:517-544.
- Schramm, P. 1970. Effects of fire on small mammal populations in a restored tall-grass prairie. In: Schramm, P., ed. *Proceedings of a Symposium on Prairie and Prairie restoration*. Galesburg, IL: Knox College:39-41.
- Schramm, P. and B. J. Willcutts. 1983. Habitat selection of small mammals in burned and unburned tallgrass prairie. In: Brewer, R. ed. *Proceeding of Eight North American Prairie Conference*. Kalamazoo, MI: Western Michigan University:49-55.
- Seastedt, T. R. 1984. Belowground macroarthropods of annually burned and unburned tallgrass prairie. *American Midland Naturalist*. 111(2):405-408.
- Seastedt, T. T. 1988. Mass, nitrogen, and phosphorus dynamics in foliage and root detritus of tallgrass prairie. *Ecology*. 69(1):59-65.
- Solecki, M. K. 1997. Controlling invasive plants. In: Packard, S. and Mutel, C., ed., The Tallgrass Restoration Handbook, Washington, D. C.: Island Press:251-278.
- Stebbins, G. L. 1981. Coevolution of grasses and herbivores. *Annals of the Missouri Botanical Garden*. 68:75-86.
- Steuter, A. A. 1997. Bison. In: Packard, S and Mutel, C. eds. *The Tallgrass Restoration Handbook*, Washington, D. C.: Island Press:339-347.
- Stewart, O. C. 1956. Fire as the first great force employed by man. In: Thomas, W. L., ed. *Man's role in changing the face of the earth*. Chicago, IL: University of Chicago Press:115-133.
- Svejcar, T. J. 1990. Response of *Andropogon gerardii* to fire in the tallgrass prairie., In: Collin, S and L. Wallace, L., eds. *Fire in north American tallgrass prairie*, Norman, OK: University of Oklahoma Press:19-27.
- Swengel, A. B. effects of management on butterfly abundance in tallgrass prairie and pine barrens. *Biological Conservation*. 83(1):77-89.
- Tainton, N. M. and M. T. Mentis. 1984. Fire in grassland. In: P. de Van Booyeb, P and N. Tainton, N., eds. *Ecological Effects of fire in South African ecosystems*. New York, NY: Springer-Verlag:117-147.
- Terri, J. A. and L. G. Stowe. 1976. Climatic patterns and the distribution of C4 grasses in North America. *Oecologia*. 23: 1-12.
- Towne, E. G., David C. Hartnett, and R. C. Cochran. 2005. Vegetation trends in tallgrass prairie from bison and cattle grazing. *Ecological Applications*. 15 (5):1550-1559.
- Transeau, E. N. 1935. The prairie peninsula. *Ecology*. 16(3):423-427.
- Umbanhowar, C. E., JR. 1992. Reanalysis of the Wisconsin prairie continuum. *American Midland Naturalist*. 127: 268-275.
- Vinton, M. A., D. C. Hartnett, E. J. Finck, and J. M. Briggs. 1993. Interactive effects of fire, bison (*Bison bison*) grazing and plant community composition in tallgrass prairie. *American Midland Naturalist*. 129(1):10-18.
- Vogl, R. 1974. Effect of fire on grasslands. In: Kozlowski, T. T. and Ahlgren., eds. *Fire and Ecosystems*. New York, NY: Academic Press:139-194.
- Walter, H. 1971. *Ecology of Tropical and Subtropical Vegetation*. Edinburgh, UK: Oliver and Boyd.
- Weaver, J. E. 1954. *The North American Prairie*. Lincoln, NE: University of Nebraska Press.
- Weaver, J. E. 1968. *Prairie plants and their environment*. Lincoln, NE: University of Nebraska Press.
- Weaver, J. E. and H. W. Roland. 1952. Effects of excessive natural mulch on development, yield, and structure of native grassland. *Botanical Gazette*. 114:1-9.
- Well, P. V. 1970a. Historical factors controlling vegetational patterns and floristic distribution in the Central Plains Region of North America. In: Dort, W. and Jones, J., eds. *Pleistocene and recent environments the Central Great plains*. Special publication 3. Lawrence, KA: University of Kansas Press:211-221.
- Wells, P. V. 1970b. Postglacial history of the Great Plains. *Science*. 167:1,574-1,582.
- Warren, S. D., C.J. Scifres, and P. D. Tell. 1987. Response of grassland arthropods to burning : a review. *Agriculture, Ecosystems and Environment*. 19:105-130.
- Winkler, M. G. 1995. Sensing plant community and climate change by charcoal-carbon isotope analysis. *Ecoscience*. 1:340-345.

- Winkler, M. G. 1997. Later quaternary climate, fire, and vegetation dynamics. In: Clark, J., Cachier, H. and Goldammer, J and Stocks, B., eds. Sediment records of biomass burning and global change., Berlin: Springer-Verlag:329-346.
- Winkler, M. g. , A. M. Swain, and J. E. Kutzbach. 1986. Middle Holocene dry period in the northern Midwestern United States: lake levels and pollen stratigraphy. *Quaternary Research*. 25:235-250.
- Wright, H. A. Effects of spring burning on tobosa grass. *Journal of Range Management*. 22:425-427.
- Wright, H. A. 1973. Range burning. *Journal of Range Management*. 27:5-11.
- Wright, H. A. 1972. Fire as a tool to manage tobosa grasslands., Tallahassee, FL: Proceeding of the Tall Timbers Fire Ecology Conference 12:153-157.
- Wright, H. A. and S. C. Bunting. 1975. Mortality of honey mesquite seedlings after burning. *Noxious Brush and Weed Control Highlights* 6:39. Lubbock, TX: Texas Technical University, Texas Department of Agriculture.
- Zedler, J. and O. L. Loucks. 1969. Differential burning response of *Poa pratensis* and *Andropogon scoparius* prairies in central Wisconsin. *American Midland Naturalist* 81:341-352.
- Zink, E. and J. E. Weaver. 1946. Annual increase in underground materials in three range grasses. *Ecology*. 27(2):115-127.