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CLIMATE EFFECTS ON FIRE REGIMES AND TREE RECRUITMENT IN BLACK HILLS PONDEROSA PINE FORESTS

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Abstract. Climate influences forest structure through effects on both species demography (recruitment and mortality) and disturbance regimes. Here, I compare multi-century chronologies of regional fire years and tree recruitment from ponderosa pine forests in the Black Hills of southwestern South Dakota and northeastern Wyoming to reconstructions of precipitation and global circulation indices. Regional fire years were affected by droughts and variations in both Pacific and Atlantic sea surface temperatures. Fires were synchronous with La Niñas, cool phases of the Pacific Decadal Oscillation (PDO), and warm phases of the Atlantic Multidecadal Oscillation (AMO). These quasi-periodic circulation features are associated with drought conditions over much of the western United States. The opposite pattern (El Niño, warm PDO, cool AMO) was associated with fewer fires than expected. Regional tree recruitment largely occurred during wet periods in precipitation reconstructions, with the most abundant recruitment coeval with an extended pluvial from the late 1700s to early 1800s. Widespread even-aged cohorts likely were not the result of large crown fires causing overstory mortality, but rather were caused by optimal climate conditions that contributed to synchronous regional recruitment and longer intervals between surface fires. Synchronous recruitment driven by climate is an example of the Moran effect. The presence of abundant fire-scarred trees in multi-aged stands supports a prevailing historical model for ponderosa pine forests in which recurrent surface fires affected heterogenous forest structure, although the Black Hills apparently had a greater range of fire behavior and resulting forest structure over multi-decadal time scales than ponderosa pine forests of the Southwest that burned more often.

Key words: Atlantic Multidecadal Oscillation; crossdating; dendrochronology; El-Niño–Southern Oscillation; fire history; fire regime; Pacific Decadal Oscillation; precipitation variation.

INTRODUCTION

Projected future climate changes will likely affect complex biogeographic shifts as a result of effects on both species demography (recruitment and mortality) and disturbance regimes (Overpeck et al. 1990, Dale et al. 2001, Burkett et al. 2005). The ability of species to tolerate changes in temperature and moisture regimes will undoubtedly be confounded by alterations in disturbances (Burkett et al. 2005). For example, recent global-change-type drought coupled with widespread bark beetle outbreaks has caused massive die-off of piñon pine (*Pinus edulis*) and other tree species across large portions of the Colorado Plateau (Breshears et al. 2005, Mueller et al. 2005). Empirical and modeling studies have largely focused on species responses to drought and drought-related impacts on disturbances, such as increased fire frequency, fire severity, or insect outbreaks. However, precipitation changes are expected to be spatially variable, with some areas probably seeing increased moisture while others become dryer (e.g., Intergovernmental Panel on Climate Change 2001). Better understanding of potential response to increased moisture is as critical for predicting future vegetation patterns as is understanding responses to drought.

Prediction of vegetation change in response to climate change can benefit from paleoecological studies that document longer-term responses of plant communities to varying climate and disturbance regimes. Here, I compare chronologies of regional fire years and tree recruitment in ponderosa pine (*Pinus ponderosa* var. *scopulorum*) forests of the Black Hills of southwestern South Dakota and northeastern Wyoming to reconstructions of precipitation and global circulation indices over the past five centuries. My objectives are to evaluate temporal linkages between climate variations, fire years, and tree recruitment patterns, and to infer the role of climate in both fire occurrences and formation of regional forest structure over time. The climate reconstructions document large annual to multi-decadal variations over the time period encompassed by fire-year and tree-recruitment chronologies, and include both severe droughts and extended pluvial periods with which to develop inferences about climatic effects on long-term forest structural change.

This study also addresses important questions about the disturbance ecology and historical variability of Black Hills ponderosa pine forests. The dominant

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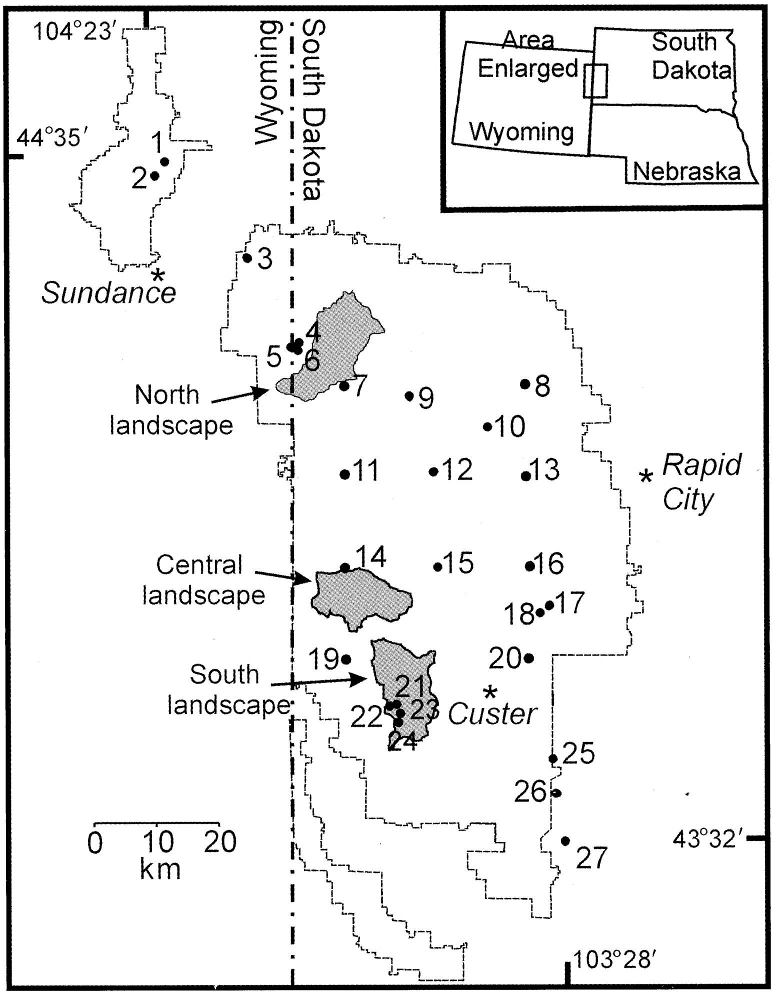

FIG. 1. Landscapes sampled for tree-recruitment data (shaded) and fire-scar site locations (numbered) in the Black Hills. The boundary of the Black Hills National Forest is marked by the dashed line.

disturbance regime in ponderosa pine forests across North America prior to Euro-American settlement in the 19th century consisted of recurrent surface fires (e.g., Swetnam and Betancourt 1998, Allen et al. 2002, Heyerdahl et al. 2002, Swetnam and Baisan 2003, Hessl et al. 2004, Brown and Wu 2005). However, early accounts from the Black Hills in the late 19th century document large areas of trees killed by fire (Graves 1899, Dodge 1965). Broad expanses of even-aged forest also were present at settlement and are thought to have been the result of widespread crown fires in the 1700s and early 1800s (Graves 1899, Shinneman and Baker 1997). Shinneman and Baker (1997) assert that a historical fire regime dominated by surface burning does not apply across much of the Black Hills landscape. This assertion has raised critical questions for both understanding ecological dynamics in Black Hills forests and for guiding forest management in this region. If crown fires and denser forest structure were fundamental features of the historical Black Hills forest, landscape-scale restoration of open, multi-aged forests and surface fire regimes as has been proposed for ponderosa pine forests in other regions (e.g., Allen et al. 2002) may be inappropriate.

METHODS

Study area

The Black Hills are a relatively isolated mountain range that rises over 1000 m above the surrounding mixed-grass prairies of the northern Great Plains. The main part of the range is in southwestern South Dakota with a smaller extension, the Bear Lodge Mountains, in northeastern Wyoming (Fig. 1). Elevations range from 1050 to 1350 m on the margins with the Great Plains to the highest point at 2207 m. The Black Hills support extensive ponderosa pine forests (Shepperd and Battaglia 2002). White spruce (*Picea glauca*) and aspen (*Populus tremuloides*) are occasional co-dominants of higher and wetter forests in the northern and central Hills. In most areas ponderosa pine is the only tree species present. Annual precipitation declines from about 740 mm in the north to about 480 mm in the south.

Euro-American settlement began after 1874. Prior to this, the area was home to the Lakota Sioux who apparently used the Black Hills only sporadically after the Prairie horse culture arose in the early to mid-18th century (Hassrick 1964). Less is known of the Native American history prior to this time. Intensive logging that began with Euro-American settlement has resulted in large areas of second-growth forest (Graves 1899, Shepperd and Battaglia 2002). The Black Hills National Forest Reserve (today the Black Hills National Forest) was the first federal forest preserve established in the United States in 1897, partly as a response to intensive and often wasteful timber practices up to that time (Graves 1899). Timber production is still a major use of much of the forest.

Tree-ring data

Tree-ring evidence is central to documenting historical fire regimes in ponderosa pine forests throughout its range (e.g., Heyerdahl et al. 2002, Swetnam and Baisan 2003, Hessl et al. 2004, Sherriff 2004, Brown and Wu 2005). These reconstructions rely on proxy evidence of fire timing and behavior recorded in long-lived trees. Fire history is typically reconstructed using two types of tree-ring evidence: (1) fire scars created during surface burning, and (2) recruitment dates of trees that potentially postdate crown-opening fires (Brown and Wu 2005).

For this study, I collected both fire-scar and tree-recruitment data. "Tree recruitment" refers to trees that established in the overstory and have persisted to the present, either as living trees or remnant trees (stumps, logs, or snags) that are able to be sampled. To reconstruct regional patterns of tree recruitment, trees were sampled from 37 plots across three landscapes on the Limestone Plateau, an area of rolling hills and canyons on the western margins of the main range (Fig. 1; Brown 2003). The Limestone Plateau has been cited as an area of extensive even-aged forest structure thought to have resulted from widespread fires (Graves 1899, Shinneman and Baker 1997). Landscapes were delineated on a precipitation gradient from wet to dry in the northern, middle, and southern portions of the Limestone Plateau (Fig. 1). Plots within each landscape were randomly chosen latitude/longitude coordinates and located in the field using a handheld GPS unit. *N*-tree distance sampling methods (Jonsson et al. 1992) were used to collect data from the nearest 30 presettlement trees to each plot center within a maximum plot radius of 40 m (~0.5-ha circular plot; Brown and Cook 2006, Brown and Wu 2005). Most plots were $\leq$0.25 ha in size (Brown 2003). Presettlement trees were defined as all remnant trees and living trees that either were not "blackjacks" (younger trees with primarily dark bark) or that were $\geq$30 cm dbh. Based on prior age sampling of ponderosa pine in the Black Hills, trees tend to have mainly dark bark (blackjacks) until about 75–100 years of age, after which it progressively changes to a buff or orange color. I assumed all blackjack trees and trees <30 cm dbh established post-settlement. Increment cores or cross sections were removed from 10 cm height on all trees in each plot. Because of past harvest in all but one plot in the northern landscape, many of the trees sampled were stumps (Brown and Cook 2006).

To reconstruct regional fire years, I compiled dates of fire scars found on the plot trees and additional data from fire-scarred trees collected at 27 other sites (Fig. 1; Brown and Sieg 1996, 1999, Brown et al. 2000, Brown 2003). These sites were selected to span elevational and moisture gradients present across the Black Hills and Bear Lodge Mountains. Older trees exhibiting multiple fire scars were selected at each site to develop the longest records of fire years (sensu Swetnam and Baisan 2003).

All cores and cross sections were dendrochronologically crossdated using locally developed master chronologies. Visual matching of ring characteristics and correlated measured ring widths were used to assure crossdating. If crossdating could not be determined, samples were not used in subsequent analyses. After crossdating of tree rings was completed on fire-scarred cross sections, dates were assigned to fire scars. On increment cores and cross sections that did not include pith but inside ring curvature was visible, pith dates were estimated using overlaid concentric circles of varying diameters that take into account both average inside ring widths and an estimated distance to pith. Plot and site chronologies were compiled using program FHX2, an integrated package for graphing and statistical analyses of fire and forest history data (Grissino-Mayer 2001).

Evaluating tree recruitment, fire year, and climate relationships

Tree pith dates from Limestone Plateau plots were combined to document regional patterns of tree recruitment from AD 1500. Pith dates at 10 cm height were first corrected to recruitment dates by subtracting five years, the average time estimated for seedlings to grow from germination to 10 cm height. This correction is based on height-growth measurements on open-grown ponderosa pine in the Front Range of central Colorado (P. M. Brown, W. D. Shepperd, and M. W. Kaye, *unpublished manuscript*) and estimation from nodal growth on seedlings in the Black Hills. A regional tree-recruitment chronology was developed from 5-yr sums of annual recruitment dates.

A regional fire-year chronology was developed from 51 site- and plot-level composite fire-year chronologies. Fire years included in each composite chronology are those recorded on $\geq$2 trees. Fire years recorded on only one tree were excluded since there may be false positives, scars not caused by fire but assumed to be fire scars (Falk 2004, Brown and Wu 2005), when determining fire dates. I assume that use of scar dates recorded on two or more trees in a stand minimizes the likelihood of false positives since it is less likely that other possible scarring mechanisms (e.g., lightning, fell-tree abrasions) affected more than one tree in an individual stand during the same year (Brown and Wu 2005). The regional fire-year chronology was made up of years recorded in ≥10% of the 51 site- and plot-level composite chronologies. Percentages of sites recording fire scars is assumed to be reflective of relative spatial scales of burning across the Black Hills during individual fire years.

Regional tree-recruitment and fire-year chronologies were graphically and statistically compared with two independently derived tree-ring based reconstructions of precipitation, two proxy indices of the El Niño-Southern Oscillation (ENSO), an index of the Pacific Decadal Oscillation (PDO), and an index of the Atlantic Multidecadal Oscillation (AMO). ENSO is a coupled atmosphere/ocean feature of the equatorial Pacific. PDO is an index of sea surface temperature (SST) anomalies in the North Pacific basin. Both ENSO and PDO have been associated with fire occurrence across the western United States through synoptic control of annual droughts that synchronize fire timing (Heyerdahl et al. 2002, Hessl et al. 2004, Brown and Wu 2005, Taylor and Beaty 2005, Sibold and Veblen 2006). AMO is an index of North Atlantic basin (0 to 70° N) SST anomalies that has recently been associated with droughts (McCabe et al. 2004, Sutton and Hodson 2005) and fire occurrence (Sibold and Veblen 2006) across the central and western United States. I used superposed epoch analysis (SEA; e.g., Brown and Wu 2005) to compare average annual climate conditions for the set of regional fire years to climate for the entire period of record. SEA also was used to compare climate during years prior to fire years to assess antecedent climate conditions that may be important for fire occurrence. Significant climate anomalies were determined using bootstrapped confidence intervals based on average annual climate values with the same number of years as regional fire-year data sets. Five climate reconstructions were used in SEA: (1) percentage of August-to-July mean precipitation from instrumental stations in the Black Hills and northern Great Plains (the reconstruction spans the period from 1596–1990; Stockton and Meko [1983], updated by D. M. Meko, *personnel communication*); (2) annual precipitation for the Bighorn Basin in north-central Wyoming (1260–1998; Gray et al. [2004*a*]); (3) Southern Oscillation Index (SOI; 1706–1977; Stahle et al. [1998]); (4) Niño3 SST (1408–1978; Cook [2000]); and (5) PDO (1661–1991; Biondi et al. [2001]). SOI is a commonly used measure of ENSO and is the difference in surface air pressure between Darwin, Australia, and Tahiti. The Niño3 index is average SST from mid-tropical Pacific recording stations, the region with the largest SST variability on ENSO (3 to 4 yr) time scales. I also tested for significant contingent states of reconstructed AMO (Gray et al. 2004*b*) with PDO and SOI on fire years recorded in ≥2 of the composite site- and plot-fire-scar chronologies. A chi-square test of expected vs. observed fire years was used to test each of eight annual combinations of anomalies (positive/negative) of the three climate indices (sensu Sibold and Veblen 2006). A larger set of fire years was used for this analysis to increase the number of observations available for the chi-square statistic. Finally, correlations were used to assess significant temporal agreement between 5-yr means of the two precipitation reconstructions to the regional tree-recruitment chronology.

Results

Tree-recruitment and fire-scar chronologies

I crossdated a total of 644 trees (of 720 trees sampled) from 24 plots in the middle and southern landscapes (Fig. 2). Plots were largely multi-aged, with at least a few older trees found with younger trees in almost every plot. An additional 110 mainly living trees (of 372 trees sampled) were dated from the northern landscape. However, I was not able to crossdate enough of the remnant trees from the northern plots to develop plot-level chronologies as in Fig. 2 (Brown 2003). The northern area is more mesic than either of the other landscapes and remnant trees did not have enough ring variability to crossdate with confidence. Although reliable pith dates were obtained on living trees from the northern landscape, results from the middle and southern landscapes showed that inclusion of data from stumps and other remnants is required for reconstruction of presettlement patterns of tree recruitment (Fig. 2; Brown 2003). Because of harvest of larger (and, thus, mainly older) trees from almost all stands, abundant living trees dating from the late 1700s to mid-1800s make the contemporary forest appear to be even-aged even though it was not at the time of initial harvest (Brown and Cook 2006).

All trees sampled were ponderosa pine except for three aspen from a single plot in the middle landscape. Many of the randomly selected plot trees, mostly stumps, recorded fire scars (Fig. 2). Heartwood of larger remnant ponderosa pine trees may last a very long time although erosion or burning of heartwood surfaces was evident on older logs or snags (almost no stumps had been burned because of fire cessation after harvest; see Plate 1). An additional five trees that dated before 1500 from plots 201, 203, and 207 are not shown in Fig. 2. Of these trees, three logs had pith dates of 1190, 1192, and 1206 and are the oldest known tree-ring dates from the Black Hills.

Composite fire chronologies from an additional 276 trees collected from the 27 fire-scar sites (Fig. 1) and fire scars recorded on trees from the 24 plot chronologies from the middle and southern landscapes are summarized in Fig. 3a. The most extensively recorded regional fire year was 1785. There was variability in frequency of regionally synchronous fires throughout the record. Regionally synchronous fires increased in the late 1800s, and fire scars were generally absent after circa 1890.

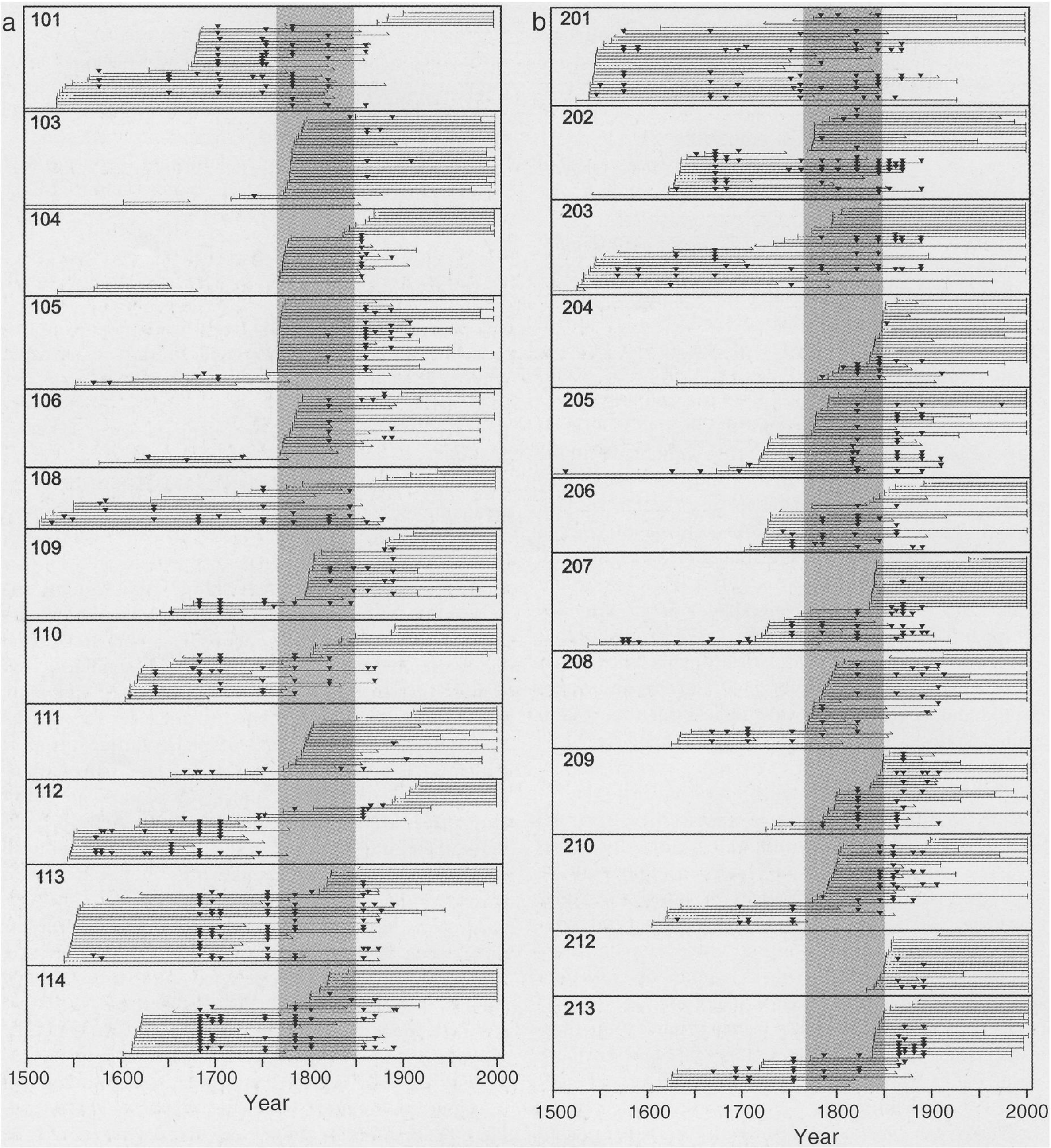

FIG. 2. Tree-recruitment chronologies from plots sampled in the (a) middle and (b) southern landscapes. Numbers in each panel refer to plot designations from Brown (2003). Horizontal lines mark time spans of individual trees, with dates of fire scars marked by inverted triangles. Dashed lines are the estimated number of years to 10-cm height pith dates. Vertical lines to the left are pith dates, with inside dates (i.e., unknown number of years to pith) marked by slanted lines. Vertical lines to the right are bark dates (death dates in remnant trees), with outside dates (i.e., unknown number of years to death date) marked by slanted lines. Vertical gray bars in each panel mark the period from 1770 to 1850 when a majority of regional tree recruitment occurred.

Climate, fire, and tree recruitment

Regional tree recruitment largely occurred during distinct episodes that were coeval with pluvial periods in the northern Great Plains and Bighorn Basin precipitation reconstructions (Fig. 3b). Recruitment dates occurring in the combined 120 years between 1520–1549, 1610–1639, 1770–1799, and 1830–1859 account for ~80% of all recruitment dates during the 401-yr period between 1500 and 1900. The most abundant pulse of establishment in the late 1700s occurred during the wettest extended period in the precipitation records and followed the most intense drought in the Great Plains record from circa 1752 to 1762. The tree-recruitment

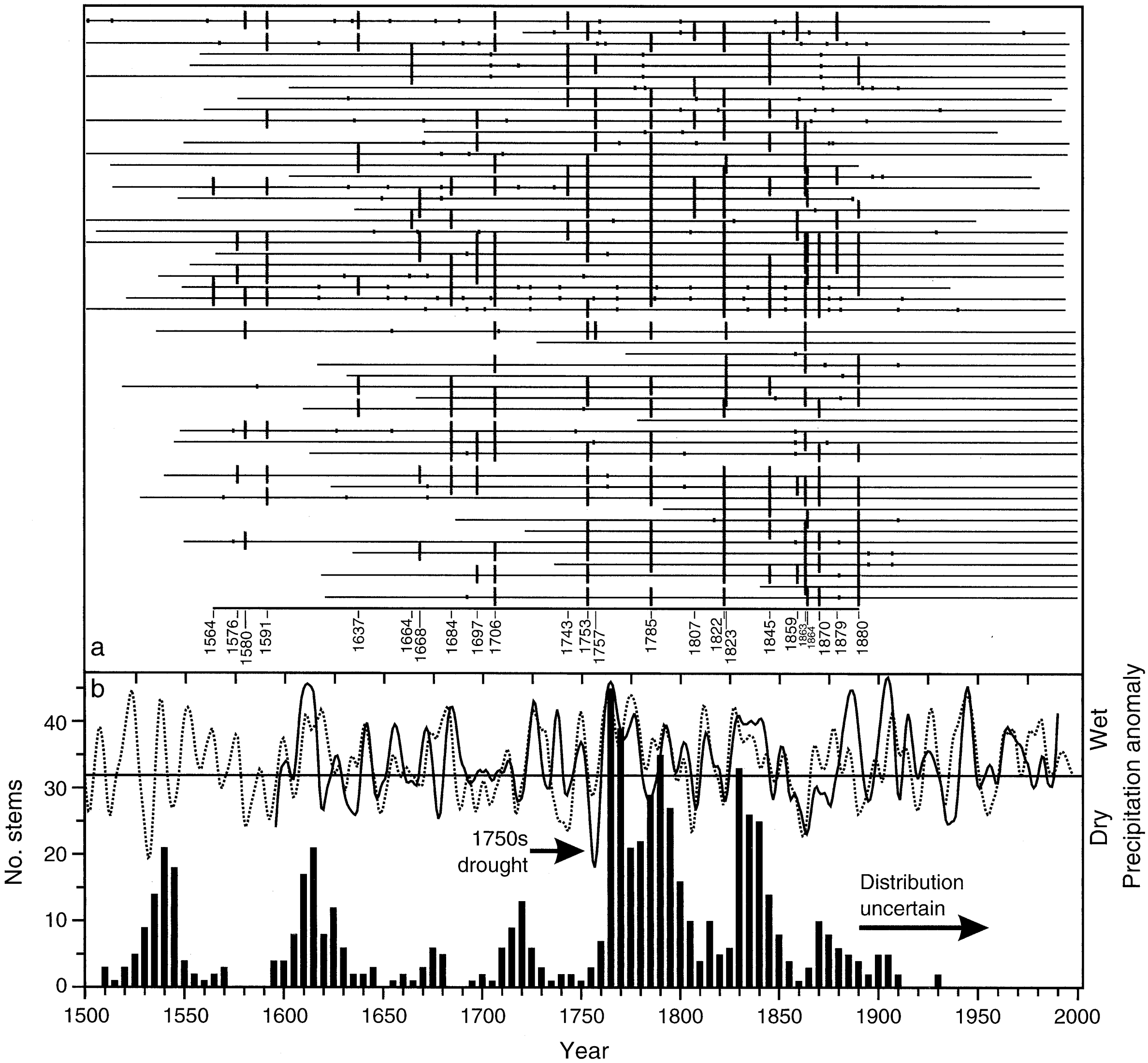

FIG. 3. (a) Composite fire-scar chronologies from 51 sites and plots. Horizontal lines mark time spans of chronologies. Long vertical lines mark regional fire years recorded on ≥10% of composite chronologies. Short vertical lines mark fire years recorded on <10% of composite chronologies. Regional fire years are listed at the bottom of the chronologies. (b) Regional tree recruitment chronology (histograms) with Great Plains (solid line) and Bighorn Basin (dotted line) precipitation reconstructions. The precipitation reconstructions have been smoothed with 10-yr smoothing splines to emphasize multi-annual variations and are plotted as standard deviation departures from the mean to show relative wet and dry anomalies. The distribution of tree recruitment dates after the late 1800s is uncertain since only presettlement trees were sampled.

chronology was significantly correlated with 5-yr averages of both the Great Plains precipitation reconstruction (1596–1900; $N = 61$, $r = 0.32$, $P = 0.015$) and the Bighorns Basin reconstruction (1500–1900; $N = 80$, $r = 0.31$, $P = 0.006$).

SEA documents that regional fire years were significantly dry on average (Fig. 4a, b). No significant lagged relationships were seen between years prior to fire years and precipitation variability. Fire years were on average La Niña years (high SOI, low SST; Fig. 4c, d). Fire years, coupled with one year prior and two years following, also were on average years of significantly cool-phase PDO (Fig. 4e). There was a strong association of fires with contingent phase combinations of climate indices, with significantly more fires from 1706 to 1900 occurring during years of combined warm (positive) AMO, cool (negative) PDO, and warm (positive) SOI (Table 1). Significantly less fires occurred during years of the opposite pattern (Table 1).

Discussion

Climate effects on regional fires

This study extends to the Black Hills the importance of drought and an emerging recognition of the central

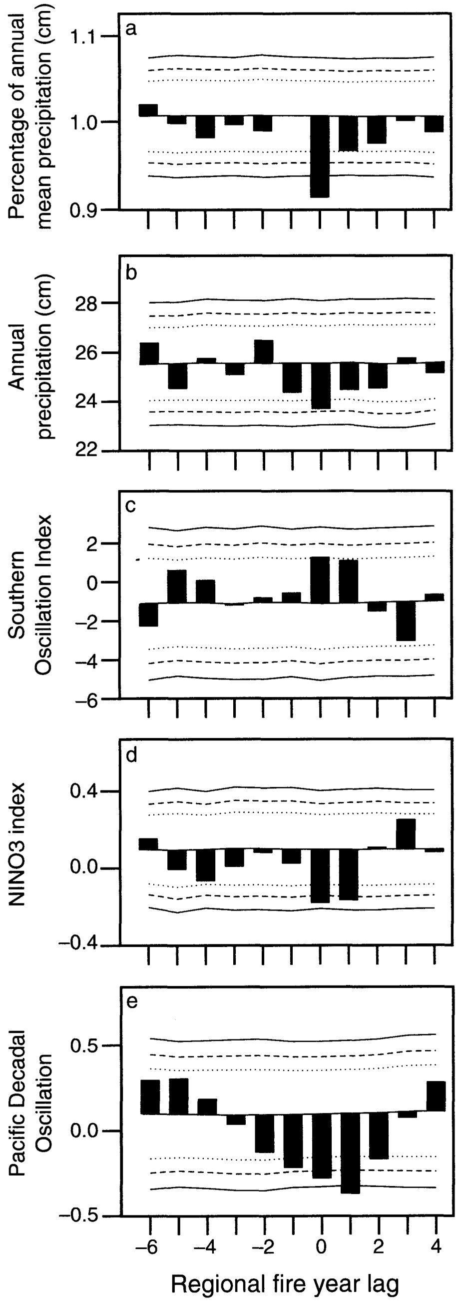

FIG. 4. Superposed epoch analyses (SEA) of average precipitation and circulation anomalies for regional fire years listed in Fig. 3a. (a) Great Plains precipitation (Stockton and Meko 1983; updated by D. M. Meko, *personal communication*); (b) Bighorn Basin precipitation (Gray et al. 2004*a*); (c) SOI (Southern Oscillation index; Stahle et al. 1998); (d) Niño3 SST (sea surface temperatures; Cook 2000); and (e) PDO (Pacific Decadal Oscillation; Biondi et al. 2001). Horizontal lines in each panel mark significant departures based on bootstrapped confidence intervals (dotted, $P < 0.05$; dashed, $P < 0.01$; solid, $P < 0.001$). SOI is reversed in terms of moisture relative to other series (dry years are high SOI, or La Niña years). Fire year lag 0 is the average climate anomaly for regional fire years, with antecedent conditions indicated by negative lags; *y*-axis units are relative anomalies from mean for each index.

role of both Pacific and North Atlantic SST anomalies on regional fire occurrence across western North America (Fig. 4, Table 1; Heyerdahl et al. 2002, Hessl et al. 2004, Brown and Wu 2005, Taylor and Beaty 2005, Sibold and Veblen 2006). Regional fire years in the Black Hills were strongly associated with droughts in both the Great Plains and Bighorn Basin precipitation reconstructions (Fig. 4a, b). No lagged relationships with prior moisture conditions were seen in SEA, which suggests that buildup of grasses and herbaceous fuels during antecedent wet years was not necessary for regional fire occurrence. This is in contrast to wet/dry oscillations typically associated with large fire years in ponderosa pine forests of the Southwest (e.g., Brown and Wu 2005). Fire frequency was generally less in the Black Hills than in the Southwest and it is likely that longer intervals between fires led to enough fine fuel accumulation that sufficient fuel drying was the only condition needed for widespread burning to have occurred (Brown 2003).

Regional fires also were strongly associated with synoptic climate features that affect drought occurrence across the western United States. Regional fires were associated with both La Niña years (positive SOI, negative Niño3 SST; Fig. 4c, d) and cool phases of the PDO (Fig. 4e). La Niñas are associated with summer-dry conditions in the Northern Plains Region (Bunkers et al. 1996), and droughts in the central United States are magnified when La Niñas occur during periods of negative PDO (McCabe and Dettinger 1999). Additional contingent states of climate system effects on fire occurrence are seen with the inclusion of AMO. The strongest signal for total fire occurrence between 1706 and 1900 was the combination of La Niñas, cool phases of the PDO, and warm phases of the AMO (Table 1). Warm AMO, especially when coupled with negative PDO, contributed to broad-scale summer droughts over the central US (McCabe et al. 2004, Sutton and Hodson 2005). Both the PDO and AMO have recently been identified as probable low-frequency (multi-annual to multi-decadal) drivers of fire occurrence across western North America (Hessl et al. 2004, Taylor and Beaty 2005, Sibold and Veblen 2006), and results from the Black Hills confirm findings from these other studies. The opposite combination of cool AMO, warm PDO, and El Niños (low SOI) led to fewer fire years than expected, probably because of increased moisture over this region. Because these circulation indices are quasi-periodic and their effects on regional climate generally predictable, advance forecasting of fire years and their likely severity across the Black Hills may be possible based on findings reported here.

Climate and fire effects on regional tree recruitment

Regional pulses of tree recruitment from 1500 to 1900 were largely coeval with pluvial periods in the northern Great Plains and Bighorn Basin precipitation reconstructions (Fig. 3b). Extended wet conditions with fewer

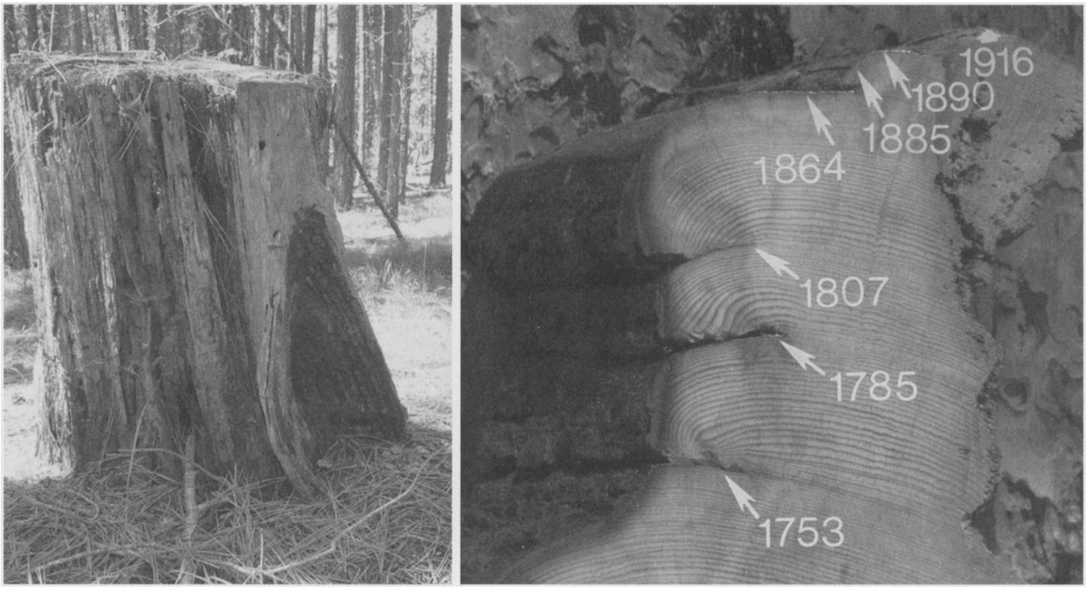

PLATE 1. (Left) A ponderosa pine stump with a "cat face" formed from repeated fire scars (visible as distinct ridges in the cat face). Bark and sapwood have eroded from the outside of the stump, and only the heartwood is left. The stump was cut with a crosscut saw, placing the date of cutting in the late 19th or early 20th centuries before widespread use of motorized chainsaws. (Right) Cross-section sample from a fire-scarred ponderosa pine snag (standing dead tree). The tree died in 1916 from a bark beetle attack as evidenced by bluestain in the sapwood. Photo credit: P. M. Brown.

droughts would have promoted seedling establishment, less seedling mortality from drought stress, and faster tree growth. Much of the presettlement forest dates from an extended pluvial that lasted from circa 1770 to 1850, the wettest period in both the Great Plains and Bighorn Basin reconstructions (see also Pederson et al. 2004). Cohorts in the Black Hills during this period also were contemporaneous with abundant recruitment in ponderosa pine forests in the Bighorn Mountains (P. M. Brown, *unpublished data*) and in the Bighorn Basin (Wentzel 2005) to the west of the Black Hills in Wyoming. The presence of synchronous recruitment over such a broad region is an example of the Moran effect (Moran 1953), in which widespread synchronization of population dynamics is affected by a strong exogenous factor, in this case optimal pluvial conditions in typically dry ponderosa pine forests.

Abundant synchronous tree recruitment affected by optimal climate forcing is probably the reason for extensive stands of even-aged forests in the Black Hills, rather than widespread crown fires as postulated by Shinneman and Baker (1997). Shinneman and Baker base their contention of extensive crown fires on age data and conclusions previously presented by Graves (1899). Graves, in an early survey of timber resources in the Black Hills, compiled an unknown amount of non-crossdated age data and ring counts to fire scars found on stump tops to propose that extensive crown fires occurred in the late 1700s and early 1800s, the largest of which he suggested occurred around 1790. The most widespread fire year found by this study was 1785 (Fig. 3a). This is likely the same fire date as estimated by Graves, and the extensive even-aged cohorts he found were undoubtedly the same found by this study dating from the late 1700s and early 1800s. However, crossdated tree-ring data document that abundant tree recruitment synchronous with pluvial conditions began before 1785 (Figs. 2 and 3b) and, thus, cannot be the result of crown opening from burning during 1785. Furthermore, crossdated data document that almost all

TABLE 1. Expected vs. observed numbers of fire years recorded in more than two composite fire-scar chronologies (Fig. 3a) from 1706 to 1900 ($N = 44$) for eight phase combinations of the AMO (Atlantic Multidecadal Oscillation; Gray et al. 2004*b*), PDO (Pacific Decadal Oscillation; Biondi et al. 2001), and SOI (Southern Oscillation Index; Stahle et al. 1998).

Case	AMO − PDO − SOI −	AMO − PDO − SOI +	AMO − PDO + SOI −	AMO + PDO − SOI −	AMO + PDO + SOI +	AMO + PDO + SOI −	AMO + PDO − SOI +	AMO − PDO + SOI +
Observed	5	6	3	5	4	6	11	4
Expected	5.4	6.1	8.8	3.2	4.1	5	6.1	5.4
Difference	−0.4	−0.1	**−5.8**	1.8	−0.1	1.0	**4.9**	−1.4

Note: Bold numbers are significantly different ($P < 0.1$) in the chi-square test.

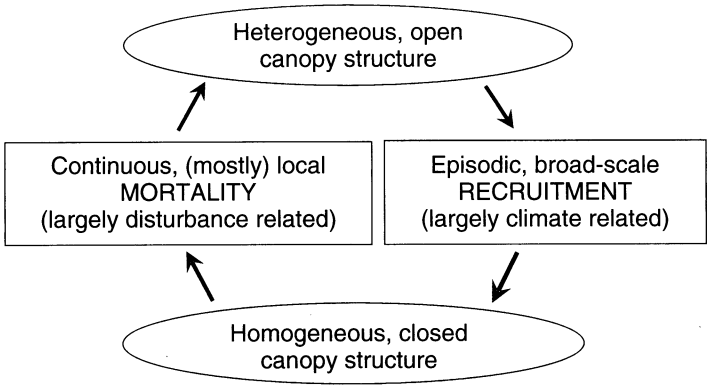

FIG. 5. A model for regional scale, multi-decadal, process-pattern linkages in Black Hills ponderosa pine forests. Heterogenous, mostly open forest structure is promoted and maintained by recurrent surface fires, droughts, and other disturbances that affect both episodic and continuous mortality on spatiotemporally varying scales. Open stands allow for abundant new trees to establish when climate forcing affects episodic, broadscale recruitment opportunities. Successful synchronous recruitment results in more homogenous, closed-canopy forest conditions for some length of time until patchy mortality results in open canopy conditions again. To put specific dates on each segment, the top condition prevailed prior to the extended pluvial of the late 1700s and early 1800s (box to the right). The bottom condition is what largely prevailed at the time of Euro-American settlement in the late 1800s. Natural disturbance processes likely would have returned the forest to the heterogeneous, open condition except for disruption by land use changes, including fire suppression and timber harvest, that accompanied Euro-American settlement beginning in 1874.

stands with trees that recruited during the 1700s and early 1800s pluvial contained trees that predated this period (Fig. 2), indicating that even if the cohort established in response to a severe fire event there was not complete canopy kill within plot boundaries (most of which were ≤.25 ha in size; Brown 2003, Brown and Cook 2005).

Trees existing at the time of cohort establishment suggest that stands were open enough for seedling recruitment to occur during the late 1700s–early 1800s pluvial (Fig. 5). Variation in tree ages in multi-aged stands would have resulted from continuous, long-term patch dynamics that included both individual and clumped (in both space and time) tree mortality by any number of factors, only one of which may have been lethal fire but also including drought stress or other disturbances such as insects, pathogens, windthrow, or lightning (Brown and Wu 2005). In the case of the late 1700s–early 1800s pluvial, this period followed the most intense drought in the Great Plains reconstruction from circa 1752 to 1762 (Fig. 3b). It is probable that this drought contributed to open conditions in many stands via both direct tree mortality from drought stress and possibly drought-related disturbance effects, such as mortality of individual trees or small patches of trees during surface fires or from outbreaks of mountain pine beetles (*Dendroctonus ponderosae*). Mountain pine beetles have been a major disturbance agent in the Black Hills during the 20th century, often causing widespread tree mortality (Shepperd and Battaglia 2002; see Plate 1). However, any trees that may have died during the 1750s drought did not contain sapwood because of decay (Fig. 2), and the presence of evidence such as bluestain indicating the possible role of bark beetles in widespread mortality during this period cannot be verified.

Variations in fire timing and frequency also likely contributed to increased survivorship of trees during climatically optimal recruitment episodes such as the late 1700s and early 1800s (Brown and Wu 2005). Longer intervals between surface fires are generally associated with cohort establishment in individual stands (Fig. 2), and regionally synchronous cohorts largely occurred during periods between regional fire dates (Fig. 3). Most seedlings and smaller trees are killed by surface fires, and longer intervals between fires would have permitted more trees to survive to reach canopy status. Trees in many southwestern ponderosa pine forests date to fire-quiescent periods in the 1700s and early 1800s (e.g., Swetnam and Betancourt 1998, Brown and Wu 2005). It is likely that variations in fire frequency and timing were more critical to structuring the historical forest than variations in fire severity as hypothesized by Shinneman and Baker (1997).

Disturbance ecology in Black Hills ponderosa pine forests

Abundant fire scars recorded on trees in all stands provide evidence that surface fires were common disturbances in Black Hills ponderosa pine forests prior to Euro-American settlement (Figs. 2 and 3a; Brown and Sieg 1996, 1999, Brown et al. 2000, Brown 2003). Mature ponderosa pine trees are well adapted to survive surface burns, with thick bark that generally protects vascular cambium from mortality and high crowns that lessen the possibility of crown scorch. The main effect of recurrent surface fires was to kill a majority of tree regeneration, limiting the number of seedlings that ultimately were able to reach maturity. Surface fires, because they were primarily driven by climatic variations (Fig. 4) and not by overstory tree density, acted as a density-independent mechanism for population regulation in ponderosa pine forests (Brown and Wu 2005). Historic accounts and early settlement photographs of ponderosa pine forests both in the Black Hills and throughout the West document often "park-like," open, multi-aged, forest stands, composed of large trees scattered across grassy understories (e.g., Graves 1899, Allen et al. 2002, Grafe and Horstead 2002). Individual seedlings or patches of seedlings were occasionally able to survive to reach maturity because of spatiotemporal heterogeneity in burning. However, even more important to regional forest structure were broad-scale variations in climate regimes that resulted in conditions optimal for seedling survival and growth and that resulted in fewer surface fires (Fig. 3; Brown and Wu 2005).

Much of the historical fire regime and resulting forest structure that has been reconstructed from the Black Hills fits with a dominant model of ponderosa pine ecosystems largely developed from the Southwest (e.g., Allen et al. 2002). In this model, recurrent surface fires resulted in broad areas of typically open, multi-aged forest stands. However, the Black Hills apparently contained a coarser-scale mosaic of dense to open stands and a greater range of variation in landscape structure over multi-decadal time scales than what was present in the Southwest, largely related to the abundant tree recruitment that occurred during the late 1700s and early 1800s (Fig. 5). These dense stands were still present at settlement (Brown and Cook 2005), and likely contributed to extensive patches of crown fire noted by early explorers and scientists during the late 1800s (Dodge 1965, Graves 1899). More extensive patches of denser trees would have contributed to ladder and canopy fuel conditions that permitted more sustained crown fire behavior across larger areas, especially given the increase in regional fire frequency in the late 1800s (Fig. 3a). However, over longer time scales, the dominant fire regime largely consisted of recurrent surface fires that contributed to and maintained heterogenous, multi-aged forest structure at both stand and regional scales (Figs. 2 and 3).

The pervasive cessation of fires that began in the early 20th century (Fig. 3a) corresponds to patterns found in virtually all ponderosa pine forests across western North America (Swetnam and Baisan 2003, Swetnam and Betancourt 1998, Allen et al. 2002, Hessl et al. 2004, Brown and Wu 2005). Fire cessation resulted from changes in land use that accompanied settlement, including livestock grazing that reduced grass and herbaceous fuels through which surface fires spread and, later in the twentieth century, active fire suppression by land management agencies. And as in ponderosa pine forests of other regions, fire cessation coupled with other impacts such as timber harvest has led to denser and more homogeneous forest structure across the Black Hills landscape (Brown and Cook 2005). Because of this shift in landscape patterns, restoration of open forest structure and multi-aged stands across large portions of the Black Hills is supported by all available historical evidence. Dense stands will likely always be present in any future forest, but what is largely missing are mosaics of open stands of variable density. However, forest management in this and other regions also must recognize that future climate change will likely lead to complex population dynamics and shifts in disturbance regimes that will complicate ecological restoration efforts (e.g., Burkett et al. 2005). Perhaps the best that forest management can do at this time is to restore as much ecosystem resiliency as possible such that ecosystem structure and function can be retained in the face of future climate change. In ponderosa pine forests throughout its range in western North America, these efforts must include restoration of surface fire regimes and resulting heterogenous forest structure.

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