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Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA

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Abstract

The frequency, extent, and severity of fires strongly influence development patterns of forests dominated by Douglas-fir in the Pacific Northwest. Limited data on fire history and stand structure suggest that there is geographical variation in fire regimes and that this variation contributes to regional differences in stand and landscape structure. Managers need region-specific fire regime data to develop process-based management schemes to manage new late-successional reserves (LSR). This study quantifies fire regimes and stand structural patterns in a LSR in Douglas-fir-dominated forests in northern California. We analyzed tree species composition, structure (diameter, age), and fire scars from 75 plots in a 1570 ha area in the northern Klamath Mountains. Tree species composition varied with elevation and aspect, and median fire return intervals were similar (12–19 years) among species composition groups. However, median fire return intervals (FRI) were shorter on south- (8 years) and west-facing (13 years) slopes than on northern (15 years) or eastern (16.5 years) aspects. Fire return intervals also varied by historical period. Median FRIs were longer (21.8 years) during the suppression period (1905–1992) than in the settlement (1850–1904) (12.5 years) or presettlement (1627–1849) (14.5 years) period. The average burn area for a fire was 350 ha, and 16 fires larger than 500 ha burned between 1627 and 1992. Fire rotations varied by century from 15.5 to 25.5 years and were longest in the fire suppression period. Stand conditions were multi-aged, and Douglas-fir recruitment occurred after fire. Patterns of past fire severity, inferred from age-classes, indicate that upper slopes, ridgetops, and south- and west-facing slopes experienced more severe fires between 1850 and 1950 than lower slopes or east- and north-facing slopes. Implications are that lower slopes and north and east aspects are more likely than other topographic positions to sustain or promote long-term, late-successional conditions. Prescribed fire will likely be an integral component of management plans that successfully maintain natural processes and structures in newly established late-successional reserves in the Klamath Mountains. © 1998 Elsevier Science B.V.

Keywords: Age-classes; Douglas-fir; Fire ecology; Fire regimes; Landscape ecology; Stand structure

1. Introduction

The structure, composition, and dynamics of Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) (nomenclature follows Hickman, 1993) -dominated

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forests in the Pacific Northwest are strongly influenced by natural disturbances such as fire, windthrow, insect attacks, and volcanic eruptions. Fires have affected most areas with the greatest frequency. The fire regime (i.e. type, intensity, return interval, and extent of fire) is a primary control on patterns of community structure, composition, succession, and diversity (Franklin and Dyrness, 1973; Agee, 1981, 1991a, 1993; Stewart, 1989; Morrison and Swanson, 1990; Spies and Franklin, 1991; Halpern and Spies, 1995; Wallin et al., 1996). Identifying the characteristics of fire regimes, and fire-generated structural patterns, is therefore central to understanding long-term dynamics of Douglas-fir-dominated forests. Moreover, data on fire regimes are needed by managers to develop plans to perpetuate forest patterns and processes in newly established late-successional reserves (LSR) in the Pacific Northwest (FEMAT, 1993). Management objectives for these reserves are to maintain late-successional forest ecosystems within their historic range of natural variability (e.g. Swanson et al., 1994) using natural processes, and to accelerate development of late-successional forest characteristics (i.e. multilayered stands, snags, coarse woody debris) in younger stands within reserves (FEMAT, 1993; USDA-USDI, 1994). Structural definitions for late-successional forests were developed from stands that have not burned in recent decades because of fire suppression. Therefore, structural attributes (i.e. multiple canopy layers, coarse woody debris, snags) often associated with late-successional forests may be, in part, an artifact of vegetation changes associated with 20th century fire suppression policies (Skinner and Chang, 1996). A better understanding of the role of frequent low- and moderate-severity fire on stand development patterns is needed by managers to evaluate risks associated with different management options, especially those that limit use of fire as a process in these ecosystems (e.g. Attiwill, 1994; Mutch and Cook, 1996; Arno et al., 1997). Furthermore, managers need place-based understanding of fire regime effects on forest dynamics because disturbance regimes and stand development patterns vary geographically (e.g. Spies and Franklin, 1989; Veblen, 1989; Veblen et al., 1992; Agee, 1993).

Fire regimes (i.e. return interval, extent, severity) in Douglas-fir-dominated forests of the Pacific Northwest seem to vary geographically and this variation may contribute to regional differences in forest structure in the Douglas-fir zone (Franklin and Dyrness, 1973; Spies and Franklin, 1989; Agee, 1991a, 1993). In the Cascades of western Washington and Oregon, extensive stands (>100 000 ha) of even-aged Douglas-firs are thought to result from large, infrequent, severe fires that kill most trees (Franklin and Hemstrom, 1981; Hemstrom and Franklin, 1982; Franklin, 1988; Agee, 1993). Douglas-fir regeneration after these coarse-scale high severity fires may occur over an extended period (>100 years) because of the lack of seed sources in large burns, reburns after the initial fire, or competition with long-lived shrubs that proliferate after fire (Franklin and Dyrness, 1973; Franklin and Hemstrom, 1981; Hemstrom and Franklin, 1982; Means, 1982; Stewart, 1986; Walstad et al., 1987; Huff, 1995). In other parts of the western Oregon Cascades, large even-aged Douglas-fir stands are punctuated by openings caused by more frequent (20–200 years) low- and moderate-severity fires (Teensma, 1987; Morrison and Swanson, 1990). Douglas-fir regenerates in these smaller scale (several hectares) openings and stands may have two or three fire-generated cohorts (Means, 1982; Stewart, 1986, 1989). In drier southern Douglas-fir-dominated forests of the Klamath Mountains in northwest California and southwest Oregon, fire regimes appear to be different from those farther north. Fires occur much more frequently, every 13–22 years, and finer scale canopy openings caused by frequent, less severe fires appear to control stand development patterns (Agee, 1991b; Wills and Stuart, 1994). However, fire regimes and the role of fire in stand and landscape dynamics have been little studied in southern Douglas-fir-dominated forests (e.g. Agee, 1991b; Wills and Stuart, 1994) and it is unclear how stand development patterns in forests prone to more frequent fires may differ from those in northern Douglas-fir-dominated forests.

The goal of this study was to describe and quantify the fire regime and patterns of stand structure at plot and landscape scales. We use fire history and age data to answer the following questions: (1) What are the characteristics (i.e. return interval, size, severity, fire rotation, seasons of fires) of fire regimes, and do they vary spatially and temporally?; (2) Do age-structural patterns reflect frequent periodic establishment of Douglas-fir after low- and moderate-severity fires or mass establishment after fires that are nearly stand-replacing? Our null hypothesis was that fire regimes in southern Douglas-fir-dominated forests are similar to northern ones and that stands are mostly even-aged. The implications of our data for management of Douglas-fir-dominated forests in LSRs of the Klamath Mountains are also discussed.

1.1. Study area

Our study was conducted in the Klamath National Forest 15 km north of Happy Camp, California on Thompson Ridge, a north-to-south trending ridge that extends from the Oregon border to the Klamath River, in the northern Klamath Mountains (Fig. 1). The terrain in the 1570 ha study area is steep (average slope pitch 33°) and rugged. Elevation ranges from 650 to 1600 m. Soils are generally deep (>100 cm) and are developed in fractured Jurassic-age meta-sedimentary and meta-volcanic rocks including granodiorite, hornblende, diorite, dacite porphyry, and amphibole gneiss (Foster and Lang, n.d.). Small outcrops of igneous peridotite or serpentine were also present.

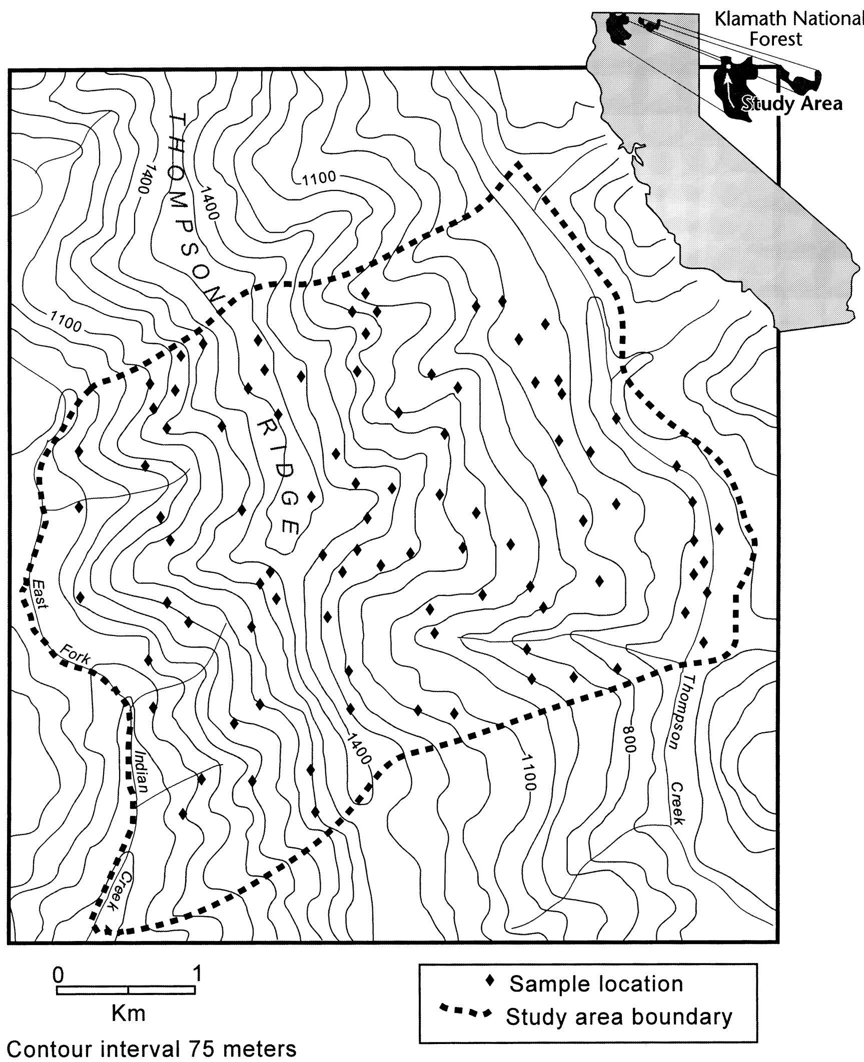

Fig. 1. Location of study area. Diamond-shaped symbols indicate sample locations.

Only two perennial streams and a few small rock outcrops occur in the study area that might act as fuel breaks to inhibit spread of fire.

The climate is Mediterranean, and temperatures are somewhat modified by proximity (75 km) to the Pacific Ocean. Average annual precipitation at Happy Camp, California (330 m) is 127.5 cm, and most (85%) falls between October and March. The average annual temperature is 16.6°C, and, on average, January is the coldest month (9.8°C) and July the warmest (25.7°C).

Forests in the study area fall within Whittaker's (1960) Douglas-fir–Sclerophyll and white fir (*Abies concolor*)–Douglas-fir, and Sawyer and Keeler-Wolf's (1995) Douglas-fir, Douglas-fir–Ponderosa pine (*Pinus ponderosa*), and mixed conifer zones. At lower elevations, a subcanopy of the evergreen hardwoods madrone (*Arbutus menziesii*), chinquapin (*Chrysolepis chrysophylla*), and canyon live oak (*Quercus chrysolepis*) and the deciduous hardwoods bigleaf maple (*Acer macrophyllum*), black oak (*Quercus kelloggii*), and dogwood (*Cornus nuttallii*) occur beneath a mixed canopy of Douglas-fir, ponderosa pine, and sugar pine (*P. lambertiana*). Stand composition is variable and strongly influenced by site moisture availability. At higher elevations hardwoods are less abundant, and Douglas-fir and white fir are canopy dominants. Douglas-fir generally decreases in abundance with elevation (Whittaker's, 1960).

People have affected fire regimes and forests in the study area during different times in known and unknown ways. Before European settlement, native Americans set fires that may have burned through the study area. Local Klamath tribes used fire extensively to promote acorn, berry, root, and fiber production and to hunt game (Lewis, 1990, 1993). In 1849, gold was discovered in the Klamath River basin, and prospectors and miners entered the Klamath Mountains. Prospectors set fires to expose rock outcrops, and settler-caused fires in the Klamath Mountains are reported to have been extensive and severe (Leiberg, 1900; Haefner, 1917; Atzet and Wheeler, 1982). However, Gannett (1902) reports that fires in the Siskiyous were rarely severe though they may have been extensive. He attributes this to the open nature of the forests with little understory. Fires set by settlers may have burned the study area, but we have no written record that they did so. In 1905, a policy of suppressing fire was implemented when the area became part of the National Forest Reserve System. Logging in the study area began in the 1960s. Small areas on the top and lower flanks of Thompson Ridge were selectively cut between 1960 and 1980, and clearcut logging began in the mid-1980s. Extensive areas were clearcut in 1988 and 1989 to salvage trees damaged or killed by a large wildfire in 1987.

Our study area was included as part of a habitat conservation area for the northern spotted owl (HCA C-5) in 1990 (Thomas et al., 1990). It has subsequently been designated as a part of the Seiad LSR through the FEMAT process (FEMAT, 1993). Fire is recognized as an important management tool to continue natural processes and reduce the potential for large, severe fires. Other silvicultural activities are now limited to treatments (site preparation, planting, thinning) designed to promote late-successional conditions where they are lacking in even-aged stands <80 years old and existing clearcuts and to help reduce the threat of large-scale severe fires (USDA-USDI, 1994).

2. Methods

2.1. Forest structure and composition

Sample sites for the study of tree structure and composition were selected by stratifying the study area by stand structure (young, mature, old), elevation (low, middle, high), and slope aspect (north, south, east, west). Elevation and aspect groups were determined from topographic maps. Stand age (young, mature, old) and structure (even-aged, multi-aged) in the study area were estimated by mapping structural units on the basis of the density and texture of tree heights on a series (1944, 1975, 1990) of aerial photographs. We also considered the location of clearcuts in choosing sample sites in an elevation, aspect, or age-structural group. We preferred to sample in clearcuts because: (1) ages of stems >1.0 m dbh could be determined more accurately from stump ring counts than from increment cores; and (2) fire evidence (i.e. series of fire scars) was more readily detected in stump cross-sections than in cores from live trees. Sample distribution was therefore not random but encompassed the observed variability in stand composition and structure throughout the study area. Seventy-five stands (28 clearcuts, 47 forested) were sampled (Fig. 1).

We used plots of variable sizes (100–2250 m^2) to sample about 20 trees (mean=22, range 14–36 stems) in a stand. Different plot sizes were used because of variability in stand density (320–2400 trees ha^{-1}). In each plot, the diameter of all live stems or stumps >5.0 cm at breast or stump height was measured, and the location (UTM coordinates), elevation, aspect, and slope pitch of each plot were recorded. Saplings (>1.4 m tall, <5.0 cm dbh) were also counted. For each plot, tree age structure was determined by coring stems of each tree at 30 cm and counting each tree's annual growth rings beneath a binocular microscope. On plots located in clearcuts, trees were aged at stump height (mean=27 cm) using the following method. First, a clear cross-section of the stump from the bark to the pith was exposed by cutting a 4 mm wide strip of wood using a wood-carving tool. Second, the exposed annual rings on each stump were then counted using a 10–20× hand lens. Hardwood stems (i.e. bigleaf maple, madrone, chinquapin, dogwood, canyon live oak, black oak) were commonly present as a minor component in our plots. However, in clearcuts they were often damaged by logging or subsequent stand treatment and therefore we could not age them. Consequently, we include data for only conifers in this study.

Some cored trees could not be aged because their stems contained internal rot or were too large (>130 cm dbh) to extract a complete core. To estimate ages of these trees (5% of stems, n=62) we used least squares regressions of age on stem diameter developed from aged stems of each species. All regression equations were significant (P<0.001) (white fir r^2=0.41, SE=33.2, n=528; incense cedar (*Calocedrus decurrens*) r^2=0.83, SE=38.8, n=39; sugar pine r^2=0.71, SE=61.2, n=25; ponderosa pine r^2=0.76, SE=42.1, n=14; Douglas-fir r^2=0.72, SE=51.1, n=648).

Groups of stands with similar composition were identified in the following way. First, importance values were calculated for each tree species in a plot as the sum of relative density and relative basal area×100 (maximum=200). Compositional groups were identified by clustering species IVS using Ward's method, and relative Euclidean distance as the similarity measure, with PC-ORD software (McCune and Meford, 1995).

Variation in forest composition data was analyzed using detrended correspondence analysis (DCA). DCA is a modified reciprocal-averaging ordination technique that calculates both species and stand scores (Gauch, 1982). The contribution of environmental variables to compositional variability was identified by correlating (Pearson product moment) DCA axis scores with elevation and slope aspect.

2.2. Fire history

Fire occurrence was reconstructed using cross-sections from fire-scarred stumps, partial cross-sections (wedges) (Arno and Sneck, 1977) from fire-scarred live trees, and increment cores from live trees (Barrett and Arno, 1988). Samples (204), including 194 cross-sections and 10 wedges from live trees were collected in a 1–3 ha area around or near each plot, with a chainsaw. An average of 3.8 cross-sections (range 1–12) was collected at each site. Evidence of fires (scars) was clear on stump tops, and samples with long fire records were easily identified and collected. Live trees, in contrast, had little external evidence of past fires (scars) because fire wounds on most trees had completely healed. We supplemented our original sample with stumps from 19 additional sites to increase the spatial extent of stump samples in the study area. These stumps were from trees cut by road building and fire line construction during and after the 1987 fire.

Fire dates were identified on full and partial cross-sections by first sanding each specimen to a high polish (400 grit), then crossdating the tree rings in each specimen with nearby tree ring chronologies (Graumlich, 1985; Holmes et al., 1986), and identifying the year and season (e.g. Baisan and Swetnam, 1990) of each fire. Only 27% (n=56) of the cross-sections crossdated because variation in radial growth of most trees was more strongly controlled by local factors such as competition and disturbance (i.e. fire) than by regional climate. At least one sample from 61% of the sites crossdated, and crossdating was more common on the west (81%) than on the east (48%) slopes of Thompson Ridge. Fire dates for samples that did not crossdate were then assigned by adjusting them to crossdated samples of known fires (e.g. 1987) that scarred trees on most (n=70) sites.

Variation in radial growth observed in stump cross-sections, wedges from live trees, and increment cores from fire-scarred and other live trees was also used to identify fire dates. Fires frequently injure trees without scarring them and cause declines in radial growth (Arno and Sneck, 1977; Barrett and Arno, 1988; Brown and Swetnam, 1994). Growth suppressions were identified as the year of sudden decrease in radial growth (>50% decrease in ring width for 5 years compared with the previous 5 years). Suppressions were considered fire-related if they corresponded to a dated fire scar on a nearby sample(s). Sudden, sustained increases in ring width (growth releases) have been used in other studies as indicators of fires (e.g., Stephenson et al., 1991; Brown and Swetnam, 1994; Mutch and Swetnam, 1995). Although releases were common, the onset of the growth release was inconsistent and often delayed for several years following the year of the fire as indicated by fire scars. Therefore, we did not use growth releases to date fires.

Median fire return intervals (FRI) were calculated for each site, and each site was then classified by tree species composition (cluster analysis of importance values), elevation (low, middle, high), and aspect (north, south, east, west). Median FRIs for each site were also calculated for the presettlement (before 1849), settlement (1850–1904), and suppression (1905–1992) periods for the study area as a whole. Median FRIs in the spatial and temporal groups were then compared using a nonparametric Kruskal–Wallis *H*-test.

Fire rotations (FR) (Heinselman, 1973) were calculated for the study area as a whole by century and for the presettlement, settlement, and suppression periods. FR is the number of years needed to burn an area the size of the study area (1570 ha) given the extent of burning in that period (Heinselman, 1973; Agee, 1993). In any given time, some parts of the study area may have burned more than once and others not at all.

Calculation of the FR requires an estimate of the area burned by each fire. We estimated fire area by first mapping dates of fires for each site and then using a ratio method to estimate fire area (Morrison and Swanson, 1990). Fire area from the point data was estimated as,

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

where, A_i is the area burned in the ith year, AT the study area, NS_i the number of sample sites with a record of the ith year burn, NST the total number of sample sites, and NRE the number of sites eliminated by subsequent fires.

The accuracy of this method decreases as NRE increases, and the method assumes that the distribution of sample sites is random. Though fires were recorded back to 1507, we chose 1626 as the cutoff date for our fire record to reduce interpretation errors that might occur because of too small sample size (n=7). Our sample sites were not placed randomly in the study area but they are well dispersed (Fig. 1).

2.3. Stand age structure and fire severity

The effect of fire severity on stand structure at plot and landscape scales was identified on the basis of the age structure of conifers and site fire chronologies. Plots were arranged into groups with similar age structure, reflecting similar stand responses to fire, using cluster analysis. The density of stems (ha^{-1}) of each species in 20-year age-classes (20–520 years) was clustered using Ward's method and relative Euclidean distance as the similarity measure. For each structural group we calculated a measure of fire severity as the average number of 60-year periods in which trees regenerated. Presumably, plots with trees in fewer 60-year age-classes characterize stands that have burned more severely than those with more age-classes. We chose a 60-year interval because it spans the maximum observed regeneration period for a post-fire cohort in our study area. The average number of fires that burned in each plot in each group was also calculated.

Landscape-scale patterns of fire severity were identified by calculating the cumulative proportion of the landscape that burned at high, moderate, and low severity between 1850 and 1950. We used the plot age data and structural patches evident on aerial photographs from 1944 and 1975 to map past fire severity. Stand boundaries were too diffuse to map earlier evidence of fire severity. Severity patches were mapped using the relative density of short even-aged stems and taller, older trees that survived successive fires. High-severity patches had <10 tall stems ha^{-1}, moderate-severity patches had 10–20 tall stems ha^{-1}, and low-severity patches had >20 tall stems ha^{-1}. The minimum mapped patch size was 1.5 ha.

3. Results

3.1. Forest composition and structure

Four groups of species composition were identified using cluster analysis of species importance values (Table 1). These groups are Psme, Psme–Pila–Pipo, Psme–Abco–Pila, and Abco–Psme (where Abco= *Abies concolor*, Psme=*Pseudotsuga menziesii* var. *menziesii*, Pila=*Pinus lambertiana*, and Pipo=*Pinus ponderosa*). Psme plots are distinguished by the almost complete dominance of Douglas-fir. Psme–Pila–Pipo plots also have high Douglas-fir importance values but sugar and ponderosa pine are characteristically common in this group. Psme–Abco–Pila plots are co-dominated by Douglas-fir and white fir and they have a significant component of sugar pine. In contrast, white fir is more abundant than Douglas-fir in Abco–Psme plots and incense cedar is the most common associate.

The DCA of species importance values separate plots on the basis of species composition (Fig. 2; Table 2). The first DCA axis separates plots with a sugar pine (r=0.38, P<0.01) and ponderosa pine (r=0.38, P<0.01) component from those with abundant white fir (axis 1, r=−0.94, P<0.01) and incense cedar (r=−0.40, P<0.01). Sugar pine is negatively correlated (r=−0.50, P<0.01) and incense cedar is positively correlated (r=0.30, P<0.01) with DCA axis 2. Compositional variation is related to elevation and slope aspect. Elevation is negatively correlated (r=0.35, P<0.01) and aspect is positively correlated (r=0.32, P<0.01) with DCA scores on the first axis. These correlations indicate that pines are concentrated at lower elevations and warmer (south–west) slope aspects. White fir and incense cedar, in contrast, are most abundant at high elevations and on cooler, more mesic sites, whereas Douglas-fir decreases in abundance with elevation (Table 2).

3.2. Fire history

Fires were recorded in the study area in 94 years during the period 1626–1992 (mean=3.9 years between fires). Median FRIs for all sample sites had a range of 5.5–116 years, and species composition groups had similar (P=0.834) median FRIs that varied from 12 to 19 years (Table 3).

Most fires (85%) burned after trees completed radial growth for the year (dormant season). In this part of California, dormant season scars are formed from burns that occur in the summer and fall after trees cease growing for the year (e.g. Caprio and Swetnam, 1995). However, some fires were recorded in latewood (11.8%) and earlywood (3.2%), indicating that these occurred in the growing season.

Patterns of fire frequency varied spatially in the study area (Table 4). Median FRIs varied by slope aspect (P<0.05, Kruskal–Wallis H-test). South- and

Table 1
Mean importance value (IV), relative frequency (RF) (%), and basal area (BA) (m^{-2} ha^{-1}) of tree species by species composition groups identified by cluster analysis of species importance values on Thompson Ridge, Klamath Mountains, California

Species	Species acronym	Psme–Pila–Pipo (n=13)			Psme (n=28)			Psme-Abco-Pila (n=15)			Abco–Psme (n=19)		
		IV	RF	BA	IV	RF	BA	IV	RF	BA	IV	RF	BA
Abies concolor	Abco	9	54	4.3	20	78	6.8	83	100	61.3	126	100	30.9
Calocedrus decurrens	Cade	3	8	0.8	4	14	2.4	5	33	13.8	13	53	2.5
Pinus lambertiana	Pila	35	77	28.7	4	25	1	14	40	7.8	5	21	11.4
Pinus ponderosa	Pipo	18	46	15.2	0	4	<1	2	7	<1	<1	5	<1
Pseudotsuga menziesii var. *menziesii*	Psme	135	100	54.5	171	100	93.9	95	100	40.2	55	79	89.9
Taxus brevifolia	Tabr	0	0	0	<1	4	<1	0	0	0	0	0	0

n is the number of samples in each group. Species composition acronyms are derived from the first two letters of the genus and species that differentiate the groups.

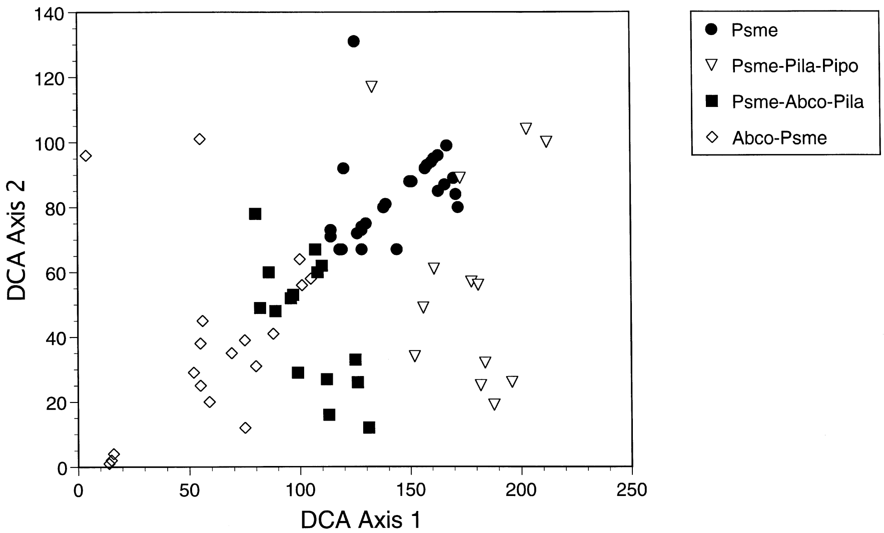

Fig. 2. Plot scores for the first and second axis of the DCA ordination of species importance values on Thompson Ridge, Klamath Mountains, California. Different symbols represent species composition group identified by cluster analysis (see Table 1).

Table 2
Pearson correlation coefficients (n=75) of species importance values (IV), elevation, and aspect with ordination scores from DCA from plots on Thompson Ridge, Klamath Mountains, California

	Axis 1	Axis 2
Abies concolor IV	−0.94[b]	−0.66[b]
Calocedrus decurrens IV	−0.40[a]	0.30[a]
Pinus lambertiana IV	0.38[a]	−0.50[a]
Pinus ponderosa IV	0.38[a]	0.17
Pseudotsuga menziesii IV	0.82[b]	0.71[b]
Taxus brevifolia IV	0.01	0.00
Elevation	−0.35[a]	−0.20
Aspect	0.32[a]	0.18

[a] $P<0.05$.
[b] $P<0.01$.

Table 3
FRIs (years) for sites by species composition group on Thompson Ridge, Klamath Mountains, California

Forest type	Median (year)	Range (year)
Psme–Pila–Pipo (n=9)	15	6.5–65
Psme (n=18)	15.5	5.5–116
Psme–Abco–Pila (n=15)	12	6–35.5
Abco–Psme (n=17)	19	4–87

n is the number of fire scar sites in each group. The fire scar record is for the period 1626–1992 and median values were similar (P=0.834, Kruskal–Wallis H-test) among forest groups.

west-facing slopes experienced more frequent fire than north- and east-facing slopes. However, there were no significant differences by slope position (lower, middle, and upper) in the median FRIs (P=0.328) (Table 4).

FRIs also varied by historical period (Table 5). Median FRIs were longer during the suppression (21.8 years), and shorter during the combined settlement (12.5 years) and presettlement (14.5 years) periods ($P<0.05$). We found no difference in the median FRIs between the settlement and presettlement period (P=0.205).

FRs for the entire study area were calculated by century and for the presettlement, settlement, and suppression periods. The average burn area was 350 (±217) ha (range 28–1340 ha) and areas >500 ha burned in 1630, 1636, 1646, 1660, 1671, 1692, 1783, 1848, 1853, 1887, 1890, 1898, 1917, 1924, 1933, and 1987. The FRs for the 17th and 18th centuries and combined presettlement period were similar at about 19 years, and the FR was shorter in the 19th century and during the settlement period (Table 6). Lower 19th century and settlement period FRs are due to the proportionally high number of large fires during these periods. FRs were longest during the suppression period (Table 6).

Table 4
Median and range of median FRIs (years) for sites by aspect and slope position for plots on Thompson Ridge, Klamath Mountains, California

Variable	*n*	Median (year)	Range (year)
Aspect			
North (315–44°)	7	15	8–54
East (45–134°)	24	16.5	5–116
South (135–224°)	11	8	4–35.5
West (225–314°)	18	13	5.5–63
Slope position			
Lower (665–969 m)	17	19	5–87
Middle (970–1269 m)	27	14	6.5–116
Upper (1270–1569 m)	16	10.5	4–37.5

n is the number of plots in each group. The fire scar record is for the period 1626–1992. Median values differed by slope aspect ($P<0.05$; Kruskall–Wallis *H*-test) but not by slope position ($P=0.328$).

Table 5
FRIs (year) by historical period for plots on Thompson Ridge, Klamath Mountains, California

Historical period	*n*	Median (year)	Range (year)
Presettlement (1626–1849)	48	14.5	6–116
Settlement (1850–1904)	40	12.5	4–200
Suppression (1905)–1992)	51	21.5	6–200

n is the number of plots with fire scar samples in each period. Median values were longer in the suppression period ($P<0.05$; Kruskal–Wallis *H*-test) but not in the presettlement or settlement periods.

Table 6
Fire rotations by period for study area on Thompson Ridge, Klamath Mountains, California

Time period	Fire rotation (year)
1626–1699	19.2
1700–1799	19.1
1800–1899	15.1
1900–1992	24.5
1850–1904	12.3
1905–1992	25.5 (31.7)[a]

[a]Without 1987 fire.

3.3. Age-classes and fire severity

Six groups were identified from clustering species age-classes (Fig. 3). Table 7 displays the average characteristics for the plots in each group in terms of age classes and number of fires recorded. At first glance there appears to be a relationship of increasing number of fires/age class and number of age classes. However, it is likely this may be, at least partly, an artifact of the influence of fire suppression. The long period without fires (1948–1987), recorded for all plots, is a greater proportion of the age of younger stands.

Group A is distinguished by the high density of white fir, with some Douglas-fir and incense cedar mostly <120 years old that established after fires in the late 19th and early 20th centuries (Table 7, Fig. 3). However, Douglas-fir, sugar pine, and ponderosa pine 140–420 years old are abundant and survived these recent fires. Ponderosa pine was found entirely on the west side of Thompson Ridge. As discussed below in more detail, the west side of the ridge was associated with higher severity fires than the east side, whereas western yew (*Taxus brevifolia*), a very fire-sensitive species, was found only adjacent to riparian areas on the east side of the ridge. This would suggest that some areas in Group A were influenced primarily by very low-severity fires. Fires in this group were probably of mixed severity.

Groups B and C are characterized by very dense populations of <100-year-old Douglas-fir, white fir, sugar pine, with some incense cedar and ponderosa pine that regenerated after moderately severe fires in

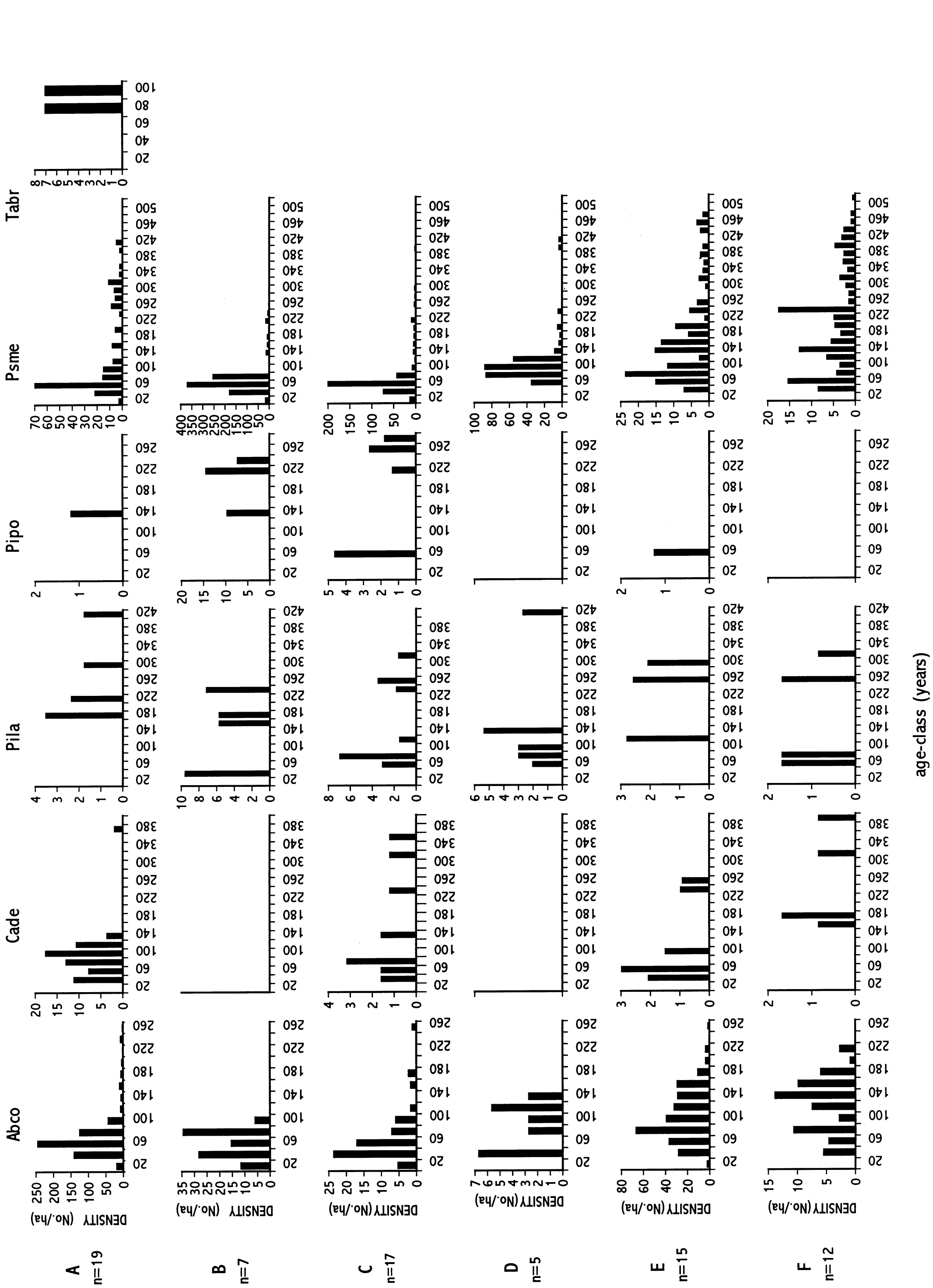

Fig. 3. Mean age–class distributions in 20-year classes for six species in the six groups (A, B, C, D, E, F) identified by cluster analysis; *n* is the number of plots. Species acronyms are the same as in Table 1. Note that only every other age-class is labeled and that the vertical scale is not the same on each graph.

Table 7
Age–class groups and fire history ordered by number of 60-year age-classes

Age–class group (n)	60-year age-classes (no.)	Mean no. fires	Fires/ age–class	Ages of younger trees (year)	Ages of older trees (year)
B(7)	2.8	7.4	2.7	<80	140–240
A(19)	3.3	12.3	3.7	<120	40–240
D(5)	3.4	12.8	3.8	80–140	140–420
C(17)	3.5	14.8	4.2	<100	140–400
E(15)	3.9	15.1	3.9	Multi-aged	220–480
F(12)	5.1	24.4	4.8	Multi-aged	260–520

n is the number of plots in each group.

the late 19th century and early 20th century fires (Table 7, Fig. 3). Relatively dense populations of 140–240-year-old Douglas-fir, sugar pine, and ponderosa pine survived these recent fires. However, Group B does not include trees >300 years that are found, at least sparingly, in all other groups.

Group D had dense populations of mixed Douglas-fir, white fir, and sugar pine 80–140-years-old that had established after moderate- and high-severity fires in the mid- to late-19th century. Some 140–420-years-old Douglas-fir and sugar pine survived repeated fires.

Groups E and F are characterized by multi-aged populations of Douglas-fir and white fir. Peaks in the age-class distributions of these two species suggest that fires of mixed low- and moderate-severity burned these plots several times during each of the last four centuries. Douglas-fir, sugar pine, and incense cedar 220–480-years-old survived repeated low-severity fires. The conditions characterized by these plots were more commonly found on east- and north-facing aspects or on lower topographic positions.

There was spatial variation in the cumulative proportions (1850–1950) of the study area burned at different levels of fire severity (Table 8). Stands experiencing only low-severity fires covered 59% of the study area, whereas 27% and 14% of the study area experienced moderate- and high-severity fires, respectively. The area of high (25%) and moderate (35%) severity burns was greater on the western side of Thompson Ridge than on the eastern side (high=6%, moderate=21%). Moreover, lower slope positions experienced mostly (75%) low-severity fires, whereas upper slopes experienced mostly (63%) moderate- and high-severity fires, with the mid-slope positions being intermediate.

Table 8
Percentage area burned between 1850 and 1950 at low (L), moderate (M), and high (H) severity in Thompson Ridge study area, Klamath Mountains, California

	East side	West side	Combined
Lower slopes			
L	91.8	52.3	75.3
M	5.2	23.7	12.9
H	3.0	2.4	11.8
Middle slopes			
L	69.0	43.7	58.3
M	22.7	33.3	27.2
H	8.3	23.0	14.5
Upper slopes			
L	64.3	0	37.3
M	33.8	28.0	31.5
H	1.9	72.0	31.2

4. Discussion

Gradients of temperature and potential soil moisture are primary controls on the distribution of tree species in the Klamath Mountains at landscape scales (Whittaker's, 1960; Sawyer and Thornburgh, 1977; Sawyer et al., 1977) and the spatial arrangement of species on Thompson Ridge reflects these controls. Mixtures of Douglas-fir, ponderosa pine, and sugar pine occur more frequently at lower elevation on south- and west-facing slopes, whereas mixtures of Douglas-fir, white fir, and sugar pine occupy cooler and more mesic sites at mid- and high-elevation on north- and east-facing slopes.

Fires burned frequently on Thompson Ridge between 1626 and 1992. Median FRIs of 12–19 years indicate that fire was an important process affecting late-successional stand development in Klamath Mountain forests. No significant trends or differences were found in the median FRIs with changes in species composition in our study area. Our plots burned with similar frequency despite compositional variation related to elevation and potential soil moisture. Different stand conditions at different slope positions had similar fire return intervals probably because of the long summer drought period and continuous nature of surface fuels. The long summer drought, characteristic of the Mediterranean climate, ensures that most of the landscape will be dry enough to support a fire by August or September despite microenvironmental differences. Additionally, continuous beds of dry forbs, grasses, hardwood leaves, and light conifer litter promote fire spread across slopes regardless of species composition. However, there was some spatial variation in FRIs – drier south- and west-facing slopes burned more frequently than other aspects.

Fire area data and FR estimates support our interpretation that fires spread among slopes and stand conditions. Average burned area was large (350 ha, 22% of study area) and more than 500 ha (32% of study area) burned in each of 17 years between 1626 and 1987. The FR for this period (1626–1987) is short at 19.5 years and shorter than for Douglas-fir-dominated forests elsewhere in the Pacific Northwest. The FR for moist Douglas-fir forests in the Cascades of western Washington is 434 years (Hemstrom and Franklin, 1982), and is 78–149 years in the Oregon Cascades (Teensma, 1987; Morrison and Swanson, 1990). FRs of 37–43 years for Douglas-fir-dominated forests in the nearby Oregon Caves National Monument in Oregon (Agee, 1991b) are most similar, but still longer than on Thompson Ridge.

Recent fires (1987, 1994) in or near our study area also suggest that fires spread easily across the landscape. In 1987, most of the study area burned as part of a complex of lightning-caused fires that eventually burned 97 466 ha in the Klamath National Forest (Biswell, 1989). In 1994, lightning ignited a fire that burned 11 000 ha just west of Thompson Ridge (USDA For. Ser., 1995). Other large fires have also burned in the 20th century in similar forests in the Siskiyou National Forest in Oregon (Atzet and Wheeler, 1982). Of course, current fuel beds may be different from those of past centuries but our historical data suggest that large spreading fires are characteristics of Klamath Mountain Douglas-fir-dominated forests.

Fire frequency varied by historical period. Fires were less frequent during the suppression than presettlement or settlement periods. Moreover, no difference in the median fire return interval was found during the presettlement and settlement periods on Thompson Ridge or in other nearby areas in the Klamath Mountains (Agee, 1991b; Wills and Stuart, 1994). This suggests that early settlers did not increase fire frequency beyond pre-Euroamerican levels. Moreover, fires were common even during the early portion of the suppression period. The median FRI during the suppression era (1905–1992) was only 21.8 years. Of the 14 years in which fires were recorded after 1905, four burned more than 500 ha. An abrupt decline in fire frequency did not occur on Thompson Ridge until after 1948. Apparently, despite policy, fire suppression did not become effective in the remote Klamath Mountains until after World War II when fire fighting became more mechanized (Pyne, 1982). Nearby studies also have similar fire scar records of 20th century fires (Agee, 1991b; Wills and Stuart, 1994). Similarly, remote forested areas in other parts of northern California burned frequently into the 1940s (e.g. Taylor, 1993; Skinner unpublished). In contrast, areas in the southern Sierra Nevada show a sharp decline of fire frequency in the late 19th or very early 20th centuries (e.g. Vankat, 1977; Vankat and Major, 1978; Kilgore and Taylor, 1979; Caprio and Swetnam, 1995).

On Thompson Ridge, fires burned frequently and contributed to multi-aged stand conditions. On average, our plots burned 14.6 times between 1626 and 1987 and had stems in four 60-year age-classes; 24% of the plots had stems in five to eight 60-year age-classes. Apparently, tree establishment can occur after fires of any severity that expose a mineral seed bed. Yet, the temporal patterns of age-classes suggest that recruitment into the canopy is mostly episodic and occurs after moderate- and higher-severity fires create openings in the canopy. Subsequently, cohorts that establish in these openings are probably thinned by lower-severity fires. Once Douglas-fir trees mature, their thick bark prevents injury by low-severity fires (Starker, 1934; Minore, 1979) and they are killed only by more severe fires. Thus, overlapping fires of mixed severity created complex stand structures at both the plot and landscape scale.

The mixed-severity fires that burned on Thompson Ridge created highly variable stand structures. Variation in fire severity is recognized as a potentially important source of landscape diversity (e.g., Stephenson et al., 1991; Christensen, 1993) that has been little studied in Pacific Northwest forests (e.g., Morrison and Swanson, 1990; Agee, 1993; Chappell and Agee, 1996). Douglas-fir forests in the central Oregon Cascades also burn with variable severity but the proportions affected by low-, moderate-, and high-severity fires are different than what we found on Thompson Ridge. In the Cascades, over a 100-year period, 37% of the fires burned at low severity, 37% at moderate severity, and 26% at high severity, whereas on Thompson Ridge proportions were 59% low, 27% moderate, and 14% high. More recent Klamath fires in 1987 (8403 ha; low=66%; moderate=22%, high=12%) (Weatherspoon and Skinner, 1995) and in 1994 (11 000 ha; low=73%, moderate=9%, high=18%) (USDA For. Ser., 1995) also burned mostly at low and moderate severity. Although the criteria for fire severity were not the same in each of these cases, they were similar. This suggests that a mixed fire regime of mostly low- and moderate-severity fires is typical of southern Douglas-fir-dominated forests.

Fire severity patterns varied with topographic position on Thompson Ridge and this spatial variation seems characteristic of forested landscapes in the Klamath Mountains. Weatherspoon and Skinner (1995) found that fire severity for the 1987 Klamath fires was positively correlated with elevation; however, this was not reported since management practices replaced elevation in their multivariate model of fire damage. The association of topographic position and fire severity is probably due to higher potential fire-line intensities on mid- and upper-slope positions in steep terrain (Rothermel, 1983).

We should note that the 1987 and 1994 fires compared here were unusual in modern times. They burned for extended times (weeks to months) under a variety of fire weather (burning) conditions (USDA For. Ser., 1995; Weatherspoon and Skinner, 1995). In contrast, most fires that have become large in recent years have burned for but a few days under extreme burning conditions and were then suppressed. This results in high-severity burns dominating the area of most modern fires (Skinner and Chang, 1996). We think that the variety of burning conditions experienced during the 1987 and 1994 fires is more typical of the range of weather conditions experienced by presettlement fires than most recent fires. The short period of effective fire suppression (generally <50 years) and the variety of burning conditions likely combined to produce severity patterns in these recent fire events that are similar to those of historical fires and unlike that found in most fires of recent years. In addition, the Dillon LSR Assessment (USDA For. Ser., 1996) concluded that most of the LSR still met standards and guidelines as functioning late-successional habitat (USDA-USDI, 1994) after the 1994 fire. This suggests that, in addition to using prescribed fires, wildfires burning under less than extreme weather conditions can be used for management in the Klamath Mountains when less than full-suppression strategies are called for by the new national fire management policies (USDA-USDI, 1995).

The cumulative effect of fire severity variation across slopes suggests that forests with late-successional characteristics (e.g. multi-layered canopy, high density of large diameter trees, snags, coarse woody debris) were more commonly found at lower slope positions as well as on north- and east-facing slopes. Upper slope positions as well as intermediate positions on south- and west-facing slopes were more likely to display a pattern of scattered, remnant, older trees and patches, exhibiting some late-successional characteristics within a coarser-grained pattern largely of younger stands. Managers designing activities to reduce the likelihood of large, severe fires (e.g. prescribed fires, thinning, fuelbreaks) while still providing for long-term, late-successional conditions in the LSRs may find it advantageous to pattern the severity and extent of treatments after these historical patterns of fire severity.

Fire regimes (i.e. return intervals, severity, fire rotations) in Klamath Douglas-fir-dominated forests were different from those in western Oregon and Washington. Fires were more frequent, generally less severe, and had shorter fire rotations. Development and dynamics of stand conditions were strongly influenced by this fire regime. Frequent fires of mixed low and moderate severity killed some overstory trees, initiated recruitment, and thinned or killed understory stems. These mixed-severity fires created multi-aged stands where tree establishment was associated with more severe fires that killed parts of the canopy. Large, severe fires were uncommon. In contrast, large stand replacing fires are more typical of northern Douglas-fir-dominated forests where Douglas-fir recruitment occurs mostly after severe fires. Subsequent stand development in the northern Douglas-fir-dominated forests may have been influenced by localized moderate- and low-severity fires that occasionally allow Douglas-fir recruitment. However, in the northern Douglas-fir-dominated forests the less severe fires usually just kill fire-intolerant trees and initiate new populations of them (Stewart, 1989).

Geographical variation in fire regimes within the Douglas-fir region has important implications for management of LSRs. Current standards and guidelines for LSRs come mostly from research in northern Douglas-fir forests, or southern forests where fire has been artificially excluded for decades. Definitions of late-successional conditions (e.g. canopy cover, coarse woody debris, snags) based on the current state of these forests may not appropriately describe late successional conditions in historically fire-prone southern Douglas-fir forests. Late successional conditions probably developed quite differently in northern areas where fire is less frequent or in southern areas where fire has been excluded compared to historic Douglas-fir forests of the Klamath Mountains that experienced frequent mixed severity fires.

Few forested regions have experienced fires as frequently and with such high variability in fire severity as those in the Klamath Mountains. This highly variable fire regime may be an important factor contributing to overall diversity in the Klamath Mountains (e.g., Martin and Sapsis, 1992). The Klamath Mountains harbor the most structurally and floristically diverse forests in the western United States (Whittaker's, 1960, 1961). Our data indicate that frequent, mixed-severity fires have been an integral process in the development of stands exhibiting structurally diverse, late-successional conditions on Thompson Ridge. Spatial variation in severity has been important in providing diversity in landscape patterns. Under the current fire regime (suppression) the influence of fire as a process has been dramatically reduced. One result appears to be the development of more homogeneous landscape patterns (Skinner, 1995). As the time since the last fire lengthens in these fire-prone forests, surface fuels and live ladder fuels will accumulate. Accordingly, the probability of large, severe fires will likely increase as has been the case throughout the western United States (e.g., Mutch and Cook, 1996). The use of fire will likely be an integral component of management plans that successfully provide long-term, late-successional conditions in the newly established late-successional reserves of the Klamath Mountains.

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