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The structure and dynamics of *Abies magnifica* forests in the southern Cascade Range, USA

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Abstract. *Abies magnifica* (Red fir) forests in the Cascade Range and Sierra Nevada of California are composed of groups, or patches, of even-sized individuals that form structurally complex stands. Patches may be even-aged, resulting from synchronous post-disturbance establishment, or multi-aged, reflecting continuous recruitment of seedlings moderately tolerant of shade. We analyze the population structure (i.e. age, size, and spatial patterning) of *A. magnifica*, and associated *A. concolor*, White fir, and reconstruct the disturbance history of two mature to old-growth *A. magnifica* forests in order to determine the relationship between disturbance and forest structure.

Within both stands examined, the distributions of *A. magnifica* seedlings, saplings, and small understory trees were clumped, with clump sizes corresponding to the area of canopy gaps. Gaps were created by frequent wildfire (mean fire return interval of 41 yr) and by windstorms. Severe fire initiated mass establishment of *Abies magnifica*, whereas gaps created by windthrow released already established individuals. Low intensity fire stimulated little recruitment, but Red fir established continuously during fire-free intervals. Thus, the complex age and structures of Red fir forests reflect both episodic and continuous recruitment, as determined by the type and severity of natural disturbance.

Keywords: *Abies concolor*; Age structure; Canopy gap; Disturbance; Fire; Red fir; Regeneration; Size structure; Spatial pattern; White fir; Windthrow.

Nomenclature: Munz & Keck (1973).

Introduction

Forest stands are commonly formed of groups, or patches, of trees in different temporal phases of development after disturbance (e.g. Watt 1947; Whitmore 1982; Pickett & White 1985). Many tree species regenerate after particular types (e.g. fire or treefall) or sizes of gap-initiating disturbance while others establish beneath intact forest canopies. Where forests are composed of diverse assemblages of tree species with distinct life histories or responses to disturbance, patterns of species' abundance may be used to reconstruct disturbance history (e.g. Heinselman 1973; Henry & Swan 1974; Marks 1974; Oliver & Stephens 1977; Foster 1988). In some forests, however, tree species have multiple modes of regeneration and may establish abundantly after various types or sizes of disturbance (e.g. *Pinus contorta*, Despain 1983; *Tsuga heterophylla*, Stewart 1986a). In these systems, the population structure of forest patches, rather than their composition, better reflects the influence of disturbance on stand development.

In the upper montane zone of the southern Cascade Range and Sierra Nevada of California, Red fir (*Abies magnifica*) is the dominant canopy and understory tree; few other species are important (Oosting & Billings 1943; Barbour & Woodward 1985). Within these mature and old-growth (> 200 yr old) stands, populations of similar-sized *A. magnifica* are distributed in groups, or patches, forming complex forest mosaics. Individual patches may range in size from hundreds of sq. m to tens of ha (Hallin 1957; Gordon 1970, 1978; Vankat & Major 1978). Spatial patterning is thought to reflect the establishment and growth of Red fir in canopy openings created by fire, windthrow, or insect attack (Oosting & Billings 1943; Hallin 1957; Gordon 1970, 1979; Parker 1986; Pitcher 1987). However, the role of natural disturbance in the patch structure and dynamics of these forests has been little studied (e.g. Pitcher 1987). Moreover, *A. magnifica* is moderately tolerant of shade; seedlings are often aggregated within shadier, cooler, understory microsites (Ustin et al. 1984; Selter, Pitts & Barbour 1986). Thus, Red fir exhibits multiple modes of regeneration.

Knowledge of the age structure of these patches is central to an understanding of the importance of disturbance in the development of these forests. In this paper, we present the results of a detailed stem analysis of two of two mature to old-growth forests in the southern Cascade Range of California. We examine the size, age, and horizontal structure of tree populations and reconstruct disturbance history to determine how the structure and dynamics of Red fir forests are influenced by the size, intensity, and spatial and temporal distribution of natural disturbance.

Study area

Our study was conducted within the Swain Mountain Experimental Forest in northeastern California (40° 26' N, 121° 7' W), at the southern tip of the Cascade Range. Two cover types of true fir species, Red fir, *Abies magnifica,* and White fir, *A. concolor*, dominate the Forest: mixed stands at elevations of 1750-1900 m and pure stands of *A. magnifica* at elevations above 1900 m (Gordon 1970). Slopes are gentle (5-15°) and soils are deep (1.0-2.5 m) and well-drained, derived from vesicular andesites (Gordon 1970). Annual precipitation averages 1100 mm, 80% falling as snow from October through May (Gordon 1979). Maximum winter snowpack is ca. 2.5 m, but may be deeper in years of high snowfall (Gordon 1979).

Two forest stands (see Table 1 for a general description) were chosen for intensive study based on the following criteria: (1) homogeneity of site and structural characteristics; (2) canopy dominance by *A. magnifica*; (3) absence of recent human disturbance; and (4) presence of trees > 1.0 m diameter at breast height (dbh) within a multi-layered canopy suggesting old-growth forest conditions (i.e. > 200 yr old). We established a 1.0 ha (100m × 100 m) plot (Plot 1) in a stand dominated by large (65 - 105 cm dbh) *A. magnifica*, interspersed with patches of *A. magnifica* seedlings, saplings, and small (5-15 cm) trees (Fig. 1). A second, 0.48 ha (60m × 80 m) plot (Plot 2) was established in a stand typified by scattered, emergent Red fir > 1.0 m dbh, with a dense understory of small to intermediate (15-30 cm dbh) sized Red and White fir (Fig. 2).

Typical of most *A. magnifica* forests (e.g. Oosting & Billings 1943), the understory in both plots was floristically depauperate, supporting a low cover of graminoids (*e.g. Carex rossii* and *Stipa californica*); herbs (*Chimaphila menziesii*, *Corallorhiza maculata*, *Hieracium albiflorum, Pyrola picta,* and *Viola purpurea*); and shrubs (*Ceanothus cordulatus*, *Castanopsis sempervirens*, and *Ribes* spp.).

Methods

Size and age structure

We constructed a 5 x 5 m grid within each plot and mapped the position and recorded the diameter of each live and dead tree ≥ 5.0 cm dbh. We also tallied the numbers of seedlings (0.2-1.4 m tall) and saplings (> 1.4 m tall, < 5.0 cm dbh) within each 5 × 5 m quadrat. Each tree was assigned to one of five relative height-classes: suppressed, intermediate, lower main canopy, upper

Fig. 1. Plot 1, Swain Mountain Experimental Forest, California, with large (> 65 cm dbh) Red fir, *Abies magnifica* (background) and a patch of seedlings, saplings and small trees with a gap of ca. 900 m^2.

Fig. 2. Plot 2, Swain Mountain Experimental Forest, California, with scattered, large (>90 cm dbh) Red and White fir, *Abies magnifica* and *A. concolor*, and a dense understory of small (5-20 cm dbh) individuals.

main canopy, or emergent. We also recorded the substrate (i.e. log or mineral soil) upon which each seedling and sapling established.

Because stand history may be interpreted from population size structure only if there is a strong relationship between the diameter and age of trees, we cored all individuals ≥ 5.0 cm dbh with an increment borer. Trees < 80 cm dbh were cored at a height of 30 cm; larger trees were cored at 1.0 m. Cores were mounted, sanded, and annual growth rings were counted using a binocular microscope. The ages of individuals > 90 cm dbh (5% of all cored trees) were estimated in the following manner because increment borers did not reach the pith.

First, we developed a regression of core length (distance from pith to inside bark) vs. diameter (dbh) for trees with complete cores in Plot 1 ($r^2 = 0.96$).

Second, the number of rings per cm was counted on 11 stump sections (from adjacent harvested stands) beginning at the pith and ending at 25 cm. We then calculated the average number of years per cm (mean and s.d. of mean, 3.9 ± 2.7 rings/cm) .

Third, the radius of each unaged tree was predicted using the core length-dbh regression and the difference between the predicted and actual radius was calculated. Finally, the number of years corresponding to the difference between the predicted and actual radius (based on the relationship derived from stump sections) was added to the age of each incomplete core (2.3% of all cored trees). A minimum tree age was used when the actual radius was greater than that predicted (2.7% of all trees). Ages were not obtained for 4.6% of cored trees due to rot or damage to cores. Because *A. magnifica* seedlings and saplings have highly variable growth rates (Gordon 1970, 1979, Pitcher 1987) depending on canopy conditions (i.e. open or closed), we did not adjust tree ages to a common coring height. Ages reported for all trees are ages at coring height.

Canopy density

Two types of data on the density of the forest canopy were collected in each plot. First, we estimated average understory light conditions by taking hemispherical photographs of the forest canopy from 16-20 systematically placed points in each plot. Percent sky cover was calculated from black and white film negatives using a light sensor calibrated to the density of clear sky and closed tree canopy (Chan et al. 1986). Second, the canopy above each 5m × 5m quadrat was classified into one of three cover classes based in the cover of intermediate or taller trees: gap (<33% cover), intermediate (33-66% cover), or closed (>66% cover) (e.g. Stewart 1986b, 1988, 1989). The second measure of canopy density has been used by others to study the distribution of smaller and younger stems with respect to canopy openings in other coniferous forests of the Pacific Northwest (Stewart 1986b, 1988, 1989).

Spatial patterns

We examined three features of the spatial distribution of Red and White fir size and age classes: the type, intensity, and scale of pattern. The type of spatial pattern was identified using Morisita's (1959) index:

$$I\delta = q \sum_{i=1}^{q} n_i \cdot \ (n_i - 1)/N \cdot \ (N - 1) \tag{1}$$

where q = number of 5m × 5m quadrats, n_i = number of individuals in the ith quadrant, and N = total number of individuals in all quadrats. Morisita's index, I_δ equals 1.0 when a population is randomly distributed, $I_\delta > 1.0$ if a population is clumped, and $I_\delta < 1.0$ if a population is regularly distributed. Each index value was tested with an F- statistic to determine if it varied significantly ($p < 0.01$) from that of a random distribution (Morisita 1959). The greater the index value for a clumped distribution the greater the intensity of clumping.

Scale of pattern (expressed in m^2) was estimated by computing Morisita's I_δ index for quadrats of varying size. Indices were calculated for square quadrats of successively larger size, whenever possible, to avoid fluctuations in I_δ due to block shape (Pielou 1977). When square quadrats were not possible, i.e. at larger block sizes, rectangular units of equivalent areas were used. I_δ values were computed only for populations with > 20 individuals because the index varies erratically when N is small.

Disturbance history

We reconstructed the disturbance history of each plot using three types of data: (1) dates of fires derived from fire-scarred trees; (2) radial growth patterns of individual trees; and (3) age structures of tree populations. Dates of fires in or adjacent to each plot were identified from: (1) scars in cores extracted from fire-scarred trees; (2) scars in stem cross-sections (wedges) cut from live, fire scarred trees adjacent to the plot (Plot 2 only); (3) scars in stump cross-sections removed from adjacent harvested stands; and 4) dates of growth declines or releases in fire-scarred and adjacent, non-scarred trees. Fires were dated by counting the number of annual growth rings from the outside ring to the fire scar (cf. Arno & Sneck 1977; Barrett & Arno 1988).

Disturbances are frequently recorded in the radial growth patterns of trees. If a disturbance severely damages a tree, its radial growth may decrease dramatically. The date of disturbance may correspond to the year of sudden decline in growth (e.g. Arno & Sneck 1977). Conversely, disturbances may improve the growing conditions of individuals by killing neighboring trees. Thus, sudden increases in growth may roughly indicate the date of disturbance (Lorimer 1984). For cored trees in each plot, we dated all growth releases (200% increase in radial growth for 5 yr compared to the previous 5 yr) and generated a time-frequency distribution of releases - an indicator of the frequency and magnitude of disturbance to the forest canopy (sensu Lorimer 1984). We dated suppressions (200% decrease in radial growth for 5 yr compared to the previous 5 yr) and display them in a similar manner.

Results

Stand characteristics and size structure

The composition, size-class distribution, and basal area of tree populations differed markedly between plots. Total basal area of Plot 1 was 36% higher than that of Plot 2, but densities of *Abies magnifica* and *A. concolor* were two to four times as great in Plot 2 (Table 1). The high basal area in Plot 1 reflects the abundance of large trees (> 65 cm dbh) in the upper main canopy height-class. White fir comprised a greater proportion of individuals and total basal area in Plot 2 than in Plot 1 due to numerous intermediate and suppressed height-class stems and to the presence of several, large emergent individuals (Table 1).

Red and White fir occurred over a wide range of height- and diameter-classes in each plot (Table 1, Fig. 3). Diameter-class distributions for both species were significantly different ($p < 0.001$, Kolmogorov- Smirnov two-sample test) within and between plots. Large (> 45 cm dbh) individuals were more common in Plot 1 than in Plot 2, but small (< 35 cm dbh) stems (except for saplings) were more common in Plot 2 (Fig. 3). Seedlings and saplings of both species were present in each stand, but *Abies magnifica* was more abundant (Table 2). Most seedlings established within quadrats which were classified as gaps (>70%) and occurred on mineral soil (> 99%).

Dead, standing stems (89% Red fir) were more abundant in Plot 2 than in Plot 1 and they were concentrated in the smallest diameter-classes in both plots (Fig. 4). Dead and down, 10-15 cm dbh stems were common in Plot 2, indicating recent thinning among small size-classes. Canopy characteristics also differed between sites. At a height of 1.8 m, percent open sky was significantly greater ($p < 0.001$) in Plot 2 than in Plot 1 (Table 1). This pattern is consistent with the greater frequency of gap quadrats in Plot 2 (55%) than in Plot 1 (42%) (Table 1) and with the greater range of continuous area beneath 5 × 5 m blocks classified as canopy gaps in Plot 2 (25-775 m^2) than in Plot 1 (25-650 m^2).

Table 1. Site and stand characteristics for Plots 1 and 2, Swain Mountain Experimental Forest, California. Densities are for trees ≥ 5.0 cm dbh; *mag* = Red fir, *Abies magnifica*, *con* = White fir, *A. concolor*. For sky cover, *n* is the number of photographs analyzed.

Site characteristics

	Plot 1	Plot 2
Elevation (m)	1970	1910
Slope (°)	5	9
Aspect (°)	326	88
Plot dimension (m)	100 ×100	60 × 80

Forest structure and composition

	Plot 1		Plot 2	
	mag	*con*	*mag*	*con*
Basal area (m^2ha^{-1})	86.4	11.7	53.2	19.1
Density (number ha^{-1})				
Emergent	0	0	17	6
Upper main canopy	104	9	17	2
Lower main canopy	24	2	19	2
Intermediate	37	11	92	31
Suppressed	66	41	752	218
Total	431	63	897	259

Forest canopy characteristics

	Plot 1	Plot 2
	$n = 20$	$n = 16$
Mean adjusted % open sky cover (± 1 SE)	45.5 (1.24)	53.5 (1.69)
No. of 5 × 5 m quadrats per canopy cover class		
Gap (< 33% cover)	169	105
Intermediate (33-66%)	121	42
Closed (>66%)	110	45

Size-age relationships

The relationship between tree diameter (dbh) and age was poor for Red and White fir on both plots. Coefficients of determination (r^2) were 0.67 and 0.48 for Red fir, and 0.54 and 0.47 for White fir in Plots 1 and 2, respectively.

Age structure

Plots 1 and 2 exhibited distinctly different age-class distributions. In Plot 1, the age structure of *Abies magnifica* was bimodal with modes in the 75-84 and 155-164 yr

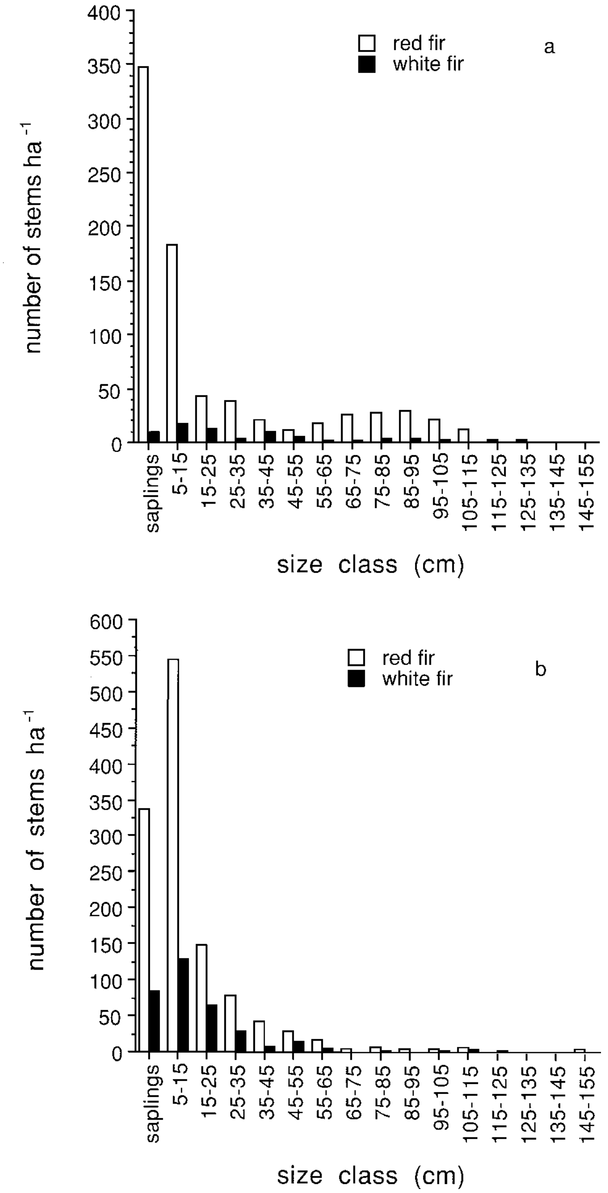

Fig. 3. Size-class distributions of *Abies magnifica* and *A. concolor* in (a) Plot 1 and (b) Plot 2, Swain Mountain Experimental Forest, California. Saplings are >1.4 m tall and < 5.0 cm dbh.

age-classes (Fig. 5a). The form of the age-class distribution of *A. concolor* in Plot 1 was similar to that of Red fir, but it exhibited an additional, small peak between 115 and 124 yr. In Plot 2, Red and White fir had unimodal age-class distributions with most individuals (89%) <110 yr old (Fig. 5b). Maximum tree age in Plot 2 (322 yr) was greater than in Plot 1 (224 yr).

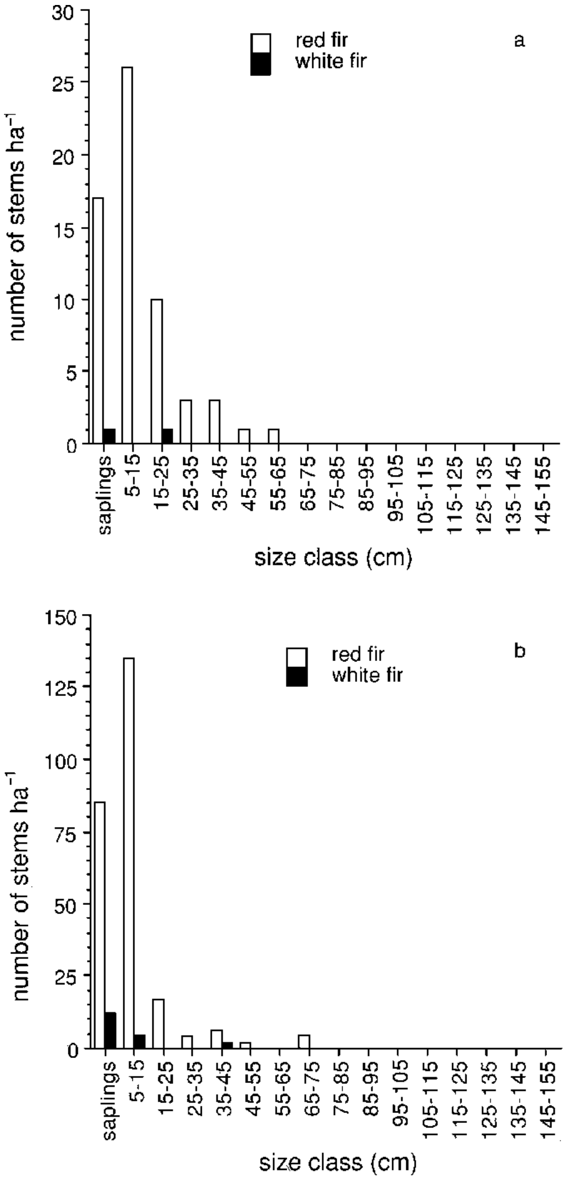

Fig. 4. Size-class distributions of dead standing stems in (a) Plot 1 and (b) Plot 2, Swain Mountain Experimental Forest, California.

Spatial patterns

Overall, both *Abies* populations displayed clumped distributions. In Plot 1, seedlings and saplings were most intensely clumped in block sizes of 25-400 m^2 (Table 3), corresponding with the range of sizes of continuous canopy gaps (see above). The clumped distributions of seedlings and saplings at larger block sizes (i.e. 5000 m^2) reflect their concentration in a large canopy gap in one

Table 2. Number (ha^{-1}) of seedlings (0.2 m - 1.4 m tall) and saplings (> 1.4 m tall and < 5.0 cm dbh) in Plots 1 and 2, Swain Mountain Experimental Forest, California within quadrats classified by canopy cover- class (Gap = < 33% canopy cover; Intermediate (Inter) = 33-66% canopy cover; Closed = >66% canopy cover).

		Gap	Inter	Closed
Plot 1				
Seedlings	*Abies magnifica*	516	176	36
	A. concolor	7	2	1
Saplings	*Abies magnifica*	251	89	8
	A. concolor	3	5	1
Plot 2				
Seedlings	*Abies magnifica*	242	27	23
	A. concolor	48	33	23
Saplings	*Abies magnifica*	219	79	40
	A. concolor	42	25	17

corner of the plot.

Small (5-15 cm dbh) Red fir were clumped at scales similar to those of seedlings and saplings, but less strongly so (Table 3). Red fir of 15-55 cm dbh were clustered at block sizes of 100-900 m^2, but less intensely so at larger block sizes; Red fir > 55 cm dbh were randomly distributed. White fir of 15-55 cm dbh were clumped at all block sizes and were concentrated in the western portion of the plot.

The spatial patterns of age-classes in Plot 1, were generally similar to those of size-classes. Trees ≤ 105 yr old were intensely clumped in block sizes of 25-400 m^2 and moderately so in sizes up to 5000 m^2 (Table 3). Trees 106-153 yr old were randomly distributed at nearly all spatial scales. The oldest trees (≥ 154 yr) were clumped at block sizes of 25 m^2, but were randomly distributed in larger blocks.

Spatial patterns of tree populations in Plot 2 resembled those in Plot 1. Red and White fir seedlings, saplings, and small (5-15 cm dbh) trees were intensely clumped in blocks ranging in size from 25 to ca. 225-900 m^2, and less so at larger scales (Table 3). Clumps of White fir seedlings and saplings were limited to a smaller range of block sizes than those of Red fir. Red fir of 15-55 cm dbh were clumped at a range of scales, but similar sized White fir were randomly distributed (except in blocks of 900 m^2). Red fir >55 cm dbh were uniformly distributed in 25 m^2 blocks but were randomly distributed at larger scales.

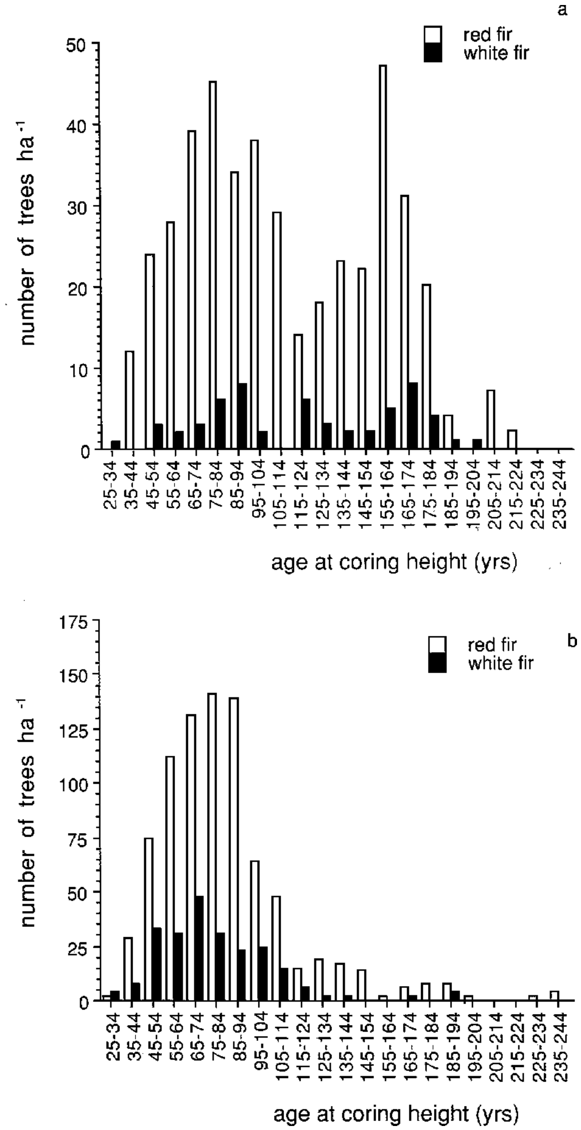

Fig. 5. Age-class distributions of *Abies magnifica* and *A. concolor* in (a) Plot 1 and (b) Plot 2, Swain Mountain Experimental Forest, California. Not shown are three red fir of 255, 293 and 322 yr in Plot 2.

Young (<110 yr) and intermediate (111-165 yr) aged stems in Plot 2 were clumped at block sizes up to 2400 m^2 (Table 3) with clumping at larger scales due to concentrations of these age-classes in opposite portions of the stand. The few old (>165 yr) trees were randomly distributed throughout the plot (Table 3).

Evidence of disturbance

Fire and wind have been common agents of disturbance in these forests. In Plot 1, for example, dates of fire scars and radial growth patterns of trees suggest that fires

Table 3. Values of Morisita's (1959) index (I_δ) for selected size-classes of Red and White fir, *Abies magnifica* (*mag*) and *A. concolor* (*con*, in parentheses) and for age-classes of both species combined, for Plots 1 and 2, Swain Mountain Experimental Forest, California. Index values were computed only for populations with > 20 individuals. There were <20 white fir seedlings and saplings in Plot 1 so these individuals were combined with red fir for analysis. Values significantly > 1.0 (*F*-test, $p < 0.01$) represent clumped distributions and are in roman, values not significantly > 1.0 are in italics.

Plot 1

Size (m^2)	Size-class (dbh)						Age-class (yr)		
	Seedlings	Saplings	5-15 cm	15-55 cm		>55 cm	<105	106-153	>154
	mag	*mag*	*mag*	*mag*	*(con)*	*mag*	*mag*	*mag*	*mag*
25	3.98	4.46	3.50	0.98	(5.16)	*1.09*	3.16	*1.21*	1.61
100	2.76	3.08	2.66	1.34	(3.22)	*1.02*	2.36	*1.05*	*1.17*
225	2.03	2.50	1.90	1.47	(2.37)	*0.95*	1.91	*1.20*	*1.12*
400	1.69	1.73	1.52	1.54	(2.79)	*1.06*	1.48	*1.06*	*1.09*
625	1.43	1.47	1.46	1.52	(2.78)	*1.03*	1.27	*1.00*	*1.05*
900	1.37	1.43	1.27	1.30	(1.91)	*0.97*	1.26	1.17	*1.03*
1225	1.19	1.24	1.31	*1.09*	(1.95)	*0.99*	1.16	*1.07*	*1.03*
1600	1.21	1.22	*1.06*	1.18	(2.00)	*0.99*	1.15	*1.03*	*1.02*
2025	1.27	1.26	*1.06*	1.25	(1.82)	0.98	1.17	1.04	1.00
2500	1.30	1.20	*1.06*	1.24	(1.85)	*1.01*	1.15	*1.03*	*0.98*
3025	1.23	1.17	*1.04*	1.15	(1.79)	*1.02*	1.11	*1.04*	*0.99*
3500	1.23	1.15	1.06	1.14	(1.80)	*1.01*	1.11	*1.02*	*0.99*
4250	1.25	1.12	1.11	1.17	(1.83)	*1.01*	1.10	*1.03*	*0.99*
5000	1.25	1.11	1.07	1.18	(1.75)	*1.02*	1.09	*1.03*	*0.99*

Plot 2

	Seedlings		Saplings		5-15 cm		15-55 cm		>55 cm	<110	111-165	>165
	mag	*(con)*	*mag*	*(con)*	*mag*	*(con)*	*mag*	*(con)*	*mag*	*mag*	*mag*	*mag*
25	7.80	(5.95)	3.60	(3.69)	2.09	(2.70)	*1.12*	(*0.72*)	*0.00*	2.09	2.38	*0.91*
100	3.89	(3.53)	2.45	(2.46)	1.71	(2.46)	1.19	(1.19)	*0.68*	1.73	1.87	*0.91*
225	2.68	(2.05)	1.90	(2.04)	1.30	(2.02)	1.15	(1.32)	*0.97*	1.62	1.69	*1.08*
400	1.72	(1.73)	1.44	(1.92)	1.30	(2.02)	1.21	(1.31)	*0.68*	1.44	1.64	*0.85*
625	1.71	(1.46)	1.35	(1.67)	1.19	(1.48)	*1.08*	(*1.18*)	*0.77*	1.32	1.44	*0.92*
900	1.53	(*1.19*)	1.25	(1.54)	1.10	(1.53)	*1.06*	(1.27)	*0.86*	1.27	1.32	*0.91*
1225	1.09	(*1.16*)	1.10	(*1.20*)	1.06	(1.27)	1.09	(*1.03*)	*0.82*	1.11	1.57	*1.06*
1600	1.18	(*1.14*)	1.09	(*1.03*)	1.04	(1.28)	1.15	(*1.05*)	*0.93*	1.09	1.55	*1.06*
2000	1.11	(*1.05*)	*1.02*	(*1.04*)	*1.01*	(1.27)	1.16	(*1.06*)	*0.93*	1.06	1.54	*1.14*
2400	1.07	(*1.04*)	*1.00*	(*1.03*)	*1.01*	(1.31)	1.17	(*1.01*)	*0.95*	1.06	1.49	*1.06*

occurred ca. 1924, 1907, 1882, and 1830 (Table 4). These dates result in a mean fire-free interval of 40 yr (range of 17-65 yr). The presence of trees in most age-classes indicates that these fires were of moderate severity and that fire-induced mortality and post-fire establishment were light and patchy. The peaks in growth releases and suppressions between 1882 and 1890 (Fig. 6a) reflect increased growth due to decreased competition and reduced growth due to injury, respectively, after the ca. 1882 fire. The large number of stems ca. 160-200 yr old, the paucity of older individuals, and a maximum age of 248 yr on five stumps adjacent to the plot, suggest that the forest originated after crown fire in the early- to mid-1700s.

Fires occurred with similar frequency in Plot 2. Fire scars and radial growth patterns indicate that fires occurred ca. 1924, 1879, 1874, and 1822, resulting in a mean fire-free interval of 42 yr (range of 5- 65 yr) (Table 4; Fig. 6b). The time of initiation of Red and White fir populations (Fig. 5b), the abundance of subsequent establishment, and the peak in growth releases (Fig. 6b) suggest that the 1874/1879 fires were severe, killing

Table 4. Dates, types, and sources of evidence of disturbance in Plots 1 and 2, Swain Mountain Experimental Forest, California.

Date	Type	Source of evidence
Plot 1		
Ca. 1973	Windstorm	Peak in frequency of growth releases between 1974 and 1976 (Fig. 6a);
1962	Windstorm	Historical record (Lynott & Cramer 1966); peak in frequency of growth releases and suppressions in 1963 (Fig. 6a);
Ca. 1924	Fire	Fire scars in two stumps adjacent to plot; suppression in one fire-scarred tree; peak in frequency of growth suppressions (Fig. 6a);
Ca. 1907	Fire	Fire scars in two stumps adjacent to plot;
Ca. 1882	Fire	Growth suppression in one fire scarred tree; peak in frequency of growth suppressions between 1885 and 1887; peak in frequency of growth releases between 1888 and 1890 (Fig. 6a);
Ca. 1830	Fire	Scars in cores of three trees.
Plot 2		
Ca. 1982	Windstorm	Peak in frequency of growth releases after 1982 (Fig. 6b);
1962	Windstorm	Historical record (Lynott & Cramer 1966); peak in frequency of growth releases and suppressions in 1963 (Fig. 6b);
Ca. 1924	Fire	Fire scar in one live tree adjacent to plot; peak in frequency of growth suppressions (Fig. 6b);
Ca. 1879	Fire	Fire scars in two live trees adjacent to plot; peak in frequency of growth releases after 1879 (Fig. 6b);
Ca. 1874	Fire	Fire scar in one live tree adjacent to plot; high frequency of growth releases after 1879 (Fig. 6b);
Ca. 1822	Fire	Three fire scars in stumps adjacent to plot; suppression in one fire-scarred tree within plot.

many trees.

Windstorms have also influenced the structure and dynamics of these forests. The 1962 Columbus Day storm blew down patches of main canopy stems in Plot 1, resulting in peaks in the frequency of releases and suppressions the following growing season (Fig. 6a). Frequent releases in 1976 also suggest significant wind-induced mortality in the early 1970s. In Plot 2, proportionally fewer trees were released after the 1962 windstorm (Fig. 6b), suggesting less extensive blowdown on that site. A peak in releases during 1983 probably stems from a more recent windstorm, ca. 1982. It is unclear if growth releases prior to 1880 (Fig. 6b) reflect frequent disturbance or are an artifact of sampling due to the few trees >110 yr old in which disturbances could be recorded.

Discussion

Populations of Red and White fir, *Abies magnifica* and *A. concolor*, on Swain Mountain exhibited size structures similar to those of mixed species stands elsewhere in the Cascade Range and in the Sierra Nevada (e.g. Oosting & Billings 1943; Parker 1986). Diameter- and age-class distributions indicate that both species are tolerant of moderate shade and can persist beneath the forest canopy. For Red fir, this pattern is consistent with the interpretation that it is a self-perpetuating, climax species on modal sites throughout its range (Oosting & Billings 1943; Barbour & Woodward 1985). However, poor diameter-age relationships for both Red and White fir indicate that only weak inferences about stand dynamics can be made from the size structure of populations, a problem noted for conifers elsewhere in the Cascade Range (e.g. Stewart 1986a).

The patchy distribution of tree size classes in Red fir forests has been attributed to gap-phase regeneration (e.g. Oosting & Billings 1943; Hallin 1957; Gordon 1978; Barbour & Woodward 1985). In our plots, seedlings, saplings, and small trees were highly clumped at spatial scales similar to the sizes of canopy gaps. In contrast, others (e.g. Barbour & Woodward 1985; Parker 1986) have found no correlation between the abundance of Red fir seedlings and characteristics of the forest canopy. Variation in site conditions, stand structure, and/or sampling methods may explain these differences. Nevertheless, the spatial distribution of natural regeneration on Swain Mountain supports the widespread correspondence between overstory and understory structure in coniferous forests of the Pacific Northwest (Stewart 1986a,b; 1988; 1989; Spies, Franklin & Klopsch 1990) and in other temperate forests (e.g. Williamson 1975; Veblen et al. 1981; Nakashizuka 1984; Veblen 1985; Taylor & Qin 1988a,b).

Fires and windstorms were the principal agents of disturbance in our stands. Plot 1 experienced four low intensity fires during the last 160 yr. Although these fires undoubtedly initiated recruitment, numerous understory trees also survived, resulting in patches with wide ranges of ages. Many individuals were also released by the 1962 Columbus Day windstorm which blew down forest stands

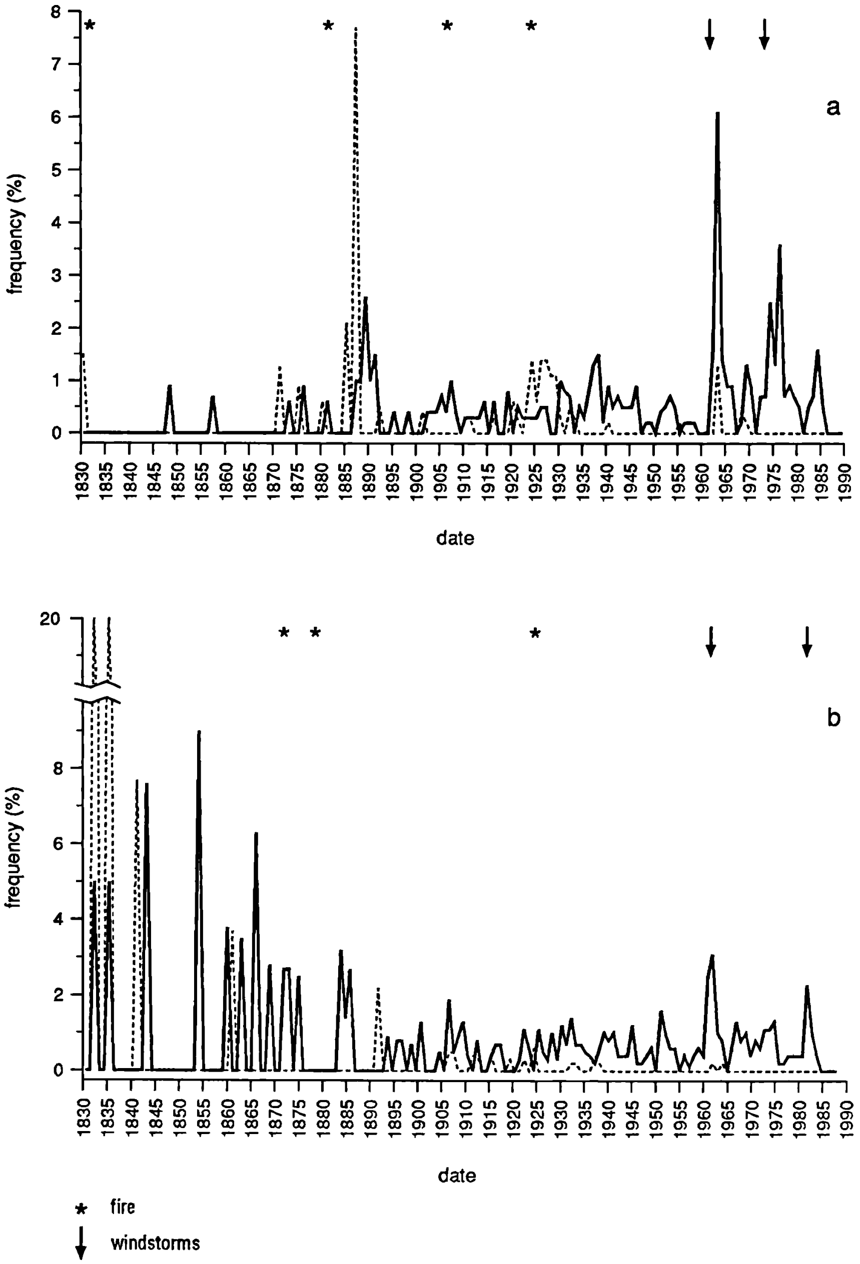

Fig. 6. Frequency (%) of aged trees exhibiting growth releases (solid) and suppressions (dashed) (sensu Lorimer 1984) in (a) Plot 1 and (b) Plot 2, Swain Mountain Experimental Forest, California.

throughout the Pacific Northwest (Lynott & Cramer 1966). Gaps created by the storm were probably colonized by Red and White fir, but because we did not census individuals <20 cm tall we cannot assess the timing and magnitude of recent establishment. In contrast to its role in Plot 1, the Columbus Day storm had little effect on stand dynamics in Plot 2. Because there were few large individuals susceptible to windthrow, blowdown was minimal and fewer understory stems were released. However, fire had a profound influence in the stand.

The 1874/1879 fires were severe and probably killed most trees. Red and White fir established immediately, but despite survival of on-site trees, restocking of the stand continued for at least 50 yr. Delayed recruitment after fire has been reported for Red fir forests in the Sierra Nevada (e.g. 50+ yr, Pitcher 1987) and for Douglas-fir (*Pseudotsuga menziesii*) stands in the Cascade Range (e.g. 100+ yr, Franklin & Hemstrom 1981; Means 1982) and is probably common in the montane and subalpine zones of both regions. Factors limiting establishment include harsh environmental conditions (e.g. temperature, water stress) on open sites (Gordon 1970; Ustin et al. 1984; Selter, Pitts & Barbour 1986) and the effects of competitors (e.g. *Arctostaphylos*, *Ceanothus*, *Ribes*) in rapidly developing shrub fields (Fowells 1965; Gordon 1970).

There are few data on fire history in Red fir forests with which to compare our results. Based on three stands from the southern Sierra Nevada, Pitcher (1987) reports a longer fire-free interval (mean of 65 yr, range of 5-126 yr) than in our southern Cascade forests on Swain Mountain (mean of 41 yr). However in both areas, forests did not burn after initiation of fire suppression earlier in the century. Several factors make it difficult to determine whether these represent true difference in fire regime. First, determinations of fire frequency are highly sensitive to fire severity and to stand structure. For example, low intensity fires may not scar trees, whereas severe fires may kill old individuals that record long histories of fire. Second, the presence of White fir in our stands suggests that they lie within the lower ecotone of the Red fir zone. Fire frequencies in lower elevation, mixed conifer forests with abundant White fir range from 9-42 yr (e.g. Kilgore & Taylor 1979; McNeil & Zobel 1980; Barbour 1988). Because fire frequency generally decreases with elevation, fire-free intervals in higher elevation, monospecific stands of Red fir on Swain Mountain may be more similar to those reported by Pitcher (1987).

During this century, widespread suppression of natural fire has undoubtedly altered the structure and dynamics of lower elevation, mixed conifer forests (Vale 1977; Kilgore & Taylor 1979; Vankat & Major 1978). Fire-free intervals during the 20th century have been greater than those of previous centuries and fire sensitive species have generally increased in density. On some sites, increased densities of Red fir have been attributed to fire suppression (e.g. Reynolds 1959; Vankat & Major 1978), but elsewhere, densities have not changed (e.g. Pitcher 1987). Fire suppression became effective in Lassen National Forest (which encompasses Swain Mountain) in the mid 1930s (Taylor 1990); fire has been absent from our plots since 1924. As a consequence, densities of smaller, younger trees may be increasing. Yet the establishment and mortality of seedlings are affected by factors other than disturbance (e.g. seed availability, precipitation, duration of snowpack). Because we did not age seedlings or saplings, we cannot determine if current rates of establishment exceed those of previous periods with more natural fire regimes. Nevertheless, we expect the fire-free interval on Swain Mountain to continue to lengthen, leading to increases in Red fir densities and to changes in the vertical structure of forests, particularly along the lower ecotone.

The role of catastrophic fire in initiating Red fir forests is implicitly suggested by descriptions of stands dominated by large, even-sized individuals (e.g. Oosting & Billings 1943; Fowells 1965; Barbour & Woodward 1985). Plot 1 on Swain Mountain supported a population of relatively even-sized stem >55 cm dbh, although their ages ranged from 160-224 yr. Stumps of similar diameter in adjacent harvested stands were 248 yr old. This suggests that the oldest cohort in Plot 1 established after stand-replacing fire 250 or more years ago. In contrast, within Plot 2 there was no distinct cohort of older trees that might have originated after stand replacing fire, nor were there in the Sierran forests studied by Pitcher (1987). However, it is possible that one or more lower intensity ground fires obscured evidence of a previous stand-replacing event. Although crown fires of >500 ha have occurred in Red fir forests of the Sierra Nevada (D. Parsons, pers. comm.), the frequency and areal extent of such large-scale disturbances remain unknown.

Red fir forests are structurally complex, despite their simple species composition. Spatial and temporal variation in disturbance and in the life history traits of Red fir contribute to this structural complexity. Red fir establishes abundantly after severe fire (e.g. Plot 2, see also Pitcher 1987), as do many conifers in fire-prone ecosystems. Yet because it is relatively shade-tolerant, Red fir may also recruit into small canopy openings (Fowells 1965; Ustin et al. 1984; Barbour 1988) created by small-scale disturbance. Moreover, low intensity fire may not restrict the development of population structures typical of continuously regenerating populations. Thus, depending on the frequency and severity of disturbance, the age structure of Red fir forest patches may reflect episodic, post-disturbance establishment or continuous recruitment during disturbance-free periods.

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