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SPATIAL PATTERNS AND CONTROLS ON HISTORICAL FIRE REGIMES AND FOREST STRUCTURE IN THE KLAMATH MOUNTAINS

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Abstract. Fire exclusion in mixed conifer forests has increased the risk of fire due to decades of fuel accumulation. Restoration of fire into altered forests is a challenge because of a poor understanding of the spatial and temporal dynamics of fire regimes. In this study the spatial and temporal characteristics of fire regimes and forest age structure are reconstructed in a 2325-ha mixed conifer forest in the Klamath Mountains. Forests were multiaged and burned frequently at low and moderate severity, but forest age structure did not vary with aspect, elevation, or topographic position. Recently there has been an increase in forest density and a forest compositional shift to shade-tolerant species. Median fire return intervals (FRI) ranged from 11.5 to 16.5 yr and varied with aspect but not with forest composition or elevation. The median area burned was 106 ha, and the pre-Euro-American fire rotation of 19 yr increased to 238 yr after 1905. Intra-annual position of fire scars in the tree rings indicates that 93% of fires occurred during the dry midsummer through fall period. Spatial patterns of sites with similar fire dates were spatially coherent and separated from others by topographic features that influence fire spread. Thus, patterns of fire occurrence tended to be fixed in space with timing of fires varying among groups of sites. Spatial and temporal patterns of fire occurrence suggest that managers using physical features to contain prescribed fire will create burn patterns consistent with historical fires in the Klamath Mountains.

Key words: California; dendroecology; fire history; fire regimes; forest age structure; landscape ecology; landscape structure; mixed conifer forest.

INTRODUCTION

Recurring fire is a process that has influenced the pattern and heterogeneity of forest ecosystems in the western United States for millennia (Swetnam 1993, Mohr et al. 2000). The effects of fire on community structure and dynamics are remarkably diverse due to short-term spatial and temporal variation in fire intensity (Ryan and Rheinhardt 1988) and longer term variation in fire regime characteristics (Swetnam 1993). Spatial and temporal variation in fire regimes are thought to be important controls maintaining diversity in fire-prone landscapes because species response to fire is strongly influenced by variation in fire regime parameters such as the frequency, extent, severity, and seasonality of fires (Martin and Sapsis 1992, Bond and van Wilgen 1996).

Nearly a century of fire exclusion in forests that once experienced frequent low- and moderate-severity fires has reduced compositional and structural diversity in forest stands and forested landscapes. For example, in California's mixed conifer forests the reduction in the frequency and extent of fire has caused an increase in forest density, a compositional shift to more fire-sensitive species, and a shift from coarse to fine grain forest mosaics (Vankat and Major 1978, Parsons and DeBenedetti 1979, Skinner 1995, Taylor 2000). Reduced fire frequency has also caused unprecedented accumulations of surface and aerial fuels and dramatically increased the risk of high-severity fires (Weatherspoon et al. 1992). Use of prescribed fire is often an integral component of fuel management strategies designed to reduce high fuel loads, reduce the risk of high-severity fire, and to restore fire as an ecosystem process in these highly altered forests (SNEP 1996, Weatherspoon and Skinner 1996, Stephenson 1999). But strategies for prescribed fire use in forest restoration are hindered by a poor understanding of the controls on the spatiotemporal dynamics of fire regimes in forested landscapes (Skinner and Chang 1996, Miller and Urban 2000*a*).

One approach to identify restoration goals is to compare forest conditions (i.e., forest structure and composition) and fire regimes for the contemporary and prefire suppression periods. Differences can be used to develop restoration strategies and specific management treatments (e.g., Weatherspoon and Skinner 1996, Stephenson 1999). Treatments to restore presettlement tree density, basal area, and fire frequencies have been applied to small areas (e.g., Covington and Moore 1994) and landscape-scale restoration is being proposed (e.g., Mutch et al. 1993, Olson et al. 1995, Weatherspoon and Skinner 1996). Yet, patterns and controls on fire

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regimes and their influence on forest structure across landscapes are poorly known (e.g., Baker 1989, Chang 1999, Miller and Urban 2000*b*). Resource managers need better information on controls and the effects of spatial and temporal variation in fire regimes on forest structure and composition so they can evaluate the ecological implications of operational strategies for landscape restoration burns. A mismatch between the characteristics of prescribed fire and prefire suppression fire regimes may produce structural patterns that fail to restore a prefire suppression condition (e.g., Baker 1994, Taylor 2000).

Topographic variation is a potentially important spatial control on variation in fire regimes. Topography directly and indirectly influences fire behavior (e.g., Rothermel 1983) and fire regimes by affecting fuel moisture, the type and arrangement of fuels, and the location of barriers to fire spread, but topographic influences on fire regimes have rarely been quantified. Variation in fire frequency and fire severity vary with topographically related variables such as aspect, species composition, elevation, and soil type in some mixed conifer landscapes (Caprio and Swetnam 1995, Fites-Kauffman 1997, Taylor and Skinner 1998, Taylor 2000, Beaty and Taylor 2001, Bekker and Taylor 2001) but not in others (Heyerdahl et al. 2001).

Alternatively, spatial variation in fire regimes may be controlled by the time-dependent process of fuel accumulation (Bonnicksen and Stone 1982, Minnich et al. 2000). Burns can influence the spatial patterns of subsequent fires by temporarily reducing fuels in a burn patch (van Wagtendonk 1995, Minnich et al. 2000). Accordingly, the fire–forest mosaic may be self-organizing and time-dependent because fuels need to accumulate before a burned patch can burn again (Minnich et al. 2000). Both topographic and self-organizing controls can contribute to spatial variation in fire-influenced forest mosaics. Yet, depending on the predominant source of variation, spatial patterns of fire occurrence may be relatively fixed or shifting (Bonnicksen and Stone 1982, Baker 1989).

The goal of this study is to better understand the spatial and temporal patterns of, and controls on, fire regimes and forest structure in mixed conifer forests of the Klamath Mountains. The Klamath Mountains are characterized by deeply incised, highly complex terrain. We hypothesized that topography exerts strong control on fire regimes and forest structure at stand and landscape scales. Specifically, we sought answers to the following questions: (1) Do fire regime characteristics vary with topographically controlled landscape characteristics such as tree species composition and/or environmental setting (i.e., aspect, slope position)? (2) Did fire regimes change with initial Euro-American settlement compared to the presettlement period? (3) Are tree populations at the plot scale mainly many-aged reflecting frequent periodic establishment after low-severity fire, or are they even- or several-aged reflecting punctuated establishment after moderate- or high-severity fires? (4) Do forest age-structural patterns vary with topography and is forest composition changing due to suppression of fires? To help answer these questions we developed a dense network of spatially explicit, multicentury, tree-ring records of fire occurrence and stand age structure in portions of two watersheds in the Klamath Mountains. We then discuss our results in the context of prescribed fire use in the Klamath Mountains. Large reserves of late-successional and old-growth forest were established in the Klamath Mountains to protect Northern Spotted Owls (*Strix occidentalis caurina* Merriam) and other forest dwelling species (USDA-USDI 1994). Fire is considered both a hazard and an important management tool for promoting and maintaining late-successional old-growth forest conditions in the reserves (USDA-USDI 1994, 2000).

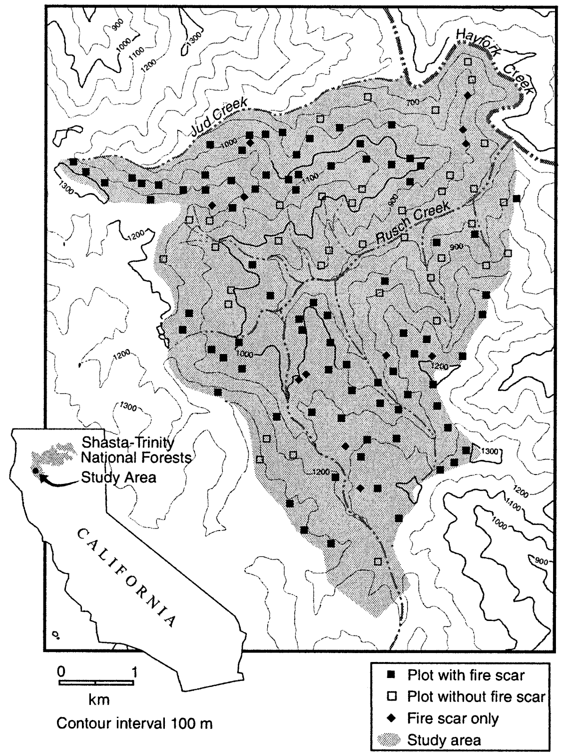

FIG. 1. Location of study area, plots, and site fire chronologies in the Hayfork study area (shaded).

STUDY AREA

Our study was conducted in a 2325-ha area of two small watersheds in the Shasta-Trinity National Forests, 8 km west of Hayfork, California in the south-central Klamath Mountains (Fig. 1). Elevations range from 640 to 1360 m. The climate is characterized by warm, dry summers and cool, wet winters. Mean monthly temperature in Weaverville (660 m), 32 km northeast of the study area, ranges from 5.9°C in December to 21.8°C in July. Thunderstorms occur in the dry season and lightning is a common cause of fire in the Klamath Mountains (Schroeder and Buck 1970). The terrain is steep, deeply dissected, and complex. Soils vary in depth from shallow (<50 cm) to deep (>100 cm) and are developed in a wide range of Jurassic-age metasedimentary and metavolcanic parent materials that include shale, rhyolite, ultramafics, and weathered granites (USFS 1983). Several perennial streams, small rock outcrops, and areas of ultramafic rock with low productivity occur in the study area and may act to inhibit the spread of low- and moderate-intensity surface fires.

Forests in the study area are diverse and any of six conifer species: ponderosa pine (*Pinus ponderosa*) (nomenclature follows Hickman 1993), Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*), incense cedar (*Calocedrus decurrens*), sugar pine (*Pinus lambertiana*), Jeffrey pine (*Pinus jeffreyi*), and white fir (*Abies concolor*) may co-occur and share dominance in a stand depending on site conditions and stand history (Barbour 1988, Parker 1994). A subcanopy of the evergreen hardwoods Pacific madrone (*Arbutus menziesii*), golden chinquapin (*Chrysolepis chrysophylla*), and canyon live oak (*Quercus chrysolepis*) and the deciduous hardwoods California black oak (*Quercus kelloggii*), bigleaf maple (*Acer macrophyllum*), Oregon white oak (*Quercus garryana*), and dogwood (*Cornus nuttallii*) occur beneath the mixed conifer canopy. Stand composition is strongly influenced by elevation, site moisture availability, and substrate.

Humans have affected fire regimes and forests in the study area in different ways. Prior to Euro-American settlement, native people in the Klamath Mountains used fire to promote production of acorns, berries, roots, fiber, and to improve hunting conditions (Lewis 1990, 1993). Euro-Americans entered the area in 1848 (Jackson 1964, Hoopes 1971) and they may have set fires for various purposes but we have no written record that they did so. A fire suppression policy was introduced in 1905 when the Trinity Forest Reserve was established as part of the National Forest Reserve System (Shrader 1965). Small-scale logging along ridgetops began in the 1960s and extensive clear-cut logging occurred between 1980 and 1990.

Methods

Forest structure and composition

The study area was stratified by elevation (low <950 m, middle 950–1149 m, high ≥1150 m) and aspect (north 315–44°, south 135–224°, east 45–134°, west 225–314°) using a topographic map. Sample sites were then distributed in each elevation or aspect group. The location of clear-cuts was considered when selecting a sample site within a group. We preferred clear-cut sites because: (1) large stems (>1.0 m dbh) could be aged using stump ring-counts but not always when they were cored because radii of larger trees were longer than increment borers; and (2) evidence of fire (i.e., series of fire scars) visible in stump cross sections was usually not apparent on the exterior surface of trees or stumps because fire wounds had completely healed since the last fire (e.g., Taylor 1993, Taylor and Skinner 1998). Only 9% of the 141 Douglas-fir stumps collected for fire dating and only 31% of all fire scar samples had external evidence of fire. ''Staggered setting'' logging had dispersed 10–20 ha clear-cuts throughout the study area so the sample distribution was not random. Areas with few clear-cuts were sampled to assure that sample sites were well distributed through both watersheds and included the observed variability in forest structure and composition on forested sites. A total of 120 plots (80 clear-cut, 40 forested) were sampled and their locations were determined with a global positioning system (GPS) and then plotted on a topographic map (Fig. 1).

Plot size varied from 150 to 2400 m^2 according to the density (range 110–2400 trees/ha) of stumps or trees so that each plot contained 20 conifer stems (mean = 24, range 13–47 stems). The location, elevation, aspect and pitch, slope position, and slope configuration of each plot was recorded and the diameter of all visible stumps or live stems ≥5.0 cm at stump or breast height in each plot was measured. The last four topographic variables were used to calculate each plot's Topographic Relative Moisture Index (TRMI), a measure of relative site moisture availability based on topographic features that ranges from 0 (xeric) to 60 (mesic) (Parker 1982).

The ages of trees ≥5 cm diameter in each plot were determined in the following way. For live tree plots, each conifer (n = 943) was cored 30 cm above the ground (a height that approximated the height of stump tops). Cores were then sanded to a high polish and tree age was estimated by cross-dating each tree's annual growth rings and determining the year of the innermost ring. In clear-cut plots, each conifer stump (n = 1973) was aged at stump height using the following technique. First, a clear cross section (radius) on each stump was exposed by cutting a 4 mm wide strip of wood from bark to pith using a woodcarving tool. Second, the radius was measured and the exposed annual growth rings were counted using a 10–20× hand lens. Hardwood stems (e.g., bigleaf maple, canyon live oak, dogwood, black oak, madrone, chinquapin) were not aged because their annual growth rings could not be consistently distinguished in cores or on stump cross sections. Consequently, our age structure analysis includes only ages for conifer species. Hand counting of rings was considered sufficiently accurate for inclusion in 20-yr age classes since no false rings were detected in the cross-dated cores and fire scar samples and missing rings were rare.

Some trees and stumps could not be aged (12%) because their stems contained rot or they were too large (>130 cm dbh) to extract a complete core. We estimated the ages of these trees in the following way. For live trees, we estimated tree age using least-squares regressions of age on stem diameter developed from all aged stems for each species. All regression equations were significant ($P < 0.001$) (white fir, $r^2 = 0.58$, $n = 251$; incense cedar, $r^2 = 0.65$, $n = 27$; sugar pine, $r^2 = 0.63$, $n = 251$; ponderosa pine, $r^2 = 0.59$, $n = 206$; Douglas-fir, $r^2 = 0.70$, $n = 1426$). For stumps, ages were estimated using the regression equations if radii were 8 cm or more short of the pith. Otherwise, we added an estimate of the number of missing rings per centimeter (Douglas-fir, 0.12 $\pm$ 0.06 rings/cm, mean $\pm$ 1 SE; white fir, 0.10 $\pm$ 0.05 rings/cm; ponderosa pine, 0.16 $\pm$ 0.08 rings/cm, sugar pine, 0.14 $\pm$ 0.06 rings/cm; incense cedar, 0.10 $\pm$ 0.04 rings/cm) for the missing portion of radii to the stump ring counts. Rings per centimeter were estimated from all core and stump samples with a complete radius for each species.

Groups of plots with similar tree composition were identified using cluster analysis. First, we calculated the importance value for each species in each plot as the sum of relative basal area, relative density, and relative frequency (range 0–300). Second, we clustered species importance values using Ward's method, and relative Euclidean distance as a similarity measure (McCune and Mefford 1995). Ward's method minimizes within group variance relative to between group variance (van Tongeren 1995). We then identified variation in species importance values and environment (elevation and TRMI) among compositional groups by comparing values for each variable using a distribution-free Kruskal-Wallis *H* test (Sokal and Rohlf 1995).

Age structural patterns were characterized in two ways. First, at the plot scale, we counted the number of stems in 20-yr age classes for each plot. This count was made for both all age classes (20–620 yr) and for age classes that established prior to the fire suppression period (>100 yr old). Second, at the landscape scale, we grouped plots by species age-class distribution to identify groups of stands with similar prefire-suppression age structures. Plots were grouped using cluster analysis and the density of aged stems per hectare of each species in 20-yr age classes for stems >100 yr old using Ward's method and relative Euclidean distance as the similarity measure. We determined potential topographic influences on stand age structure at landscape scales by comparing the frequency distribution of plots in each age-class group by aspect ($n = 4$), elevation ($n = 3$), and topographic position (ridgetop, upper slope, middle slope, lower slope) ($n = 4$) using Kolmogorov-Smirnov two-sample tests (Sokal and Rohlf 1995).

Compositional shifts that may be related to fire suppression were identified using the age structural groups and ordination. We ordinated the average density of ≤100-yr-old and >100-yr-old stems/ha of each species in each age-class group using detrended correspondence analysis (DCA) (Gauch 1982). This approach assumes that differences in the composition and abundance of younger vs. older stems represent recent shifts in regeneration patterns related to fire suppression. Compositional differences were displayed in DCA species' space by joining the younger and older groups with a vector.

Fire regimes

Fire regime parameters (i.e., return interval, season, size, rotation, severity) were reconstructed using cross-dated fire scars in wood cross sections or wedges from fire scarred stumps and live trees, respectively. A total of 329 cross sections or wedges were removed from stumps and trees in 3-ha areas in or near each plot using a chainsaw. An average of four cross sections (range 1–9) were collected at each of 92 sites. The location of each collection site was determined with a GPS and plotted on a topographic map.

Fire dates in the cross sections or wedges were identified by first sanding them to a high polish and then cross-dating each specimen's tree-ring series (e.g., Stokes and Smiley 1968). Most specimens (98%) were visually cross-dated, but complacent ring patterns in a few samples required statistical dating by comparing tree-ring widths measured to the nearest 0.01 mm from each sample to ring widths from nearby tree-ring chronologies using program COEFCHA (Grissino-Mayer 2001). The calendar year of each tree ring with a fire scar in it was then recorded as the date of the fire.

The season of burn for each fire was identified from the position of each scar within the annual growth ring (cf. Baisan and Swetnam 1990). The position of each scar was assigned to one of five ring position categories: (1) early (first one-third of earlywood); (2) middle (second one-third of earlywood); (3) late (last one-third of earlywood); (4) latewood (in latewood); and (5) dormant (at ring boundary). In this area of strongly seasonal rainfall (winter-wet, summer-dry), dormant season fires are interpreted as fires that burned later in the dry season after radial growth in the adjacent latewood cells had ceased for the year (e.g., Caprio and Swetnam 1995).

Spatial variation in fire return intervals (FRI) across the study area was identified by first assigning each fire-scar site ($n = 92$) to a forest composition, aspect (N, S, E, W), and elevation (low, middle, upper) group. Next, for each site, we calculated a median FRI based on fires recorded on all scar samples at the site. Finally, median FRI for forest composition, aspect, and elevation groups were compared using a distribution-free Kruskal-Wallis *H* test (Sokal and Rolf 1995).

Analysis of spatial variation in FRI at only the study-area scale may mask important differences in fire occurrence within slopes caused by smaller-scale topographic variation. Features such as stream courses, or abrupt changes in aspect, influence fire spread and behavior and may control spatial variation in fire occurrence that is not evident at watershed scales. Spatial patterns of fire occurrence at finer scales were identified using cluster analysis (Ward's method) to group sites by fire date. Only sites ($n = 82$) with a record of fire spanning the period 1751–1900 were used for identifying fire occurrence groups. A longer period was not used because the number of sites that recorded fires declines before 1750. We also omitted fire years recorded by only one site from the analysis to minimize the influence of spot fires on group formation. Sites in each fire occurrence group were then mapped and we calculated group median FRI and group FRI distributions and then compared them using distribution-free statistical tests (e.g., Kruskal-Wallis H test, Kolmogorov-Smirnov two-sample tests) (Sokal and Rohlf 1995).

The potential influence of previous burns on the occurrence of subsequent fires was assessed by using the fire dates of burns for each site in a fire occurrence group. The dates of all consecutive pairs of fires were used to estimate the frequency that the second fire in a consecutive fire pair burned in the same, another, or in the same and another fire occurrence group. A similar approach was used to evaluate the influence of burns on the occurrence of subsequent fires within a group. Frequencies were calculated for sites that did and did not burn in consecutive fires in the same fire occurrence group. This statistic provides a measure of how often consecutive fires within a group burned the same or a different site.

Temporal variation in FRI that may be related to land use change was identified by comparing fire frequency during the pre-Euro-American (before 1850), settlement (1850–1904), and fire suppression (post-1905) periods using a composite of all the site fire chronologies. An all-site composite may be more sensitive to changes in temporal burning patterns than samples from a more restricted area (Dieterich 1980).

No attempt was made to estimate the extent or boundary of each fire (e.g., Agee 1991). Rather, burned area was estimated by applying a ratio method to the number of sites that recorded a fire in each fire year (e.g., Morrison and Swanson 1990, Taylor and Skinner 1998). Burned area was estimated as

$$A_i = (\mathrm{AT} \times \mathrm{NS}_i)/(\mathrm{NST} - \mathrm{NRE}_i)$$

where A_i is the area burned in the ith year, AT is the study area (in hectares), NS_i is the number of sites with the ith year fire, NST is the total number of sites, and NRE_i is the number of sites without trees of sufficient age to record fires in the ith year. Accuracy of this method decreases as NRE_i increases. Though the earliest fire recorded in our samples was in 1426, we chose 1628 as the cutoff date for fire area estimates to reduce estimation errors associated with small sample size ($n = 19$).

Fire rotation (FR) (Heinselman 1973), or the number of years needed to burn an area equal in size to the study area, was estimated using the burned area estimates. FR was calculated for the whole study area by century and for the presettlement, settlement, and fire suppression periods. In any given period, some parts of the study area may have burned repeatedly but others not at all.

Stand age structure and patterns of fire severity

Patterns of fire severity at both plot and landscape scales were interpreted using the age structure groups and counts of 20-yr age classes occupied by each species. Fires burn with variable severity across a landscape, killing many trees in some stands and few in others. This variation is reflected in the age structure of forest stands. For example, stands that have experienced severe fires are usually even-aged, while multiaged stands reflect moderate-severity fires that killed only portions of the stand. Low-severity fires, in contrast, may not produce discrete age classes (Agee 1993). We counted the number of occupied 20-yr age classes in each plot for all age classes and for age classes in the prefire suppression period (>100 yr). Presumably, plots with trees in many 20-yr age classes experienced less severe fires than those with stems in fewer age classes. Finally, we calculated a grand mean fire frequency for each age structural group using the site fire chronologies in each group.

Results

Forest composition

Five forest compositional groups were identified from the cluster analysis of species importance values and the groups are segregated by elevation and potential soil moisture ($P < 0.05$, Kruskal-Wallis H test) (Table 1). The ponderosa pine–sugar pine group ($n = 18$) occupies mainly south- and west-facing slopes and xeric upper slopes and ridgetops. The two pines share codominance and canyon live oak and Douglas-fir are important associates. The Douglas-fir group ($n = 30$) occupies mesic north-facing slopes at mid-elevations and is strongly dominated by Douglas-fir with sugar pine and hardwoods as important associates. The Douglas-fir–ponderosa pine–incense cedar group ($n = 17$) occupies mainly east-facing slopes at low and midelevation and is a variable mixture of the three species. The Douglas-fir–sugar pine group ($n = 41$) is compositionally variable and occupies midslope positions on north- and east-facing slopes. Ponderosa pine is the most important associate and a diverse assemblage of hardwoods is characteristic of this group. The Douglas-fir–white fir group ($n = 13$) occupies higher elevation sites on north- and east-facing slopes with sugar pine and ponderosa pine as the most important associates.

Fire regimes

Fire record.—A total of 228 fire years were detected in 1778 cross-dated scars in 329 samples from the 92 sites in the two watersheds. The fire record spanned the period 1426–1953. For the period analyzed in this

TABLE 1. Mean importance value (IV; maximum 300), basal area (BA; m^2/ha), and density of trees ≥5.0 cm dbh (Den.; no./ha) in forest compositional groups identified by cluster analysis of species importance values.

		Forest compositional group														
		Pipo-Pila			*Psme*			*Psme-Pipo-Cade*			*Psme-Pila*			*Psme-Abco*		
Species	Species abbreviation	IV	BA	Den.	IV	BA	Den.	IV	BA	Den.	IV	BA	Den.	IV	BA	Den.
Abies concolor†	*Abco*	8	22	56	8	18	54	1	12	35	4	10	34	26	44	93
Acer macrophyllum	*Acma*										<1	1	18			
Arbutus menziesii†	*Arme*	1	5	26	1	5	29	7	8	35	5	8	33	3	7	29
Calocedrus decurrens†	*Cade*				<1	3	20	20	17	69	1	3	26	12	16	54
Chrysolepis chrysophylla	*Chch*	2	4	31	2	11	39				3	6	26	5	12	36
Cornus nuttallii	*Conu*				2	23	51				<1	3	20			
Pinus jeffreyi	*Pije*							5	4	33	2	1	26			
Pinus lambertiana†	*Pila*	130	20	91	20	5	44	7	11	44	15	10	49	22	8	48
Pinus ponderosa†	*Pipo*	149	23	76	8	6	43	32	16	74	14	9	39	20	5	40
Pinus sabiniana	*Pisa*										10	11	59			
Pseudotsuga menziesii†	*Psme*	26	30	77	80	71	180	36	57	123	44	44	118	41	26	85
Quercus chrysolepis†	*Quch*	37	36	71	2	15	45	2	10	36	7	28	58	3	11	35
Quercus kelloggi†	*Quke*	1	3	23	8	6	43	7	12	44	3	5	24			
Median elevation (m)†		1130			992			972			1080			1220		
Median TRMI (range 0–60)†		20			32			28.5			27			25		

Note: Not listed is a single plot group containing *P. attenuata* (IV-100, BA-78, Den. 213) and *Q. chrysolepis* (IV-13, BA-22, Den.-87).

† Compositional groups with different environmental characteristics (elevation, topographic relative moisture index [TRMI]) and species IV ($P < 0.05$, Kruskal-Wallis H test).

TABLE 2. Median fire return interval (yr) for fire chronology sites by forest compositional group, elevation group, and slope aspect group.

Group	n	Median	Range of medians
Forest composition			
Pipo-Pila	10	11.5	9.0–22.0
Psme-Pila	20	13.5	9.0–64.0
Psme-Pipo-Cade	13	12.5	5.5–76.0
Psme	37	13.0	5.5–35.0
Psme-Abco	12	13.0	6.0–44.5
Elevation			
Low (750–949 m)	15	12.5	5.5–76.0
Middle (950–1149 m)	45	14.0	7.0–60.5
High (≥1150 m)	32	12.0	5.5–23.0
Slope aspect			
North (315–44°)	35	16.5	5.5–76.0
East (45–134°)	16	11.3	5.5–21.0
South (135–224°)	11	12.5	7.0–22.0
West (225–314°)	30	12.0	5.5–64.0

Notes: See Table 1 for description of forest compositional groups. Median fire return intervals varied with slope aspect ($P < 0.01$, Kruskal-Wallis H test) but not with forest composition or elevation. n is the number of sites.

study (1628–1995), 184 fire years were recorded. The average period between fires detected for all sites in the study area was 2.0 yr.

Fire season.—The position of fire scars within annual growth rings indicate that fires mainly burned in the midsummer through fall period (76.2% at ring boundary) after trees had stopped radial growth for the year. Growing season fires were less frequent with 17.3% in latewood, 3.6% in the last third of early wood, 2.3% in the middle third of early wood, and 0.6% in the first third of the early wood.

Fire return intervals.—

1. *Spatial patterns*.—Median site FRIs were statistically longer on north-facing slopes than on other aspects ($P < 0.05$, Kruskal-Wallis H test) (Table 2). However, median FRIs did not significantly vary by forest compositional or elevation group ($P > 0.05$, Kruskal-Wallis H test).

2. *Temporal patterns*.—Fire occurrence over the entire study area varied by historical period (Table 3). The average period between fires was similar ($P > 0.05$, t test) for the pre-Euro-American (1.6 yr) and settlement (1.5 yr) periods and longer (4.4 yr) during

TABLE 3. Mean (± SE) composite fire return intervals (yr) for all burned sites during the presettlement (before 1850), settlement (1850–1904), and fire suppression (1905–1995) periods.

Sites scarred	Presettlement	Settlement	Suppression
Any	1.6 ± 0.1	1.5 ± 0.2	4.4 ± 2.1
≥3	2.6 ± 0.4	2.1 ± 0.4	12.0 ± 9.1
≥5	4.0 ± 0.8	3.5 ± 0.8	···
≥10	6.1 ± 1.4	6.7 ± 2.3	···
≥15	10.3 ± 2.4	9.4 ± 3.9	···

Notes: Mean values for the presettlement and settlement period were not significantly different ($P > 0.05$, t test). Fire occurrence declined dramatically after 1905.

TABLE 4. Fire rotations (yr) for the Hayfork study area by time period.

Time period	Fire rotation
1628–1995	25
1628–1699	30
1700–1799	19
1800–1899	15
1900–1995	196
1628–1849	20
1850–1904	18
1905–1995	238

the fire suppression period. Only 12 fires burned during the fire suppression period and most (83%) burned between 1905 and 1920; only two fires scarred trees on our sites after 1920. With the exception of the fire suppression period, the temporal pattern of variation for larger burns (3–15 sites scarred) was identical to that for all fires (Table 3).

Annual area burned.—Burned area varied among fire years and by time period (Fig. 2). The estimated median burn area for the entire 1628–1995 period was 106 ha (range 25–1541 ha) and the median area burned in the pre-Euro-American (128 ha, range 25–1541 ha) and settlement (106 ha, range 25–1188 ha) periods were similar. Median area burned was smaller (25 ha) in the fire suppression period. The burn area distribution was positively skewed and >500 ha burned in 13 yr since 1628 (Fig. 2).

Fire rotation.—Fire rotations also varied by time period (Table 4). Fire rotation for the pre-Euro-American periods was 20 yr. Fire rotations were shorter during the 19th century (15 yr) and settlement period (18 yr) due to the proportionately greater area burned during these periods. Fire rotation length increased dramatically during the 20th century and is now 12–15-fold longer than anytime in the previous three centuries.

Spatial patterns of fire occurrence.—Six fire occurrence groups were identified from the cluster analysis of fire dates. Sites in each fire occurrence group are spatially segregated from sites in other groups and boundaries coincide with streams or changes in slope aspect (Fig. 3). Overall, there was a difference ($P <$ 0.001, Kruskal-Wallis H test) in median FRI among fire occurrence groups (Table 5; Fig. 4) but paired comparisons indicate that only group 2 had a different (shorter) median FRI ($P < 0.05$, Mann-Whitney U test) than the other groups. Group 2 sites occur mostly on ridgetops along the southeastern boundary of the study area with a few in the lower reaches of Rusch Creek. The lower median FRI here may be related to import of fire from outside the study area that burned ridgetops but did not extend further into the study area. Variation in the pattern of FRI distributions among groups was the same as for median FRI. Only fire occurrence group 2 had a different FRI distribution ($P < 0.05$, Kolmogorov-Smirnov two-sample test), other groups had similar FRI distributions. The average similarity (Sorensen's Index) of fire dates among groups was 57% (range 36–75%).

The temporal pattern of burns among fire occurrence groups suggests that consecutive pairs of fires tended to burn different groups. Consecutive fires only rarely burned in the same group (mean = 5%, range 0–9%)

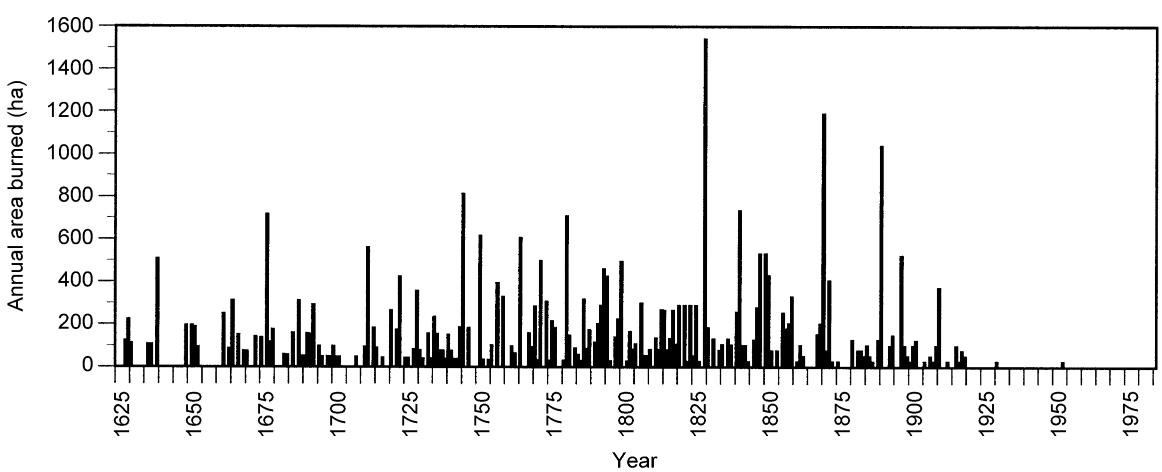

FIG. 2. Annual area burned between 1628 and 1995 in the Hayfork study area.

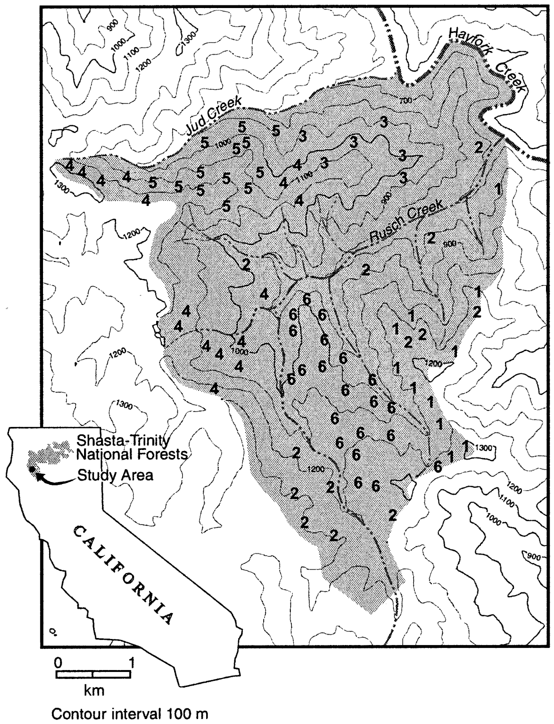

FIG. 3. Location of fire occurrence groups identified by cluster analysis of fire dates for 82 sites for the period 1751–1900 in the Hayfork study area. Group characteristics are given in Table 6 and Fig. 4.

but they frequently burned the same and another group (mean = 46%, range 26–71%) (Table 6). The largest percentage of consecutive fires burned a different group (mean = 49%, range 20–74%) and more fires ($P < 0.05$, Mann Whitney U test) burned a different group than burned the same and another group. Moreover, consecutive fires that did occur in the same and another group rarely (10%) reburned sites that recorded the earlier fire. Fires mainly (90%) burned different sites. Certainly, the lack of a scar at a particular site in a specific year does not necessarily indicate that fires that scarred trees on nearby sites did not burn there. Fuel conditions following a preceding fire may have been sufficiently altered so that fuels were discontinuous or fire intensities were too low to scar a tree.

Forest age-class patterns

Seven age-class groups were identified from the cluster analysis of stems >100 yr old (Fig. 5; Table 7). Douglas-fir is well distributed among age classes, is represented in all groups, and is among the oldest trees found in all groups except group 6.

Groups 1 and 2 are low density plots with stems of Douglas-fir, ponderosa pine, sugar pine, and white fir in a wide range of age classes. White fir >300 yr old were found in plots in both groups. On average, plots burned 10.3–13 times and the average number of age classes present in the plots in the group (4.6–7.3) suggests a pattern of punctuated tree establishment after mostly low- and perhaps moderate-severity fires.

Group 3 plots are moderately dense and distinguished by the high density of 180–240-yr-old stems of Douglas-fir, ponderosa pine, sugar pine, and white fir. Older (>240 yr) stems of Douglas-fir and ponderosa pine were common. Plots in this group burned on average 11.5 times and had stems in 7.3 age classes suggesting a long-term pattern of intermittent regeneration under a regime of frequent low-severity fires.

Group 4 plots are moderately dense and distinguished by the large number of <120-yr-old stems of Douglas-fir, sugar pine, ponderosa pine, and white fir and sparse populations of 200–420-yr-old stems of each of the same species. Douglas-fir and sugar pine are the oldest trees and stems of white fir >300 yr old were also present in plots in this group. Plots burned on average 12.4 times and on average they had trees in 4.9 age classes. Frequent tree establishment and the high frequency of fire suggest that fires were mainly low severity with some moderate-severity fire.

Group 5 plots are also intermediate in density and they are distinguished by the large number of <180-yr-old ponderosa pine, sugar pine, white fir, and especially Douglas-fir stems. Douglas-fir and sugar pine >300 yr old are also present and plots burned on average 12.3 times and had stems in 6.3 age classes. Frequent tree establishment and the high frequency of fire suggest that fires were again mainly of low and moderate severity.

Group 6 plots are moderately dense and they are distinguished by large numbers of <120-yr-old Douglas-fir, sugar pine, ponderosa pine, and white fir. There are no stems in this group >280 yr old. Stems 140–240 yr old are present and plots burned on average 10 times and had stems in 4.3 age classes. Peaks in the age-class distributions suggest the plots experienced a mix of both low- and moderate-severity fires.

Group 7 plots are dense and they are distinguished by the large number of 120–240- yr-old stems of Douglas-fir, white fir, and especially ponderosa pine and sug-

TABLE 5. Fire interval statistics for fire occurrence groups identified by cluster analysis of fire dates from 82 sites for the period 1751–1900 in the Hayfork study area.

Group	Sites (n)	Fire frequency	Fire return interval (yr) Mean	Median	SD	Minimum	Maximum
1	12	38	3.9	3	3.0	1	13
2	15	74	2.0	1	1.6	1	11
3	6	28	5.0	4	3.7	1	16
4	16	41	3.7	3	2.9	1	14
5	13	41	3.7	3.5	2.9	1	16
6	20	44	3.4	3	2.0	1	7

Notes: Median fire return intervals varied among groups ($P < 0.01$, Kruskal-Wallis H test), but paired comparisons indicate that the median fire return intervals was only shorter in group 2 ($P < 0.05$, Mann-Whitney U test); n is the number of sites.

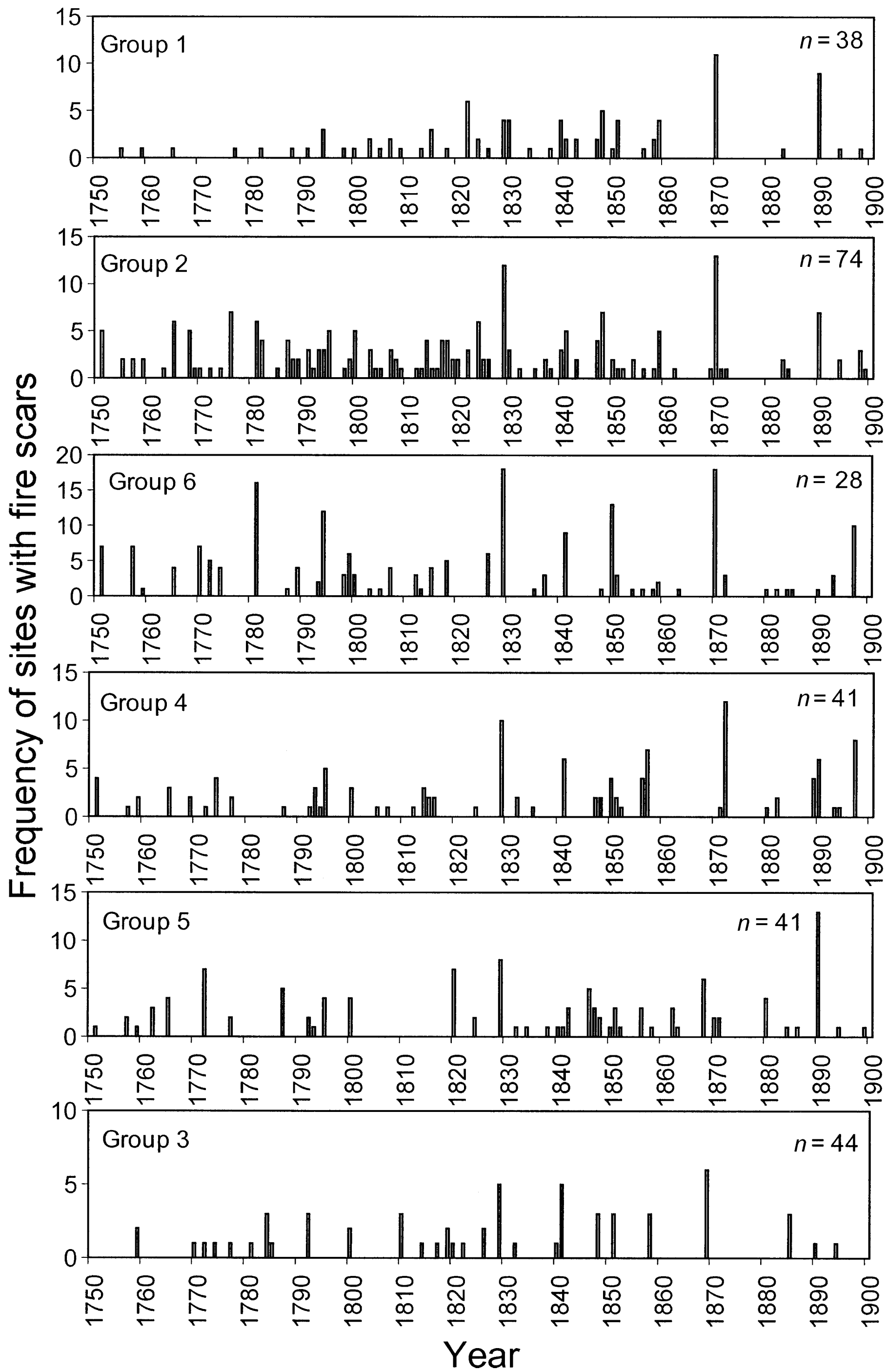

FIG. 4. Frequency of sites recording a fire year in the fire occurrence groups between 1751 and 1900 in the Hayfork study area. Group characteristics and location are given in Table 6 and Fig. 3, respectively; *n* is the number of fire years in each group.

ar pine. There are few stems >240 yr old. Douglas-fir and ponderosa pine are the species with the oldest stems. Plots burned on average 13.5 times and had stems in 4.1 age classes. Again, this suggests that fires in these plots were a mix of both low- and moderate-severity burns.

The landscape-scale pattern of plots in age-class groups was heterogeneous and not associated with topography. There was no significant difference ($P > 0.05$, Kolmogorov-Smirnov test) in the frequency distribution of age-class groups by aspect, elevation, or topographic position class. Moreover, there was no as-

TABLE 6. Percentage of consecutive fires that burned the same, another, or the same and another fire occurrence group between 1751 and 1900 in the Hayfork study area.

Group	Same	Another	Same and another	n
1	0	74	26	35
2	9	20	71	69
3	3	53	44	36
4	5	55	39	38
5	8	61	32	38
6	0	53	47	45
All	5	49	46	261

Notes: Fire occurrence groups were identified by cluster analysis of fire dates from 82 sites for the period 1751–1900. See Fig. 3 for location of groups; n is the number of consecutive fires.

sociation between topographic variables and the density of stems ≤100 yr old in the age-class groups. However, there were more stems ≤100 yr old than >100 yr old in each group ($P < 0.05$, Kruskal-Wallis H test) suggesting that fire suppression may have caused an increase in density in all age-class groups.

Forest compositional change

The ordination of ≤100-yr-old and >100-yr-old stems shows that Douglas-fir and white fir have regenerated more successfully than other conifer species during the fire suppression period. Differences in overstory (>100 yr) and understory (≤100 yr) composition are shown with vectors and vector length is proportional to compositional differences between the layers (Fig. 6). The magnitude of difference varies among the age-class groups. Compositional differences were greatest in groups 1, 4, and 7, which have a pine or mixed pine–Douglas-fir dominated overstory and an understory of mainly Douglas-fir and white fir. In groups 3, 5, and 6, which exhibit the least compositional difference, Douglas-fir was the overstory and understory dominant although pines and white fir were present in both layers in each group. In group 2, Douglas-fir and white fir were proportionally most abundant in the overstory and white fir was more abundant in the understory.

DISCUSSION

The primary controls on tree species distribution in the Klamath Mountains are temperature (elevation) and

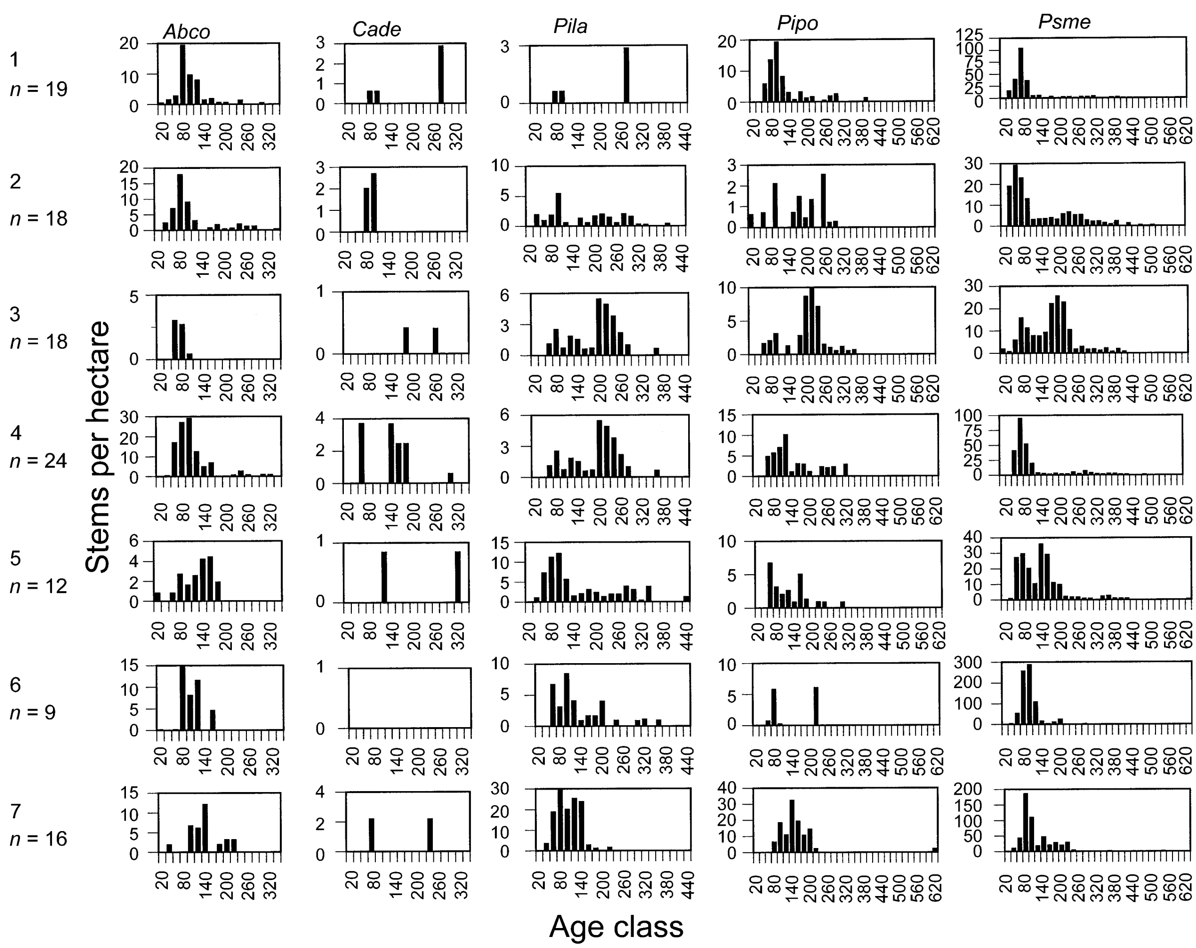

FIG. 5. Mean age-class distribution for the five dominant species in the seven age-class groups identified by cluster analysis of stems/ha >100 yr old in 20-yr age classes; n is the number of plots. Species abbreviations are defined in Table 1. Note that only every third age class is labeled and that the scale of the vertical axis is different on each graph.

TABLE 7. Mean density (stems/ha) of aged stems >100 yr and all aged stems, mean number of occupied age classes, and fire history characteristics for age-class groups identified by cluster analyses of stems >100 yr old in plots in the Hayfork study area.

Group	n†	Stems >100 yr Mean	Stems >100 yr Range	Stems >100 yr SD	All stems Mean	All stems Range	All stems SD	20-yr age classes >100 yr Mean	20-yr age classes >100 yr Range	20-yr age classes all stems Mean	20-yr age classes all stems Range	Mean number fires	Fires/age class
1	19	94	48–161	32	381	192–767	182	4.6	2–9	7.3	4–12	10.3	2.2
2	18	85	19–132	32	220	85–734	153	7.3	1–13	9.4	3–14	13.0	1.9
3	18	196	123–278	42	245	151–435	79	7.3	4–10	8.9	4–12	11.5	1.6
4	24	167	65–314	62	477	160–1212	274	4.9	1–9	7.2	4–11	12.4	2.5
5	12	159	63–262	67	268	145–586	117	6.3	2–9	8.3	5–11	12.3	2.0
6	9	216	104–312	64	947	417–1900	578	4.3	3–6	6.7	5–9	10.0	2.3
7	16	382	192–655	130	874	370–1500	618	4.1	2–7	6.6	4–9	13.5	3.3

† Number of plots.

soil moisture (Whittaker 1960, Sawyer and Thornburgh 1977, Sawyer et al. 1977), and these same controls influenced relative species abundance patterns in the mixed species forests in the Hayfork study area. Ponderosa pine, sugar pine, and canyon live oak were most abundant on dry south-facing slopes and ridgetops while white fir was most abundant on high elevation mesic sites. In contrast, Douglas-fir, California black oak, Pacific madrone, and golden chinquapin were most abundant on more mesic north-facing slopes at low elevation. Overall, the topographic controls on tree species distribution and abundance patterns we identified in the Hayfork study area are similar to those of montane forests elsewhere in the Klamath Mountains (Whittaker 1960, Sawyer and Thornburgh 1977, Sawyer et al. 1977, Taylor and Skinner 1998). The prevalence of Douglas-fir and the diversity of hardwood species distinguish mixed conifer forests in the Klamath Mountains from those elsewhere in the Cascade Range, Sierra Nevada, San Bernardino Mountains, and Sierra San Pedro Martir (Whittaker 1960, Barbour 1988).

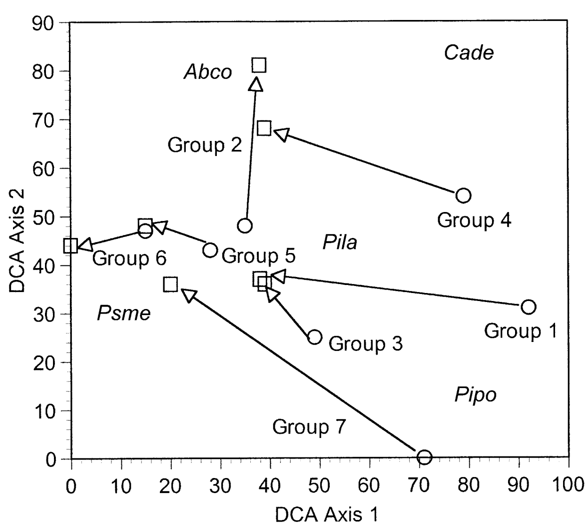

FIG. 6. Compositional differences in the density (stems/ha) of ≤100-yr-old (squares) and >100-yr-old (circles) trees in the seven age-class groups identified by cluster analysis. Vectors show the direction and magnitude of compositional difference between the two age classes for each group in DCA species space. The position of species abbreviations represent regions of relative dominance. Species abbreviations are given in Table 1.

Variation in elevation, aspect, and tree species composition can potentially influence spatial patterns of fire frequency by affecting the production, moisture, arrangement, and structure of fuels (Skinner 1978, Biswell 1989). Spatial variation in fire frequency associated with elevation has been identified in the southern Cascades and Sierra Nevada where differences in temperature and duration of snowpack combine to favor stands dominated by long-needled pines (e.g., ponderosa pine, Jeffrey pine, sugar pine) at low elevation and short-needled species (e.g., white fir, red fir) at high elevation (e.g., Parker 1994, Taylor 2000). The negative correlation between elevation and fire frequency in these landscapes is caused by several factors that affect flammability. First, fuel production rates on warmer, low-elevation, pine-dominated sites are higher than on cooler, higher elevation, fir-dominated sites (Agee et al. 1978, Stohlgren 1988; J. W. van Wagtendonk, *personal communication*). Consequently, fuel recovery after fire is faster so a low elevation site can burn again sooner. Second, fuels dry out sooner each year on low elevation sites so the period fires can burn each year is longer than at higher elevation. Finally, litter beds of short-needled species (i.e., fir) are dense, slowing fire spread and reducing intensity (Albini 1976, Rothermel 1983, van Wagtendonk et al. 1998), reducing the probability of fire being recorded at a particular site.

In the Hayfork study area, spatial variation in fire frequency was associated with aspect and not elevation or forest species composition. Fires were less frequent on north-facing slopes than on other slope aspects. Although this difference was statistically significant, the small difference in median FRI between north-facing and other aspects may not be significant from a management perspective. What may be more important is the greater variation in median FRIs on the north- and west-facing aspects compared to the south- and east-facing aspects. The variation in FRIs on the west-facing aspects may be due to the dry, shallow soils of low productivity associated with them (cf. USFS 1983). Indeed, these slopes were more likely to have a greater component of canyon live oak. Where canyon live oak makes up a major portion of the canopy, it is often associated with sites of low productivity (USFS 1983) characterized by sparse, discontinuous surface fuels that do not carry fire well except under more extreme conditions (Skinner and Chang 1996). Instead of more humid, mesic conditions inhibiting fires, the xeric, steep, west-facing slopes may not have been able to consistently produce fuels to carry fires as often as the south- or east-facing slopes.

Spatial variation in fire frequency with aspect has been identified in other landscapes with strongly contrasting terrain in the Klamath Mountains (Taylor and Skinner 1998), the Cascade Range (Beaty and Taylor 2001), and the Blue Mountains (Heyerdahl et al. 2001), where many of the same species occur on all slope aspects, albeit in different relative proportions. Spatial variation in fire regimes in the Hayfork landscape was also associated with finer-scale topographic features that affect the spread of fire across slope aspects (e.g., Skinner 1997).

The cumulative patterns of burns in the Hayfork landscape are spatially coherent and areas with similar patterns of fire occurrence are separated from others by features (i.e., streams, riparian zones, sharp changes in aspect, changes in parent material) that act as impediments to fire spread. The spatial patterns of fire occurrence are consistent with low intensity fire behavior (e.g., Rothermel 1983) where frequent fire maintains fuels below threshold levels needed for landscape-scale burns, except in years with more extreme fire-weather conditions (Miller and Urban 2000*a*). Even small streams and narrow riparian strips with water, higher humidity, and vegetation with high live fuel moisture are effective barriers to fire spread in forests that experience frequent, low-intensity surface fires (Skinner 1997). Moreover, differences in fuel bed characteristics that occur at abrupt changes in aspect, in riparian areas, or at parent material boundaries are sufficient to inhibit the spread of fire under typical conditions (e.g., Taylor 2000, Stephens 2001). Parent materials, especially where ultramafic rock is interspersed with other rock types as in our study area, may affect fire spread patterns due to different levels of fuel production. Historically, even bare foot paths were reported to stop many fires in the vicinity of our study area (Wilson 1904).

The interactions of topography and fire behavior promoted fire occurrence patterns that were related to topography. Fire occurrence groups had similar fire regimes (median FRI, FRI distributions) but fires in the groups tended to occur in different years. The average similarity of 57% between fire occurrence groups indicates that the boundaries between groups did not act as simple barriers but as filters to fire spread. Fires in some years were contained within the group area and did not spread across boundaries. Yet, at other times, often in dryer years, fires would spread across boundaries. Between 1751 and 1900, on average, fivefold more sites burned in the study area during the 10 driest years than in the 10 wettest years (PDSI-GP-5; Cook et al. 1996). Patterns of consecutive burns within and between the fire occurrence groups also suggest that the spatial structure of fires in the fire occurrence groups may be influenced by the time-dependent process of fuel buildup. However, the coincidence of fire occurrence group boundaries with topographic features known to affect fire behavior suggests that topography is the primary control on the spatial pattern of fire in the highly complex terrain in our study area. Relatively high rates of fuel production and low rates of fuel decomposition may reduce the importance of the burn patch mosaic on the spatial structure of fire regimes (Chang 1999, Miller and Urban 2000*b*).

Species response to fire is strongly influenced by season of burn (Kauffman 1990), and the position of fire scar lesions within annual growth rings indicates that burns in the Hayfork study area occurred mainly (76%) after growth had ceased for the year. In the Klamath Mountains, ignitions peak in July and August when lightning is most frequent (Schroeder and Buck 1970). Compositionally similar forests in the Klamath Mountains and southern Cascades also experienced mainly (80–90%) dormant season burns (Taylor and Skinner 1998, Beaty and Taylor 2001), but those in the central and southern Sierra Nevada experience mainly late growing season burns (latewood) (Caprio and Swetnam 1995). Further south, in the Sierra San Pedro Martir, mixed conifer forests usually burn early (91% earlywood) in the growing season (Stephens et al. 2003). This latitudinal gradient in season of burn is probably related to geographic variation in the onset and length of the summer drought period (south-early, north-late) (Major 1977, Parker 1994), which would influence the period fuels are dry enough each year to burn. Despite overall high similarity in tree species composition along the latitudinal gradient (Barbour 1988, Minnich et al. 2000), vegetation response to fire may be regionally distinct and promote regional variation in vegetation development after fire. Consequently, reference conditions for fire regimes developed from distant areas may not be appropriate (e.g., Minnich et al. 2000) as models for local restoration.

Variation in fire severity is an important source of structural diversity in forested landscapes because burns may kill all trees in some stands and few in others. Stands that have experienced high-severity fires are even aged or several aged with stems in relatively few age classes while those that experience mainly low- and moderate-severity fires have stems in a wide range of age classes because fires kill few trees in the stand (Agee 1993). Forest stands in our study area were multiaged and virtually all stands had stems >250 yr old, and many included older stems of relatively fire-sensitive white fir. This suggests that burns were mainly low or moderate in severity and patchy enough to allow white fir to grow to a fire-resistant size (e.g., Agee 1993). On average, plots had stems in 5.5 different 20-yr age classes and had burned 12.1 times. Additionally, 30% of the plots had stems in 8–13 different 20-yr age classes. Few plots had distinct cohorts of trees. Similar forests of multiaged or multisized stems that experienced frequent, low-severity fires occur throughout the mixed confer zone in the Sierra Nevada, southern Cascade Range, and the Klamath Mountains (e.g., Parsons and DeBenedetti 1979, Taylor and Skinner 1998, Taylor 2000). The lack of obvious fire-generated cohorts and presence of stems in a wide range of age classes in the plots suggest that periods of postfire recruitment overlapped, which makes cohorts indistinguishable. The age structure of mixed conifer forests, however, are not uniformly multiaged. In the Klamath Mountains and southern Cascades, large (>100 ha) mainly even-aged patches of trees are present indicating that high-severity burns played an integral role in shaping forest structure at stand and landscape scales at least in some areas (e.g., Taylor and Skinner 1998, Beaty and Taylor 2001, Bekker and Taylor 2001). Even-aged stands in the Klamath Mountains and southern Cascade Range, are proportionately more abundant on upper slope positions suggesting that topography may also be an important control on fire severity and stand age structure at landscape scales (Skinner 1995, Taylor and Skinner 1998, Beaty and Taylor 2001). Mid- and upper-slope positions often experience higher fire intensities than lower slopes due to preheating of fuels, higher effective windspeeds, and lower canopy cover (Rothermel 1983, Weatherspoon and Skinner 1995, Taylor and Skinner 1998). While most stands in our study area were multiaged at all slope positions, there was evidence of high-severity fire in several stands in Rusch Creek and in adjacent watersheds. Stands of knobcone pine (*P. attenuata*) and montane chaparral (*Arctostaphylos* sp.; *Ceanothus* sp.) were present on some upper slopes and ridgetops. Knobcone pine and chaparral dominate the sites that have recently experienced high-severity fires (Keeley 1977, Vogl et al. 1977). Our understanding of the influence of topography on patterns of fire severity is currently insufficient to untangle the potential long-term effects of topography from the short-term effects of extreme fire weather on fire severity and forest age structure patterns.

Fire regimes varied with historical period, and fire occurrence and burned area declined after 1905 when a policy of suppressing fires was implemented on National Forest lands. The 10-fold increase in fire rotation from 20 to 238 years is a clear indicator of how dramatically fire suppression has altered fire regimes in the Hayfork study area. Similar dramatic declines in the frequency and extent of fires have been reported for mixed conifer forests in the Sierra Nevada (Kilgore and Taylor 1979), Cascade Range (Taylor 2000, Beaty and Taylor 2001, Bekker and Taylor 2001) and the Klamath Mountains (Wills and Stuart 1994, Taylor and Skinner 1998). In some parts of the Sierra Nevada, an earlier settlement period decline in fire frequency occurred, perhaps due to decreased Native American ignitions or livestock grazing (Kilgore and Taylor 1979, Caprio and Swetnam 1995). No settlement period decline in fire frequency occurred in the Hayfork study area or in other mixed conifer forests in the Klamath Mountains (Wills and Stuart 1994, Taylor and Skinner 1998) or the Cascade Range (Taylor 2000, Beaty and Taylor 2001, Bekker and Taylor 2001). In fact, fires were frequent in our study area until about 1920 and fire frequency did not decline in some parts of the Klamath Mountains until after World War II when fire fighting became more mechanized (Taylor and Skinner 1998). Clearly, there is considerable regional variation in when and why fire regimes changed in California and this may be reflected in the type and magnitude of vegetation change that is associated with altered fire regimes.

Forest changes caused by fire suppression have been documented in the mixed conifer forests in the Sierra Nevada (Vankat and Major 1978, Parsons and DeBenedetti 1979), the San Bernardino Mountains (Minnich et al. 1995, Savage 1997), and southern Cascade Range (Dolph et al. 1995, Taylor 2000). Overall, forests have increased in density and shifted in composition from more fire-resistant to more fire-sensitive species, reducing the structural diversity of forests at both stand and landscape scales (Vankat and Major 1978). The forest density increases in our study area are consistent with this view except for the importance of Douglas-fir in these changes. Douglas-fir declines with decreasing latitude in the Sierra Nevada and is absent from the southern Sierra Nevada southward. In most mixed conifer forests, fire-resistant ponderosa, sugar, and Jeffrey pine are set to be replaced by white fir and incense cedar (e.g., Parsons and DeBenedetti 1979, Savage 1997, Taylor 2000). However, this pattern was evident only on mesic and higher elevation sites in our study area where white fir and incense cedar were already relatively abundant in the overstory. The predominant increase in density was for Douglas-fir or a mixture of Douglas-fir and white fir. Douglas-fir is shade tolerant on drier sites in the Klamath Mountains (Herman and Lavender 1990), and Douglas-fir and white fir are more fire-sensitive than the pines when they are small. But Douglas-fir is as fire tolerant as the pines when it matures due to its thick bark, which prevents injury by low- and moderate-intensity fires (Agee 1993). The large increase in young Douglas-fir during the fire-suppression period in the Klamath Mountains suggests that compositional shifts in mixed conifer forests that are associated with reduced fire frequency may vary regionally despite overall high similarity in tree species composition in California's mixed conifer forests.

Decades of fire exclusion have dramatically altered the historical effects of frequent low-and moderate-severity fires on forest structure and on the abundance and spatial arrangement of understory fuels historically created by frequent low- and moderate-intensity fires. Land managers are seeking ways to use prescribed fire, among other fuel management techniques, both to reduce the heightened risk of severe fire due to changing fuel conditions and to reintroduce fire as an integral ecosystem process in late-successional and old-growth reserves in the Klamath Mountains (USDA-USDI 1994, 2000). Yet, it is uncertain if common prescribed burning practices (i.e., sequences of burns with boundaries at defensible terrain features) will restore a more natural fire regime to fire-prone landscapes or if they will create potentially undesirable consequences for landscape structure because of the scale of burning (Baker 1994, Taylor 2000). In our study area, quantitative measures of prefire suppression fire regimes demonstrate that areas with similar fire regimes (FRI, FRI distributions, scheduling or timing of fires) were often bounded by topographic features such as stream courses, aspect changes, and ridgetops. Using topographic features as fire boundaries is a common management practice for prescribing surface fires in the highly complex terrain of the Klamath Mountains. Spatial and temporal variation of fire regimes in our study area suggest that this tactical approach to prescribed burning is consistent with prefire suppression burn patterns, at the watershed scale, and that it is an appropriate strategy for reintroducing surface fire into late-successional reserves in the Klamath Mountains. It may also be an appropriate strategy in other landscapes where the scale and arrangement of landscape features strongly affect fire behavior and fire effects (e.g., Taylor and Skinner 1998, Taylor 2000, Beaty and Taylor 2001, Heyerdahl et al. 2001). However, the scale threshold for landscape control on variation in fire regime parameters remains unexplored in most ecosystems. Matching scales of a prescribed fire program with topographic controls is a useful framework for guiding landscape restoration in forests highly alerted by nearly a century of fire exclusion.

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