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DISTURBANCE AND STAND DYNAMICS IN PONDEROSA PINE FORESTS IN ROCKY MOUNTAIN NATIONAL PARK, USA

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Abstract. Fire is thought to be the dominant disturbance agent in pure ponderosa pine (*Pinus ponderosa* Laws.) forests, but fire severity and disturbances other than fire, and the effects of these events over time, have rarely been analyzed. We first created systematic criteria to (1) identify the causes of tree regeneration and mortality events and (2) classify the severity of these events. These criteria were then applied to understand the effect of events on ponderosa pine forests in Rocky Mountain National Park (RMNP), Colorado.

For each of nine intensive study plots sampled in the pure ponderosa pine zone of RMNP, we mapped and dated live and dead trees and the spatial extent of fire and non-fire events using dendrochronology. Events were identified using evidence of disturbance agents, such as blue-stain fungus in the case of mountain pine beetles, fire scars, and climatic reconstructions. Disturbance severity was classified based on amounts and spatial distribution of regeneration, mortality, and survivors. We studied the temporal and spatial relationships between events and tree age structures to determine historical and contemporary stand dynamics.

We identified 103 events among the nine study plots; 97% of these events were fire. High-severity events were 7% of events, 2% of events were mixed-severity, and the other 70% were low-severity. The severity of 20% of events could not be determined. All but one of the high-severity events were fire. In seven plots, at least one crown fire occurred within the last 300 years. In RMNP, pre-EuroAmerican settlement crown fires led to dense, even-aged stands. Subsequent surface fires killed some trees and facilitated the regeneration of others, leading to less dense, uneven-aged stands after ~200–300 years. Climate may be the cause or co-cause of one or two regeneration pulses within the last 300 years, but most regeneration and mortality is associated with fire. The historical occurrence of crown fires, as well as surface fires, in pure ponderosa pine forests in RMNP indicates that the fire regime is more variable than previously thought. Suppression of crown fires, though not completely possible, would move the fire regime outside its historical range of natural variability.

Key words: crown fire; disturbance severity; Pinus ponderosa; *ponderosa pine; range of natural variability; Rocky Mountain National Park (USA).*

INTRODUCTION

A large body of ponderosa pine (*Pinus ponderosa* Laws.) research from the southwestern United States (Arizona, New Mexico) has culminated in efforts to restore historical structure and function of ponderosa pine forests to a state within its range of natural variability (Swanson et al. 1994, Landres et al. 1999), or as close as possible considering modern constraints (Covington et al. 1997, Moore et al. 1999). Reconstructions of historical fire frequency, age structures, and stand density have been used to provide baseline data for restoration efforts in the Southwest (Fulé et al. 1997, Mast et al. 1999). Generally, southwestern ponderosa pine forests are thought to have experienced only high-frequency, low-severity fires (Weaver 1959, Cooper 1960, Biswell 1972, Harrington and Sackett 1992, Covington and Moore 1992). Density and spatial pattern of trees in these ponderosa pine forests vary with site-specific environmental conditions, but have in common an open, grassy understory (Moore et al. 1999). Frequent low-severity fires are thought to have thinned young trees and reduced the potential for crown fire (e.g., Covington and Moore 1992). Fire suppression is commonly thought to have led to forests with a dense understory of small trees that increases the likelihood of crown fires (Cooper 1960, Covington and Moore 1992, 1994*a, b*). Because much research in ponderosa pine forests has been done in the Southwest, a paradigm based on these forests has emerged. However, there is evidence that the age structures and disturbance dynamics of ponderosa pine forests throughout their geographical range are more variable than in the Southwest (Shinneman and Baker 1997).

It remains unclear how fire and other disturbances contribute to geographic variation in ponderosa pine forest structures. Fire, for example, has been cited as having dual roles in preparing mineral seedbeds that

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facilitate regeneration (Show and Kotok 1924, Cooper 1960, Sackett 1984, White 1985) and in killing young trees and preventing dense understories (Show and Kotok 1924, Cooper 1960, Covington and Moore 1992, 1994*a*, *b*). Cooper (1960) hypothesized that apparently even-aged tree groups regenerated in openings, and that this pattern was maintained by surface fires. In contrast, White (1985) documented uneven-aged groups, hypothesizing that individual trees were killed and consumed by surface fires, creating a seedbed for regeneration. Yet, these studies lacked data on disturbance history and the correlation of the spatial extents of disturbances and tree ages. A direct link between fire and the age structure and spatial distribution of trees remains elusive.

Fire history and age structure studies by themselves often leave unanswered questions about stand dynamics, and related methodological and interpretive issues are problematic. Fire history studies are usually conducted over large areas and provide coarse-scale fire data (e.g., Savage and Swetnam 1990). Age structure reconstructions usually include only live trees, often subjectively judged to have originated prior to EuroAmerican settlement, and ignore smaller trees (Fulé et al. 1997, Mast et al. 1999) and dead wood (White 1985, Covington and Moore 1994*a, b*). Some researchers have begun to collect fire-history and age-structure data from the same sampling locations (Mast et al. 1999). However, it is difficult to infer the degree of influence that fire has on age structure without fine-scale fire data, tree establishment and death data, and spatial information about both. It is also difficult to determine the chronology of past disturbance events, fire severity, and spatial extent of past disturbances without studying dead wood.

Fire is thought to be the dominant natural disturbance agent in ponderosa pine forests (Cooper 1960, Covington and Moore, 1994*a*, *b*), but little effort has been directed toward determining fire severity. Most early foresters assumed that only surface fires occurred based on ''ubiquitous'' fire scars (e.g., Weaver 1943), as well as the generally open canopy, especially in the Southwest. However, while widely spaced trees in pure ponderosa pine stands were described as being common, the occasional occurrence of areas with dense growth was also mentioned (Show and Kotok 1924). Crown fires likely occurred in pure ponderosa pine forests in the Black Hills of South Dakota and Wyoming (Shinneman and Baker 1997), and some even-aged stands in the Northwest may have been caused by crown fires (Weaver 1943). Crown fires have been documented in mixed-conifer forests containing ponderosa pine in Colorado (Brown et al. 1999), but crown fires in mixed-conifer forests are not an unusual occurrence (Arno et al. 1995). A review of pure ponderosa pine forests suggests that very sparse forests in Colorado would not have supported crown fires, but some crown fires may have occurred in denser stands (Veblen 2000). This is suggested by early historical photographs, which show that stand-replacing fires occurred near or somewhat before the time of EuroAmerican settlement (Veblen and Lorenz 1986). Also, Mast et al. (1998) identified even-aged cohorts consistent with postfire regeneration close to our study plots, but did not identify crown fires as the cause (Mast et al. 1998). That crown fires occurred before EuroAmerican settlement thus is probable, but their prevalence and importance remain unknown, largely due to insufficient study, as well as the assumption that crown fires are not natural in ponderosa pine forests (Baker and Ehle 2003).

Some early foresters noted non-fire disturbance agents in ponderosa pine forests. Weaver (1943, 1961) argued that even-aged groups within an all-aged forest regenerated after crown-killing events such as insect outbreaks, windthrow, or fire. Seedlings germinated after these events in the newly created openings. Subsequent surface fires kill some or all of these seedlings and consume the original beetle-killed or windthrown trees. When the seedlings are old enough or tall enough to survive surface fires, they are thinned by fires or by insects. Young trees that survive these attacks are then susceptible to windthrow or insects, and the process repeats. Disturbance agents other than fire may also kill trees over relatively large areas. Weaver (1943:9), for example, noted a pine white butterfly (*Neophasia menapia* Felder) outbreak that ''. . . killed a major portion of the ponderosa-pine stand on several townships of the Yakima Indian Reservation on the east slope of the Cascades in southern Washington'' in the early 1900s.

There are three major categories of disturbance known in ponderosa pine forests in our study area: fire, mountain pine beetle (*Dendroctonus ponderosae*) and associated blue-stain fungus (*Ophiostoma* spp.), and windthrow. These agents are capable of acting as stand-replacing events, and potentially leave long-term evidence of their presence. Mountain pine beetles carry blue-stain fungus on their bodies, and trees are essentially inoculated with the fungus when the beetles penetrate the cambium to lay their eggs. The sapwood of trees may be blue-stained 2–3 wk after infestation by mountain pine beetles (Hansen and Lewis 1997). Single pieces of dead wood from isolated tree deaths that contain blue-stain fungus may not have been actually killed in mountain pine beetle epidemics, as nonlethal, endemic-level infestations of mountain pine beetles also result in blue-stain fungus inoculation. When a number of trees is killed by a wind event, they will all tend to lie in the same direction. However, when individual trees are windthrown, it is virtually impossible to discern the mortality agent in retrospect, as no long-term evidence remains that can be used to identify the disturbance agent with confidence. Other agents such as lightning, drought, western gall rust (*Endocronartium harknessii*), Comandra blister rust (*Cronartium comandrae*), Armillaria root disease (*Armillaria* spp.), and dwarf mistletoe (*Arceuthobium* spp.), also kill trees (Hawksworth and Wiens 1996, Hansen and Lewis 1997). However, these agents usually kill individual trees, or they do not leave long-term evidence of their presence.

Climate is also a potential agent of change in ponderosa pine forests in RMNP. Episodes of favorable or unfavorable climate (i.e., wet periods, droughts) can promote regeneration or mortality of ponderosa pine (Savage et al. 1996, Allen and Breshears 1998). When a large tree-regeneration pulse or some mortality is present, it can be difficult to determine the potential role of climate. Instrumental climate records do not extend far back in time. Thus, standardized tree-ring widths from chronologies are often used as an indicator of past climate (Mast et al. 1999) or climate is reconstructed (Grissino-Mayer 1996).

The goals of this study are to (1) determine disturbance histories of stands of pure ponderosa pine by creating and applying systematic criteria to identify fire, wind, mountain pine beetle (*Dendroctonus ponderosae*), and climate events, (2) classify the severity of those events using numeric and spatial criteria, and (3) examine how disturbance history and severity, and climate and fine-scale spatial patterns of regeneration and mortality have shaped historical and present ponderosa pine stands. An understanding of the historical dynamics of these forests increases the chances of effective management geared toward keeping these forests within their range of natural variability in the face of changing conditions, such as climate and resulting fire regimes.

METHODS

Field research was conducted in 1999 in pure ponderosa pine forests of Rocky Mountain National Park (RMNP), Colorado, in stands away from the pine–grassland ecotone. Sampling was restricted to pure ponderosa forests, because the presence of other tree species may alter the fire regime and stand dynamics. An age-structure study was conducted at the pine–grassland ecotone (Mast et al. 1998), but not in stands on higher slopes. Elevation range of pure ponderosa pine forests in RMNP is ~2100–3000 m. Climate for Estes Park at 2293 m is based on data since 1961, where mean annual precipitation is 36 cm, with the highest levels in May and July. Maximum mean daily temperature of 26°C occurs in July, and minimum mean daily temperature of −9°C occurs in January. Mean annual snowfall is 86 cm (Western Regional Climate Center).[2] RMNP is affected by the North American monsoon, which causes almost daily afternoon lightning and thunder storms from July through September (Adams and Comrie 1997).

Settlement in Estes Park, just outside RMNP, began in 1860 with one family (Buchholtz 1983). Organized fire suppression began in 1915, the year the park was established, when the park superintendent began issuing firewood cutting permits (in a subalpine forest stand) to area residents with the understanding that permittees were to help suppress fires (U.S. National Park Service, Superintendent Monthly Report, on file in the RMNP library). Historical periods used here are: (1) pre-EuroAmerican settlement, before 1860, (2) settlement, 1860–1914, and (3) suppression, 1915–present.

Field plots

Sampling locations were identified using a stratified-random design based on two categories of aspect (north and south) and three categories of geologic substrate (Biotite schist, Silver Plume granite, and glacial till/alluvium/dikes) to evaluate the influence of aspect and/or geologic substrate on age structure and disturbance history. Digital maps of the ponderosa pine zone, geology, and a digital elevation model were obtained from RMNP and entered into the GRASS GIS (U.S. Army Construction Engineering Research Laboratory [USA-CERL] 1997). The GRASS r.le.setup program (Baker and Cai 1992) was used to place the stratified-random samples. Sampling locations were placed a minimum of 200 m apart (Fig. 1), and potential locations at the pine–grassland ecotone and within 200 m of a road or trail were rejected. Paired plot samples were used when forests in the vicinity of a randomly located sampling location appeared to have two different stand structures. UBMN and UBMS, and HPW and HPE are the two sets of adjacent paired sampling locations. Table 1 has names and abbreviations of sampling locations. Plots were well distributed within the pure ponderosa pine zone in RMNP.

At each sampling location, age-structure plots were nested within fire-scar plots. All trees visibly scarred by fire within a 50 × 50 m fire-scar plot were located, and increment cores or a wedge was removed from each to date fires (Arno and Sneck 1977, Sheppard and Lassoie 1986, Means 1989). When scars were increment bored, cores from each healing curl of the scar(s) were removed, and a core without a fire scar was also taken from the base of the tree. Age-structure plots originated in a randomly chosen corner of each fire-scar plot and extended to the size necessary to encompass a minimum of 50 live trees (DME is an exception with only 35 live trees). Locations of the corner where the age-structure plot originated and all fire scars outside the age-structure plot (but inside the scar plot) were documented with a Global Positioning System (GPS). All GPS positions were differentially corrected. All live, standing-dead, and dead-and-down trees were mapped using an x, y coordinate system. Distances were measured with an electronic distance meter (Sonin, Scarsdale, New York, USA).

Scar-centered plots, a third type of plot, were sampled to determine whether the regeneration from a fire

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[2] URL: ⟨www.wrcc.dri.edu⟩

occurs in the immediate vicinity of where the fire is documented by a scar. Scar-centered plots were created by centering a 10 m diameter circle on a subset of fire scars within fire-scar plots. Within the circle, the distance and azimuth of each tree from the center fire-scarred tree was recorded. Live and dead trees were sampled as in the age-structure plots. When fire scars from within the same sample plot recorded the exact same fires, one was randomly omitted from the analysis.

Live trees were increment bored as near the base as possible, with the increment borer aimed at an angle toward the root collar of the tree. Trees were bored until a core was obtained that contained rings within 5 yr of the center, based on visual estimation in the field. Trees less than 5 cm dbh were labeled seedlings, and whorls were counted to estimate age, as destructive sampling was considered inappropriate in the park. Increment cores were extracted from standing-dead trees with little rot, usually above the base to avoid the presence of some rot. Wedges for dating tree origin and death were removed with a cross-cut saw from partially rotten standing-dead trees and all dead-and-down trees at least 1 m long and 10 cm wide at the widest point. Usually only one cross section per tree was taken (1) as close to the base of the tree as possible to improve the estimate of earliest live year, and, when the base was not discernible, (2) where log diameter was largest to improve the estimate of last live year. Diameter at breast height (dbh) was recorded for each live and standing-dead tree, and diameter at each end was recorded for dead-and-down trees.

Sample preparation

Increment cores were processed following Stokes and Smiley (1968). Increment cores and fire scars from live trees were visually crossdated using the Deer Ridge chronology from RMNP (Veblen et al. 2000). Cores from live trees that could not be crossdated were counted. The actual number of rings to center was estimated by fitting a circle to the earliest ring in the core, measuring and averaging the earliest 10 rings in the core, and dividing the earliest ring radius by the mean width of the earliest 10 rings (Norton et al. 1987). Cores were sometimes taken above the tree base due to rottenness or obstacles. To estimate number of years to core height, regression equations for mean years to coring height from the nearest site location in Mast et al. (1998) were used.

Annual ring widths on wedges and cores from all dead-and-down trees and from standing-dead trees whose rings could not be visually crossdated were measured using the tree ring measurement program TRIMS (Madera Software, Tucson, Arizona, USA). Measurement files were crossdated against existing tree-ring chronologies: Monarch Lake, D. A. Graybill; Deer Mountain, D. A. Graybill; Jefferson County, D. A. Graybill; Great Sand Dunes Lower, H. D. Grissino-Mayer (International Tree-Ring Data Bank),[3] and Deer Mountain, T. T. Veblen (Veblen et al. 2000) using the program COFECHA (Holmes 1983) and visually checked when necessary. Some standing-dead and dead-and-down trees contained fire scars, and all fire years were visually crossdated after the entire ring series was crossdated using COFECHA.

Event diagrams, events, evidence rules, and agents

We explored the relationship between tree origins and fires or wet periods by testing the null hypotheses that tree origins are independent of time since fire and time since a wet period. Fires were separated into two classes, low-severity or high-severity, for this analysis. Ponderosa pine regeneration is favored by above-average precipitation for more than one growing season after germination (Pearson 1942, 1950, Mast et al. 1998). We identified past wet periods using reconstructed Palmer Drought Severity Indices (PDSI) for station 58 near our study area (Cook et al. 1999). PDSI values of $+0.5$–1.0, defined as a ‘‘developing wet spell,’’[4] were uncommon (only 32 yr between AD 1700–1978), as were PDSI values of 1.00–2.00, defined as a ‘‘mild wet spell’’ (only 25 yr), while only 10 moderate or severe wet spells with PDSI value >2.0 occurred. Successive wet years that might favor ponderosa pine regeneration were rarer—we defined a ‘‘low-severity wet spell’’ as two or more successive years with PDSI ≥ 0.5 ($n = 12$) and a ‘‘high-severity wet spell’’ as two or more successive years with PDSI ≥ 1.0 ($n = 4$). Chi-square analysis was used to test the null hypothesis that the observed (extant) number of ponderosa pine seedlings is no different than expected if seedling regeneration is independent of time since fire or time since a wet spell. Because successive fires interrupt the possibility of ongoing regeneration, expected values were calculated from the actual distribution of fire-free intervals. This initial analysis, reported in the results, revealed that tree origins are elevated during a period of ~20 yr after a fire, in agreement with observations that fires release nutrients, increase soil moisture, and expose mineral soil favorable to establishment of ponderosa pine seedlings (e.g., Sackett 1984).

Given that fire was found in the initial analysis to be associated with tree origins, an ‘‘event’’ was tentatively identified by (1) a fire scar date, (2) a regeneration pulse, or (3) a mortality pulse. More than one of these indicators may be evident for an event. Events, such as regeneration pulses, are commonly identified by visual analysis of age distributions (e.g., Duncan and Stewart 1991, Villalba and Veblen 1997). The date of an event was estimated from crossdated fire scars, the approximate year of the onset of a regeneration pulse, and the approximate year following an episode

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[3] URL: ⟨www.ngdc.noaa.gov/paleo⟩

[4] URL: ⟨nadss.unl.edu/pdsi/doc⟩

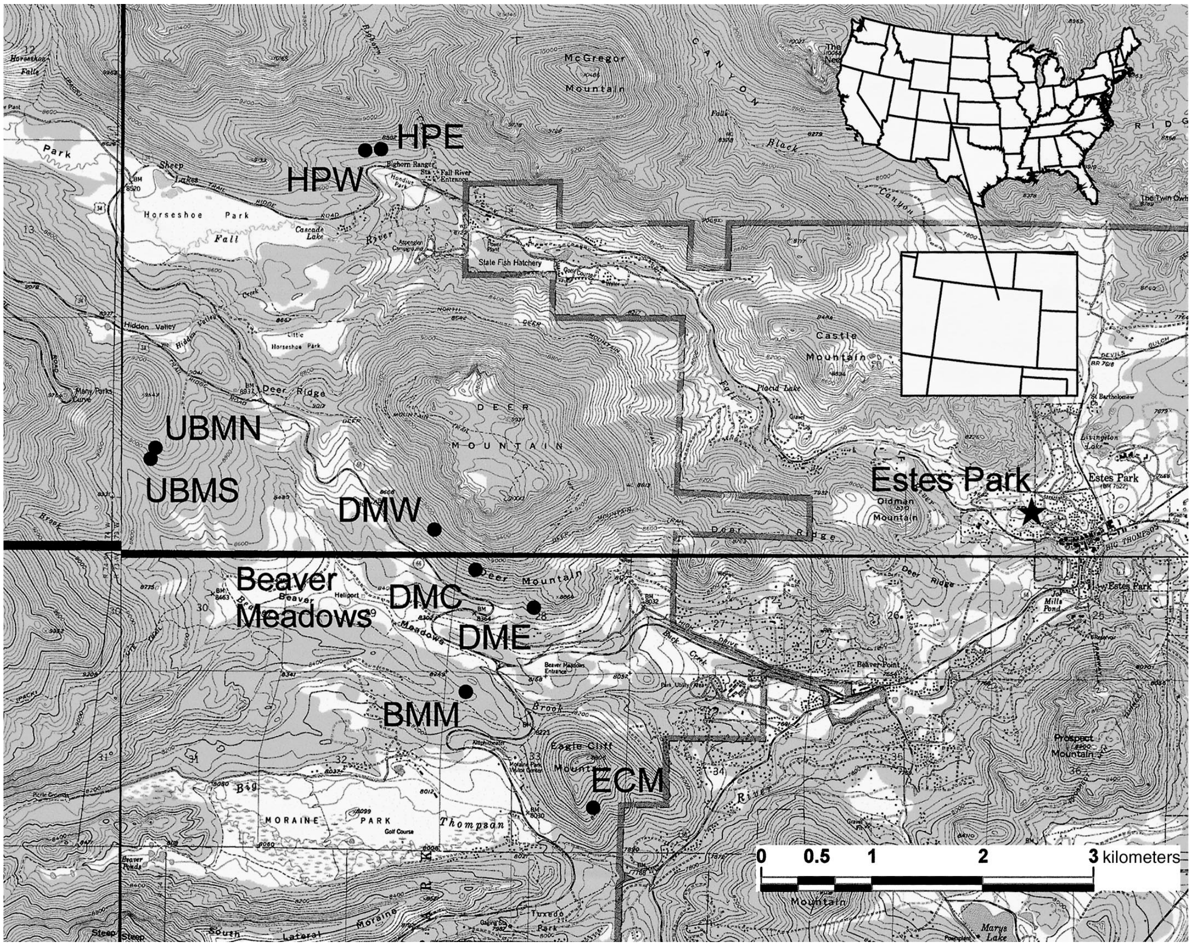

FIG. 1. Locations of plots within the ponderosa pine zone of Rocky Mountain National Park (see Table 1 for plot names). This zone occupies only a small part of the park adjoining the eastern boundary, shown as a wide line.

of mortality. Ninety-three percent of event dates are from visually crossdated fire scars. Event diagrams, modified from Johnson et al. (1994) and Grissino-Mayer (1995), constructed for each plot, display the lifespan of each live and dead tree along a time continuum, with event years also shown (Fig. 2).

For the second phase of the analysis, timing criteria were created to associate individual tree origins and deaths with dated events, as not all tree origins or deaths occur at the time of events. A live tree was assumed to have originated as a result of an event if it originated within 20 yr after the event, consistent with the initial analysis. The 20-yr cutoff was also chosen to account for possible error in estimating the number of rings to center in cores that do not include the pith and possible error if the core is taken above the root collar (i.e., the number of rings to core height).

Dates for dead trees are less certain. A dead-and-down tree was assumed to have germinated as a result of the event if the earliest ring year was within 40 yr after the event. Forty years were chosen to account for the unknown number of rings to height of sampling above the root collar, potential lost rings due to decomposition and consumption by subsequent fires. The actual interval is somewhat arbitrary, but there is only a 10% difference in the number of trees assumed to have been killed by fire if a 20-yr cutoff is used, rather than a 40-yr cutoff. A standing-dead tree was assumed to have been killed by an event if the last ring was within 20 yr before the event.

Based on these evidence rules, the number of fire scars (in the case of fire), tree origins, tree deaths, mortality groups, and surviving trees was compiled for each event. A mortality ‘‘group’’ is at least three trees within 10 m of each other and no surviving trees in between. Each piece of evidence associated with an event was also located on a map of tree locations created from the *x*, *y* coordinates of all trees, and these maps were used to assist in the analysis of event severity and minimum fire size.

Evidence of an agent coincident with an event suggests the agent is at least partly responsible for the event (Table 2). While most disturbance agents are visually detectable when trees are alive (see Eckberg et

TABLE 1. Size of age-structure plots, time since last high-severity event, mean diameter at breast height (dbh), tree density, number of dead wood pieces/ha, percentage of dead wood crossdated in age-structure plots only, clumping distances, geologic substrate, and aspect.

Abbreviation	Plot name	Plot size (m)	Time since event (yr)	Mean tree dbh (cm)	Total tree density (no./ha)
Younger stands					
BMM	Beaver Meadows Moraine	25 × 25	140	16.3	992
UBMS	Upper Beaver Meadows south	15 × 15	140	9.2	3052
HPW	Hondius Park west	20 × 20	120	13.5	1601
Older stands					
DME	Deer Mtn. east	50 × 50	unknown	36.5	68
DMC	Deer Mtn. center	50 × 75	240	34.0	140
DMW	Deer Mtn. west	75 × 50	300	35.1	137
UBMN	Upper Beaver Meadows north	50 × 50	200	30.9	286
HPE	Hondius Park east	50 × 105	210	41.2	98
ECM	Eagle Cliff Mtn.	50 × 80	200	39.7	136

al. 1994), or died recently (Lundquist 2000, Lundquist and Negron 2000), only agents that leave long-term evidence are detectable in retrospective studies such as this. Fire scars implicate fire, blue-stain fungus indicates mountain pine beetles, dead wood oriented in a consistent direction suggests wind, and correspondence with tree-ring chronologies or climate reconstructions (i.e., PDSI) implies a climate influence (either drought or a wet period), as reviewed in the introduction. All dead wood was examined in the laboratory for blue-stain fungus. Orientation of downed wood was recorded in the field and evaluated later. To evaluate climatic effects, we used standardized tree-ring indices of the Deer Mountain chronology (Veblen et al. 2000) near our plots and a reconstructed Palmer drought severity index, which varies from +6 to −6 as drought increases (Cook et al. 1999). Mortality pulses were compared with indices for the decade before and the decade during the pulse, and regeneration pulses were compared with indices during the decade following the onset of the pulse. The evidence associated with an event is then used to determine the agent(s) most likely responsible for the event (Table 2).

Severity and extent of events

Severity of events was classified as high, mixed, or low using guidelines set after preliminary analysis (Table 3). High-severity events are usually documented by high mortality and a subsequent large regeneration pulse (Fig. 3a). High-severity events may cause high, but not always complete, overstory mortality (Fig. 3b). Some high-severity fires could have been intense surface fires, rather than crown fires (Turner et al. 1994). Mixed-severity events are group-replacing events defined by mortality of at least one group (Fig. 3c) with possible additional mortality (Fig. 3d). Low-severity events are defined as having low mortality with low or no regeneration (Fig. 3e) or no mortality with low regeneration (Fig. 3f). Either mortality or regeneration or both may indicate low-severity events. Spreading fires are identified by evidence in more than one part of a plot: either one fire scar accompanied by evidence of mortality or regeneration, or more than one fire scar. Where events are only labeled ‘‘fire,’’ a single fire scar was the only evidence.

Older regeneration pulses cannot be identified as regenerating after a stand-replacing event based on initial tree growth as indicated by tree ring widths. Trees in regeneration pulses after known crown fires show wide variation in the mean width of the earliest 10 rings (Fig. 4). High variation in initial growth of trees in the same cohort indicates that the development of a size hierarchy within even-aged stands (Mast and Veblen 1999) begins within the first 10 yr after germination.

Tree spatial pattern was determined to evaluate possible clump-related regeneration mechanisms hypothesized by Cooper (1960) and White (1985). Clumping of live-tree spatial locations was evaluated by calculating L_{hat}, a variance-stabilizing form of Ripley’s K function that includes an edge correction, using S-Plus Spatial Statistics (Insightful, Seattle, Washington, USA). For each plot, the cumulative intertree distance distribution was compared to that from a Poisson point process. A graph was produced for each plot showing the cumulative distance distribution of trees in the plot and its departure from a Poisson distribution. L_{hat} values greater than the 95% confidence intervals indicate clumping of tree locations, while L_{hat} values less than the 95% confidence intervals indicate regular spacing of trees (Kaluzny et al. 1998). While other studies have analyzed tree clumping by age class (Mast and Veblen 1999), we instead compared young vs. old stands.

Areas of fires cannot be exactly reconstructed, but their minimum size within a plot can be estimated by a polygon that just encompasses the evidence, including scars, mortality, and regeneration. This analysis helps evaluate within-stand regeneration and mortality processes in relation to fire size. Differences in mean minimum fire size and number of fires between younger and older stands and over the three time periods (pre-

TABLE 1. Extended.

Dead wood density (no./ha)	Percentage of dead wood crossdated	Clumping distances (m)	Geologic substrate	Aspect (degrees)
816	67	2–4.5, 7–15	Glacial till	40
400	44	3–6.5	Biotite schist	268
250	60	1–4	Silver Plume granite	203
120	77	10–13	Biotite schist	210
61	26	0–35+	Biotite schist	194
96	67	None	Biotite schist	230
28	86	0–5, 10–12.5	Biotite schist	200
17	56	0–18	Silver Plume granite	193
25	30	0–2.5, 6–11, 14–22	Biotite schist	118

EuroAmerican settlement, to AD 1860; EuroAmerican settlement, AD 1860–1914; suppression, AD 1915 to the present) were evaluated using contrasts in a repeated measures analysis of variance (Hand and Taylor 1987) using SPSS 10.0 (SPSS, Chicago, Illinois, USA). Older stands are defined as those that originated before EuroAmerican settlement (200–300 yr ago), and younger stands are those that originated at or near the beginning of the EuroAmerican settlement period (120–140 yr ago). The focus was on stand-development processes following a high-severity fire, so mean minimum fire area and number of fires exclude the high-severity fire and events before it.

RESULTS

A total of 501 live trees and 154 fire-scarred trees, including internal fire scars (fire scars not outwardly visible) inside age-structure plots, was sampled. A mean of 17 fire-scarred trees was sampled per plot (range 8–23). A total of 185 dead trees were sampled inside the age-structure plots, and 110 were successfully crossdated. The percentage of successfully crossdated wood for all plots ranges from 26 to 86% (Table 1). Wood that could not be successfully crossdated was not used in the analysis.

Disturbance agents, severity, and extent

Ninety-seven percent of 103 events were caused by fire (Fig. 2). Only one event was identified as being non-fire: a mid-1970s mountain pine beetle outbreak in plot BMM (Fig. 2a). The agents of about 2% of the events were considered ‘‘ambiguous.’’ Six potential additional events were also identified (Fig. 2), although these older events caused by an ambiguous agent failed to meet the minimum event criteria (Table 3). However, based on reasonable evidence (e.g., the 1560 event in plot DME had four origins and one death) for events that occurred so long ago, a subjective decision was made to call them ‘‘potential events.’’ A mean of 11 events (range 10–20) was identified in each plot.

High-severity events were 7% of the 103 identified events (Fig. 2). A high-severity event occurred in each of six plots, and two crown fires may have burned in plot UBMS (Fig. 2h). All but one of the high-severity events were identified as fire; the disturbance agent for the other event is ‘‘ambiguous’’ (Fig. 2g). A high-severity fire occurred in BMM in 1860, in DMC in 1751–1757, in DMW in about 1700, in UBMS in 1860 or 1863, in HPW in either 1875 or 1878–1896, and in HPE in 1797–1799 (Fig. 2). The 1878–1896 fire date in HPW was based on fire scar cores that could not be dated more precisely. Because the regeneration pulse began about 1884, the fire likely occurred at or shortly before this. A high-severity event caused by an ambiguous agent occurred in ECM in about 1800. Three events were identified as mixed-severity within a plot. One of these was an 1802 fire in UBMN (Fig. 2e), the second was a 1793 fire in DMW (Fig. 2b), and the third was a mid-1970s mountain pine beetle outbreak in plot BMM (Fig. 2a). No other insect-caused or wind-related events were identified. Seventy percent of events were low-severity. However, due to the potential for lost evidence, especially from older events, severity may sometimes be underestimated.

The severity of 20% of events could not be identified at all (Fig. 2), largely due to long time since the event or occurrence before crown fire. The largest proportion of the events of ambiguous severity occurred in the BMM plot. All of these events of ambiguous severity in BMM occurred before an 1860 crown fire, and include all the events before the crown fire. If the BMM plot is excluded, the severity of 9% of events could not be identified. Fire severity has not increased during the suppression period. Except for the high-severity fire that occurred at or just after EuroAmerican settlement, all postsettlement fires were low severity (Fig. 2).

Many fires were restricted to a single plot, but several spread among plots, varying in severity. Six plots form an approximate circle around Beaver Meadows (Fig. 1). Two more are on a hillside facing a different park,

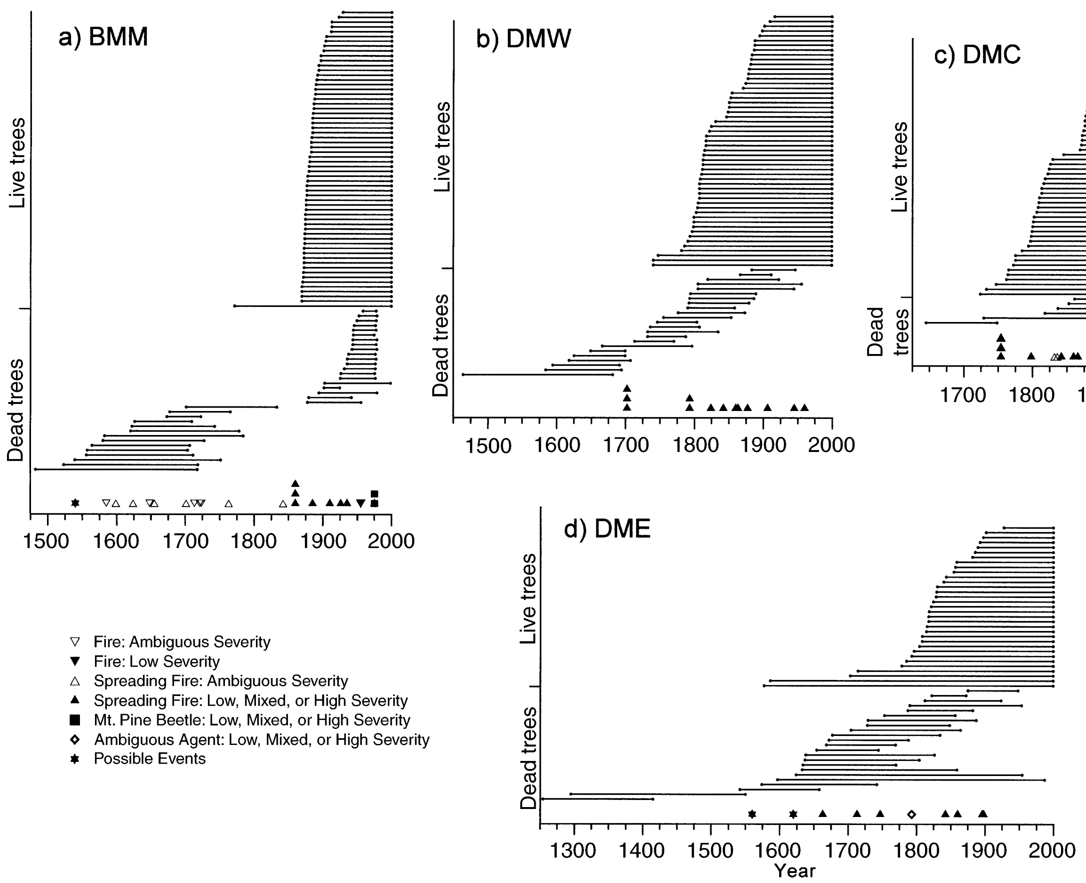

FIG. 2. Event diagrams for the nine sample plots. The last year shown is 1999, the year the samples were taken. The severity of an event is indicated by the number of symbols stacked vertically: 1, low severity; 2, mixed severity; 3, high severity. A crown fire burned in plot HPW in either 1875 or sometime between 1878 and 1896; it was impossible to determine which fire was the crown fire. The 1878–1896 fire could not be dated more precisely due to difficulty dating these fire-scar cores. Because the regeneration pulse began about 1884, the fire likely occurred shortly before this.

and one is on the side of a mountain away from the other plots. Fires in 1842 (low-severity, ambiguous severity) and 1860 (possibly all severities) burned in all plots (Fig. 2), likely exceeding 1000 ha in area. Fires in 1713 (low, mixed, and ambiguous severity) and 1863 (low, possibly high or ambiguous severity) burned in four plots, with at least one plot not around Beaver Meadows, possibly indicating a minimum of two ignitions. Low-severity fires in 1906 and 1968 burned three plots, with at least one plot not around Beaver Meadows. An 1898 low-severity fire burned in three plots surrounding Beaver Meadows.

The size of the crown fire (high-severity) component of past fires cannot be determined very well with our data. Only one fire, in 1860, may have burned as a crown fire in two plots (BMM and UBMS), which are ~3 km apart. If the intervening area also burned in the crowns, this fire could have exceeded a few hundred hectares in area. However, the 1860 fire was also a crown fire in lodgepole pine to the west of plots UBMN and UBMS (A. Buechling, *personal communication*).

Fire severity, timing, regeneration, and mortality

Most regeneration in scar-centered plots resulted from the same high-severity fires that burned in the age-structure plot, rather than from the fire(s) that scarred the center tree (compare Figs. 5 and 6). A scar corresponding to the fire associated with regeneration was not usually found inside the scar-centered plot itself. Rather than being one of the oldest trees within the scar-centered plot, the scarred tree at the center of the plot was a part of, or younger than, the largest cohort in 60% of the plots. Spatial configurations of fire scars, tree mortality, and regeneration from a 1945 fire in HPW (Fig. 7), as well as scar-centered plots (Fig. 6), show that regeneration may or may not occur next to a scarred tree or a tree killed by the fire.

Most tree regeneration appears visually to be temporally associated with, and probably is the result of fire (Fig. 5). The null hypothesis that the frequency of extant regenerating trees is independent of time since fire is rejected for low-severity fires (Fig. 8a; $\chi^2 = 45.27$, df $= 8$, $P = 0.000$) and high-severity fires (Fig.

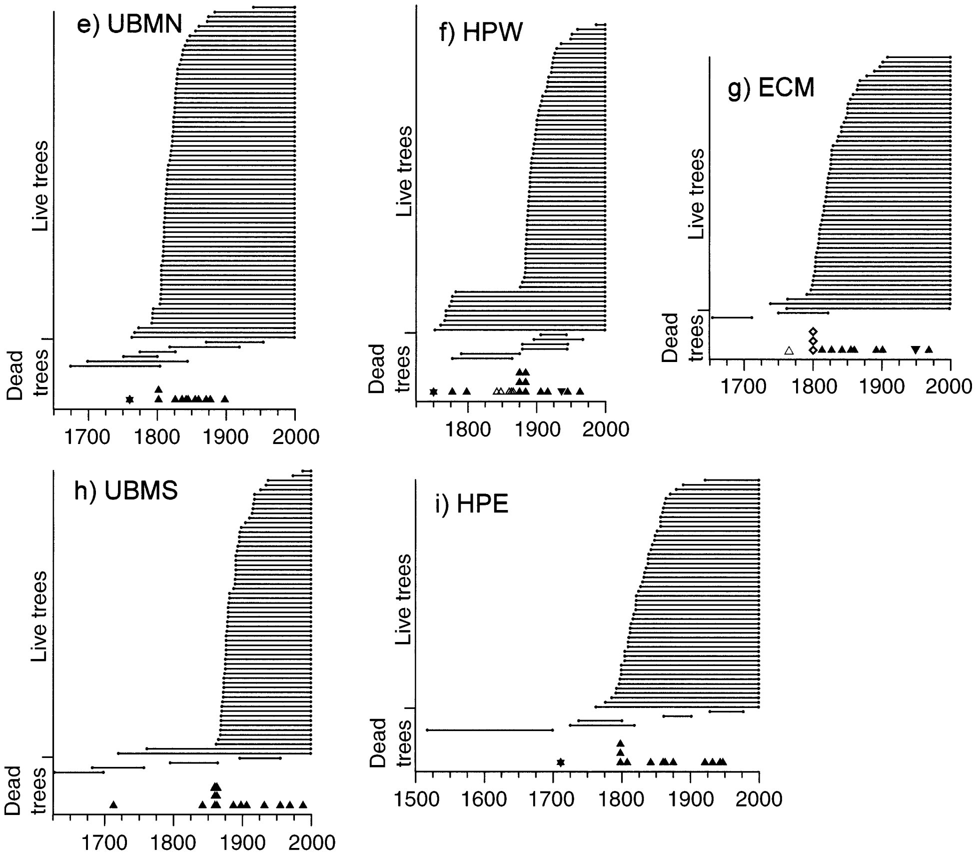

FIG. 2. Continued.

8b; $\chi^2 = 36.86$, df = 6, $P = 0.000$). Regeneration drops off sharply about 20 years after a low-severity or high-severity fire and decreases steadily with time since fire (Fig. 8a, b). More of the regeneration occurs within 10 yr of low-severity fires (Fig. 8a) than within 10 yr of high-severity fires (Fig. 8b), suggesting that low-severity fires create a briefer window of opportunity for regeneration.

The apparent higher amount of regeneration immediately after low-severity fires is due to the higher number of low-severity fires. The null hypothesis that the mean number of extant trees that regenerated within

TABLE 2. Possible combinations of agents, given fire scar, mortality, and regeneration evidence.

Agent(s)						Mortality pulse			Regeneration pulse
Fire	Beetles	Wind	Drought	Wet period	Fire scar	Blue stain	Oriented wood	Drought	Wet period
X					yes	no	no	no	no
X	X				yes	yes	no	no	no
X		X			yes	no	yes	no	no
X			X		yes	no	no	yes	no
X				X	yes	no	no	no	yes
	X				no	yes	no	no	no
	X	X			no	yes	yes	no	no
	X		X		no	yes	no	yes	no
	X			X	no	yes	no	no	yes
		X			no	no	yes	no	no
		X	X		no	no	yes	yes	no
		X		X	no	no	yes	no	yes
			X		no	no	no	yes	no
			X	X	no	no	no	yes	yes
				X	no	no	no	no	yes

TABLE 3. Criteria used to identify event severity.

Evidence	Attribute	High severity	Mixed severity	Low severity
Mortality pulse	number of trees	variable; can be absent due to later events and passage of time	≥3 trees per group (high-severity component) possibly scattered mortality (low-severity component)	variable; can be absent if regeneration is present
	distribution of trees	contiguous	within 10 m of each other (a group) and no survivors between (high severity) scattered (low severity)	if ≥3, then have survivors between them
	group number/size	one, large	≥1, small	0
	duration/timing	DD: Within 40 yr before regeneration peak or fire scar, or to previous scar within 40 yr SD: Within 20 yr before regeneration peak or fire scar, or to previous scar within 20 yr	DD: Within 40 yr before regeneration peak or fire scar, or to previous scar within 40 yr SD: Within 20 yr before regeneration peak or to previous scar within 20 yr	DD: Within 40 yr before regeneration peak or fire scar, or to previous scar within 40 yr SD: Within 20 yr before regeneration peak or to previous scar within 20 yr
Regeneration pulse	number of trees	≥7 (pre-1800) ≥15 (post-1800)	variable	variable; can be absent if mortality present
	distribution of trees	contiguous with dead wood pulse	contiguous with dead wood pulse if one is present (high severity) possibly scattered (low severity)	scattered or in small clusters
	number of groups	one, large	≥1, small clusters	none or small
	duration/timing	live trees: Origins up to 20 yr after event or until next event dead trees: First ring year within 40 yr after event or until next event	live trees: Origins up to 20 yr after event or until next event dead trees: First ring year within 40 yr after event or until next event	live trees: Origins up to 20 yr after event or until next event dead trees: First ring year within 40 yr after event or until next event
Survivors	number of trees	≤5	>5	>5
	distribution of trees	no particular distribution	none within at least one group; otherwise well distributed	well distributed

Note: Key to abbreviations: DD, dead-and-down wood; SD, standing-dead wood.

20 yr after fire is independent of the severity (high vs. low) of the fire is rejected ($\chi^2 = 7.17$, $P = 0.007$). The mean number of extant trees per plot that regenerated after a low-severity fire is 3.0, much lower than the mean of 19.9 trees per plot after a high-severity fire.

Tree mortality is similarly strongly associated with fire (Fig. 9). The null hypothesis that the frequency of tree deaths is not different before and after a low-severity fire is rejected ($\chi^2 = 17.26$, $P = 0.000$). Eighty-two percent of crossdated dead-and-down wood is associated with, and was probably killed by low-severity fires (Fig. 9).

The temporal spacing of fires affected tree recruitment. For example, fires in plot DMC from 1832–1866 have short temporal spacing and burned overlapping areas within the plot (Fig. 10). These frequent, overlapping fires appear to have largely delayed successful seedling establishment until after 1866. The resulting regeneration pulse after the 1866 fire (Fig. 5d) appears similar to pulses after high-severity fires (e.g., Fig. 5b), but 1866 was a low-severity fire, because there are many survivors.

Climate influences on regeneration and mortality

Tree origins are not independent of wet events, but do not appear to be favored by them either (Fig. 8c, d). The null hypothesis that the frequency of extant regenerating trees is independent of time-since-event is rejected for low-severity wet events (Fig. 8c; $\chi^2 = 59.42$, df = 5, $P = 0.000$) and for high-severity wet events (Fig. 8d; $\chi^2 = 62.50$, df = 8, $P = 0.000$). However, tree origins are less than expected in the first 10 yr after wet episodes (Fig. 8c, d), and more than expected 30–60 yr later (low severity) or 10–40 yr later (high severity). Such a long-delayed regeneration response to a brief climate episode is unlikely, suggesting

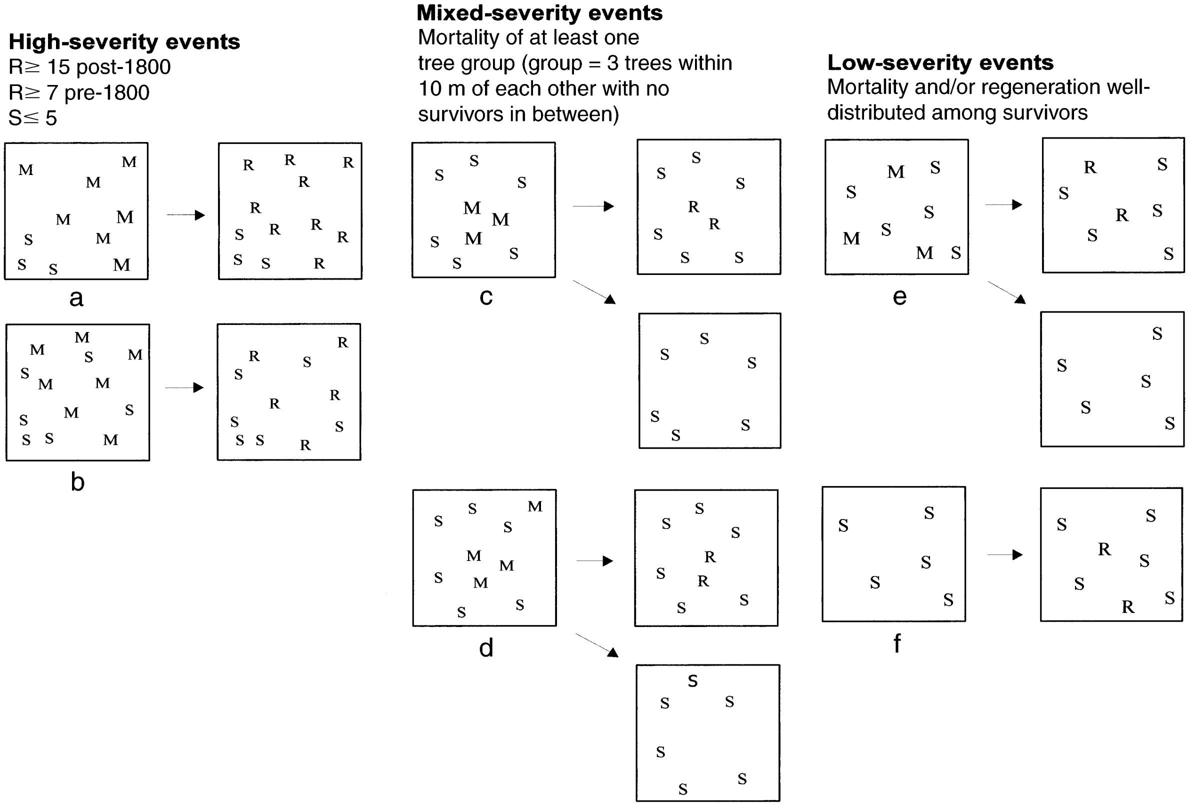

FIG. 3. Generic graphical representations of (a, b) high-severity, (c, d) mixed-severity, and (e, f) low-severity events (R, regeneration after event; M, mortality caused by event; S, survivor of, or tree unaffected by, event).

that wet episodes are not generally the cause of tree regeneration, particularly since the wet episodes are followed by fires that are related to regeneration (Fig. 8a, b).

Using the tree-ring chronology from Deer Mountain and reconstructed wet spells as indicators (Fig. 5a), climate also does not visually appear to be related to regeneration pulses in the plots, except in two possible instances. Between 1760 and 1770, tree-ring indices are 20% higher than both the chronology mean and pre-EuroAmerican settlement period mean, although the closest prior wet spell is 1753–1754 (Fig. 5a). There are small corresponding regeneration pulses beginning about 1760 in six of the plots, suggesting favorable climate could have played a role. However, this interpretation is clouded by the fact that a crown fire occurred between 1751–1757 in DMC, a 1763 fire of ambiguous severity occurred in BMM, and a 1763–1768 fire of ambiguous severity occurred in ECM (Fig. 2). The lowest Palmer Drought Severity Index (PDSI) value derived from tree rings that occurred during the 1750 decade was about -3 (Cook et al. 1999). This is in contrast to a -5 value during the 1950s, during which some ponderosa pine trees died from a drought in New Mexico (Allen and Breshears 1998). Thus, dry years that occurred during the 1750 and 1760 decades were likely not dry enough to kill trees and lead to regeneration, although the dry conditions may have contributed to the occurrence of fire that led to regeneration. It is unclear whether climate, fire, or both led to the regeneration pulses in about 1760 in six plots.

A regeneration pulse in one or two cases is associated with favorable climate after a fire, but ample regeneration also occurs without favorable climate, and episodes of favorable climate may have no regeneration. Tree-ring indices during the 1790 decade, corresponding to a pulse in only one plot, HPE (Fig. 5i), are 22% and 23% higher than the chronology mean and pre-EuroAmerican settlement period mean, respectively, and 1792–1795 was one of the longest periods of PDSI exceeding $+0.5$ since AD 1700 (Fig. 5a). However, regeneration beginning in the 1790 decade also corresponds with a high-severity fire, although there is no evidence of a mortality pulse occurring just before regeneration began. Tree-ring indices during the 1800 decade, corresponding to pulses in UBMN and ECM, are only 2% and 3% larger than the chronology mean and pre-EuroAmerican settlement mean, respectively, and this was not a period containing any wet spells, based on the PDSI reconstruction (Fig. 5a). These pulses correspond with a high-severity fire in UBMN, but no fire from this time was documented in ECM. From 1860 to 1880, corresponding to pulses in BMM, UBMS, and HPW, tree-ring indices are 28%, 18%, and

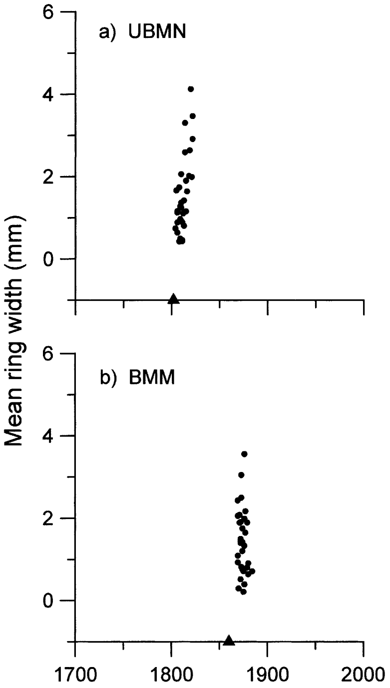

FIG. 4. Mean ring widths of the earliest 10 rings from live trees that germinated within 20 years after a high-severity fire in (a) 1802 and (b) 1860. Trees from which cores were taken above the base were excluded. Triangles on the *x*-axis indicate the year in which a high-severity event occurred.

33% smaller than the chronology mean and 18%, 8%, and 24% smaller than the settlement period mean, respectively, and there are no wet spells (Fig. 5a), suggesting climate is unlikely to provide a direct explanation for the pulses. Regeneration from 1860–1880 also corresponds with high-severity fire. An exceptional wet spell in 1903–1907 (PDSI > 0.9) does not appear to have led to much regeneration (Fig. 5a).

Stand development

Stands regenerating after high-severity fires 120–140 yr ago (BMM, UBMS, and HPW) are presently relatively dense and have small trees (see Plate 1, left), with mean dbh ranging from 9.2 to 16.3 cm (Table 1). Trees in older stands have mean dbh ranging from 30.9 to 41.2 cm (Table 1). Mean dbh of trees in younger stands is significantly smaller than in older stands ($t = -9.01$, $P = 0.0004$). After ~200 yr, fires have decreased the density of stands (Table 1; $t = 2.84$, $P = 0.052$). Since most mortality is associated with fire (Fig. 9), and 120–140-yr-old stands are still very dense, natural thinning due to shade intolerance or competition among trees is not likely the primary cause of density decreases. Density appears to have stayed low between 200 and 300 yr after a high-severity event (Table 1), but low-severity fires may continue to cause tree turnover. For example, in plot HPW, the 1945 fire killed three trees (two are standing dead, one is dead and down) and led to the regeneration of two trees (Fig. 7).

Clumped tree pattern occurs in eight of nine age-structure plots, but is weak in seven plots, evidenced by L_{hat} values that are only slightly outside 95% confidence intervals (e.g., Fig. 11a). Trees in DMC show a strong clumped pattern, possibly due to fuel discontinuity or limited regeneration sites caused by the abundant rock outcrops in this stand (Fig. 11b). Trees in most plots were weakly clumped at short (0–5 m) and intermediate (8–15 m) distances (Table 1). Clumping at only short distances in HPW and UBMS may be due to small plot size; it is unknown whether trees in these areas are also clumped at intermediate distances. After about 200 yr from the last stand-replacing event, age structure is uneven (e.g., Fig. 5i) and trees are weakly clumped up to intermediate distances (Table 1). It appears that, after ~300 yr, age structure is uneven (e.g., Fig. 5c), and trees may become located in a spatially random pattern (Table 1).

Suppression-period regeneration and changes in fire regime

There is very little suppression-period regeneration in any of the stands (see Plate 1, right), except the three younger stands (Fig. 5b, g, h). Unless trees were too small to core, trees <5 cm dbh were dated the same way as larger trees in UBMS and HPW, because they were a large component of the age structure. Nearly all of these trees, despite their small size (Table 1), were 120–130 yr old. The few, more recent trees germinated after fire (e.g., Fig. 5h). There is a total of only eight seedlings in the other six age-structure plots, and no one of these plots contains more than three seedlings. Whorl counts ranged from five (HPE) to 26 (UBMS), but are only a crude estimation of age. Many seedlings were growing in rock cracks and had thick bases relative to seedling height, suggesting they are suppressed. A mixed-severity mountain pine beetle outbreak that affected at least 85% of the area of BMM in the mid-1970s did not result in any regeneration (Fig. 5b).

There was no significant difference in the number of low-severity fires per decade per square meter between the pre-EuroAmerican settlement and EuroAmerican settlement periods ($F_{1,7} = 0.239$, $P = 0.640$) or the EuroAmerican settlement and suppression periods ($F_{1,7} = 1.802$, $P = 0.221$). There was also no significant difference in the number of low-severity fires per decade per square meter between older and younger stands from the pre-EuroAmerican settlement period to the settlement period ($F_{1,7} = 0.199$, $P = 0.669$) or from the settlement to suppression period ($F_{1,7} = 1.896$, $P = 0.211$).

The null hypothesis that mean minimum low-severity fire sizes are equal over the three periods is rejected ($F_{2,14} = 7.51$, $P = 0.006$). The null hypothesis of equal mean minimum low-severity fire sizes is not rejected

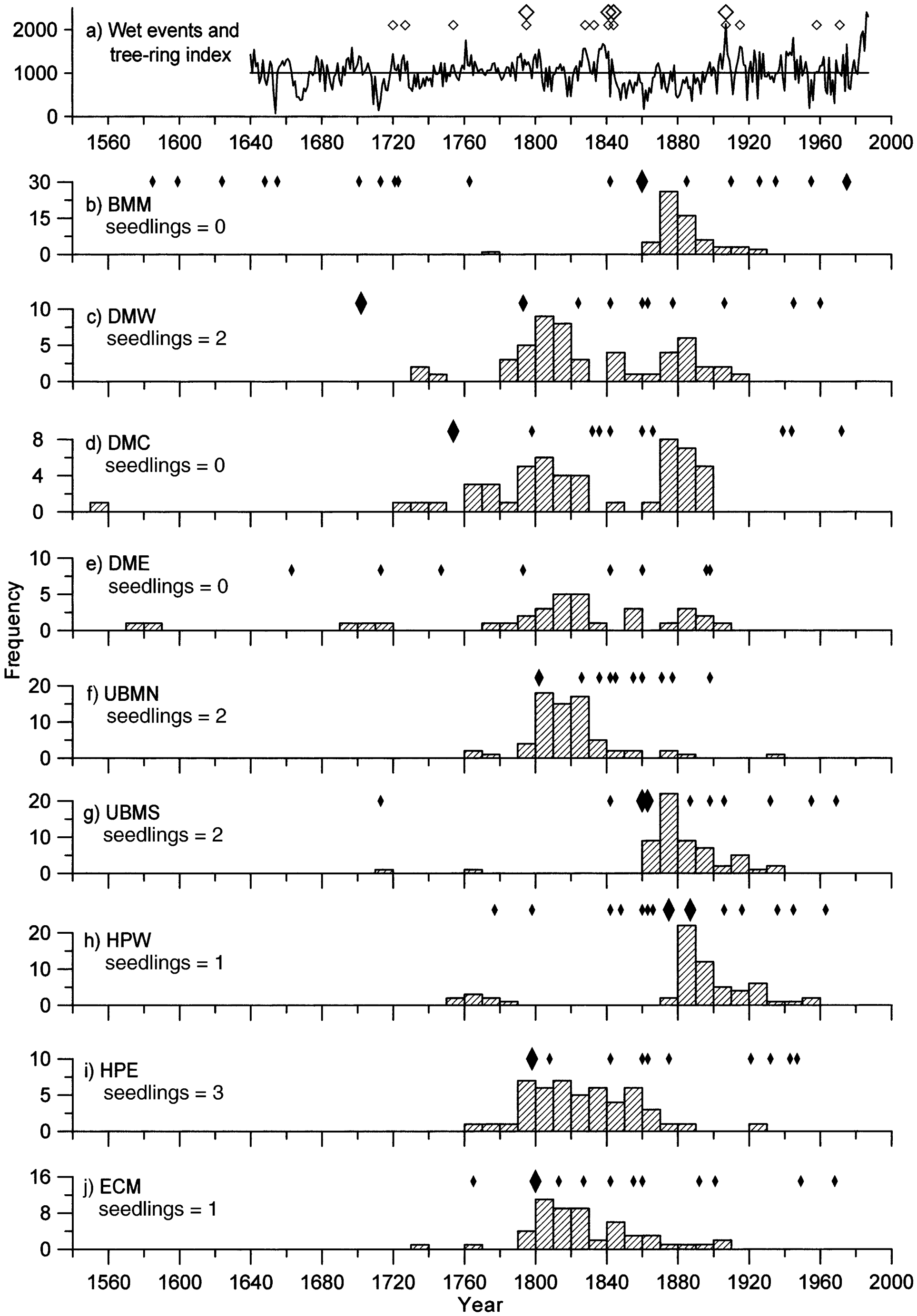

FIG. 5. (a) Wet events and tree-ring index for Deer Mountain and (b–j) age frequency distributions and disturbance events for the nine age-structure plots. Large diamonds in (a) are high-severity wet events (two or more consecutive years of PDSI ≥ 1.0), and smaller diamonds are low-severity wet events (two or more consecutive years of PDSI ≥ 0.5). The horizontal line in (a) is the mean, and the fluctuating line is the tree-ring index for Deer Mountain. In (b–j), the number of seedlings is listed below the plot name, except in HPW and UBMS where seedlings were aged and included with the other live trees. Black diamond symbols above each histogram are disturbance event years, with three increasing sizes for low-severity, mixed-severity, and high-severity events, respectively. In plot HPW, it is unknown whether the crown fire occurred in 1875 or sometime between 1878 and 1896.

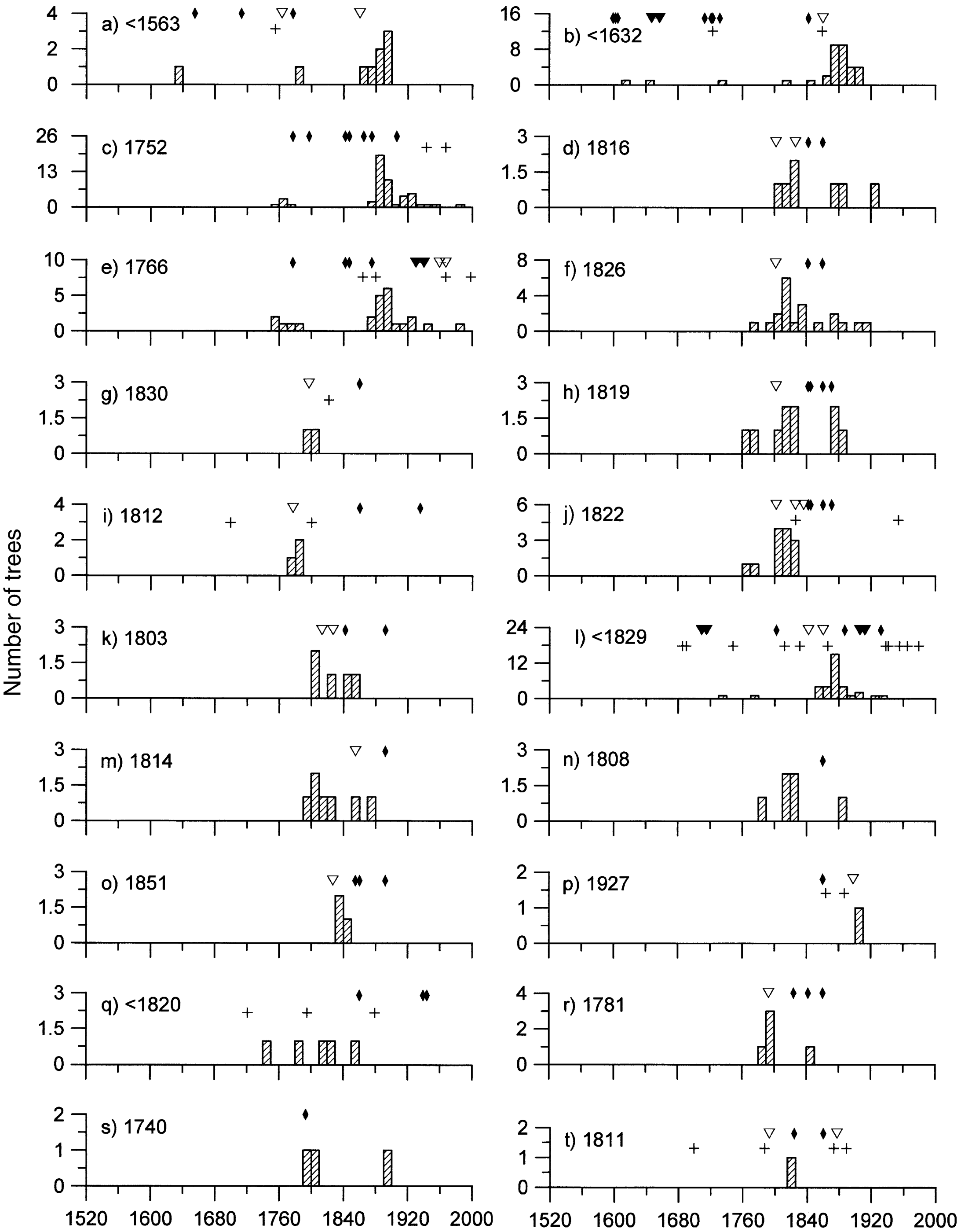

FIG. 6. Age frequency distributions for 20 scar-centered plots. The origin year of the scarred tree at the center of the plot (not included in the histogram) is listed by the letter denoting each plot. Some origin years are conservative, because the trees were rotten at the base. Black diamond symbols on the first line indicate fire years. Fire years include fires that scarred the tree at the center of the plot, as well as fires that scarred trees elsewhere inside the scar-centered plot. Open, downward-pointing triangles indicate fires that burned in the scar-centered plot, but the scar is located inside the age-structured plot. "Plus" symbols (+) on the second line indicate the most recent ring of dead trees. Plots are (a) BMM scar 2, (b) BMM scar 5, (c) HPW scar 4, (d) UBMN scar 3, (e) HPW scar 5, (f) UBMN scar 6, (g) HPE scar 1, (h) UBMN scar 7, (i) HPE scar 2, (j) UBMN scar 8, (k) ECM scar 1, (l) UBMS scar 3, (m) ECM scar 6, (n) DME scar 3, (o) ECM scar 9, (p) DME scar 4, (q) DMC 1998 scar 3, (r) DMW scar 4, (s) DMW scar 2, and (t) DMW scar 5.

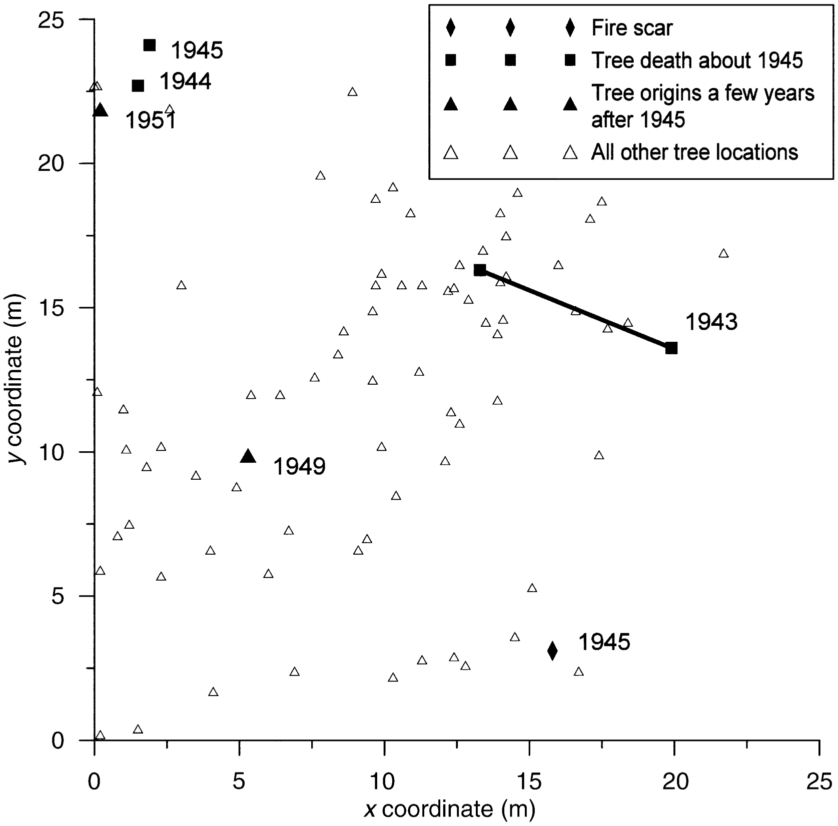

FIG. 7. Locations of fire scars, regeneration, and mortality, indicating minimum spatial extent of the 1945 low-severity fire in HPW.

for the individual contrast between the pre-EuroAmerican settlement and settlement periods ($F_{1,7}$ = 0.309, P = 0.596), but is rejected for the contrast between the suppression period and the two earlier periods ($F_{1,7}$ = 14.775, P = 0.006). Estimated mean minimum low-severity fire size, including older plots only, declined from 0.24 ha in the pre-EuroAmerican settlement period to 0.03 ha in the suppression period. Older stands have experienced more low-severity fires per decade per square meter since the last high-severity fire than have the younger stands (BMM, UBMS, and HPW) (t = 4.95, P = 0.002). All events after the high-severity fire were included.

DISCUSSION

Prevalence of fire as disturbance agent

High-severity fires occur less frequently than low-severity fires, but are a prominent feature of the fire regime of ponderosa pine in RMNP. High-severity (i.e., crown) fires occurred in mixed-conifer forests at higher elevations in Colorado before EuroAmerican settlement (Brown et al. 1999), but have not been commonly documented in pure ponderosa pine forests before EuroAmerican settlement (but see Weaver 1943, Shinneman and Baker 1997). Crown fires in three plots (BMM, UBMS, HPW) occurred at or shortly after the beginning of Euro-American settlement. While the severity of one of the 1875 or 1878–1896 fires in HPW is ambiguous, at least one was a crown fire. The 1859/1860 fire year (fires in BMM, UBMS, and perhaps HPW) is probably climatically related, as it appears to be widespread in the Colorado Front Range (Veblen et al. 2000) and has been documented in Montana (Freedman and Habeck 1984), the Black Hills (Fisher et al. 1987), the Southwest (Dieterich 1980, Swetnam and Dieterich 1985, Grissino-Mayer and Swetnam 1995, and Fulé et al. 1997), and Utah (Stein 1988). In RMNP, the 1860 fire was probably extensive, burning with varying severity through many of our stands, those sampled by Mast et al. (1998), and in the nearby lodgepole pine zone (Arne Buechling, *personal communication*).

The potential for crown fire is thought to have increased due to fire suppression and resulting dense understories (e.g., Covington and Moore 1992, 1994*a*, *b*), but fire severity has not increased to date during the suppression period in ponderosa pine stands in RMNP. The three crown fires that occurred near the beginning of EuroAmerican settlement occurred too soon after settlement to have been caused by unnatural

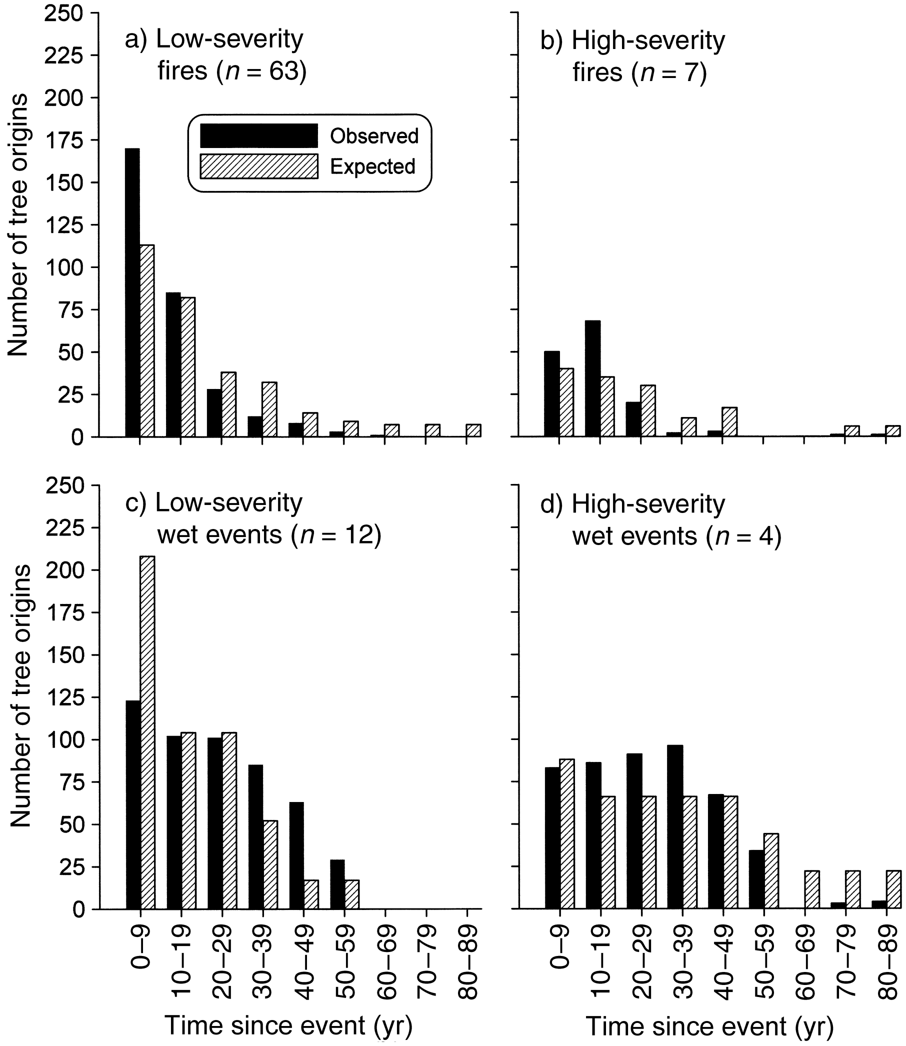

FIG. 8. Number of observed extant tree origins and expected tree origins following (a) a low-severity fire, (b) a high-severity fire, (c) a low-severity wet spell and (d) a high-severity wet spell for increasing intervals of time since the fire or wet spell. Expected values are based on actual intervals between fires or wet spells but represent regeneration independent of the length of interval.

fuel accumulation resulting from fire suppression. All other postsettlement fires were low severity or possibly mixed severity in some cases. Because crown fires occurred historically in ponderosa pine forests in RMNP, it is likely that crown fires will occur in the future, regardless of suppression efforts.

The majority of extant mortality evidence was associated with fire. Other agents, such as endemic-level mountain pine beetles and Armillaria root disease, likely caused some mortality, but evidence of rot-causing agents may have disappeared entirely, whereas charred wood may be preferentially preserved. Decay of trees killed by mountain pine beetles in plot BMM in the mid-1970s is advanced, so it seems likely that evidence of trees killed during past mountain pine beetle outbreaks disappears more quickly than wood killed by agents that do not cause accelerated rot. The majority of these trees were relatively small, but small trees were also attacked in the same epidemic in Lory State Park north of RMNP (McCambridge et al. 1982). Without blue stain, in contrast, charred wood is often very old but sound. Such wood was especially resinous throughout, giving the wood a golden-brown color. Robertson and Bowser (1999:258) also documented what they referred to as ''skeleton wood.'' This wood was ''. . . very old resin-laden, decay-resistant heartwood. Frequently this skeleton wood had 'charcoaled' surfaces.'' These authors hypothesize that this wood is decay-resistant despite high resin content, and may persist after several fires. The cause of the high resin content is unknown. This differential preservation of wood may mean that the wood record may provide a biased record of mortality agents that must be evaluated cautiously.

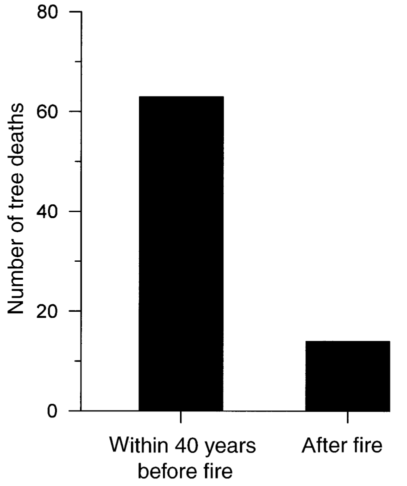

FIG. 9. Number of trees whose last ring is within 40 yr before a low-severity fire (because of potential loss of rings due to decomposition or consumption by subsequent fires) or whose last ring is after a low-severity fire, and so was likely not killed by it. Dead wood was omitted if the last visible ring was more than 40 yr before the earliest documented fire in the plot or was not associated with the fire (e.g., beetle-killed trees).

Disturbance-driven stand development

Most regeneration and mortality is associated with fire (Figs. 8 and 9). A sharp drop in regeneration after ~20 yr following high-severity fires (Fig. 8b) indicates that a large, cohesive pulse of regeneration occurs after high overstory mortality (see also Fig. 5). A low-severity fire often occurs within 20 yr after a high-severity fire. Depending on the size and degree of severity of this first low-severity fire, this may act as an initial thinning mechanism, potentially causing varying degrees of mortality.

In general, regeneration is high only after high-severity events (Figs. 5 and 8b), and regeneration associated with low-severity events often does not occur near the scars that document those fires (Fig. 7). Scarred trees are often surrounded by trees of the same age, which germinate together after a high-severity event documented either within the age-structure plot (when scars are inside the age-structure plot) or somewhere else in the fire-scar plot (in the case of scars outside the age-structure plot), rather than trees that germinated after the fire that scarred the center tree. The overall lack of regeneration near scars caused by low-severity fires may be due to recruitment failure resulting from competition with large trees nearby, local variability in fire severity, and spatial patchiness of fire. This pattern lends support to mapping minimum

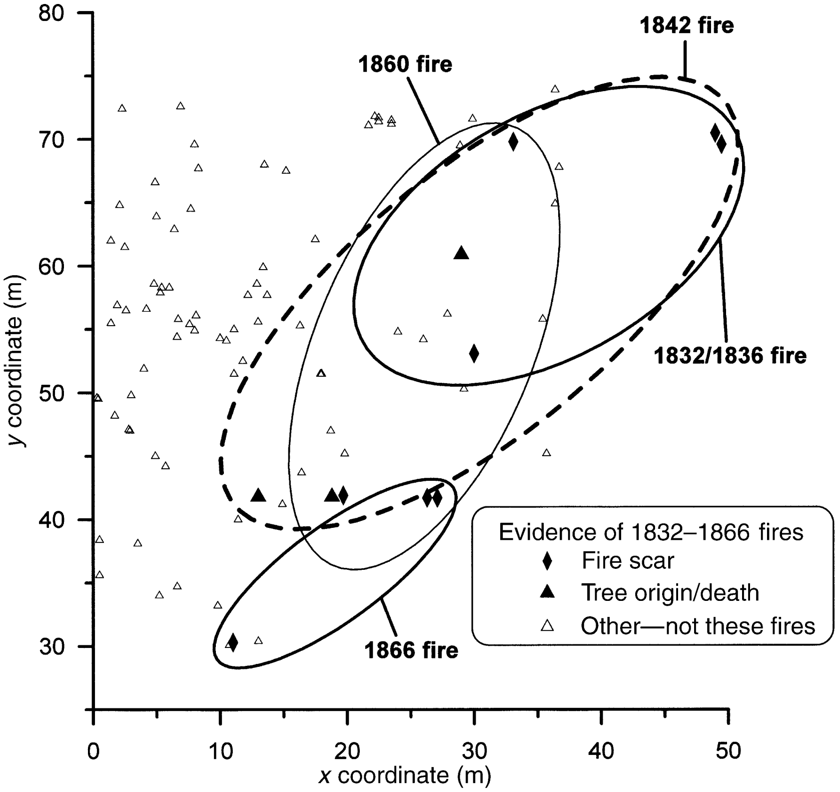

FIG. 10. Polygons encompassing fire scars and regeneration from the 1832/1836, 1842, 1860, and 1866 fires in the DMC plot.

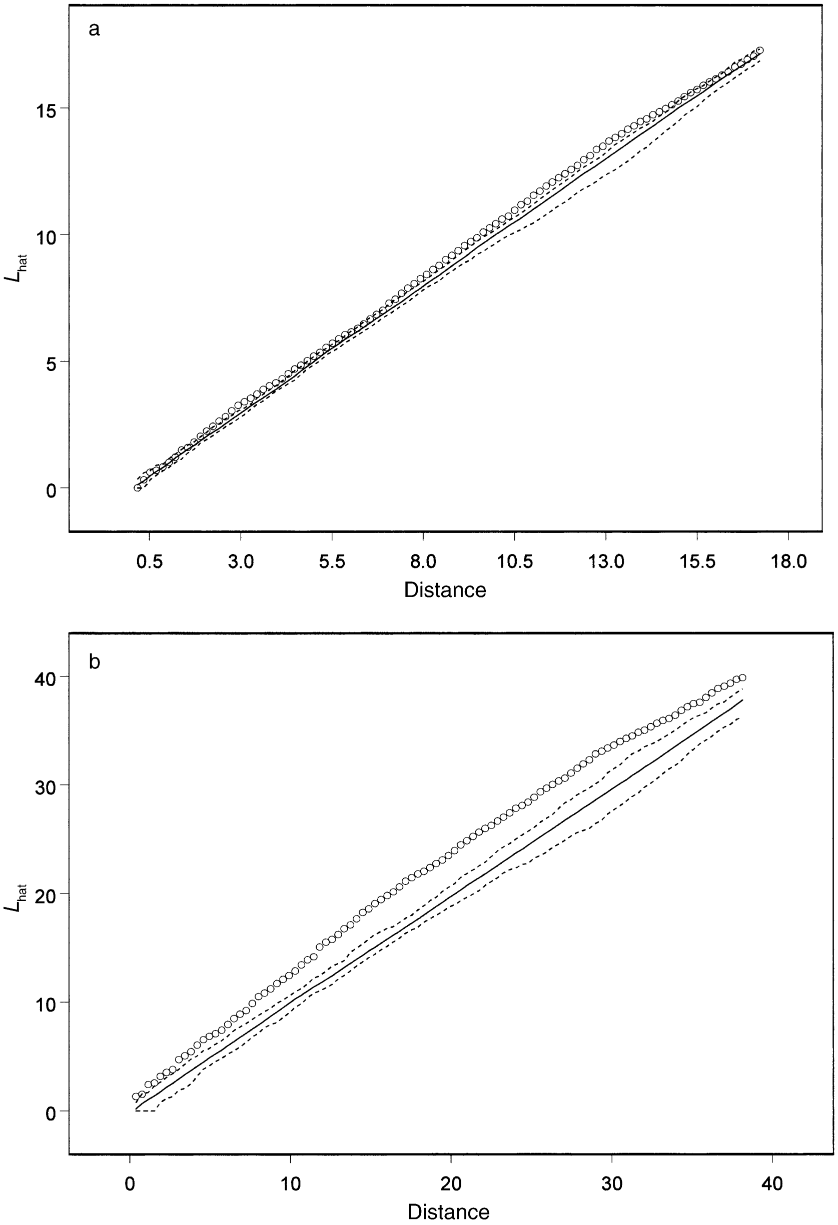

FIG. 11. L_{hat} graphs showing cumulative distance distribution of trees (open circles) in plots (a) BMM and (b) DMC and the departure from a Poisson distribution (solid line). Dashed lines indicate 95% confidence intervals. L_{hat} values above the 95% confidence intervals indicate clumping of tree locations, and values below the 95% confidence intervals indicate regular spacing of tree locations.

fire-size boundaries based partly on the assumption that a tree that regenerated within 20 yr after a fire is a result of the fire, even though it may not be located near the fire scar documenting the fire.

The absence of regeneration near fire scars and the weak clumping suggest that the clump-related regeneration mechanisms hypothesized by Cooper (1960) or White (1985) for the Southwest do not operate in ponderosa pine forests in RMNP. In the Southwest, clumped spatial arrangement and interspersed vegetation may influence fire spread and regeneration. It is also possible that patterns of fire spread cause a clumped pattern after regeneration has occurred. Crown fires in RMNP, in contrast, essentially erase previous tree patterns and their effects on fires and regeneration. Surface fires lead to regeneration in locations that do not correspond to fire-scar evidence. Mast and Veblen (1999) documented tree clumping at the pine–grassland ecotone, but did not specify the strength of the clumping pattern. Clumping in stands away from the ecotone in RMNP is present, but is so weak as to be nearly negligible in most plots (Table 1).

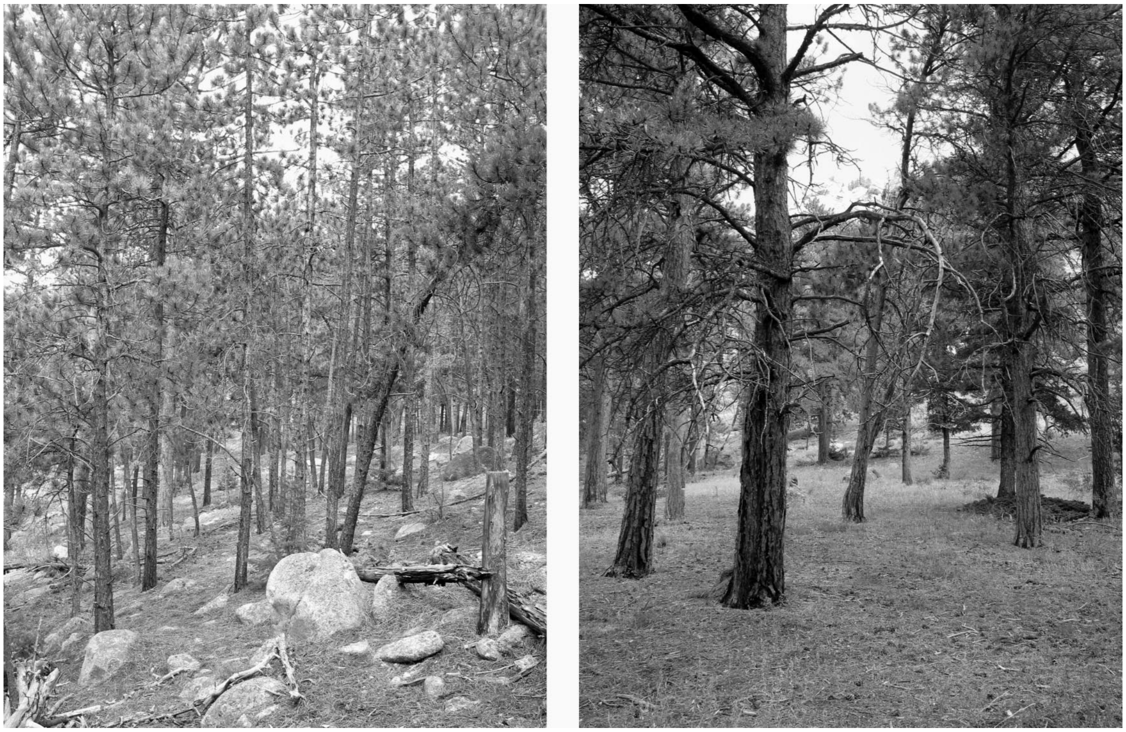

PLATE. 1. Ponderosa pine forests in Rocky Mountain National Park: (left photo) naturally dense, young forest that regenerated after a high-severity fire; (right photo) old-growth ponderosa pine forest that is deficient in young trees due to fire suppression. Photos by W. L. Baker.

High-severity fires cause initially even-aged stands that became less dense and more uneven-aged over time due to tree turnover caused mainly by surface fires (Fig. 5). Mast et al. (1998) also documented initially even-aged stands at the pine–grassland ecotone in RMNP that originated after fires in 1860. Dense, even-aged stands were also likely not uncommon before Euro-American settlement in the Black Hills (Shinneman and Baker 1997). As subsequent low-severity fires occur, a tail forms in the later part of the age-structure, indicating recruitment of younger trees (e.g., Fig. 5h). Repeated low-severity fires cause pockets of mortality and/or regeneration that lead to uneven age-structure (e.g., Fig. 7). After ~300 yr, and quite possibly less in the absence of fire suppression, it appears that the age distribution is relatively flat (Fig. 5e), indicating a more uneven age-structure than in younger stands. Net mortality must be higher than net recruitment (such as occurred after the 1945 fire in HPW), because density decreases through time until stands exceed 200 yr of age (Table 1). Older stands have experienced more low-severity fires per unit of time and space than have younger stands, indicating a possible feedback of stand structure on surface fires.

Relatively frequent surface fires that burn over the same area can delay tree recruitment. For example, low-severity fires from 1832 to 1866 in plot DMC effectively delayed recruitment until after a fire-free period following 1866 lasting 73 yr (Figs. 5d and 11). The need for 50 or more years after germination for ponderosa pine trees to survive fire has been suggested elsewhere (Baker and Ehle 2001). Unfortunately, evidence of mortality from fires between 1832 and 1866 may have been consumed in later fires or decomposed. It is impossible to know definitively whether trees germinated after each fire. If so, they would have been small when the next fire burned the area, and evidence of their existence would have likely been destroyed. The lack of fire in the period from 1866 to 1939 appears to have been one factor in the survival of the post-1866 pulse.

In normal years, regeneration in ponderosa pine stands appears to be predominately limited by drought and competition with grass for moisture, and regeneration does not usually occur unless grass is at least temporarily decreased. Studies of seedling–grass competition show that initial ponderosa pine regeneration may be high, but mortality is also high, due to competition with grasses for moisture (Pearson 1942, Kolb and Robberecht 1996). Grass roots grow faster than seedling roots and dominate the upper soil layers. Temporary removal of grass via burning, clipping, scarification, or root exclusion gives seedlings enough competitive advantage that survival increases (Pearson 1942, Foiles and Curtis 1965, Larson and Schubert 1969, Haase 1986, Kolb and Robberecht 1996). Removal of the overstory via natural or mechanical means without removing herbaceous understory does not generally result in high recruitment (Pearson 1910, Heidmann et al. 1982, Ffolliott and Gottfried 1991), but seedlings may occasionally be abundant (Weidman 1921, Pearson 1923, Weaver 1943). It may be that abundant regeneration comes in after overstory removal where grass density is low, seed crop is abundant, climate is favorable, or some combination of the three occurs.

Grazing pressure by native herbivores does not appear to have had a large effect on regeneration, because regeneration appears to be closely tied to fire occurrence regardless of herbivore population fluctuation. However, grazing cannot be excluded as an influence. Further research on the potential effect of grazing is warranted.

Fires, climate, and regeneration

Extant tree origins suggest that regeneration is elevated within 10 yr of a low-severity fire and 20 yr of a high-severity fire (Fig. 8a, b), but not by wet episodes (Fig. 8c, d). Enhanced regeneration of ponderosa pine after fires has been observed in prescribed burning experiments (Sackett 1984). Similarly, the extant regeneration pulses present in the plots appear visually to be the result of past high-severity fires, rather than climate (Fig. 5).

However, climate may sometimes play a role. The small 1760 pulse in many plots may have been co-caused by fire and climate, or climate may have only promoted recruitment after fire. Potentially favorable climate existed at that time, but fires occurred in at least three plots just before the pulses began. It is unlikely that a dry period during the 1750s was severe enough to kill overstory trees and potentially lead to regeneration. Mast et al. (1998) also have evidence of a 1760 regeneration pulse in their plots at the pine–grassland ecotone. The lack of evidence of mortality just before the beginning of the 1760 pulse, and the widespread occurrence of the pulse, point toward climate. Evidence of fire (at least one of them a crown fire) in half of the plots with the pulse and the potential for lost evidence due to long time since event point toward fire. Thus, there is evidence both for and against both climate and fire as the cause of the 1760 pulse. The event in ECM in about 1800 has not been positively connected to fire, but potentially favorable climate at this time was barely higher than average. There is no compelling evidence of either fire or climate as the cause of the pulse, but neither can be ruled out.

Relatively wet climatic conditions during the 1970s (Mast et al. 1998) and periods of high tree-ring index in the 1980s in RMNP (Fig. 5a) did not appear to increase tree recruitment in the pure ponderosa pine zone away from the pine–grassland ecotone. We found few seedlings (Figs. 2 and 5). Stohlgren et al. (1998*a*) similarly found only 12 ponderosa pine seedlings or saplings in ∼3 ha sampled in ponderosa pine transects in RMNP. However, Mast et al. (1998) found few post-1950 seedlings in six plots facing east and west, but many seedlings in six plots facing north and south. It is difficult to reconcile the difference in seedlings in our plots and in the transects of Stohlgren et al. (1998*a*) with the large number of seedlings documented by Mast et al. (1998) in half their plots. However, Mast et al. present aggregated plot data, their plots were apparently subjectively chosen, and fire scars were also subjectively selected. Aggregated plot data could by chance emphasize a pattern dominant in a small number of plots. Subjectively chosen plots may, by accident, contain high numbers of seedlings. Subjectively chosen scars may miss recent fires that are the cause of seedlings. The most recent fire detected in any of the Mast et al. plots in RMNP is AD 1900, while we found 28 fire scars dating after 1900 in our nine plots (Fig. 5), an average of three scars per plot. Although many post-1900 fires in our plots were not followed by tree regeneration, the regeneration that did occur is strongly associated with fires (Figs. 5 and 8). Our field experience in the ponderosa pine zone of RMNP is that the abundant seedlings found in half of Mast et al.'s plots are atypical of the zone in general, but could reflect a tendency in the ecotone with grasslands where Mast et al. sampled.

Due to localized cooling in and around RMNP, it is difficult to determine whether global warming has had an effect on regeneration. Mann et al. (1999) documented a warming trend beginning in the early 1900s, which leveled off from about 1945 to the 1970s, then continued to increase to a maximum of about 0.75°C above the mean of the calibrated period 1902–1980. Stohlgren et al. (1998*b*), in contrast, found that mean July temperatures in and around RMNP have decreased by more than 2°C in some areas near RMNP in the last 45 yr, likely due to cooler, wetter, local conditions created by irrigation on the plains east of the park. While a climatic influence on regeneration cannot be excluded using available data, most regeneration only occurred after fire both before and after the onset of global warming. Regeneration in plot HPW (Fig. 7) after a 1945 fire, for example, shows that regeneration occurred after temperatures had warmed and immediately after a fire.

Spatial variation in the environment likely accounts for some variation in fire regime and regeneration (Shinneman and Baker 1997), as well as spatial pattern of trees. Plots on Deer Mountain, for example, may more closely resemble stands in the Southwest than do other plots in RMNP that receive less direct sunlight. Two of the Deer Mountain plots experienced crown fires 200–300 yr ago. Plot HPW may have experienced two crown fires ∼80 yr apart (The 1800 regeneration pulse still present in neighboring HPE in Fig. 5i and the 1875 or 1878–1896 pulse in HPW in Fig. 5h). Both Deer Mountain plots and Hondius Park plots are south facing, but Hondius Park plots are partially shaded by nearby hillsides, and Deer Mountain plots are on a convex, unshaded hillside. Stands that receive more direct solar radiation are drier, so fire-spread may be greater and competition with grasses for moisture may be more intense, which may result in higher seedling mortality, as well as slower development of ladder fuels that facilitate crown fire.

High age-structure complexity across the landscape is due to small crown-fire size and variability in time since crown fire. Since our plots are small, we cannot readily determine whether fires that were fully crown fires at the plot level might be mixed-severity at the landscape level, burning some areas as surface fires and other areas (our plots) as crown fires. Fires in 1713, 1860, and 1863 appear to have been mixed severity at the landscape scale, but our data cannot exclude the possibility that other crown fires might have been more extensive. We do know that the present ponderosa pine landscape in RMNP is a mosaic of even- and uneven-aged patches delineated by crown-fire extent. This is in contrast with the Southwest, where it is thought that frequent surface fires led to a relatively homogeneous landscape of open, old-growth forest (Covington and Moore 1994*a*, *b*).

Effects of EuroAmerican settlement

The lack of difference in fire size or number of fires from the pre-EuroAmerican settlement to settlement period and the continued occurrence of crown fires at the beginning of the settlement period likely indicate that EuroAmerican presence did not have an appreciable effect on the dynamics of these stands until fire suppression efforts became effective and fire size declined. The transition from the pre-EuroAmerican settlement period to the settlement period is coincident with the change from generally cooler, drier conditions during the Little Ice Age (Petersen 1994) to warmer, wetter, climatic conditions today. Thus, the lack of difference in fire size and number of fires spanned the transition from one set of climatic conditions to another. It is unknown whether the fires that occurred during EuroAmerican settlement were set by humans. Regardless of ignition source, widespread fires and high-severity fires, such as occurred during 1859/1860, would not occur unless natural fuel accumulations and climatic conditions were suitable for a high-severity fire.

Estimates of tree density during the pre-EuroAmerican settlement period are much lower in the Southwest than in RMNP. Estimated pre-EuroAmerican tree densities in the Southwest range from ~7 to 60 trees/ha (Covington and Moore 1994*a*, Mast et al. 1999). One stand in the Southwest has current density of 507 trees/ha; 75% of these trees are <4 cm dbh (Covington et al. 1997), but the ages of these smaller trees are unknown. These estimates are much lower than current density in our study plots, which range from ~70 to 3000 trees/ha (Table 1). Current density in the older plots, in particular, is an underestimate of pre-EuroAmerican density, because density has decreased through time. Variation in density is expected within and between regions, because site conditions, disturbance history, and time since last disturbance all vary. Our findings do not support the idea that ''. . . increased density of ponderosa pine stands during the period of fire exclusion has changed the susceptibility of these forests to stand-replacing fires, pathogen infestation, and perhaps insect outbreaks'' (Veblen 2000:37). Tree density was always comparatively high in these forests, relative to the Southwest, and stand-replacing fires have not increased since EuroAmerican settlement.

Currently dense (BMM, HPW, and UBMS) ponderosa pine stands in RMNP are likely dense primarily due to the relatively short time since the last crown fire, although smaller surface fires in the suppression period have also contributed. Differences in density in adjacent paired plots are not due to differences in geologic substrate (Table 1), reinforcing the role of fire history in explaining density differences. The effect of fire suppression in RMNP is smaller fires, leading to a prolonged time for tree turnover from surface fires to occur. In younger stands, it will take longer for age structure to become uneven and density to decrease. Older stands already have a more uneven age structure and are less dense (Fig. 5c, d, e; Table 1).

An important distinction between dense stands in RMNP (Plate 1, left) and dense stands in the Southwest is that dense young stands appear to be a natural mode of regeneration in RMNP. Dense stands in the Southwest, in contrast, are thought to be dense due largely to suppression of frequent surface fires that formerly killed young trees (Covington and Moore 1994*a*, *b*).

Relatively little regeneration dates since the beginning of fire suppression in RMNP ponderosa pine forests (Plate 1, right) in contrast with the Southwest. There is no regeneration in a stand affected by a recent mountain pine beetle outbreak (Fig. 5b). Recent relatively moist climatic conditions during the 1970s have not resulted in regeneration pulses, except possibly in ecotones with grasslands (Mast et al. 1998). Over the last 200–300 yr, most regeneration has occurred after fire (Figs. 5 and 8). Long-term fire suppression in RMNP may lead to general recruitment failure. Fire suppression in the Southwest is commonly believed to be the cause of stagnating forests dense with young trees that would ordinarily have been thinned by fire (Weaver 1951, Cooper 1960, Covington and Moore 1994*a*, *b*). The effects of fire suppression are different in the Southwest because of the presence of the 1919 regeneration pulse (Savage et al. 1996), which is absent in RMNP.

If crown fires are successfully suppressed over a long period in RMNP, both stand structure and landscape structure throughout the pure ponderosa pine zone will be less heterogeneous than before suppression. Fire suppression in these forests nearly arrests the tree turnover (mortality and regeneration) process, rather than causing fuel buildup that could facilitate a crown fire that would not have otherwise occurred. Reintroducing surface fires in RMNP may actually restore the possibility of mixed- and high-severity fires somewhat by encouraging patches of tree regeneration that could offer a way for surface fires to climb into the canopy. Trees killed by fire and other causes may affect the severity and spatial pattern of future fires. If restoration is the goal, dead wood should be left in place, due to its role in severity and pattern of fires, in addition to its role as habitat and nutrient provider during decomposition. Some dead-and-down wood appears to naturally persist on the forest floor for hundreds of years in RMNP (Fig. 5).

A goal of fire restoration in the Southwest may be to kill many young trees that regenerated after settlement, while preserving older trees. In RMNP, the goal of fire restoration in older stands should be to restore regeneration as well as to kill some young, as well as old, trees. Unfortunately, young trees are presently rare in older stands due to fire suppression (Plate 1, right). In younger stands, the goal should be to restore the process of density reduction, although not necessarily accomplished by one fire. Some recruitment of younger trees will likely occur in burned areas, and the overall effect should be tree turnover, and wood on the forest floor.

Conclusion

The historical occurrence of crown fires in RMNP indicates that the paradigm of ponderosa pine structure and function drawn from forests in the Southwest does not accurately describe structure and function of all ponderosa pine forests. The range of natural variability of disturbance and resulting age structures is wider than previously thought, including crown fires and surface fires as well as even-aged and uneven-aged stands that must be taken into account in formulating regional restoration plans. Baseline information on the dynamics of these stands under historical conditions provides a foundation of information that may be helpful, along with future research, in determining future management objectives under potentially different climate conditions. Fire managers in Rocky Mountain National Park and similar urban-interface areas in which both surface and crown fires burned historically face a difficult dilemma. Surface fires alone will not fully restore the historical fire regime and stand dynamics, particularly if they do not lead to occasional overstory mortality and regeneration. Naturally occurring crown fires are an inherent component of the natural fire regime in ponderosa pine forests in Rocky Mountain National Park. Thus, thinning of these forests (via prescribed burns or mechanical means) and removal of dead trees and downed wood to reduce crown fire potential or fire spread may satisfy sociopolitical objectives, but should not be labeled as restoration.

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