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Ecological effects of changes in fire regimes in *Pinus ponderosa* ecosystems in the Colorado Front Range

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Abstract

Question: What is the relative importance of low- and high-severity fires in shaping forest structure across the range of *Pinus ponderosa* in northern Colorado?

Location: Colorado Front Range, USA.

Methods: To assess severities of historic fires, 24 sites were sampled across an elevation range of 1800 to 2800 m for fire scars, tree establishment dates, tree mortality, and changes in tree-ring growth.

Results: Below 1950 m, the high number of fire scars, scarcity of large post-fire cohorts, and lack of synchronous tree mortality or growth releases, indicate that historic fires were of low severity. In contrast, above 2200 m, fire severity was greater but frequency of widespread fires was substantially less. At 18 sites above 1950 m, 34 to 80% of the live trees date from establishment associated with the last moderate- to high-severity fire. In these 18 sites, only 2 to 52% of the living trees pre-date these fires suggesting that fire severities prior to any effects of fire suppression were sufficient to kill many trees.

Conclusions: These findings for the *P. ponderosa* zone above ca. 2200 m (i.e. most of the zone) contradict the widespread perception that fire exclusion, at least at the stand scale of tens to hundreds of hectares, has resulted in unnaturally high stand densities or in an atypical abundance of shade-tolerant species. At relatively mesic sites (e.g. higher elevation, north-facing), the historic fire regime consisted of a variable-severity regime, but forest structure was shaped primarily by severe fires rather than by surface fires.

Keywords: Douglas-fir; Fire history; Fire severity; Historic range of variability; Ponderosa pine; *Pseudotsuga menziesii*.

Nomenclature: Weber (1976).

Introduction

Large, severe wildfires in recent decades in many parts of the world from tropical to boreal forests have led to the widespread belief that "fires are behaving differently now than at any time in history," and much of the difference in fire behavior has been attributed to alteration of historic fire regimes (Anon. 2004). A common paradigm applied to many temperate and tropical ecosystems has been the belief that prior to modern fire suppression relatively frequent but low-severity fires characterized many xeric woodland environments, and that restoration of such fires is essential for maintaining biodiversity and ecosystem resiliency (Anon. 2004). However, the universality of this paradigm has been questioned on the basis of insufficient knowledge of past variability in fire regimes, and especially of the intensities and ecological effects of past fires (Anderson et al. 2005; Bradstock et al. 2005). A driving factor for forest management in the U.S. West is the belief that fuel reduction through thinning will not only protect life and property but will also simulate the fuel effects of formerly frequent, low-severity fires and promote ecosystem resilience (Anon. 2002a, b; Healthy Forest Restoration Act, HFRA: Anon. 2003). However, the social and ecological context surrounding wildfire is complex and defining vegetation management objectives to meet the goals of maintaining ecological integrity, biodiversity and community safety are challenging (e.g. DellaSala et al. 2004; Dombeck et al. 2004).

The HFRA and related policies are based on three important premises (Anon. 2003): (1) fire suppression since the early 20th century has reduced fire frequency, particularly in dry forest types formerly characterized by frequent, low-intensity fires; (2) this reduction in fire frequency has resulted in atypically dense forests and in-growth of shade-tolerant species such as *Pseudotsuga menziesii*; and (3) this increase in woody biomass has resulted in a greater risk of severe wildfires. Support for these premises is mainly from research on dry *Pinus ponderosa* ecosystems, including parts of the Southwest and inland Northwest, showing that thinning of dense modern forests could both reduce the hazard of crown fire and restore forests to historic conditions (Covington & Moore 1994; Everett et al. 2000; Allen et al. 2002; Hessburg et al. 2005a). However, other research has stressed the variability in the historic frequency and severity of fires in some *P. ponderosa* ecosystems, and consequently, the effects of fire exclusion on current fuel characteristics and fire hazard have been questioned (Shinneman & Baker 1997; Veblen 2003; Brown et al. 2004; Schoennagel et al. 2004; Hessburg et al. 2005b).

Some *P. ponderosa*-dominated forests, such as those on the eastern slope of the Colorado Rocky Mountains, have been shown to have had a variable-severity (also termed 'mixed and variable') fire regime in which both low- and high-severity fires occurred historically (Brown et al. 1999; Kaufmann et al. 2000; Ehle & Baker 2003). In a variable-severity fire regime, fire intervals tend to be longer than in an exclusively low-severity fire regime, and more importantly there are some high-severity fires (i.e. lethal to a large fraction of canopy trees in a stand) that strongly influence forest structure (Brown 1995; Brown et al. 2004; Hessburg et al. 2005b). Although recent studies in the Front Range have documented the occurrence of variable-severity fire regimes in *P. ponderosa* forests (Brown et al. 1999; Kaufmann et al. 2000; Ehle & Baker 2003), there have been no systematic examinations of how the ecological effects of high- vs. low-severity fires vary with elevation within this forest zone.

In the current study spanning the full elevation range of *P. ponderosa* on the eastern slope of the northern Colorado Front Range we address the following questions: 1. Has the rate of tree establishment increased since active fire suppression began around 1920? 2. Since 1920, is there evidence of in-growth of *Pseudotsuga menziesii* into *P. ponderosa* stands? 3. In this variable-severity fire regime, how significant were low-severity versus high-severity fires in shaping forest structures prior to fire exclusion? The primary focus of this study is on discriminating between forest structures that historically were shaped mainly by frequent low-severity (i.e. surface) fires that killed mostly juvenile trees versus structures that were shaped mainly by infrequent high-severity fires that killed high percentages of canopy trees in naturally dense stands.

Methods

Study area

The study area extends from ca. 1800 to 2800 m in Boulder County and southern Larimer County in the northern Front Range. Soils in the montane zone are primarily derived from Precambrian granitic rocks and are typically poorly developed, coarsely textured, and shallow (Peet 1981). At low elevations mean annual precipitation is ca. 48 cm, and a trend towards increasing precipitation and cooler temperatures with elevation results in greater moisture availability at higher elevation as reflected in vegetation patterns (Peet 1981). The drier montane zone extends from approximately 1800 to 2850 m and is largely defined by the distribution of *P. ponderosa* (Marr 1961). In the lower montane zone (1800 to 2350 m), forests vary from open park-like stands of *P. ponderosa* at the plains-grassland ecotone to dense stands mixed with *Pseudotsuga* at more mesic sites and north-facing slopes. In the mid- to upper montane zone (2350 to 2850 m), topographic position becomes increasingly important with dense stands of *P. ponderosa* and *Pseudotsuga* on north-facing slopes and pure, less dense stands of *P. ponderosa* on south-facing slopes. *Populus tremuloides*, *Pinus flexilis* and *P. contorta* (var. *latifolia*) often co-occur with *P. ponderosa* and *Pseudotsuga* at higher elevations in the montane zone.

Lightning-ignited fires are common throughout the montane zone with at least some small lightning-ignited fires occurring in every year (Veblen & Donnegan 2006). Although Native Americans set some fires mainly for hunting purposes, the abundance of lightning ignitions in the modern record (post-1910) imply that fire occurrence is not limited by ignitions. Furthermore, the tree-ring record indicates that fires were only widespread during years of unusually dry conditions so that it is likely that weather rather than ignition was the main limitation to years of widespread fire (Veblen et al. 2000). The zone of greatest Native American impact on fire occurrence would have been at the lowest elevations, near the Plains grassland where settlement was concentrated and where fuels dried sufficiently in most years to allow at least moderate fire spread (Veblen & Donnegan 2006). Permanent Euro-American settlement in conjunction with a mining boom in the second half of the 19th century was associated with an increase in the number of fire ignitions across the montane zone. However, the second half of the 19th century also was a period of more extensive droughts compared to the previous ca. 50-year period and all years of widespread fire coincided with weather conditions conducive to fire spread (Veblen et al. 2000). Thus, although it is impossible to quantify the relative contributions of humans and climatic variation to the increase in fire occurrence in the mid-19th century, the widespread pattern of drought and fire across the Rocky Mountain region suggests that regional-scale climatic variation was the predominant driver of the change in fire regime (Donnegan et al. 2001; Sibold & Veblen 2006). In the montane zone, fire frequency declined dramatically at the end of the 19th century and beginning of the 20th century (Veblen et al. 2000). At the lowest elevations reduction of grass fuels by livestock grazing probably contributed importantly to this decline in fire. However, above ca. 2200 m analysis of the tree-ring record of fire does not show any climatic dependence on moister antecedent years favorable to grass production (Sherriff 2004). This implies that grass fuels were not limiting to fire at higher elevation; consequently, livestock grazing probably did not contribute significantly to the decline in fire frequency in the mid- to upper montane zone. Instead, over most of the montane zone the reduced fire frequency after ca. 1920 coincides with implementation of fire suppression policies by federal and local authorities, improved infrastructure for fire suppression (e.g. automobile roads), and the end of the mining boom and associated anthropogenic ignitions (Veblen & Lorenz 1991; Veblen & Donnegan 2006).

Field sampling and sample processing

Twenty-four areas were sampled for tree age structures throughout Boulder County on Boulder Open Space and Arapaho-Roosevelt National Forest lands and in Larimer County in Rocky Mountain National Park (Fig. 1). Sample sites were limited to areas dominated or nearly dominated by *P. ponderosa* which is mapped as the dominant species in approximately 75% of the zone from 1800 to 2850 m (USDA Forest Service unpubl. data; Sherriff 2004; Sherriff & Veblen in press). General areas for sampling were first subjectively located to maximize the elevation range of sites where *P. ponderosa* was dominant, and to eliminate areas that showed significant signs of logging. Sites were chosen to focus on *P. ponderosa* stands, but also to be representative of the distribution of cover types within the montane zone with 10 sites in pure *P. ponderosa* (≥ 90% *P. ponderosa*), eight sites in *P. ponderosa* - *Pseudotsuga* (≥ 10% *Pseudotsuga*), and six sites in mixed conifer stands that are dominated by *P. ponderosa* (but include ≥ 10% of two or more co-dominant species).

Our focus was on *P. ponderosa*-dominated ecosystems, and consequently there was a bias towards aspects that were not north-facing at higher elevations which

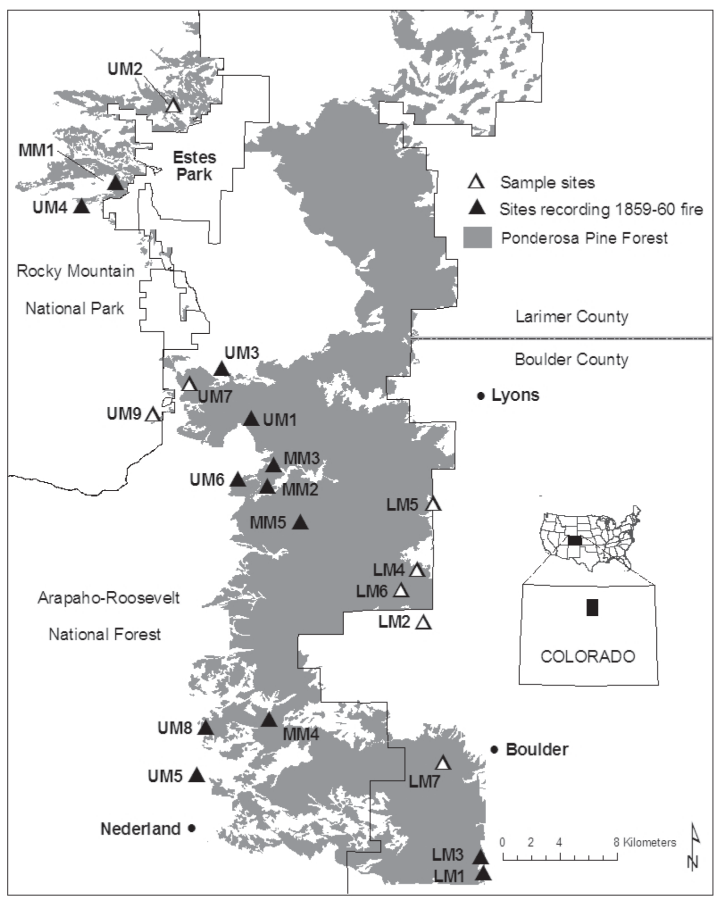

Fig. 1. Locations of sample sites of fire history and age structure throughout the *Pinus ponderosa* zone of the northern Colorado Front Range. Only 21 of 24 sites are shown because of the close proximity of LM3 east, west and north. Black triangles indicate sites that record the fire date of 1859-1860.

Table 1. Summary of site and sample information.

Site	Elevation (m)	Aspect	Slope (°)	No. fire scars	No. tree ages	Area (ha)	No. sectors	Crossdated dead trees
Lower Montane Zone								
LM1	1870	E-NE	11	18	109	100	4	13
LM2	1910	E	16	15	38	25	2	4
LM3-east[1]	1930	E-SE	18	37	118	30	4	8
LM3-west[1]	1930	W	15		101	50	4	
LM3-north[1]	1930	N	20		126	25	4	
LM4	1950	W-SW	20	7	103	50	4	
LM5	1950	W-SW	17	14	134	200	4	12
LM6	2090	W	28	13	44	12	1	
LM7	2200	E-NE	14	10	125	42	4	4
Mid-Montane Zone								
MM1	2440	E-Flat	5	20	133	80	4	8
MM2	2460	E-SE	12	21	144	95	4	
MM3	2480	NW	11	11	53	18	2	
MM4	2490	SE	21	18	164s	40	4	4
MM5	2520	W	16	16	124	191	4	
Upper Montane Zone								
UM1	2550	E	22	21	123	60	4	
UM2	2550	S-SW	20	16	123	50	4	6
UM3	2580	SW	11	32	134	135	4	5
UM4	2580	S-SW	15	21	131	50	4	19
UM5	2600	E	8	20	131	130	4	4
UM6	2620	E	13	11	67	55	2	
UM7-west[2]	2650	W	15	9	60	80	2	4
UM7-north[2]	2650	N	15	10	59	60	2	5
UM8	2700	E-SE	8	19	85	49	2	3
UM9	2750	E-SE	17	13	90	25	2	10

[1] LM3 was sampled as three separate sites for age and forest structure; 37 total fire-scar samples were taken across LM3 east, west and north sites; crossdated dead trees are for all three sites. [2] UM7 was originally sampled as one site and later divided into two separate sites because of differences in site conditions and forest structure.

tend to be pure stands of *Pseudotsuga* (Table 1) We also rejected sites for sampling if they contained more than a few cut stumps (> 20 stumps/ha). Because prior work has shown that cut stumps > ca. 25 cm diameter persist for over 100 years in this dry climate, the absence or near absence of cut stumps indicated that the sample sites had not been significantly affected by logging (Veblen & Lorenz 1986). Logging in the late 1800s and early 1900s was common in the montane zone, especially near roads and mines, but the widespread distribution of our sample sites on different topographic settings and wide range of stand ages sampled implies that while avoiding logged sites our sample sites are representative of the range of the *P. ponderosa* ecosystem.

Sampling of age structure and fire history

Stand structure and fire history were sampled in areas of relatively uniform forest structure and physical environment (elevation range and topography). The extent of each sample area varied in size from 12 to 200 ha according to tree density and the extent of the apparently homogeneous age structure. The sampling goal was to systematically obtain at least 50 tree ages from > 200 objectively located and measured trees. At 16 sites it proved feasible to sample > 100 tree ages but at eight sites low tree densities and/or smaller extent of the homogeneous, unlogged forest structure limited the age structure sample size to 38 to 90 trees (Table 1). To spread the sampling across each sample area, transects were randomly located in four ca. equal-area sectors in small and large sample areas, respectively. Fewer sectors were used in smaller and more homogeneous sample areas. Fire scars were collected opportunistically along transects and near the outer boundaries of each sector to produce a rough estimate of the spatial extent of past fire types across the entire site. Data from each sector were interpreted separately to test for consistency before aggregating data from multiple sectors to represent an entire sample site. At points of constant distances along each transect, trees (i.e. ≥ 4 cm in diameter) were systematically selected following the closest individual method (ca. 33 trees per sector; Cottam & Curtis 1956) for coring and age determination. Tree size, species, and status (i.e. live, dead, cut stump) were recorded in 10 m × 200 m belt transects for all except six sites (LM4, LM6, MM2, MM3, MM5 and UM6) that were sampled using only the closest individual method for both tree age and these other tree parameters. All trees > 1.4 m in height were included in the sample of size and stand structure. In addition, seedlings (< 30 cm height) and saplings (> 30 cm height and < 4 cm diameter) were counted in the belt transects at all sites.

To estimate the ages of trees too small to core (< 4 cm in diameter) and to estimate the number of rings missed due to coring height (ca. 20 cm above the root-shoot boundary), basal disks from juvenile trees were cut at sites of different elevation and aspect. Relatively open sites were selected to mimic post-fire growth conditions. Seedlings and saplings (< 4 cm in diameter) were sampled from 11 sites for *P. ponderosa* (*n* = 5-15 per site), eight for *Pseudotsuga* (*n* = 4-13 per site), and two to three sites each for *Juniperus* (*n* = 4 per site), *P. contorta* (*n* = 10-12 per site) and *P. flexilis* (*n* = 2-8 per site). For sites where seedling data were not collected, the median age-to-coring height was used from a site of similar elevation and aspect.

Tree-core and fire-scar sample processing

Annual rings on all cores were counted and visually cross-dated by comparison with a master chronology from nearby *P. ponderosa* sites (Veblen et al. 2000). For core samples that did not reach the pith, a geometric model of annual tree growth was used to estimate the number of rings to the pith (Duncan 1989). Cores that missed the pith by more than 20 years were not used. To date establishment and mortality of dead trees, samples were quantitatively cross-dated using the program COFECHA (Holmes 1983). Partial cross-sections from fire scars were initially cross-dated using marker rings, and when necessary were also measured and quantitatively cross-dated with COFECHA (see Sherriff 2004 for details).

Analytical methods

As detailed below, severity and regeneration impacts of past fires were interpreted from the spatial distribution of fire scars, percentages of living trees that survived a fire, abundance of tree establishment following a fire date, presence of synchronous tree mortality related to a fire date, and tree-growth suppressions and releases (Table 2) based on procedures from previous studies in nearby ponderosa pine forests (Veblen & Lorenz 1986; Goldblum & Veblen 1992; Kaufmann et al. 2000; Ehle & Baker 2003). For each fire event at each site, we considered alternative explanations of the apparent post-fire age cohorts. Specifically, we examined tree-ring evidence to rule out the alternative hypotheses that favorable climate alone (i.e. in the absence of a previous severe fire) or that widespread tree mortality caused by insect outbreaks triggered massive new tree establishment. Possible decadal-scale climatic influences on tree establishment were examined by comparing recruitment peaks (≥ 10 trees) and a 10-year smoothing average of moisture availability based on the departure from mean tree-ring growth from a regional ponderosa pine tree-ring chronology (Sherriff 2004). We did not find a consistent relationship between ponderosa pine establishment and decadal-scale climatic variation, and all episodes of abundant tree establishment occurred soon after fire-scar evidence of a fire (Sherriff 2004). Although tree cores at some sites showed growth releases or suppressions in relation to 20th century outbreaks of bark beetles or defoliating insects, we did not detect major episodes of tree establishment dating from these outbreaks (Sherriff 2004).

Duration and timing of tree establishment and mortality

Previous age structure studies of *P. ponderosa* in our study area have shown that durations of periods of elevated seedling recruitment following fire are highly variable, but commonly last several decades and sometimes over fifty years (Veblen & Lorenz 1986; Mast et al. 1998; Ehle & Baker 2003). In this study, we assumed tree establishment that occurred within a 40-year period following a fire-scar date within the same sector of a site to be associated with that particular fire date. Tree establishment over longer periods (i.e. 40 to 60 years following a fire-scar date) was assumed to be associated with the fire-scar date if tree establishment was continuous at a 10-year time scale. A widespread fire (i.e. fire-scarred trees recording a fire date in more than one sector) was more likely to be of higher severity and to have created conditions more favorable for tree establishment than a fire of limited extent (i.e. a fire event recorded by a single fire-scar date). Thus, if both a single and a widespread fire-scar date occurred in the same sector (within a period of 40 years or less), post-fire tree establishment was attributed to the widespread fire. Due to decay and disappearance of evidence, we did not attempt to quantify the amount of tree mortality associated with past fire events, and instead tree mortality is classified as present or absent. The date of the outermost ring on dead trees was defined as the mortality date even though ring erosion would have resulted in some inaccuracies. Most mortality dates (> 98%) were within two years of the fire event date in question. For the small number of mortality dates not within two years of the fire event date, it was assumed that if the date of the outermost ring preceded the fire date by fewer than 10 years that the tree was killed by the fire in question.

To investigate changes in forest age structures potentially related to fire exclusion, we compared establishments dates of living trees for three different time periods: Pre-EuroAmerican settlement (prior to 1861), settlement (1861-1920), and fire suppression (1921 to present). The time period of 1921 to present was selected to determine if substantial increases in tree density and in-growth of

Table 2. Classification of fire severity based on remnant live trees, recruitment of live trees, death dates (presence or absence), ring-width changes and tree spatial pattern. Remnant trees are the percentage of trees that survived the most recent fire in the severity class, and recruitment pulse indicates the percentage of live trees that post-date the fire. Fires of low and moderate severity occur at more variable frequencies than high-severity fires that occur at longer intervals (> 50 years).

Fire severity class	Frequency	Remnant live trees	Recruitment pulse live trees	Mortality pulse	Ring-width change	Tree spatial distribution
Low	Variable	40 - 100 %	≤ 20% or < 3 trees	Present or absent	No change in growth	Patchy or clustered
Moderate	Variable	20 - 70 %	20 - 70 %	Present	Release or suppression	Patchy or dispersed
High	Infrequent	0 - 19 %	71 - 100 %	Present	Release or suppression	Uniform

young *Pseudotsuga* occurred during the fire exclusion period. Tree establishment associated with the fire suppression period actually refers to trees that established between 1921 and ca. 1980 because the youngest trees (≥ 4 cm diameter) aged were ca. 20 years old. Large-scale permanent EuroAmerican settlement began in the late 1850s (Veblen & Lorenz 1991), and consequently the 1861 to 1920 settlement period is equivalent in length and directly comparable to the fire exclusion period. χ^2-tests were used to test for differences in frequencies of *P. ponderosa* establishment by time period and elevation (lower versus mid- and upper montane zones), and of *Pseudotsuga* establishment since 1921 compared to the previous 60 years.

Fire severity classification

We evaluated past fire types and fire effects by: (1) visual inspection of frequency distributions of tree establishment and fire dates within each sector; and (2) a quantitative approach to classifying fire regime types within each sector and across sectors of each site using fire scars, remnant living trees that survived a fire, post-fire tree establishment, synchronous tree mortality, and tree-ring growth responses (Table 2). Fire severity was classified as high, moderate or low (Table 2) based on estimates of canopy tree mortality associated with modern fires in Colorado (Romme et al. 2003). Fire events in which the severity class applied to all sectors were designated as 'extensive' or as 'patches' if applicable to fewer than all sectors.

A high-severity fire was identified as an event in which more than 70% of the live trees established during the post-fire establishment period and fewer than 20% of the live trees pre-dated the fire event (i.e. remnant trees in Table 2). Thus, high-severity fires are interpreted to have been events that killed high percentages of canopy trees within a fire perimeter, and initiated establishment of a new cohort of canopy trees as is typical of *P. ponderosa* (Romme et al. 2003). Low-severity (surface) fires were identified by a fire-scar date that had little or no post-fire establishment (fewer than 20% of the live trees) in the same sector and at least 40% of the live trees pre-dated (remnant trees) the fire-scar date (Table 2). The presence of mortality and/or an abrupt change in ring width (release and/or suppression) would more likely be associated with a high-severity event than a low-severity fire. At some sites evidence of past fire types (i.e. fire scars, post-fire age structure, tree-ring growth responses and mortality events) was more variable. Fires that did not fit either the high- or low-severity criteria were classified into the intermediate class of moderate- fire severity (Table 2). A moderate-severity fire was defined as having 20 to 70% post-fire establishment and fewer than 70% of the live trees pre-dating the fire event. This classification discriminated between forest structures that prior to the beginning of fire exclusion (ca. 1920) were shaped primarily by frequent low-severity fires that killed mostly juvenile trees, versus infrequent high-severity fires that occurred in naturally dense stands where fires killed high percentages of canopy trees.

Results

Stand age structures and tree establishment dates

Ages were determined from a total of 2519 living trees and 109 dead trees in the 24 stands (Table 1). Age structure is based on an average of 105 (range of 38-164) tree ages for each site (12-200 ha). Of the cores sampled at each site, 55-85% are within two years of the pith and 93-100% are within ten years of the pith by either observing the pith or as estimated by Duncan's (1989) geometric method. Of the cores from each site 93-100% are within ten years of the pith. Fewer than 20 cut stumps/ha are present at most of the sample sites and differences in median numbers of cut stumps among the three elevation zones are small (Fig. 2; App. 1); although no quantitative cut stump information was collected at LM4, LM6, MM2, MM3, MM5 and UM6, cut stumps are scarce at those sites.

To estimate tree establishment dates, age at coring height was adjusted by the median age-at-coring height from destructive sampling of seedlings at the same site or a site of similar elevation and aspect. The median age-at-coring height ranges from 6-22 years for *P. ponderosa*, 12-21 years for *Pseudotsuga*, 7-17 years for *Juniperus*, 12-19 years for *P. contorta* and 16-21 years for *P. flexilis*. An estimate of three years is used for *Populus* based on seedling ages collected by Baker et al. (1997) at a nearby site. For each site, the age range represented by saplings is assumed to span from the median seedling age into the ages represented by 4 to 6 cm diameter trees for that species. Thus, although sapling ages are not precisely quantified, they represent establishment dates mostly or exclusively within the most recent 40 years. Tree establishment dates were grouped into 20-year tree age classes as a conservative basis for interpreting age structure patterns.

Stand densities are highly variable across the distribution of *P. ponderosa*. Median stand density is 348 trees/ha (range of 39-670) in the lower montane, 806 trees/ha (range of 242-933) in the mid-montane, and 665 trees/ha (range of 123-1624) in the upper montane zones (Fig. 2; App. 1). In the lower and mid-montane zones (below 2520 m) *P. ponderosa* is overwhelmingly dominant in tree density (Fig. 2; App. 1). At most upper montane sites (2550-2750 m) it is also dominant, but *Pseudotsuga*, *P. contorta* and *Populus* are more abundant at one site each on a northerly exposure and at high elevation (UM7-north, UM8, and UM9, respectively). At two sites (UM7 and LM3), differences in forest composition and/or structure between sectors justified subdividing the sites into two or more separate areas for evaluating stand development and fire history (Fig. 3). Relatively little *Pseudotsuga* was present at most sites with an average of 14% (range of 0-53%) of the tree population across all sites (Fig. 2; App. 1).

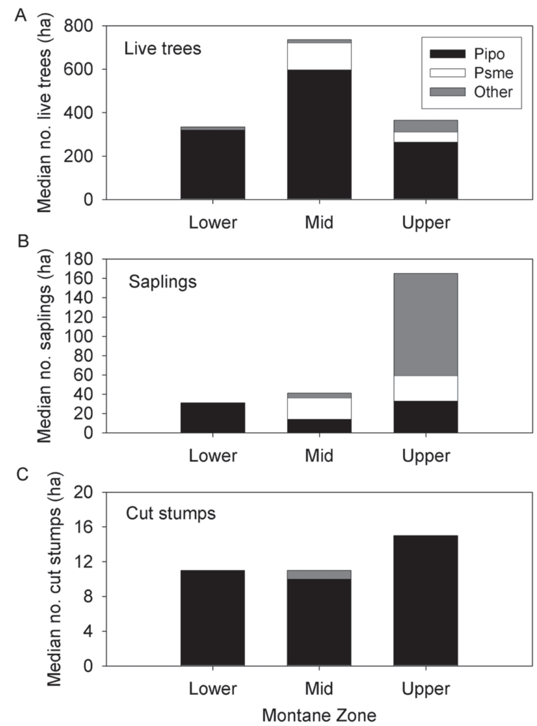

Fig. 2A-C. Median density of (**A**) live trees ($\geq$ 4 cm diameter), (**B**) saplings, and (**C**) cut stumps for each species per hectare for each elevation zone. Species are *Pinus ponderosa* (Pipo) and *Pseudotsuga menziesii* (Psme); category 'other' represents *Pinus contorta*, *Pinus flexilis*, *Populus tremuloides* and *Juniperus scopularum*. Other species are primarily *Juniperus* in the lower montane (1870-2200 m), *Populus* in the mid-montane zone (2440-2520 m), and *P. contorta* and *Populus* in the upper montane (2550-2750 m) zones.

Age structure by elevation zone

In the lower montane stands, tree populations are relatively young (Fig. 3); 28% of the living trees in these nine stands established since 1921 as compared to 53% that established in the previous 60-year period (Fig. 4). Even though tree establishment did not become more frequent after 1921, the number of *P. ponderosa* that established since 1921 is greater in the lower montane sites than in the mid-montane (P < 0.001, χ^2-test) and upper montane sites (P < 0.001). Tree establishment dates (Fig. 3) and the abundance of saplings at many sites (Fig. 2; App. 1) in the lower montane zone indicate that tree establishment continued through the end of the 20th century. Establishment of *P. ponderosa* was relatively high during the early 20th century at all lower montane sites, but there is some variation in the timing of this increase (Fig. 3). Major pulses of establishment had begun by 1880 at some sites (e.g. LM3-east, LM4) while at other sites no increase occurred until after 1900 (e.g. LM3-west, LM7; Fig. 3). The only two sites (LM3-north and LM7) that record abundant saplings (App. 1) and tree establishment of *Pseudotsuga* since 1921 also contain older trees of this species (Fig. 3); in these stands, there were no significant differences between the number of *Pseudotsuga* that established from 1860-1920 or after 1921, (P > 0.05, χ^2-test).

In the mid- and upper montane zones (above 2200 m), relatively few trees established during the 20th century in comparison with the lower montane sites (Fig. 3). Many sites have pulses of establishment initiating in the 1860s to 1900, and some sites contain the apparent remnants of pulses of establishment from the early 1800s or earlier (Fig. 3). *P. ponderosa* establishment dates are consistently less common after 1920 in comparison with the previous 60-year time period (Fig. 3). Aggregated establishment dates for all species are substantially greater from 1861 to 1920 than after 1920 (P < 0.001, χ^2-test; Fig. 4). Numbers of saplings of *P. ponderosa* and *Pseudotsuga* are relatively low (Fig. 2B; App. 1) further indicating that there has not been a major increase in tree establishment during the fire suppression era. *Pseudotsuga* trees that established after 1921 on average account for $\leq$ 3% of the trees in both the mid- and upper montane zones (Fig. 4). *Pseudotsuga*

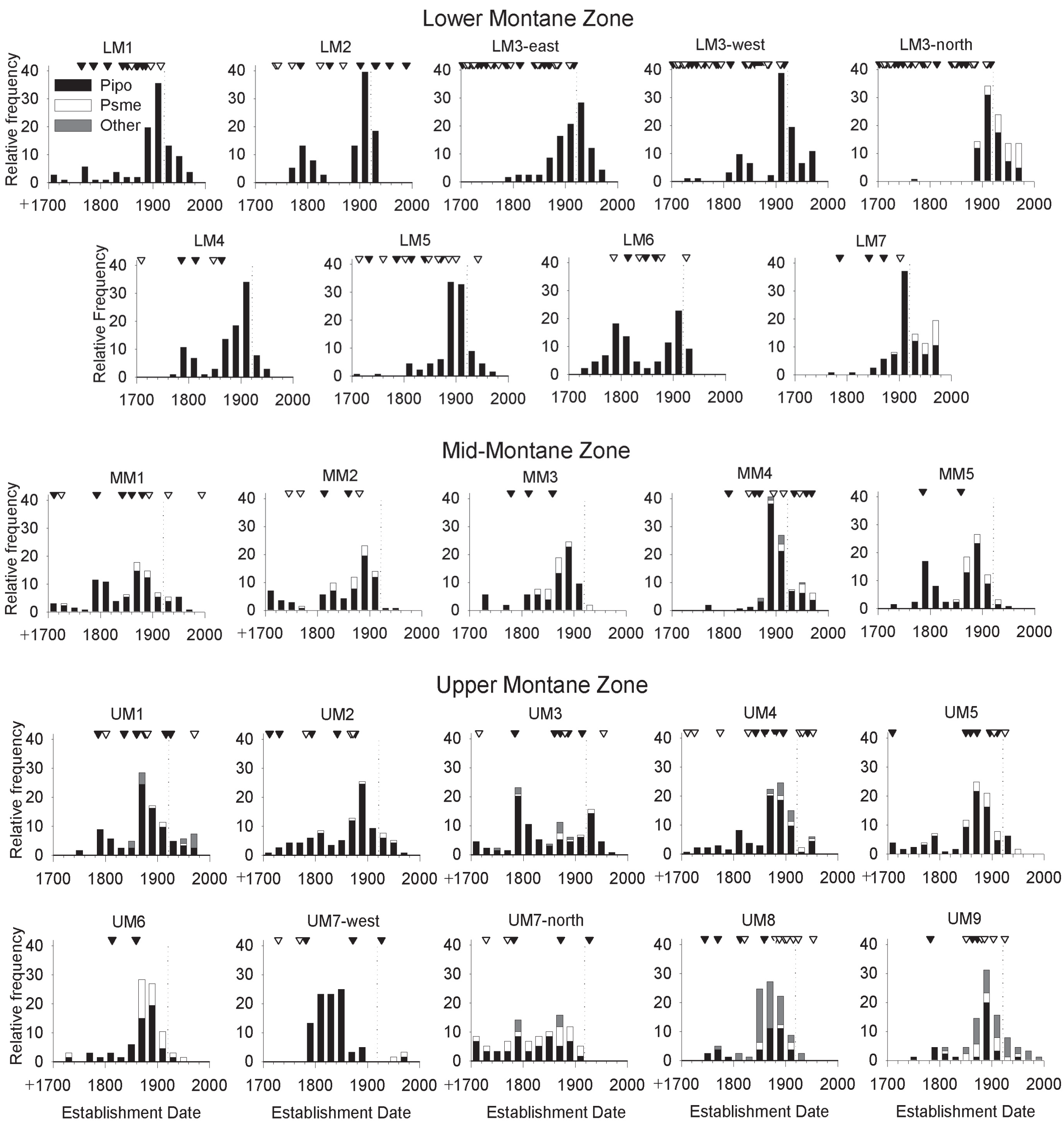

Fig. 3. The relative frequency (%) of all aged trees (≥ 4cm diameter) in 20-year establishment classes for each site in the lower (1870-2200m), mid- (2440-2520m) and upper (2550-2750m) montane zones. White triangles represent local fires (single fire-scars) and black triangles represent more widespread fires (multiple fire-scars). The dashed horizontal line marks the post-1920 fire suppression period. Other species primarily represent *P. contorta* at UM8 and *Populus tremuloides* at UM9.

saplings are moderately abundant at some sites, but in each case these are sites where tree ages indicate that this species has long been present as shown by no differences in the frequencies of pre- and post-1921 establishment dates (Figs. 2-3; $P > 0.05$, χ^2-test).

Past fire types and fire effects

During the pre-fire exclusion period (1700-1920) two to 29 fire events (i.e. at least one fire scar per fire event) occurred at individual sites and a total of 160 fires occurred across the 24 sites (tree-level fire history charts for each site are presented in Sherriff 2004). At all sites,

Table 3. The percentage of surviving trees (remnants), tree establishment, change in ring-width of live trees and mortality presence at each site associated with the most recent moderate- to high-severity fire. Bracketed fire years spanning two or more years were used when the exact fire dates were undetermined. Mortality presence indicates death of one or more trees associated with the fire event. Spatial pattern of the respective fire severity is described as 'extensive' when the fire occurred in all sectors or as 'patches' when the fire occurred in fewer than all sectors of a sample site. The estimate of minimum fire extent is based on evidence of fire occurrence across sectors within each site. There were no moderate- or high-severity fires identified at LM1 and LM3.

Site	Fire year	Remnant (% live trees)	Establishm. (% live trees)	Establishm. period (years)	Ring change (% live trees)	Mortality presence[4]	Fire severity	Spatial pattern	Min. fire extent (ha)
Lower Montane									
LM1									
LM2[1]	1786		21	28			low-moderate	patches	6
LM3									
LM4	1863-66	23	53	42			high	patches	50
LM5	1871	22	60	33	9.6	present	high	patches	200
LM6	1866-69	52	41	43			moderate	extensive	12
LM7	1870	6	45	44		present	moderate	extensive	42
Mid-Montane									
MM1	1880	27	62	43	9.5		moderate	extensive	80
MM2	1859	50	35	44			moderate	extensive	65
MM3	1859-60	43	53	50			moderate	extensive	18
MM4	1859	5	47	41	12.5		high	patches	40
MM5	1859	38	52	46			high	patches	191
Upper Montane									
UM1	1859-60	27	49	39	3.3		moderate	extensive	60
UM2	1876	45	38	43	14.3	present	moderate	extensive	50
UM3[2]	1913	70	23	42	2.7		moderate	patches	135
UM4	1880	48	43	38			high	patches	50
UM5	1859-60	35	52	46	2.2		high	patches	130
UM6	1859	28	60	44			high	patches	55
UM7-west[3]	1782	2	45	45	6.2	present	moderate	extensive	85
UM7-north[3]	1782	25	34	60			moderate	patches	55
UM8	1859	17	80	48	14.3	present	high	extensive	49
UM9	1872	47	43	26	36.4	present	moderate	extensive	25

[1] Too few trees existed prior to late 1800s to assess the percentage of surviving trees (remnants); [2] The low-severity fire of 1913 was mixed severity in 1 sector and low severity in 3 sectors; [3] Estimated minimum extent of the 1782 fire is 140 ha for the entire sampling area; [4] Death dates were not sampled at LM4, LM6, MM2, MM3, MM5, or UM6.

tree establishment began within 12 years after a fire-scar date (Fig. 3). No major peaks in tree establishment (≥ 10 trees) are observed that could not be associated with a fire-scar date during the 1700 to 1920 period. Recruitment periods range between 19 and 60 years for fires interpreted as moderate to high severity (according to the criteria in Table 2). Tree establishment periods following low-severity fires were often shorter than 10 years. However, destruction of evidence by subsequent fires at the same location prevented a reliable assessment of fire severity for 73 of the 160 total fire events. Thus, we systematically describe fire severities and associated evidence only for the most recent moderate- to high-severity (i.e. evidence destroying) fire events, most of which occurred in the second half of the 19th century. Fire severity at each site is designated as extensive when applied to all sectors or as patches where the severity class applied to fewer than all sectors.

Fire severity by elevation zone

In the lower montane zone below 1950 m, the relatively high number of fire scars recorded on dispersed trees (i.e. sites LM1-LM3; Fig. 3), and the scarcity of evidence of large post-fire cohorts, growth releases, or tree mortality imply that fires were generally widespread but of low severity. With the exception of two fire events at LM2, these relatively frequent low-severity fires ceased after 1920 (Fig. 3). Below 1950 m, forest density was historically low and it is doubtful that high-severity crown fires could have occurred prior to the early 1900s, although a moderate-severity fire occurred at LM2 in 1786 (Table 3; Fig. 3). At higher elevations (1950 to 2200 m) within the lower montane zone, moderate- and high-severity fires in the late 1800s are evident in all four sites (i.e. LM4-7; Table 3).

In the mid- and upper montane zone (above 2200 m), the pre-1921 frequency of widespread fires was substantially less than in the lower montane zone (Fig. 3). For example, some sites (e.g. MM5 and UM6 with 16 and 11 fire scars, respectively) record only two dates despite the presence of trees that established prior to 1750 (Fig. 3). Although fewer widespread fires occurred in the mid- and upper-montane zones, fire dates such as 1859-60 were regionally synchronous that could have been a single

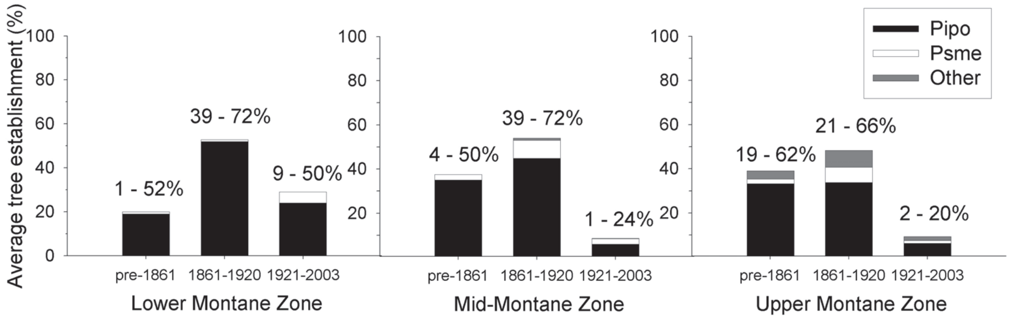

Fig. 4. The average percentage of tree establishment (trees ≥ 4 cm diameter) for time periods prior to the fire suppression period (pre-1861 and 1861 to 1920) and during the fire suppression period (1921 to present) for the lower (n = 9 sites), mid- (n = 5 sites) and upper (n = 10 sites) montane zones. The tree establishment dates during the fire suppression period range from 1921 to 1980. The range in percentages of establishment for each site within each elevation (montane) zone is given above each bar graph.

widespread fire event or multiple fires (Fig. 1 and see Veblen et al. 2000). In 1859-1860, extensive moderate- to high-severity fires occurred at six of the seven highest density stands (MM2, MM3, MM5, UM5, UM6 and UM8; Table 3; App. 1) and patchy moderate- to low-severity fires occurred at seven other sites (i.e. LM1, LM3, MM1, MM4, UM1, UM3, and UM4; Table 3; Fig. 3). The occurrence of widespread fires declines dramatically after about 1920 (Fig. 3). The high frequency of single fire scars at some sites (e.g. UM8, UM9) well into the fire-exclusion period probably reflects the burning of one or two trees by fires that did not spread. However, tree establishment linked to the extensive fire events of 1859 (UM8) and 1872 (UM9) dominate the present forest structure, whereas new tree establishment cannot clearly be related to the 20th century surface fires in these stands (Table 3; Fig. 3).

Across the distribution of *P. ponderosa*, the most recent moderate- to high-severity fires occurred mostly in the second half of the 19th century and strongly influenced the abundance of tree establishment dates in the modern forest (Table 3). At 18 sites, 34 to 80% of the live trees date from establishment associated with the last moderate- to high-severity fire; only 2 to 52% of the living trees pre-date these fires suggesting that fire severities prior to any effects of fire suppression were sufficient to kill many trees (Table 3). Remnant age structures, widespread fire scars and abrupt changes in tree radial growth suggest that more than one moderate- to high-severity fire occurred at most sites since ca. 1700, although subsequent high-severity fires destroyed much of the earlier evidence of fires. High-severity events are evident across these sites of 12 to more than 200 hectares, but probably burned much larger areas than the maximum sizes of our sample areas, as indicated by widespread occurrence of dense post-fire cohorts and fire-scarred trees in years such as 1859-1860 recorded in nearby studies (Fig. 1; Veblen & Lorenz 1986; Mast et al. 1998; Ehle & Baker 2003).

Discussion

Stand age structures and tree establishment

Although environmental variation associated with topography (aspect, slope steepness) is important in determining forest composition and structure in the montane zone of the Front Range (Peet 1981), major patterns of age structure in our study area are evident in broadly defined elevation zones. Tree ages in the lower montane zone (ca. 1870-2200 m), indicate that formerly sparse *P. ponderosa* stands increased substantially in density during the 20th century and that nearly treeless grasslands have been invaded by trees (Figs. 2-4). This increase in *P. ponderosa* densities at the lowest elevations has been documented in other studies of tree ages (Veblen & Lorenz 1986; Mast et al. 1998) for small parts of the study area and by historical photographs (Veblen & Lorenz 1991).

The increase in stand densities in the lower montane zone coincides with a decline in years of widespread fire that begins in the 1880s to 1890s in some stands (Fig. 3), which is a general pattern for this elevation zone (Veblen et al. 2000). Fire occurrence may have declined earlier at the lower elevations due either to reduction of grass fuels by grazing or to more effective fire suppression close to settlements. However, fire reduction is probably not the sole explanation for increased tree establishment at low elevations in the late 19th to early 20th centuries. Cattle grazing was widespread along the ecotone between the plains grasslands and the foothill forests during the late 19th century and has long been hypothesized to trigger tree establishment in grasslands (Marr 1961) as has been demonstrated in *P. ponderosa* ecosystems elsewhere (Madany & West 1983; Rummell 1951). Additionally, the 1890s to the 1920s was a period of moister climate (Mast et al. 1998; Veblen & Donnegan 2006), and establishment of *P. ponderosa* in the lower montane zone depends on above-average spring moisture (League &

Veblen 2006). Although cut stumps are rare at most sites (Fig. 2), the soil disturbance associated with the extraction of a few logs could also have created favorable conditions for establishment of tree seedlings (Kaufmann et al. 2000). Grazing, logging, and favorable climate probably all contributed to increased establishment of *P. ponderosa* in the late 19th and early 20th century, but seedling survival also depended on the long fire-free period that initiated coincidentally with these other environmental changes.

Although there is a general pattern of increased *P. ponderosa* stand density in the lower montane zone since the late 19th century, the magnitude of this change varies with topographic and edaphic conditions. Sites located on more xeric slopes of fine-grained sedimentary materials exhibit low stand densities that have not increased substantially over the last 80 years (e.g. LM2 in Fig. 3). Increases in stand densities have been more prominent on mesic (northerly) slopes (e.g. LM3-north and LM7; Fig. 3). Similarly, comparison of air photos from the 1930s to 1990 shows more tree encroachment on north-facing slopes at the lower forest-grassland ecotone (Mast et al. 1997).

In contrast to the lower montane zone, at mid- to upper elevations (ca. 2440-2750 m), only small percentages of living *P. ponderosa* established in the post-1920 fire exclusion period (Fig. 4). For example, at no site above 2200 m did more than 24% of the trees of all species (> 4 cm diameter trees) establish after 1920. Even when saplings (i.e. < 40 years old) are considered, there is no evidence of abundant establishment of *P. ponderosa* after 1920 (Fig. 2). Similarly, tree ages do not support the hypothesis that *Pseudotsuga* has invaded previously pure stands of *P. ponderosa* during the post-1920 fire exclusion period (Fig. 4). In the lower montane stands, establishment of *Pseudotsuga* is absent except on mesic aspects with a northerly component (e.g. LM3-north and LM7; Fig. 3). In the mid- and upper montane zone, *Pseudotsuga* is more abundant as trees and saplings (Figs. 2-3), but where young (i.e. post-1920) *Pseudotsuga* are abundant tree ages indicate that the species was also common prior to fire exclusion. Such stands do not show evidence of *Pseudotsuga* invading formerly pure or nearly pure *P. ponderosa* stands, and instead appear to be mixed *P. ponderosa-Pseudotsuga* stands recovering from pre-20th century fires.

A potential limitation to our interpretations is the rejection of sample sites that showed abundant evidence of logging if such sites were characterized by particular site or stand conditions not represented by unlogged sites. However, that bias would have the effect of reducing the abundance of old trees in our samples if there was a preference for cutting stands of large, old trees. As noted previously minimal logging in some sectors of our study areas might have favored new tree establishment tending to increase the number of trees that established after the late 1800s. The direction of these biases cannot explain our main finding of rare *P. ponderosa* establishment in the lower montane zone or scarcity of in-growth of *Pseudotsuga* across all the sites during the fire exclusion period. However, late 19th and early 20th century logging clearly had an impact over the larger landscape (Veblen & Lorenz 1991) and contributes to younger tree ages today, even though our sampling avoided such heavily logged sites.

Past fire types and fire effects

Previous studies of *P. ponderosa* pine forests in the Colorado Front Range have shown that the historic fire regime was one of variable severity, and in particular that fire intervals were longer and fire severity greater than for most dry *P. ponderosa* woodlands of the Southwest (Veblen & Lorenz 1986; Brown et al. 1999; Kaufmann et al. 2000; Ehle & Baker 2003). However, the present study is the first to systematically show that the relative importance of lower- and higher-severity fires varies between the lower montane zone and the mid- and upper montane zone within *P. ponderosa*-dominated forests. In our study area, more frequent low-severity fires characterize areas of low elevation (below 2000 m) where *P. ponderosa* ecosystems border or intermingle with grasslands. Due to the overriding influence of grasslands at low elevation, other factors such as topographic position may be inconsequential for determining fire frequency in areas adjacent to the plains-grassland ecotone. Greater proximity to grassland in lower elevation areas probably promotes more frequent fire because of a greater abundance of fine, herbaceous fuels. In this environment, the historic fire regime consisted mainly of low-severity fires that killed only tree seedlings but were not lethal to the generally sparse population of large trees. This pattern is especially evident below 2000 m, but also occurred at higher elevations on xeric south-facing slopes and/or where montane grasslands were abundant. In the northern Front Range, the cessation of formerly frequent surface fires coincides with increased stand densities broadly throughout the lower montane zone. At increasing distance from grasslands, lower amounts of fine fuel may hinder frequent fire occurrence.

In the mid- and upper montane zone there is no evidence that surface fires formerly maintained open woodlands of low density tree populations. Instead, the historic fire regime at higher elevations and on more mesic north-facing slopes consisted of a variable-severity regime in which stand structures were shaped primarily by severe fires rather than by non-lethal surface fires. Many stands experienced intervals of 50 to over 100 years between successive widespread fires. Such long intervals would have been sufficient for conifer seedlings to reach sizes that would survive low-severity surface fires. Thus, the lack of evidence of frequent fires in combination with frequent tree establishment dates (Fig. 3) indicates that these stands were not maintained as open woodlands by non-lethal surface fires. Instead, primarily infrequent high- and moderate-severity fires shaped current forest age structures in the mid- and upper montane zone. Variable-severity fires occurred historically in pure *P. ponderosa* and *P. ponderosa*-dominated stands regardless of *Pseudotsuga* presence or absence. More than half of the existing tree population in many such fires established within a few decades after the fire (Table 3).

The cohort age structures identified in this and other studies in the *P. ponderosa*-dominated forests of the northern Front Range are interpreted to be mainly a response to past severe fires that create open conditions favorable to the regeneration of this shade-intolerant species (Veblen & Lorenz 1986; Mast et al. 1998; Ehle & Baker 2003). As a shade-intolerant tree species (Kimmins 2003), the regeneration of *P. ponderosa* rarely occurs beneath relatively closed canopies. However, we caution that climatic variability, insect outbreaks, and seed availability may sometimes confound the attribution of pulses of tree establishment to the conditions created by severe fire. Although there is no consistent association of the tree establishment patterns with tree-ring records of moisture availability, small increases in establishment in two stands (UM4 and UM5) appear to coincide with increased moisture availability in the late 1790s to early 1800s (Sherriff 2004). Similarly, tree mortality caused by outbreaks of mountain pine beetle (*Dendroctonus ponderosae*) and spruce budworm (*Choristoneura occidentalis*) may create open conditions favorable for *P. ponderosa* establishment, but is likely to be less favorable to tree establishment than fire which exposes bare mineral soil. Although favorable climate conditions and/or insect outbreaks may have influenced recruitment during fire-free periods, none of the sampled sites show major peaks in establishment without evidence of fire. In addition, lags of one to many decades in the establishment of *P. ponderosa* may occur because of variable seed production (Krannitz & Duralia 2004) and/or because of loss of seed source in the most severe fires. Thus, the use of cohort age structures to identify severe fires may underestimate fire severity.

Implications for management and for other Pinus ponderosa ecosystems

Our study demonstrates that within the zone dominated by *P. ponderosa* in the northern Front Range, historic fire regimes varied from mainly low-severity fires at the lowest elevations to a variable-severity fire regime at higher elevations in which higher-severity fires were the primary determinant of stand structure. Widespread fire years that document high- and moderate-severity fires, as illustrated by the 1859-1860 fire year, are within the historical range of variability for *P. ponderosa* forests at a regional scale. Currently, high stand densities over much of the range of *P. ponderosa* in this large study area are due to past severe fires and not due to 20th century fire exclusion. Both high-severity fires and high stand densities are within the historic range of variability for these forests, which needs to be taken into account when forest management goals include restoring forest conditions to pre-fire-exclusion conditions. Tree ages show that mixed stands of *P. ponderosa* and *Pseudotsuga* were part of the historic range of forest conditions, and that young *Pseudotsuga* in mixed stands are not in-growth due to fire exclusion. This finding contrasts with the in-growth of *Pseudotsuga* reported for the southern Front Range (Kaufmann et al. 2003), and serves as a caution to extrapolating management implications beyond the geographic area of the forests studied.

Most previous studies of fire history in the U.S. West have stressed variations in fire regimes among cover types, and few studies have recognized important variation *within* cover types. Our results indicate that within the *P. ponderosa pine* forests of the northern Front Range the historic fire regime was a mixed-severity regime more comparable to that of the mixed-conifer forest type of the Pacific Northwest and California (e.g. Morrison & Swanson 1990; Taylor & Skinner 1998; Minnich et al. 2000; Beaty & Taylor 2001) than to the uniformly low-severity regime of *P. ponderosa* ecosystems of the Southwest (e.g. Covington & Moore 1994). Variable-severity fire regimes are less clearly candidates for thinning than are low-severity fire regimes and a cautious approach to restoration efforts has been recommended (Brown et al. 2004). For the *P. ponderosa* cover type, a few studies in the Pacific Northwest (Arno et al. 1995; Wright & Agee 2004; Everett et al. 2000; Hessburg et al. 2005a, b) have also documented fire regimes of variable severity. These studies and ours illustrate the importance of collecting evidence on the severity of past fires (i.e. cohort ages, growth releases, episodes of tree mortality) because fire severity cannot be reliably interpreted from fire interval data alone, which is often the approach applied to the study of fire history in *P. ponderosa* forests (e.g. Brown & Shepperd 2001; Grissino-Mayer et al. 2004).

Although current implementation of national fire policies (Anon. 2006) recognizes differences in fire regimes of the same cover type for different geographical regions, it makes the simplifying assumption that within a single region the fire regime of a cover type is relatively uniform. Our study shows that such an assumption of uniformity is not valid for the *P. ponderosa* cover type in the northern Front Range, and challenges ecologists and managers to re-consider the degree of variation in fire regimes within broadly distributed forest types. In many parts of the world, ecosystem managers assume that preservation of biodiversity is dependent on re-introduction of fire but often knowledge of past fire frequencies and severities is inadequate (Anon. 2004). Although natural disturbance regimes have been proposed as models for management of many forest types (Hunter 1993; Perera & Buse 2004), numerous studies (e.g. Cumming et al. 2000; Anderson et al. 2005; Bradstock et al. 2005), including the present one, are showing that variability of fire regimes within the same ecosystem type is greater than previously believed.

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References

Anon. 2002a. *National Fire Plan*. USDA. URL: http://www.fireplan.gov/.

Anon. 2002b. *Healthy forests: an initiative for wildfire prevention and stronger communities*. Whitehouse, Washington, DC, US. URL: http://www.whitehouse.gov/infocus/healthy forests/Healthy_Forests_v2.pdf.

Anon. 2003. An initiative for wildfire prevention and *stronger communities*. Healthy Forests Restoration Act. URL: http://www.whitehouse.gov/infocus/healthyforests.

Anon. 2004. *Fire, ecosystems and people: A preliminary assessment of fire as global conservation issue*. The Nature Conservancy. URL: http://nature.org/initiatives/fire/science/

Anon. 2006. *Landfire*. URL: http://www.landfire.gov/Products_Rapid_Assessment.html.

Allen, C.D., Savage, M., Falk, D.A., Suckling, K.F., Swetnam, T.W., Schulke, T., Stacey, P.B., Morgan, P., Hoffman, M. & Klingel, J.T. 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. *Ecol. Appl*. 12: 1418-1433.

Anderson, A.N., Cook, G.D., Corbett, L.K., Douglas, M.M., Eager, R.W., Russell-Smith, J., Setterfield, S.A., Williams, R.J. & Woinarski, J.C.Z. Fire frequency and biodiversity conservation in Australian tropical savannas: implications from the Kapalga fire experiment. *Aust. Ecol*. 30: 155-167.

Arno, S.F., Scott, J.H. & Hartwell, M.G. 1995. *Age-class structure of old-growth ponderosa pine Douglas-fir stands and its relationship to fire history*. USDA Forest Service, Research Paper, INT-RP-480. Intermountain Research Station, Ogden, UT, US.

Baker, W.L., Munroe, J.A. & Hessl, A.E. 1997. The effects of elk on aspen in the winter range in Rocky Mountain National Park. *Ecography* 20: 155-165.

Beaty, R.M. & Taylor, A.H. 2001. Spatial and temporal variation of fire regimes in a mixed conifer forest landscape, Southern Cascades, California, USA. *J. Biogeogr*. 28: 955-966.

Bradstock, R.A., Bedward, M., Gill, A.M. & Cohn, J.S. 2005. Which mosaic? A landscape ecological approach for evaluation interactions between fire regimes, habitat and animals. *Wildlife Res*. 32: 409-423.

Brown, J.K. 1995. Fire regimes and their relevance to ecosystem management. In: *Proceedings of the Society of American Foresters National Convention 1994 Sept. 18-22,* pp. 171-178. Anchorage, AK, US.

Brown, P.M. & Shepperd, W.D. 2001. Fire history and fire climatology along a 5° gradient in latitude in Colorado and Wyoming, USA. *Paleobotany* 50: 133-140.

Brown, P.M., Kaufmann, M.R. & Shepperd, W.D. 1999. Long-term, landscape patterns of past fire events in a montane ponderosa pine forest of central Colorado. *Landscape Ecol*. 14: 513-532.

Brown, R.T., Agee, J.K. & Franklin, J.F. 2004. Forest restoration and fire: principles in the context of place. *Conserv. Biol*. 18: 903-912.

Cottam, G. & Curtis, J.T. 1956. The use of distance measures in phytosociological sampling. *Ecology* 37: 451-460.

Covington, W.W. & Moore, M. 1994. Southwestern ponderosa forest structure. *J. For*. 92: 39-47.

Cumming, S.G., Schmiegelow, F.K.A. & Burton, P.J. 2000. Gap dynamics in boreal aspen stands: Is the forest older than we think? *Ecol. Appl*. 10: 744-759.

Dellasala, D.A., Williams, J.E., Williams, C.D. & Franklin, J.F. 2004. Beyond smoke and mirrors: a synthesis of fire policy and science. *Conserv. Biol*. 18: 976-986.

Dombeck, M.P., Williams, J.E. & Wood, C.A. 2004. Wildfire policy and public lands: integrating scientific understanding with social concerns across landscapes. *Conserv. Biol*. 18: 883-889.

Duncan, R.P. 1989. An evaluation of errors in tree age estimates based on increment cores in Kahikatea (*Dacrycarpus dacrydioides*). *N.Z. Nat. Sci*. 16: 31-37.

Ehle, D.S. & Baker, W.L. 2003. Disturbance and stand dynamics in ponderosa pine forests in Rocky Mountain National Park, USA. *Ecol. Monogr*. 73: 543-566.

Everett, R.L., Schellhass, R., Keenum, D., Spurbeck, D. & Ohlson, P. 2000. Fire history in the ponderosa pine/Douglas-fir forests on the east slope of the Washington Cascades. *For. Ecol. Manage*. 129: 207-225.

Goldblum, D. & Veblen, T.T. 1992. Fire history of a ponderosa pine Douglas-fir forest in the Colorado Front Range. *Phys. Geogr*. 13: 133-148.

Grissino-Mayer, H.D., Romme, W.H., Floyd, M.L. & Hanna, D.D. 2004. Climatic and human influences on fire regimes of the southern San Juan Mountains, Colorado, USA. *Ecology* 85: 1708-1724.

Hessburg, P.F., Agee, J.K. & Franklin, J.F. 2005a. Dry forests and wildland fires of the inland Northwest USA: contrasting the landscape ecology of the pre-settlement and modern eras. *For. Ecol. Manage.* 211: 177-139.

Hessburg, P.F., Salter, R.B. & James, K.M. 2005b. Evidence for the extent of mixed-severity fires in pre-management era dry forests of the Inland Northwest, USA. In: Taylor, L., Zelnick, J., Cadwallader, S. & Hughes, B. (eds.) *Proceedings of the symposium on Mixed-Severity Fire Regimes: Ecology and Management, Spokane, Washington, November 17-19, 2004,* pp. 89-104. The Association for Fire Ecology, Misc. Publ. 3. Davis, CA, US.

Holmes, R.L. 1983. Computer assisted quality control. *Tree-Ring Bull.* 43: 69-78.

Hunter, M.L. 1993. Natural fire regimes as spatial models for managing boreal forests. *Biol. Conserv.* 65: 115-120.

Kaufmann, M.R., Regan, C.M. & Brown, P.M. 2000. Heterogeneity in ponderosa pine/Douglas-fir forests: age and size structure in unlogged and logged landscapes of central Colorado. *Can. J. For. Res.* 30: 698-711.

Kaufmann, M.R., Huckaby, L.S., Fornwalt, P.J., Stoker, J.M. & Romme, W.H. 2003. Using tree recruitment patterns and fire history to guide restoration of an unlogged ponderosa pine/ Douglas-fir landscape in the southern Rocky Mountains after a century of fire suppression. *Forestry* 76: 231-241.

Kimmins, J.P. 2003. Ecological role of solar radiation. In: *Forest ecology – A foundation for sustainable management*, pp. 153-180. 3rd ed. Prentice Hall, NJ, US.

Krannitz, P.G. & Duralia, T.E. 2004. Cone and seed production in *Pinus ponderosa*: A review. *W. N. Am. Nat.* 64: 208-218.

League, K. & Veblen, T.T. 2006. Climatic variability and episodic *Pinus ponderosa* establishment along the forest-grassland ecotones of Colorado. *For. Ecol. Manage.* 228: 98-107.

Madany, M.H. & West, N.E. 1983. Livestock grazing-fire regime interactions within montane forests of Zion National Park, Utah. *Ecology* 64: 661-667.

Marr, J.W. 1961. *Ecosystems of the east slope of the Front Range in Colorado*. University of Colorado Studies Series in Biology 8. Boulder, CO, US.

Mast, J.N., Veblen, T.T. & Hodgson, M.E. 1997. Tree invasion within a pine/grassland ecotone: an approach with historic aerial photography and GIS modeling. *For. Ecol. Manage.* 93: 181-194.

Mast, J.N., Veblen, T.T. & Linhart, Y.B. 1998. Disturbance and climatic influences on age structure of ponderosa pine at the pine/grassland ecotone, Colorado Front Range. *J. Biogeogr.* 25: 743-755.

Minnich, R., Barbour, M., Burk, J. & Sosa-Ramirez, J. 2000. Californian mixed-conifer forests under unmanaged fire regimes in the Sierra San Pedro Martir, Baja California, Mexico. *J. Biogeogr.* 27: 105-129.

Morrison, P.H. & Swanson, F.J. 1990. *Fire history and pattern in a Cascade Range landscape*. U.S. Forest Service General Technical Report PNW-GTR-254, Corvallis, OR, US.

Peet, R.K. 1981. Forest vegetation of the Colorado Front Range: composition and dynamics. *Vegetatio* 45: 3-75.

Perera, A.H. & Buse, L.J. 2004. Emulating natural disturbance in forest management: An overview. In: Perera, A.H., Buse, L.J. & M.G. Weber (eds.) *Emulating natural forest landscape disturbances,* pp. 3-7. Columbia University Press, NY, US.

Romme, W.H., Veblen, T.T., Kaufmann, M.R., Sherriff, R. & Regan, C.M. 2003. Ecological effects of the Hayman fire, Part I: Historical (pre-1860) and current (1860 - 2002) fire regimes. In: Graham, R.T. (ed.) *Hayman fire case study*, pp. 181-195. USDA Forest Service, General Technical Report, RMRS-GTR-114. Rocky Mountain Research Station, Fort Collins, CO, US.

Rummell, R.S. 1951. Some effects of livestock grazing on ponderosa pine forest and range in central Washington. *Ecology* 32: 594-607.

Schoennagel, T., Veblen, T.T. & Romme, W.H. 2004. The interaction of fire, fuels, and climate across Rocky Mountain forests. *BioScience* 54: 661-676.

Sherriff, R.L. 2004. *The historic range of variability of ponderosa pine in the northern Colorado Front Range: past fire types and fire effects*. Ph.D. Dissertation University of Colorado, Boulder, CO, US.

Sherriff, R.L. & Veblen, T.T. In press. A spatially-explicit reconstruction of historical fire occurrence in the ponderosa pine zone of the Colorado Front Range. *Ecosystems*.

Shinneman, D.J. & Baker, W.L. 1997. Nonequilibrium dynamics between catastrophic disturbance and old-growth forests in ponderosa pine landscapes of the Black Hills. *Conserv. Biol.* 11: 1276-1288.

Sibold, J.S. & Veblen, T.T. 2006. Relationships of subalpine forest fires in the Colorado Front Range to interannual and multi-decadal scale climatic variation. *J. Biogeogr.* 33: 833-842.

Taylor, A.H. & Skinner, C.N. 1998. Fire history and landscape dynamics in a late successional reserve, Klamath Mountains, California, USA. *For. Ecol. Manage.* 111: 285-301.

Veblen, T.T. 2003. Historic range of variability of mountain forest ecosystems: concepts and applications. *For.Chron.* 79: 223-226.

Veblen, T.T. & Lorenz, D.C. 1986. Anthropogenic disturbance and recovery patterns in montane forests, Colorado Front Range. *Phys. Geogr.* 7: 1-24.

Veblen, T.T. & Lorenz, D.C. 1991. *The Colorado Front Range: A century of ecological change*. University of Utah Press, Salt Lake City, UT, US.

Veblen, T.T. & Donnegan, J.A. 2006. *Historical range of variability of forest vegetation of the national forests of the Colorado Front Range*. USDA Forest Service, Rocky Mountain Region and the Colorado Forest Restoration Institute, Fort Collins, CO, US.

Veblen, T.T., Kitzberger, T. & Donnegan, J. 2000. Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado Front Range. *Ecol. Appl.* 10: 1178-1195.

Weber, W.A. 1976. *Rocky Mountain Flora*. Colorado Associated University Press, Boulder, CO, US.

Wright, C.S. & Agee, J.K. 2004. Fire and vegetation history in the eastern Cascade Mountains, Washington. *Ecol. Appl.* 14: 443-459.

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