

Historical variability in fire at the ponderosa pine - Northern Great Plains prairie ecotone, southeastern Black Hills, South Dakota¹

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Abstract: Ecotones are boundaries between plant assemblages that can represent a physiological or competitive limit of species' local distributions, usually through one or more biotic or abiotic constraints on species' resource requirements. However, ecotones also result from the effects of chronic or episodic disturbances, and changes in disturbance regimes may have profound effects on vegetation patterns in transitional areas. In this study, centuries-long chronologies of surface fire events were reconstructed from fire-scarred ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) trees in three sites at the ecotone between ponderosa pine forest and Northern Great Plains mixed-grass prairie in the southeastern Black Hills of South Dakota. The fire chronologies provide baseline data to assess the possible role of fire in this transitional area and to document historical variability in fire regimes in this region of the Northern Great Plains. Regular fire events were recorded at all three sites from the beginning of the fire chronologies in the 1500s up to the late 1800s or early 1900s, at which time spreading fires ceased. Fire frequencies derived from the fire chronologies were compared to each other and to four sites from interior ponderosa pine forest in the south-central Black Hills. Mean fire intervals at the savanna sites were between 10 to 12 years, whereas Weibull median probability intervals were one year shorter. Fire frequency at the savanna sites was twice as high as at the interior forest sites, and most likely was due to spatial extent of fires on the mixed-grass prairie coupled with warmer and drier climate regime. Post-settlement shifts in the ponderosa pine savanna during the twentieth century in this area may be largely attributed to lack of fire occurrences, although grazing and other factors also likely contributed to observed changes in forest and grassland margins.

Keywords: dendrochronology, crossdating, fire chronology, fire frequency, Northern Great Plains, grassland fire regimes.

Introduction

Ecotones are boundaries between plant assemblages where environmental conditions presumably change enough to provide species with competitive advantages or disadvantages over others. Much of the research on ecotones has focused on quantifying present-day abiotic (e.g.,

climatic or edaphic) or biotic (e.g., competition for light or soil moisture) environmental gradients to understand spatial dynamics of vegetative patterning across transitional areas (Peet, 1981; Hansen & Di Castri, 1992; Gosz, 1993; Risser, 1995). This approach has often succeeded in explaining transitions between plant assemblages at a biome or regional scale, but may not fully explain patterning at smaller landscape or patch scales (Gosz, 1993; Risser, 1995).

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At smaller scales, vegetation patterns at ecotones are often the result of more complex interactions between factors that control plant reproduction, establishment, growth, and mortality. The position of an ecotone can be the result of historic events or processes that may not be related to any measurable environmental factor. Abrupt climate change, such as a major drought or an anomalous cold period that causes widespread mortality of a species at its environmental limit, can be a cause of major shifts in ecotones (Risser, 1995; Allen & Breshears, 1998). Conversely, climate conditions favorable for plant regeneration may occur more slowly or episodically and lead to lags in re-establishment of an ecotone to some former position (Taylor, 1995). For example, drought in the early 1950s in the southwestern U.S.A. caused large uphill elevational shifts in woodland grassland ecotones (Betancourt et al., 1993; Swetnam & Betancourt, 1998) and woodland - forest ecotones (Allen & Breshears, 1998) that have not yet returned to previous positions even after wet periods in the 1970s and 1980s (Gosz, 1991; Swetnam & Betancourt, 1998).

Ecotones also shift in response to changes in either natural or human-induced disturbance regimes (McPherson, 1997). Tree invasion into grasslands has been noted world-wide in response to changes in disturbance frequency or severity (Richardson, Williams & Hobbs, 1994; McPherson, 1997; Mast, Veblen & Linhart, 1998). A review of possible explanations for recent woody plant encroachment in southwestern U.S.A. grasslands by Archer (1994) concluded that widespread and intensive grazing practices that began after non-Native American settlement has been largely responsible for invasion of woodlands into what were formerly pure grassland communities. Archer (1994) also suggested that cessation of surface fire regimes has contributed to observed shifts in woodland ecotones during recent decades.

The Black Hills of southwestern South Dakota and northeastern Wyoming are often described as an island of predominately ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) forest surrounded by seas of mixed grasslands of the Northern Great Plains prairie (Raventon, 1994). The often broad transition zone between forest and grassland on the periphery of the Black Hills, hereafter referred to as the ponderosa pine savanna (McPherson, 1997), is usually considered to be controlled mainly by climate, with tree establishment and growth on the prairie margins precluded by lower precipitation and warmer temperatures that lead to reduced soil moisture regimes (*sensu* Daubenmire, 1943; Peet, 1981). However, there is evidence that the ecotonal mosaic of ponderosa pine forest, savanna, and grasslands on the periphery of the Black Hills has shifted over the past century in response to changes in land use that began in the late 1800s. Ponderosa pine trees have established in what were formerly grassland communities (Progulske, 1974; Bock & Bock, 1984; Fisher, Jenkins & Fisher, 1987). Sequences of aerial photographs from the southeastern Black Hills (Figure 1) document often dramatic changes in ponderosa pine stand density and landscape coverage during very short time periods in recent decades (34 years between scenes in Figure 1). Changes in the pine - grassland ecotone in the Black Hills are similar to tree and shrub encroachment seen in many areas of the Northern and Central Great Plains region (Steinauer & Bragg, 1987; Archer, 1994;

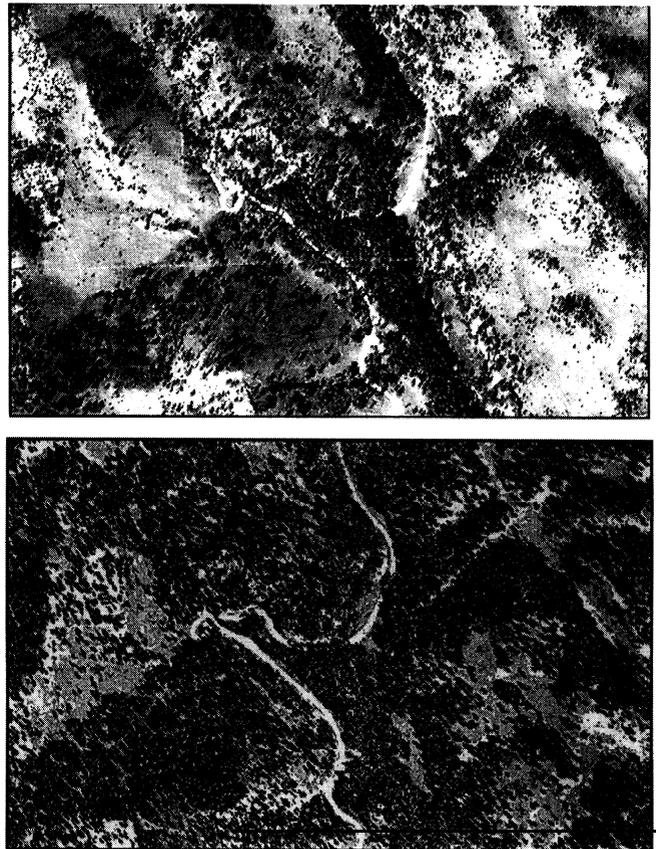


FIGURE 1. Aerial photographs from September 19, 1938 (top photograph), and September 17, 1972 (bottom photograph), from the vicinity of the Pigtail Bridge (PIG) site. Dark areas in the photographs are ponderosa pine trees and light areas are grasslands. Fire-scarred trees at PIG were collected from the area between the roads in the center of the photographs.

McPherson, 1997; Mast, Veblen & Hodgson, 1997; Mast, Veblen & Linhart, 1998).

In this study, we used dendrochronologically-crossdated fire-scarred ponderosa pine trees to document timing and frequency of historical fire occurrences at three sites in the ponderosa pine savanna at Wind Cave National Park in the southeastern Black Hills. We have two objectives with the data described here. First, fire chronologies from Wind Cave provide baseline information on the possible role of fire as a control of forest - grassland ecotones in this area. Shifts in forest and grassland patterns in the Black Hills have been attributed at least in part to the disruption of pre-settlement fire regimes of frequent, generally low-intensity surface fires (Gartner & Thompson, 1972; Progulske, 1974; Bock & Bock, 1984; Fisher, Jenkins & Fisher, 1987). Frequent surface fires would have tended to maintain the ecotone by killing ponderosa pine seedlings and saplings before they could become established on the prairie margins.

Our second objective with this study was to document historical variability in the fire regime of the Northern Great Plains mixed-grass prairie. Although fire has long been recognized as a pervasive factor influencing the structure and function of prairie ecosystems of North America (Sauer, 1950), there are few studies that have quantified pre-settlement fire regimes in these areas (but see Bragg,

1985; Fisher, Jenkins & Fisher, 1987; Umbanhower, 1996). We contrast fire data from Wind Cave National Park with similar data from four interior ponderosa pine forest sites at Jewel Cave National Monument in the south central Black Hills, approximately 35 km northwest of Wind Cave (Brown & Sieg, 1996). Fire data from Wind Cave National Park offer a larger regional view of the historical range of variability (Morgan *et al.*, 1994) in pre-settlement fire regimes in the Black Hills, and provide some of the most detailed fire history information yet available for this area of the Northern Great Plains grasslands.

Methods

STUDY AREA

The Black Hills are an isolated dome of often rugged mountains that rise over 1000 m above the surrounding relatively flat Great Plains of southwestern South Dakota and northeastern Wyoming. Elevations in the Black Hills range from around 1050 m to 1350 m on the margins of the Great Plains to Harney Peak, the highest point, at 2207 m. The Black Hills cover an elliptical area roughly 200 km north to south and 100 km east to west. Often considered as the easternmost extension of the Rocky Mountains, the Black Hills were originally formed from an intrusive granitic pluton (Froiland, 1990). The Black Hills are both wetter and cooler than the surrounding Great Plains, and support extensive coniferous forests in contrast to the adjacent mixed-grass prairies (Hoffman & Alexander, 1987; Froiland, 1990). There is a strong decreasing moisture gradient from northwest to southeast across the Black Hills (Bunkers, Miller & DeGaetano, 1996). Lead, in the northern part of the range, received an average of 673 mm precipitation between 1931 and 1990. In contrast, Hot Springs, in the southeastern Black Hills, received an average of 440 mm during the same period. The surrounding Great Plains area receives an average of 350 to 430 mm. Approximately 65% to 75% of the precipitation in the Black Hills falls from April to September (Froiland, 1990).

Extensive ponderosa pine forest dominates up to 95% of the forested areas (Thilenius, 1971; Boldt, Alexander & Larson, 1983), with white spruce (*Picea glauca* [Moench] Voss), the other major coniferous species of the higher and wetter forests of the northern Hills (Hoffman & Alexander, 1987). Limber pine (*Pinus flexilis* James), lodgepole pine (*Pinus contorta* [Dougl.]), and Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) are minor components of the coniferous forest. There is also a considerable deciduous tree component from eastern forests, many species of which reach their westernmost extent in the Black Hills.

Wind Cave National Park is in the southeastern foothills of the Black Hills at the ponderosa pine forest - Northern Great Plains prairie ecotone (Figure 2). Elevations at the Park range from 1100 m to 1530 m and slopes are usually moderate to flat. Ponderosa pine forests and savannas and prairie grasslands form a complex landscape mosaic across the Park (Figures 1 and 2). Contiguous ponderosa pine forest is primarily concentrated in the northwest and west. Forests grade irregularly into scattered savanna stands, with clusters of trees found on isolated scaps or

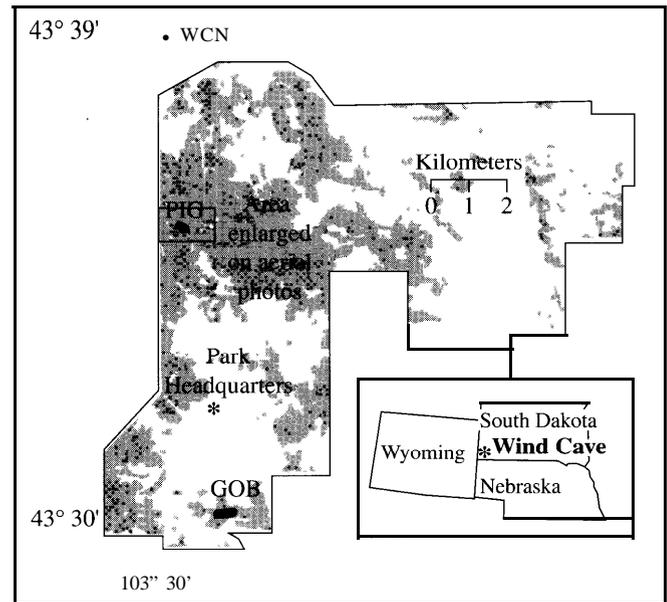


FIGURE 2. Locations of three sites (WCN, PIG, and GOB) collected for fire chronologies at Wind Cave National Park. Light grey areas on map are locations of ponderosa pine forest and savannas; white areas are grasslands. Area enlarged on aerial photographs is that shown in Figure 1. Data on the landscape patterning of ponderosa pine forest were not available for the vicinity of site WCN.

steeper drainages in the south and east (Shilts *et al.*, 1980). Ponderosa pine stands are occasionally dense with little understory vegetation, especially in areas with continuous canopy, although stands are more often open with abundant grassy or herbaceous understories. Prairie grasslands are most continuous at lower elevations in the south and east (Gartner & Thompson, 1972; Shilts *et al.*, 1980; Bock & Bock, 1984).

RECONSTRUCTION OF FIRE HISTORY

Fire-scarred ponderosa pine trees were collected from three sites near the present day limit of ponderosa pine forest in and near Wind Cave National Park (Figure 2). Wind Cave North (WCN) is in Black Hills National Forest just to the north of the Park boundary in relatively continuous ponderosa pine forest. Pigtail Bridge (PIG) is also in more continuous ponderosa pine forest closer to the Black Hills proper. The third site, Gobbler Ridge (GOB), is located as far out on the savanna as we could find old (*i.e.*, pre-settlement) ponderosa pine trees.

The overall methodology of fire history reconstruction at these three sites follows that described by Brown & Sieg (1996). The goal of collection at each site was to obtain comprehensive, long-term inventories of fire events using annually-resolved proxy fire scar records from individual trees (Swetnam & Baisan, 1996; Brown & Sieg, 1996). Fire scars result when surface fire kills cambial tissue along a portion of a tree's growing circumference, forming a characteristic lesion visible in the tree rings. Long-term sequences of fire scars often are recorded on individual trees owing to repeated fire events during the life of a tree. Sites ranged from 20 to 25 ha in size, *i.e.*, the scale of forest stands. Sites were selected in old-growth ponderosa pine stands in order to find long fire scar records on individual

trees. Visual inspection and increment core sampling of living trees in many areas of the Park suggested that much of the present-day ponderosa pine forest at Wind Cave consists of relatively young trees (< *ca.* 100 years) that are not old enough for reconstruction of long-term fire history.

At each site, cross sections were collected from fire-scarred trees using a chainsaw. We selected individual trees at each site based upon the numbers of fire scars visible in either fire-created "cat-faces" or on stump tops. Generally full circumference cross sections were removed from stumps or logs, whereas partial cross sections were removed from the vicinity of scarred areas on living or standing dead trees. Once returned to the lab, cross sections were surfaced using a hand planer, belt sander, and hand sanding to 320 or 400 grit sandpaper. Fine sanding was crucial for observation of cell structure within tree rings and at fire scar boundaries.

Cross sections were crossdated using standard dendrochronological procedures such as skeleton plotting (Stokes & Smiley, 1968). After crossdating was assured on all cross sections at a site, dates were then assigned to fire scars seen within the dated ring series. Intra-annual positions of fire scars were also noted when possible (Dieterich & Swetnam, 1984; Brown & Sieg, 1996). Dormant season scars were those that occurred between two rings and were assigned to either the earlier or later year (i.e., fall fires occurring after annual growth had ceased for a year or spring fires occurring before growth began for the next) based upon positions of scars for the same years on other trees (Brown & Sieg, 1996). If only dormant season scars were recorded on all trees for a specific fire date, the fire date was assigned to the previous year (i.e., a fall fire) based the almost ubiquitous presence of late season scars on other trees in the Black Hills (Brown & Sieg, 1996). Once cross-dating was verified on all trees at a site, fire chronologies were compiled from all fire dates recorded (*sensu* Dieterich, 1980). Compilation of fire chronologies minimized any potential incompleteness of scar records on individual trees. Fire events may not be recorded on every tree at the time of occurrence or fire scars may be lost by erosion or burning in subsequent fire events (Swetnam & Baisan, 1996; Brown & Sieg, 1996).

FIRE FREQUENCY

Fire frequency in each fire chronology was described using three measures: mean fire interval (MFI), Weibull median probability interval (WMPI; Grissino-Mayer, 1995; Swetnam & Baisan, 1996), and a regression-derived measure from cumulative fire dates (Brown, Kaufmann & Shepperd, 1999). MFI is the average number of years between fire dates in a composite fire chronology and has been widely used to describe fire frequency (Heyerdahl, Berry & Agee, 1995). Variance in fire intervals is described by the first standard deviation and range of intervals. WMPI is the fire interval associated with the 50% exceedance probability of a modeled Weibull distribution of all fire intervals in a fire chronology and is considered to be a less biased estimator of central tendencies in fire interval data (Grissino-Mayer, 1995; Swetnam & Baisan, 1996). If fire interval data are distributed normally, MFI and WMPI will be the same. Variance with the Weibull model is described by the 5%

and 95% exceedance intervals (Grissino-Mayer, 1995). Program FHX2 (Grissino-Mayer, 1995) was used to calculate MFI and WMPI for each site. The third descriptor for fire frequency is a regression-derived measure determined by piecewise regression procedures (Neter, Wasserman & Kutner, 1989) fit through a cumulative sequence of fire dates. The use of piecewise regression for describing fire frequency permits both statistical and visual assessments of changes in frequency through time (Brown, Kaufmann & Shepperd, 1999).

We compared fire frequency in the three sites at Wind Cave National Park to four sites at Jewel Cave National Monument that were collected using similar methodology (Brown & Sieg, 1996). Sites at Jewel Cave are located in the interior of the ponderosa pine forest of the Black Hills northwest of Wind Cave. The Jewel Cave sites are higher (1580 m to 1750 m elevation) than those at Wind Cave (1220 m to 1510 m), with correspondingly cooler and wetter climate regimes. Significant differences between MFIs and WMPIs at the three Wind Cave sites, and between the Wind Cave and Jewel Cave sites were assessed using a generalized F-test with a Bonferroni adjustment (Weerahandi, 1995).

Results

FIRE CHRONOLOGIES

Fire chronologies from three sites at Wind Cave National Park are shown in Figure 3. Frequent, episodic surface fires were recorded on trees beginning from dates in the 1500s or 1600s until the late 1800s or early 1900s. Fire dates recorded on trees at all three sites included 1591, 1652, 1706, 1724, 1739, 1768, 1822, 1845, 1853, 1863, 1870, 1875, and 1881. Trees at both Wind Cave North (WCN) and Pigtail Bridge (PIG) showed generally synchronous fire scars recorded on most trees during fire years, whereas Gobbler Ridge (GOB) trees showed generally less synchrony in scars recorded, especially before 1822. Synchronous fire events stopped at all three sites in the late 1800s, although we found fewer trees that extend into the 1900s, especially at WCN. Trees at sites PIG and GOB recorded two widespread fire dates (recorded on most trees) in the early 1900s. After these two fire dates, there were occasional fire scars recorded on one or two trees, but fire scars were much less common at all three sites during the twentieth century.

Most fire scars recorded on trees at Wind Cave occurred later in the growing season or as dormant season scars between two rings (Table I). In general, years when only dormant season or unknown position scars were recorded were dated to the prior year. However, nine out of 13 trees at GOB recorded dormant season scars between the 1909 and 1910 rings that were dated to 1910. This date was determined from a reference in the Wind Cave National Park's annual Superintendent's records of a fire that burned in March, 1910, on the south side of the Park where the GOB trees were collected. It is possible that other fire dates prior to the twentieth century that were recorded only as dormant or unknown position scars could have been spring fires and are therefore recorded in the fire chronologies as one year earlier than the actual calendrical date.

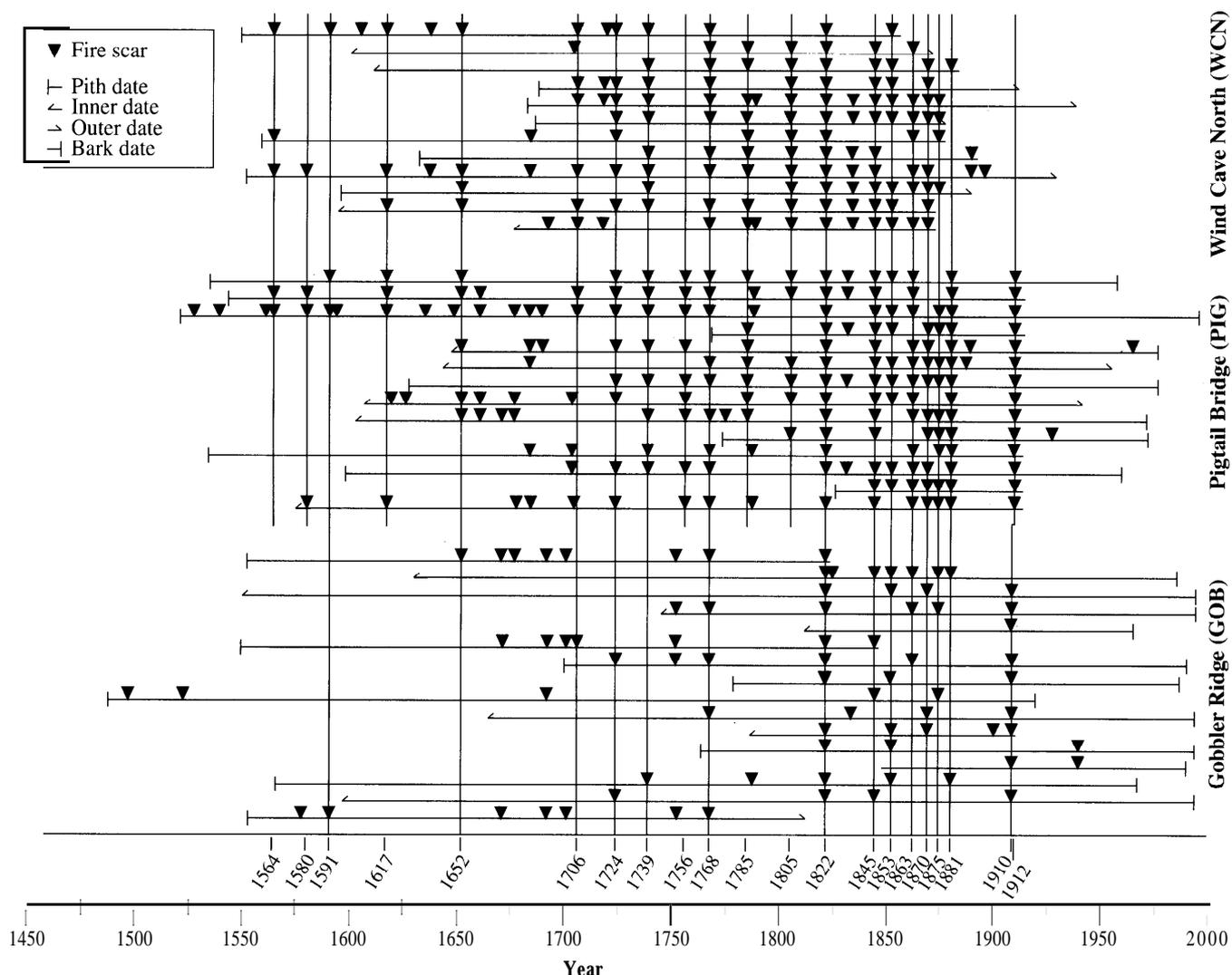


FIGURE 3. Fire chronologies for Wind Cave National Park sites. Time spans of individual trees are represented by horizontal lines, with fire scars noted by triangles at the dates they were recorded. Dates at the bottom of the fire chronologies are those years when fire scars were recorded at more than one site, except for 19 10 and 19 12 which were recorded only at sites GOB and PIG, respectively.

TABLE I. Numbers of fire scars by season of occurrence from trees at Wind Cave National Park. Numbers in parentheses are percentages of the total number of fire scars with an assigned season of occurrence (excluding unknown position fire scars)

Site	Early season ¹	Middle season ²	Late season ³	Unknown dormant ⁴	Unknown position	Total fire scars
WCN	12 (10.4)	2 (1.7)	71 (61.7)	30 (26.1)	22	137
PIG	14 (8.8)	3 (1.9)	106 (66.3)	37 (23.1)	39	199
GOB	9 (15.3)	0	19 (32.2)	31 (52.5)	20	79

¹ Includes fire scars recorded as early dormant or in first third of the earlywood.

² Includes fire scars recorded in middle third of earlywood.

³ Includes fire scars recorded in last third of earlywood band, in the latewood band, or as late dormant.

⁴ Includes years when only dormant season position fire scars were recorded (i.e., not associated with earlywood or latewood scars on other trees for that period).

FIRE FREQUENCY

Mean fire intervals (MFIs) and Weibull median probability intervals (WMPIs) were not significantly different ($p < 0.01$) between the three sites at Wind Cave National Park in a generalized F-test (Table II). WMPIs were generally one year less than mfiS, reflecting the positive skew in fire intervals distributions. The three Wind Cave sites also recorded similar variances in fire intervals as reflected by the standard deviations, ranges of intervals, and Weibull 5% and 95% exceedance probability intervals. MFIs and WMPIs for the Wind Cave sites were approximately half as long as the four ponderosa pine forest interior sites at Jewel Cave National Monument (Table II), which also tended to record greater variability in lengths of fire intervals (Brown Sieg, 1996). There were significant differences in fire frequency between sites from the two areas. The measures

TABLE II. Measures of fire frequency for three ponderosa pine savanna sites at Wind Cave National Park (GOB, PIG, and WCN) and four forest interior sites at Jewel Cave National Monument (JC site designations; Brown & Sieg, 1996). Fire intervals used in calculations are for all dates recorded on any tree at each site for the period of analysis

Site	Period of analysis	No. of intervals	MFI (\pm SD) ¹	Range of intervals ²	WMPI ³	5% to 95% prob. inter. ⁴	Fire frequency (from Figure 4) ⁵
WIND CAVE NATIONAL PARK							
WCN	1564 to 1896	27	12.3 \pm 6.9	3 to 32	11.6	3.5 to 22.7	0.077
PIG	1528 to 1912	38	10.1 \pm 5.8	2 to 23	9.3	2.3 to 20.3	0.100
GOB	1652 to 1910	21	12.3 \pm 7.2	3 to 34	11.5	3.5 to 22.6	0.078
JEWEL CAVE NATIONAL MONUMENT							
JCN	1576 to 1890	16	19.6 \pm 13.5	4 to 45	17.4	3.9 to 40.3	0.045
JCC	1388 to 1890	22	22.8 \pm 17.6	1 to 63	18.8	2.6 to 57.0	0.042
JCE	1591 to 1890	13	23.0 \pm 22.0	1 to 77	16.9	1.6 to 63.9	0.043
JCS	1591 to 1900	13	23.8 \pm 23.1	7 to 93	20.1	4.6 to 46.3	0.043

¹ Mean and first standard deviation of all intervals in composite fire chronology in years.

² In years.

³ Weibull median (50% exceedance) probability interval in years.

⁴ Weibull 5% and 95% exceedance probability intervals in years.

⁵ Slope of line of cumulative fire dates (number of fires year⁻¹).

of fire frequency for all sites were calculated for the period of record up to the late 1800s or early 1900s, as there were few fire events recorded at any site after that time.

Fire frequency determined by regression slopes fit through sequential fire dates also show similarity in the three Wind Cave sites and differences from the four Jewel Cave sites (Figure 4, Table II). Piecewise regression (Neter, Wasserman & Kutner, 1989) through fire dates recorded before 1652 at GOB is significantly different than the longer-term trend in fire frequency after 1652 and this earlier period was not used for calculations of measures of fire frequency. The fire scar record at GOB before the 1652 fire date was determined to be too sparse (see also Figure 3) to reflect a true record of past fire events (Brown, Kaufmann & Shepperd, 1999). Visual assessment of patterns through time also suggests shorter-term shifts in fire frequency,

although none of these shifts were significant in piecewise regression. However, sites at both Wind Cave and Jewel Cave recorded slightly increased fire frequency from the middle to the end of the nineteenth century (Figure 4; also see Figure 3). Slightly reduced fire frequency was also evident in both the Wind Cave and Jewel Cave sites in the early 1700s (Brown & Sieg, 1996).

Discussion

FIRE AT THE MARGIN OF THE NORTHERN GREAT PLAINS GRASSLAND

Fire intervals found at Wind Cave National Park are among the shortest documented for northern ponderosa pine forests. Fire frequencies at Wind Cave sites are comparable to those found in southwestern U.S.A. ponderosa pine forests and some lower elevation ponderosa pine sites in the northern Rocky Mountains (Arno, 1976; Wright & Bailey, 1982; Heyerdahl, Berry & Agee, 1995; Swetnam & Baisan, 1996; Barrett, Arno & Menakis, 1997). In the southwest, stands often recorded fire once every 3 to 15 years, depending on climate regimes and fuel conditions. Northern Rocky Mountain ponderosa pine forests generally had longer intervals between fires, but some stands burned as often as every 7 to 15 years (Arno, 1976; Barrett & Arno, 1982).

Fire was twice as frequent in ponderosa pine savanna at Wind Cave National Park as in the forest interior ponderosa pine stands at Jewel Cave National Monument in the central Black Hills (Table II, Figure 4). Higher fire frequency in the Wind Cave area may have been due to differences in climate regimes and/or fuel dynamics at the ponderosa pine forest - grassland ecotone. Wind Cave ponderosa pine forests are lower in elevation and both warmer and drier than those at Jewel Cave. Warmer and drier conditions would have led to more years when fuels were able to carry fire. Also, the fire history recorded on ponderosa pine trees at Wind Cave should be considered to more closely reflect the fire regime that was present in the mixed-grassland prairies surrounding the Black Hills rather than that of the ponderosa pine forest of the interior of the Hills. Grasslands have, in general, greater spatial continuity and uniform loadings of fine fuels, which result in larger potential

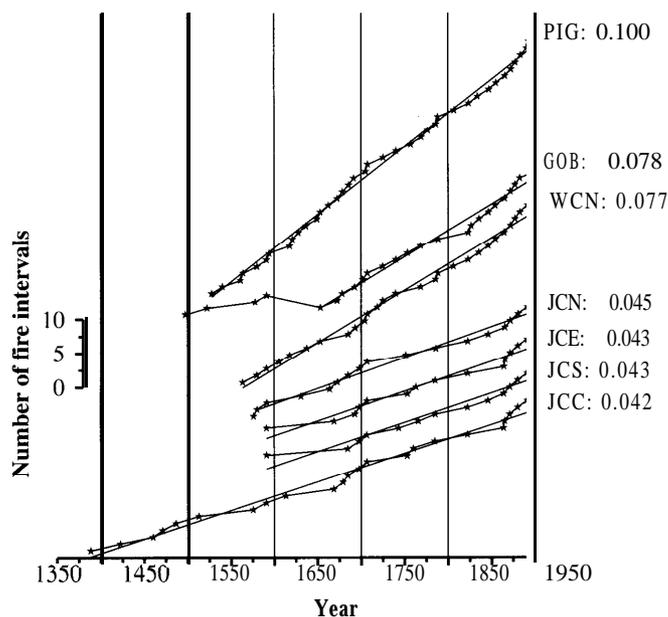


FIGURE 4. Fire frequencies determined by slopes of line fit through cumulative fire dates for Wind Cave National Park (top three lines) and Jewel Cave National Monument (bottom four lines) sites. Numbers after site designations are slope of best-fit regression line (number of fires per year).

“firesheds” over which fire can potentially burn from any ignition point. If ignition and not fuels was a limiting factor in fire occurrences, then more extensive fires should result in more frequent fires at any one location. Early accounts from the Northern Great Plains often described single fires burning over vast areas of grassland (possibly > 100 000 ha; e.g., Higgins, 1986). In contrast, spatial patterns of fire at Jewel Cave suggested that there were topographic breaks present in the interior area that limited fire spread between sites (Brown & Sieg, 1996). Vegetative and topographic discontinuities in the more mountainous and rocky interior of the Black Hills would have limited fire spread from an ignition location, resulting in smaller potential burn areas in any one year.

Although fire frequency was different between the Wind Cave and Jewel Cave sites, there was synchrony in fire timing in the two areas over the past several centuries. Many of the same fire years, including 1591, 1706, 1785, 1822, 1845, 1863, and 1870, were recorded at sites in the two areas. Both areas recorded slightly decreased fire frequency in the 1700s and slightly higher fire frequency in the late 1800s (Figure 4). Lower fire frequency in the early 1700s appears to have been a regional pattern across the Black Hills (Brown, unpubl. data). Higher fire frequency in the late 1800s may have been the result of either increased use of this area by Native Americans at the time of widespread non-Native American settlement of this area beginning in 1875 (Progulske, 1974) or early settlement activities such as mining and land clearing for farming. Fisher, Jenkins & Fisher (1987) attributed an increase in fire frequency from the 1700s to late 1800s in the western Black Hills at Devil’s Tower National Monument to an increase in aboriginal activity in this area.

The presence of late season scars for most fire years at Wind Cave National Park (Table I) corresponds to seasonal patterns seen in both recent fire records for the Northern Great Plains (Higgins, 1984) and in the fire scar data from Jewel Cave National Monument (Brown & Sieg, 1996). Most historic lightning-caused fires in the Northern Great Plains occurred in July and August (Higgins, 1984) and fire scars in trees at Jewel Cave occurred almost exclusively later in the growing season. Tree growth in the Black Hills area is probably complete by early to late August (Brown & Sieg, 1996). An exception to the pattern of late season scars at Wind Cave was the March, 1910, fire at Gobbler Ridge. The fire season of 1910 was the most widespread fire year for which written records exist in the northern Rocky Mountains, including the Black Hills (Plummer, 1912), and was largely responsible for the U.S. Forest Service’s “10 a.m.” policy (all fires suppressed by 10 a.m. of the following day; Pyne, 1992) that contributed to fire exclusion in forests throughout the western U.S.A.

FIRE, GRAZING, AND ECOTONAL DYNAMICS

Cessation of fires at Wind Cave beginning in the early twentieth century (Figure 3) corresponds to patterns seen in other ponderosa pine ecosystems of the western U.S.A. (Cooper, 1960; Savage, 1991; Grissino-Mayer, 1995; Touchan, Swetnam & Grissino-Mayer, 1995; Swetnam & Baisan, 1996; Brown & Sieg, 1996; Fule, Covington &

Moore, 1997). Fire cessation was usually coincident with the beginning of widespread, intensive livestock grazing, and often preceded, occasionally by several decades (Savage, 1991; Touchan, Swetnam & Grissino-Mayer, 1995), direct fire suppression efforts by land management agencies.

Intensive livestock grazing and loss of surface fire regimes were also contemporaneous with the beginnings of shifts in plant community structure and composition at ecotones between forests and grasslands, with woody plant encroachment into what were formerly prairie areas (Archer, 1994; McPherson, 1997; Mast, Veblen & Hodgson, 1997; Mast, Veblen & Linhart, 1998). However, it is difficult to disentangle cause-and-effect relationships between changes in vegetation and possible driving factors because of the presence of both positive and negative feedbacks between environmental components. In savannas, a positive feedback exists between fuels and fire. Fires promote grasses and herbaceous plants by killing woody plants before they can establish and exclude understory individuals through shading or allelopathic mechanisms. Grazing contributed indirectly to a reduction in fires by removing grasses and other fine fuels that were necessary for fire spread (Zimmerman & Neuenschwander, 1984; Archer, 1994; Touchan, Swetnam & Grissino-Mayer, 1995). However, herbivory by livestock also directly changed the competitive relationships between grasses and woody plants by selectively removing grasses to favor unpalatable woody species in a community (Archer, 1994). Archer (1994) concluded that although herbivory, fire exclusion, minor climate changes, and possibly atmospheric CO₂ enrichment have interacted to produce recent changes in woodland grassland patterns and species associations, the proximal cause for change in most cases has been grazing by large numbers of livestock.

In the Wind Cave savanna, as in other areas of tree invasion in the western U.S.A., it is difficult to determine the timing and magnitude of driving factors and ecosystem responses. It is likely that extensive ponderosa pine forest expansion in this area began in the early 1900s (e.g., Progulske, 1974). There does not appear to have been any major changes in either precipitation or temperature regimes at that time that could explain movement of trees into lower elevation grasslands (e.g., Meko, 1992; Cook *et al.*, 1996). Conversely, herbivory by livestock may only partially explain observed shifts in ponderosa pine forest savanna. Wind Cave National Park was established in 1906 and the area has not been grazed by livestock since that time. After extensive non-Native American settlement of this area starting around 1875 up to the time the Park was established, this area was most likely grazed by livestock, although we have not been able to find records of numbers of animals or specific locations grazed during this period. The last extensive fire (recorded at all three sites) at Wind Cave was in 1881 (Figure 3). Fire cessation may have been precipitated by livestock grazing that started around 1875 and continued until the Park was established in 1906. Geographical fragmentation caused by road and fence construction and cattle grazing in areas adjacent to the Park would also have stopped the spread of what would have formerly been landscape fire events. Active fire suppression after the Park’s establishment would have further contributed to fire exclusion from the landscape during recent decades.

A further complicating factor to understanding the driving factors of ecotonal change in the Black Hills savanna is that extensive bison (*B. bison*) herds are native to this area. Bison were extirpated from virtually the entire Northern Plains about the time of the introduction of livestock and later reintroduced to the Park in 1913 (Turner, 1974). The Park supports a large bison herd at the present time. The impacts of bison on dynamics of fire regimes in the Great Plains are not well understood. Herbivory by bison during the pre-settlement period may not be ecologically equivalent to herbivory by cattle since temporal and spatial patterns of disturbance tend to be different between the two species (Laurenroth & Milchunas, 1989). Bison traveled in large herds that likely moved on when resources were depleted. Laurenroth & Milchunas (1989) suggest that bison grazing was likely of heavy intensity but low frequency for a given area, whereas cattle grazing is high frequency but low intensity. Under a pre-settlement bison grazing regime, it is probable that grass fuels would have had time to recover between periods of herbivory, a pattern that could have led to frequent surface fires as found by this study (Figure 3).

By assuming that bison grazing in Wind Cave National Park over this past century is not ecologically equivalent to livestock grazing, this would exclude grazing as a significant control on the encroachment of ponderosa pine into grassland communities. It is likely that recent encroachment has been more the result of fire exclusion than possible shifts in competitive relationships between grasses and woody plants that resulted from grazing alone. The Park has begun to re-introduce prescribed fires in recent decades and these often kill ponderosa pine trees that established in what were formerly grassland areas (Bock & Bock, 1984). These results suggest that a return to historical patterns of fire regimes should restore the ecotonal mosaic to more of a pre-settlement configuration in the Wind Cave area.

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