SOIL-DEPENDENT FIRE FREQUENCY: A NEW HYPOTHESIS FOR THE DISTRIBUTION OF PRAIRIES AND OAK WOODLANDS/SAVANNAS IN NORTH CENTRAL AND EAST TEXAS

George M. Diggs, Jr.

Department of Biology &
Center for Environmental Studies
Austin College
Sherman, TX 75090, U.S.A.
and
Botanical Research Institute of Texas
Fort Worth, TX 76102-4060
gdiggs@austincollege.edu

Peter C. Schulze

Department of Biology &
Center for Environmental Studies
Austin College
Sherman, TX 75090, U.S.A.
pschulze@austincollege.edu

ABSTRACT

The distinctive historical vegetation pattern of alternating tallgrass prairies on clay soils and oak woodlands/savannas on sandy soils in North Central Texas and East Texas has been described for more than a century. Many authors have attributed this pattern to relatively high levels of soil moisture available for tree growth on areas of sandy soil, and conversely, inadequate levels of soil moisture for tree growth on clay soils. However, this explanation is not consistent with present day observations of rapid invasion of clay soils by woody vegetation. We propose an alternative hypothesis, that the historical distribution of prairies and woodlands in North Central and East Texas can be explained by soil-dependent variations in grass biomass and resulting differences in fire frequency and intensity.

RESUMEN

El patrón histórico de vegetación en el que alternan praderas con hierbas altas en suelos calcáreos y robledales /sabana en suelos arenosos en el centro-norte y este de Texas ha sido descrito durante más de un siglo. Muchos autores han atribuido este patrón a los niveles relativamente altos de humedad en el suelo disponible para el crecimiento de los árboles en áreas de suelo arenoso, y por el contrario, niveles inadecuados de humedad en el suelo para el crecimiento de árboles en suelos calcáreos. Sin embargo, esta explicación no es consistente con las observaciones actuales de invasión rápida de suelos calcáreos por vegetación arbórea. Proponemos una hipótesis alternativa, que la distribución histórica de las praderas y bosques en el centro-norte y este de Texas puede ser explicada por las variaciones dependientes del suelo en la biomasa de las gramíneas y las diferencias resultantes en la frecuencia e intensidad del fuego.

INTRODUCTION

Conditions at the time of European Settlement, Approximately 1800 A.D.

The vegetation of North Central and East Texas at the time of European settlement (hereafter referred to as presettlement vegetation) was characterized by well-defined zones of tallgrass prairie and oak woodlands/savannas (Fig. 1).

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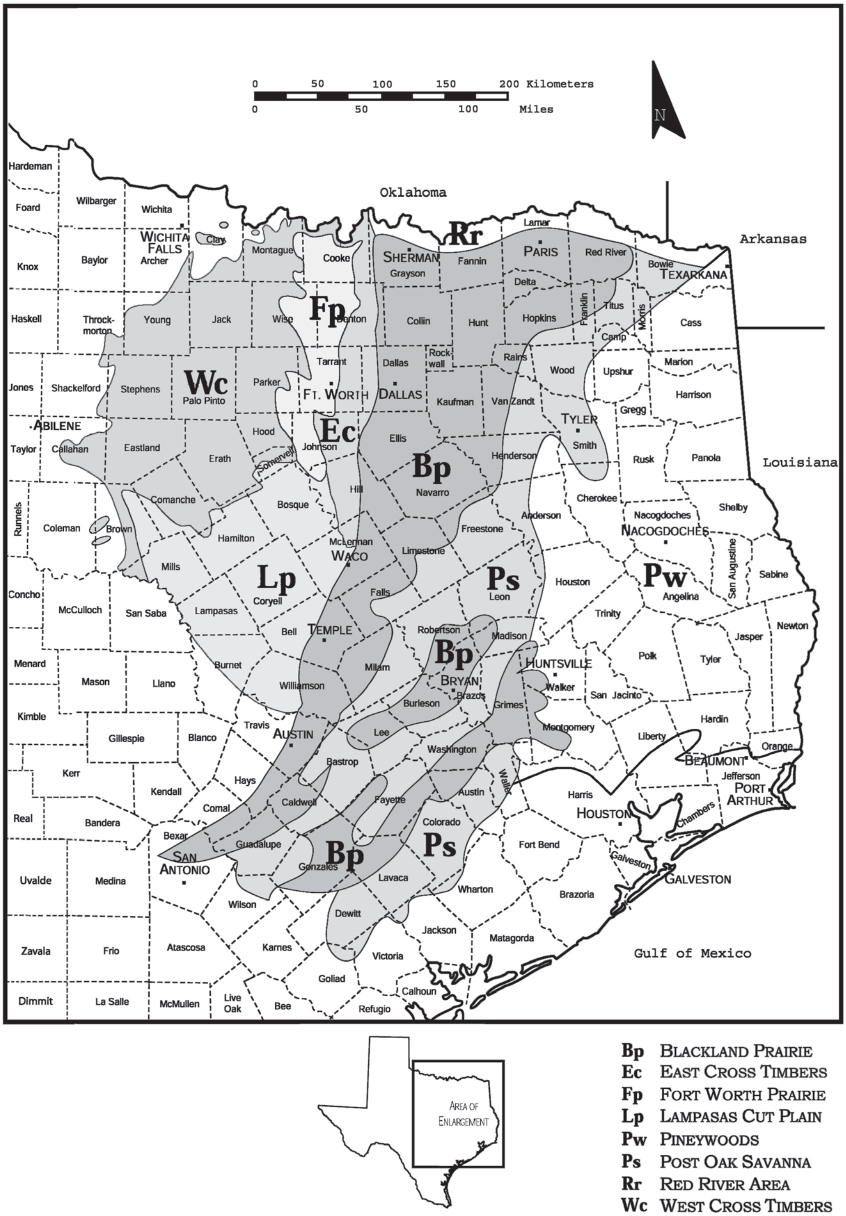

Fig. 1. Vegetational areas of North Central and East Texas. The Prairies are in shades of blue while the Woodlands/Savannas are in shades of green. Two vegetational areas of North Central and East Texas are not shown in color—the Pineywoods (forest) and the Red River Area (somewhat transitional between the Pineywoods and the Post Oak Savanna).

From west to east, the prairie bands are the Grand Prairie (composed of the Fort Worth Prairie and the Lampasas Cut Plain), the main belt of the Blackland Prairie, the San Antonio Prairie, and the Fayette Prairie, whereas the oak woodland/savanna belts are the West Cross Timbers, the East Cross Timbers, and three bands of Post Oak Savanna. These were highly recognizable areas of vegetation, with the Cross Timbers appearing on the earliest maps and the presettlement prairies described by numerous explorers, early settlers, and researchers as almost devoid of trees (e.g. Gregg 1844; Brooke 1849; Parker 1856; Dyksterhuis 1946; Thomas 1962; Correll & Johnston 1970; Hatch et al. 1990; Diggs et al. 1999; Telfair 1999; Francaviglia 2000). Hereafter we refer to these two vegetation types as Prairies and Woodlands. The current climate of the region, presumably relatively unchanged since presettlement times, is characterized by wet springs, dry summers with occasional thunderstorms, moderate to strong winds, and periodic multi-year droughts. As in many areas of central North America, prairie fires were common prior to settlement (Stewart 1951; Komarek 1965, 1966; Wells 1970; Wright and Bailey 1982; Collins & Wallace 1990; Bragg 1995). The relative frequency of ignition by lightning versus Native Americans is unclear.

The Woodlands represent the westernmost extension of the eastern deciduous forest. In general, the vegetation was composed of an oak overstory with tall grasses. The grasses were dominated by *Schizachyrium scoparium* (little bluestem), with *Andropogon gerardii* (big bluestem) and *Sorghastrum nutans* (Indian grass) as lesser dominants. While varying locally, the woody vegetation was in general dominated by two trees, *Quercus stellata* (post oak) and *Quercus marilandica* (blackjack oak). The tree density of the oak woodlands was variable, ranging from quite open to dense thickets. Some early accounts described woodlands through which wagons could easily pass (e.g. Marcy 1853, 1866), while others described almost impenetrable thickets (e.g. Kendall 1845). Gregg (1844) observed a variety of tree densities, noting that, "Most of the timber appears to be kept small by the continual inroads of the 'burning prairies;' for, being killed almost annually, it is constantly replaced by scions of undergrowth; so that it becomes more and more dense every reproduction. In some places, however, the oaks are of considerable size, and able to withstand the conflagrations."

The presettlement Prairies were vast grasslands dominated by *Schizachyrium scoparium* (little bluestem), with *Andropogon gerardii* (big bluestem) and *Sorghastrum nutans* (Indian grass) as lesser dominants, and woody vegetation generally limited to areas along the larger watercourses, as scattered mottes, or associated with locations that were protected from fire, such as mesas and buttes (Smythe 1852; Parker 1856; Hill 1901; Diggs et al. 1999). For example, Hill (1887) described the Grand Prairie as "a prairie region, utterly destitute of timber" and Kendall (1845) wrote, also of the Grand Prairie, "As far as the eye could reach … , nothing could be seen but a succession of smooth, gently-undulating prairies." Early accounts of the Blackland Prairie were similar. Smythe (1852) described the eastern edge of the Blackland Prairie as having "... a view of almost boundless Prairie stretching to the north, as far as the eye could reach. ..." and further, as "nearly destitute of trees."

Soils of North Central and East Texas

Most soils of the Prairies of North Central and East Texas are derived from lime-rich Upper Cretaceous rocks which weather to form soils with substantial levels of clay. Outlying segments of the Blackland Prairie (Fayette and San Antonio prairies) have soils developed from younger Tertiary age deposits. While the majority of Tertiary deposits in East Texas are sandy in nature (i.e., those supporting the Pineywoods and Post Oak Savanna), those underlying Prairie (e.g., Fleming, Oakville Sandstone, and Cook Mountain formations) in general have a relatively high clay content and in some cases develop soils which display the gilgai microtopography so typical of certain high clay soils (Launchbaugh 1955; Smeins & Diamond 1983; Miller & Smeins 1988). Further, where clay lenses are found in other geologic strata outcropping in isolated pockets of the Cross Timbers, Post Oak Savanna, and Pineywoods, areas of prairie vegetation can again be found (Dyksterhuis 1948; Hill 1991). It is thus clay that appears crucial in the development and maintenance of the grassland vegetation characteristic of the Prairies. In some cases clay is abundant throughout all soil horizons, while in others there is a clay-loam or loam surface layer—all the Prairie soils, however, have significant amounts of clay (Godfrey et al. 1973; Diamond & Smeins 1985). Conversely, the Woodlands are developed in general from Cretaceous and Tertiary sandstone rocks of such geologic layers as the Antlers/Trinity, Woodbine, Carrizo, and Wilcox, and can be generally described as sandy (Sellards et al. 1932; Hartmann & Scranton 1992).

Prevailing Explanation for the Distribution of Prairies and Woodlands

As discussed above, the presettlement distribution of the Prairies corresponds to the distribution of limestone parent material overlain by alkaline soils with a high clay content, while the presettlement Woodlands occurred on either sandy, slightly acidic soils or, in the westernmost part of the region, on gravelly and rocky substrates (Sellards et al. 1932; Dyksterhuis 1948; Diggs et al. 1999). The striking correspondence of vegetation and soil types led early writers to propose that the distribution of Prairies and Woodlands was due to the different water holding capacities of clays and sands. While the basic hypothesis has been stated many ways, its essence is that greater infiltration and water storage at depth in sandy soils permits tree survival, while clay soils do not support trees because of inadequate infiltration of water (and reduced root penetration) due to the clay's relative impermeability.

Hill (1887) appears to have been the first to propose this hypothesis. He argued that,

> "The reason why the timber confines itself to [the sandy soils is that they] … afford a suitable matrix for the penetration of the roots of trees, and a constant reservoir for moisture, thus furnishing two of the greatest essentials to forest growth. … The barrenness of the prairies, so far as forest growth is concerned, is owing to the absence of the requisite structural conditions for preservation of moisture, as well as the excess of carbonate of lime in their soils."

Subsequent authors reiterated Hill's contention. For example, Tharp (1926) suggested that the sandy soils increased available soil moisture for tree growth. Weaver and Clements (1938) argued that, "… the oaks … have been able to maintain themselves against the competition of the grasses by virtue of the favorable chresard of the sandy soil." Dyksterhuis (1948) summarized much of this information, and apparently agreed with the general idea of sandy soil-moisture availability favoring the growth of trees. Allred and Mitchell (1955) reiterated these ideas:

> "Sandy, gravelly and rocky areas … also improve local soil-moisture conditions in the grassland formation. Rainfall intake is high on these soils, which also yield up moisture to plants more readily and more completely than do heavier soils. … In these areas, soil-moisture conditions have been improved sufficiently over the climatic normal so that trees or shrubs, particularly oaks, form savannah with the understory composed of grassland dominants of the True Prairie."

This reasonably intuitive explanation for the historic distribution of the Prairies and Woodlands has been nearly universally accepted, including by recent authors (e.g., Diggs et al. 1999; Francaviglia 2000).

However, the hypothesis that the Woodlands are restricted to sandy soils because of inadequate moisture availability on clay soils cannot be correct because, in fact, trees occur extensively on the clay soils. As noted above, early accounts noted woody vegetation along the larger watercourses and as isolated mottes or clumps of trees in scattered locations on the clay soils of the Prairies. More impressive, however is the current invasion of trees onto extensive upland areas of clay soil that can be widely observed throughout the Prairies (e.g., Launchbaugh 1955; Smeins & Diamond 1986). Indeed, the few remaining prairie remnants require active management to prevent loss to invading woody vegetation (Smeins & Diamond 1986). In the absence of fire, mowing, or some other suitable disturbance, trees such as *Juniperus virginiana* (eastern red cedar), *Gleditsia triacanthos* (honey-locust), *Celtis laevigata* (hackberry), *Maclura pomifera* (bois-d'arc), *Prosopis glandulosa* (mesquite), and *Ulmus crassifolia* (cedar elm) rapidly invade the native prairie and cause the vegetation to convert to a thicket and then a woodland/forest. A glance from the road along almost any major highway on the present day Blackland Prairie provides abundant evidence of rapid invasion by woody species in the absence of disturbance (Fig. 2). In areas no longer cultivated or otherwise disturbed, the invasion by trees can be observed within a relatively few years—this is particularly obvious in the numerous areas that were cultivated until relatively recently. It therefore seems clear that there is sufficient moisture for tree growth on the clay soils and

Fig. 2. Area of Blackland Prairie in Grayson County showing invasion by woody vegetation under current fire supression conditions (photo by W. Cole Weatherby)

some other mechanism or mechanisms must have been responsible for the historical difference in the vegetation on the clay Prairies and sandy Woodlands.

It should be noted that the woody species present on the modern day Prairies and Woodlands are largely different, probably due to the different soil requirements of the various species, and we do not view woody plant encroachment on the Prairies as simply an expansion of the Woodlands. Nonetheless, woody vegetation is now extensive on many formerly Prairie areas. The woody species currently encroaching on areas of Prairie vegetation were probably not in general major components of the adjacent presettlement Woodland vegetation. Rather, they are probably species that in presettlement times were present in low numbers on the Prairies themselves near streams or where topography made fire unlikely. On the other hand, some species (e.g., *Juniperus ashei*, *J. virginiana*) are at present highly invasive on both the Prairies and Woodlands.

HYPOTHESIS

Soil-dependent fire frequency

We propose that the presettlement distribution of Prairies and Woodlands in North Central and East Texas was not due to insufficient moisture for tree growth on clay soils, but rather to differences in fire frequency on different soil types. We hypothesize that higher fuel quantity on clay soils increased the frequency and intensity of fire, and that fire in turn suppressed the growth of trees. Prairie fires are fueled primarily by grasses, as opposed to forbs or woody vegetation, so an increase in grass biomass leads to an increase in the quantity of fuel. We predict that grass biomass is typically higher on clay than on sandy soils due to better moisture and nutrient availability at the shallower rooting depth of grasses versus woody plants.

This situation would represent two alternative positive feedbacks. High fuel quantity on clay would encourage fire, which would suppress woody vegetation and under certain conditions (e.g., depending on season of burn—Howe 1995) stimulate subsequent grass growth (by removing dead biomass which hinders new growth), thereby maintaining high fuel quantity. Low fuel quantity on sand would reduce the chance of fire, which would foster invasion by trees that would then further suppress grass biomass (e.g., by shading or other competition) and the subsequent frequency and intensity of fire. These alternative feedbacks would lead to alternative stable states, Prairies and Woodlands (Fig. 3). This particular hypothesis for the distribution of Prairies and Woodlands is consistent with the more general conclusions of Scholes and Archer's (1997) review of tree-grass interactions around the world. They write that "Moist fertile environments [e.g. our Prairies] support a vigorous grass growth that, if not grazed, leads to frequent intense fires.... Semi-arid environments on sandy, low fertility soils [e.g. our Woodlands] are seldom treeless."

Soil type (and its effects on grass biomass) is not the only variable that affects the frequency or intensity of fire. Whether a fire ignites, how hot it burns, and its ability to spread also depend on a number of other variables including frequency of ignition events, season of year, rainfall, humidity, wind speed, topography, and grazing (some of which also affect grass biomass). These variables would combine in a stochastic manner to increase or decrease the frequency and/or intensity of fire in any given location at any particular time. For example, fire frequency and intensity would be low during a wet summer, but the resulting grass growth could combine with a subsequent windy drought to increase fire likelihood and intensity the following year. Thus, the systematic effect of soil type on fire would be increased or decreased at any given location at any particular time by the net effect of these other variables, with the result being substantial variation in the time since the last fire in different areas of both the Prairies and the Woodlands. When this stochastic variation is taken into account, the fire-frequency hypothesis can explain not only (1) the historical distribution of Prairies and Woodlands, but also: (2) the historically dominant tree species of the Woodlands; (3) the historical occurrence of isolated groves of trees on clay soils; (4) the present invasion of Prairies by trees; and (5) the difference between the historically dominant tree species of the Woodlands and the species that are increasing in abundance on the Woodlands and invading the Prairies today (e.g., *Juniperus* species).

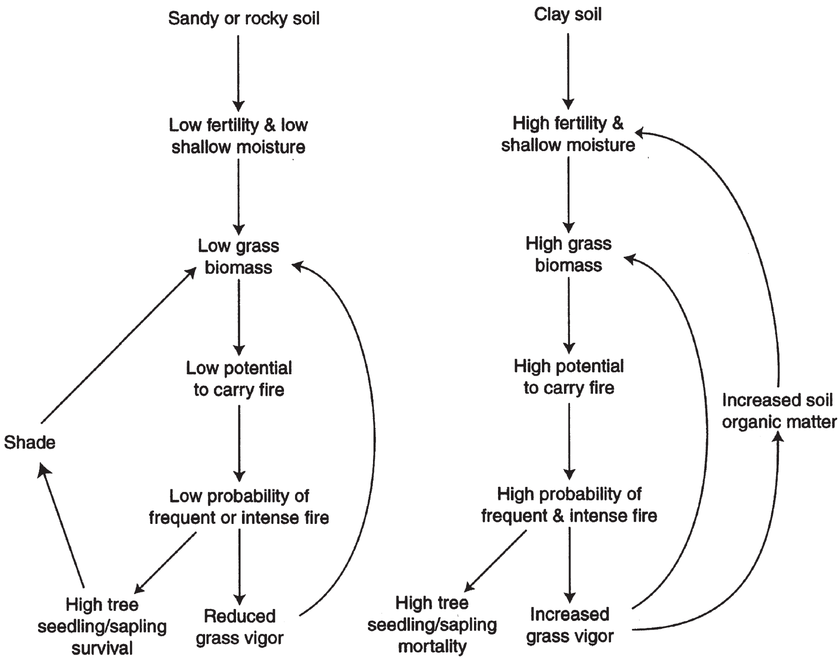

Fig. 3. Flow diagram showing two positive feedback routes to two alternative stable states.

The Woodlands were historically dominated by oaks, species with thick bark, stubby branches, and the ability to resprout from roots, features that impart resilience to grass fires. Further, occasional extended periods without fire on the Prairies would have allowed the establishment of the isolated groves of trees that were observed by Western settlers. Once established, such groves would have been unlikely to burn due to the suppression of grass growth by the trees and the resistance of large trees to fire.

The present invasion of the Prairies by trees can be explained by a lack of fire that has resulted from intentional fire suppression plus numerous and extensive fire breaks that have been created by human activities (roads, cultivated fields, overgrazed areas). Moreover, once this process begins, any Prairie area that becomes substantially invaded by trees would lose grass biomass and come to serve as an additional firebreak, thereby further reducing the likelihood of fire on adjacent remaining prairies. Finally, the present tree invasion of many (but certainly not all) areas of the Prairies (and of the Woodlands understory) is dominated by *Juniperus virginiana* (eastern red cedar) and *Juniperus ashei* (Ashe's juniper), species that are sensitive to fire (easily scorched/ignited and unable to resprout from roots).

The key assumption of our hypothesis is that the difference in grass biomass was sufficiently higher on the Prairies than the Woodlands to raise the likelihood, frequency, and intensity of fire on the clay soils of the Prairies compared to the sandy or rocky soils of the Woodlands. In addition, our hypothesis leads to the prediction that patches of open grassland on sandy soil are very rare except in instances of active management (e.g., suppression of woody species) or immediate proximity to clay soils (which would result in more frequent fires due to closeness to the fire-prone prairie vegetation).

We have not measured grass biomass on intact remnants of the Prairies and Woodlands, and therefore do not have the data necessary to estimate differences in a number of variables associated with fire (e.g., frequency, intensity, extent, pattern, season, etc.). Further, while some biomass and fuel loading data are available in the literature (e.g., Johnson & Risser 1974; Engle & Stritzke 1995), we have been unable to find directly comparable data for the area of study. However, substantial indirect evidence is consistent with the assumption of higher grass biomass on clay soils. First, during dry periods clay soils generally hold more water at grass rooting depths than do sandy soils. This is due to the relatively large surface areas of the individual clay particles and the large number of very small pores which act as billions of capillary tubes collectively holding large amounts of water (Vankat 1979). The result of this increased water holding capacity is that plants rooted in such soils may continue active growth much later in the dry season than plants rooted in coarser soils (Daubenmire 1974; Burgess 1995; McAuliffe 1995; Tucker 1999; Greeves et al. 2000; Ball 2001). Furthermore, undisturbed Blackland soils form gilgai, microtopographical surface features that function like shallow basins, increasing water retention during heavy rains (Hayward & Yelderman 1991; Diamond & Smeins 1993). Early settler accounts and observations of existing prairie remnants (e.g., the Nature Conservancy's Clymer Meadow preserve in Hunt County, the Matthews-Cartwright-Roberts Prairie in Kaufman County, and Austin College's Garnett Prairie in Grayson County) suggest that these "hog wallows," (as they were known to early settlers) were abundant on Vertisols of the presettlement Blackland Prairie. Temporary water storage in gilgai depressions of one-half acre foot of water per acre of flat prairie have been estimated. As much as six inches of rain could be temporarily trapped in these structures before runoff began (Hayward & Yelderman 1991). Meanwhile, the high surface area and negative surface charges of clay particles give clay soils high cation exchange capacity. This allows these soils to hold more ionized minerals or nutrients, including those essential for plant growth (Foth 1990; Whitehead 2000; Harpstead et al. 2001; O'Connell 2001). It is therefore not surprising that indirect evidence, such as agricultural productivity, suggests that the Blackland clay soils were among the most fertile soils west of the Mississippi River (Haywood & Yelderman 1991). In addition, the high below-ground biomass of Prairie vegetation serves to continually add organic matter to the soil, thereby functioning as a positive feedback mechanism to increase fertility and water holding capacity (in part due to the surface area provided by the additional organic material). Conversely, sandy soils have larger pores that allow water to drain more easily. They not only dry earlier during dry periods but "the more water that percolates through the soil, the more nutrients are washed out—particularly nitrogen, potassium and sulfur" (Tucker 1999). Therefore, soils that are high in sand, like those of the Woodlands, are often poor for plant growth since they are relatively infertile and often too well-drained (Vankat 1979).

Confounding factors

Several other factors have the potential to operate synergistically or in opposition to the soil-mediated fire frequency hypothesis in influencing the balance between grass-dominated and woody vegetation. Of particular importance is the grazing regime. Van Auken (2000), for example, has identified high levels of herbivory by domestic animals as the primary cause of brush encroachment in the semiarid grasslands of the southwestern U.S. This influence is probably the result of a combination of disturbance and reduced fire frequency. The grazing regime during presettlement times was certainly very different than at present. Instead of domestic animals continuously confined to limited areas of pasture, the primary herbivores were large dense herds of migratory bison free to move over vast distances. The grazing regime would thus have been extremely irregular both temporally and spatially. While a large herd could move through an area of Blackland Prairie and crop the vegetation very short (thus preventing fires), in some seasons or years a given area would probably be missed entirely leaving large amounts of standing biomass (heavy fuel load for fires). Under such conditions fire would not be expected every year, nor would it be essential every year for the maintenance of the grassland. Rather, fire would be critical only with enough regularity to prevent trees from growing large enough to become invulnerable to grass fires.

Another grazing related influence is the role of dense herds of grazers on controlling woody vegetation and stimulating grasses. Savory (1998) has stressed the importance of herding grazers on maintaining grasslands and has emphasized the extremely different consequences of typical human-controlled grazing regimes (long periods of exposure to low densities of animals) and natural systems (large migratory herds at high density due to threat of predation). He has noted that extremely high densities of grazers (and thus damage to woody plants) may be of critical importance in preventing encroachment of woody vegetation and shifting the balance in favor of grazing adapted grasses. A different impact of grazers is that seed dispersal may be of major importance in the invasion of grasslands by certain woody species. Data of Brown and Archer (1999) suggest that rates and patterns of seed dispersal may be the primary determinants of encroachment by mesquite (*Prosopis glandulosa*) on present-day landscapes in semi arid regions of the American southwest.

Still another confounding factor is the competition for resources between grasses and woody species in an intact prairie ecosystem. Under certain conditions (e.g., of soil, water, grazing, etc.) on an intact prairie, grasses might be able to out compete woody species or at least resist their invasion, with or without the influence of fire. However, the impact of fire and grazing are of critical importance since under natural conditions it is unlikely that either of these factors would be absent for any significant length of time.

CONCLUSION

The soil-mediated fire frequency hypothesis is merely a particular case of a group of mechanisms that, by reducing the frequency and intensity of fire, enable trees to grow where grass would otherwise dominate. The fire induced state of grasslands on the Prairies is therefore apparently destabilized when fire is suppressed for any of a number of reasons. In addition to the hypothesized effect of soil on grass biomass, other variables that can hinder fire and thus allow trees to invade include precipitation, grazing, and topography (Collins & Wallace 1990; McPherson 1995). Trees invade when rainfall prevents fire throughout the year (e.g., in areas of eastern deciduous forest in the eastern U.S). Likewise, reduced grass biomass from grazing on the Prairies reduces fire likelihood, which in turn enables invasion by trees (Smeins et al. 1982; Scholes & Archer 1997; Van Auken 2000). As noted by Van Auken (2000), "the driving force [for brush encroachment] seems to be chronic, high levels of herbivory by domestic animals. This herbivory has reduced the aboveground grass biomass, leading to the reduction of fine fuel and a concomitant reduction or complete elimination of grassland fires. This combination of factors favors the encroachment, establishment, survival and growth of woody plants." Finally, where relief is extreme, as on scarps or cliffs, woodlands are often present. This is due to both the thin rocky soil (and hence low grass biomass) and the topography (e.g., abrupt scarps), which often creates natural firebreaks (Wells 1965, 1970; Axelrod 1985). Thus, any factor that reduces fire likelihood, frequency, or intensity can be expected to allow trees to invade grasslands in areas where there is sufficient moisture for tree growth. The soil-mediated fire frequency hypothesis for the historical distribution of the Prairies and Woodlands of North Central Texas and East Texas is consistent with both historical vegetation patterns and recent changes in the vegetation, and is simply a special case of a generally accepted explanation for tree-grass interactions.

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