Identifying Reference Conditions for Prescribed Fire Management of Mixed Conifer Forests in Yosemite National Park, California.

Final Report to the Joint Fire Science Program
Prepared By Alan H. Taylor and Andrew E. Scholl

Project #01-3-3-12 Local Needs

Principal Investigators and contact information

Ms. Kara J. Paintner, Fire Ecologist & Natural Resource Liaison, Fire Management Program Center and Natural Resource Program Center, BRMD, 1201 oak ridge drive Fort Collins, CO 80525; Tel: 970.267.2121, Fax 970.225.3585, kara_paintner@nps.gov

Dr. Alan H. Taylor, Department of Geography, The Pennsylvania State University 302 Walker Building, University Park, PA 16802; Tel:814.865.1509, FAX 814.863.7943, aht1@psu.edu

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Key Findings

Fire History

- Both mixed conifer forests in Yosemite National Park experienced frequent fire before the onset of fire suppression. Mean return intervals for fires scarring 10% or more of the grid points and 25% or more of the grid points were 2.5 years (range 1-12) and 7-10 years (range 1-48), respectively. The mean point fire return interval was 12.4 years (range 2-84) in Big Oak Flat and 9.9 years (range 1-60) in South Fork Merced.
- The position of fire scars within tree rings was mainly in latewood (46.5%) and at the ring boundary indicating that fires burned most frequently in late summer and fall.
- Both mixed conifer forests experienced a dramatic decrease in fire occurrence and extent in the early 1900s and the frequency of fire was similar in the pre-Euro American and settlement period in both forests.
- Fire extent varied among years, and mean and median fire extent were similar in both areas (202 ha and 123 ha, respectively). A total of six fires in both study areas burned >1000 ha.
- There were more small than large (>350 ha) fires and larger burns (19%) accounted for nearly 50% of the area burned since AD 1575.
- Fire rotations for the pre-Euro American and settlement period ranged from 10-13 years and increased to 211-378 years during the fire suppression period depending on study area.
- Fire severity was inferred from forest age structure and there was no evidence of high severity fire in either study area. Burns were either low or moderate in severity.
- The location and extent of burns in one year affected burn patterns in subsequent years and this was evident in both the pre-Euro American and settlement period.

Stand Structure

- Contemporary forest structure was different than the reconstructed reference forest (AD 1899) due mainly to fire suppression.
- Average density of trees >10 cm dbh in the contemporary forest (576.8 ha^{-1} , range 90-2060 ha^{-1}) was higher than in the reference forest (133.3 ha^{-1}, range 10-520 ha^{-1}).
- Average basal area of trees >10 cm dbh in the contemporary forest (66.2 m^2 ha^{-1}, range 20.7-150.8 m^2 ha^{-1}) was higher than in the reference forest (42.7 m^2 ha^{-1}. range 4.9-103.7 m^2 ha^{-1}).

- Average quadratic mean diameter of trees >10 cm dbh in the contemporary forest (42.1 cm, range 19.2-84 cm) was smaller than in the reference forest (67.6 cm, range 28.3-131.2 cm).
- Average structural diversity (mean Shannon's Diversity Index) was similar between reference and contemporary forests (1.9 vs. 1.9)
- Much of the forest change was caused by a dramatic increase in establishment of white fir and incense-cedar that began with the onset of fire suppression.
- Forest changes since 1899 altered the shape of tree diameter distributions. Diameter-class distributions were different between the reference and contemporary forest for incense-cedar, sugar pine and Douglas-fir.
- There was a high incidence of spatial autocorrelation in the ages of trees in the reference forest. Small and intermediate sized patches of similar aged trees were a conspicuous structural feature of pre fire suppression forests.

Implications for Management

- Quantitative data on reference conditions for forest structure and fire regimes are essential for developing restoration plans, management treatments, and evaluation metrics to judge success of fire and resource management programs.
- Reference forest structure data indicate that restoration objectives should emphasize: 1) density and basal area reduction, mainly of small diameter trees; 2) increasing structural heterogeneity across the forest landscape.
- There was considerable spatial variability in reference forest structure within each study area. Consequently, management plans and treatments should emphasize variability in outcomes across a landscape rather than achieving an average condition.
- Reference fire regime data indicate that re-introducing frequent fire is essential for restoring the functional relationships between fire and forest structure that regulated pre fire suppression forests.
- Prescriptions should emphasize a mixture of small and large later season burns over several decades to be consistent with historical burn patterns.

INTRODUCTION

A guiding policy for management of landscapes inside national parks (NPS) calls for maintenance of natural conditions and processes. This policy assumes that natural and unnatural influences on landscape change are distinguishable and that natural processes can maintain a desired landscape structure. Current policy guidelines permit natural change to proceed within limits, while managers are directed to arrest or reverse unnatural or anthropogenic change. An important need for fire and resource managers implementing this policy in forests highly altered by a century or more of fire suppression is quantitative information on pre-fire suppression reference conditions. Managers use information on reference conditions for both understanding how fire suppression has changed ecosystems, and for identifying restoration goals and management treatments if contemporary conditions are outside the range of desired conditions (Fule et al. 1997; Stephenson 1999; Taylor 2004).

A critical need for knowledge of reference conditions for mixed conifer forests was identified by fire and resource managers in developing Yosemite National Park's Fire Management Plan (USDI 2004). Fire suppression in YNP has dramatically altered the mixed conifer forest landscape. Exclusion of fire for a century or more has caused an increase in forest density, an increase in live and dead forest fuels, and a shift in forest composition towards more fire intolerant tree species. Research on fire regimes and forest structure in old-growth mixed conifer forests in the Sierra Nevada suggests that frequent (e.g. 3-20 years) low intensity surface fires created relatively open forests with a fine-grained multi-aged forest structure (Parsons and Debenedetti 1979; Caprio and Swetnam 1995; Swetnam et al. 2000). Yet, these studies provide little quantitative reference information for forest structure (species composition, basal area, density, spatial patterns) that could be used by managers as a foundation for restoration plans or for developing metrics to evaluate the success of management treatments. Moreover, there is little information on pre fire suppression fire severity and fire extent for mixed conifer forests in the Sierra Nevada. Quantitative data on reference fire regimes and forest structure for mixed conifer forests are needed by both YNP fire and resource managers, and managers in the Sierra and Stanislaus National Forest, for development of cross-agency objectives for prescribed fire use on lands adjacent to YNP. Knowledge of reference conditions is also essential for building a flexible fire program that can shift from restoration to maintenance burning as its goals are met. In YNP, prescribed fire is currently the predominant tool used to achieve fire and resource management goals in the highly altered mixed conifer forest zone.

SUMMARY OF OBJECTIVES

The objectives of this project were to:

1) Determine fire regimes (frequency, return interval, size, severity, season) for the pre-settlement (pre-1850), settlement (1850-1904), and suppression periods (1905-present) in the Merced and Tuolumne drainage mixed conifer forests;

2) Determine how fire regimes vary with topographic and forest compositional gradients in the Merced and Tuolumne drainage mixed conifer forests;

3) Determine pre-fire suppression forest characteristics (basal area, density, and size structure) of mixed conifer forests at plot and landscape scales in the Merced and Tuolumne drainage mixed conifer forests;

SUMMARY OF MATERIALS AND METHODS

Study Areas

Mixed conifer forest structure and fire regimes were studied at two sites in YNP, Big Oak Flat (BOF) and the South Fork of the Merced (SFM). These areas were chosen for study because they are the largest extant tracts of mixed conifer forest in YNP that have not been extensively burned by wildfire or prescribed burning since 1900. Unburned areas were needed because fires remove evidence (wood) needed to reconstruct reference conditions using dendroecological methods. The BOF and SFM study areas covered 2125 ha and 1600 ha, respectively (Figure 1). The composition of the mixed conifer forests on the sites was typical of those in the montane zone of the Sierra Nevada (Barbour 1988). The forests were a mix of any of five conifer species: ponderosa pine (Pinus ponderosa), Douglas-fir (Pseudotsuga menziesii var. menziesii), incense-cedar (Calocedrus decurrens), sugar pine (Pinus lambertiana), Jeffrey pine (Pinus jeffreyi), and white fir (Abies concolor) that co-occur and share dominance depending on site conditions. California Black oak (Quercus kelloggii) is an important hardwood associate in these forests, particularly at lower elevations. Jeffrey pine (Pinus jeffreyi), a common component of Sierra Nevada mixed conifer forests, was not found in either study area.

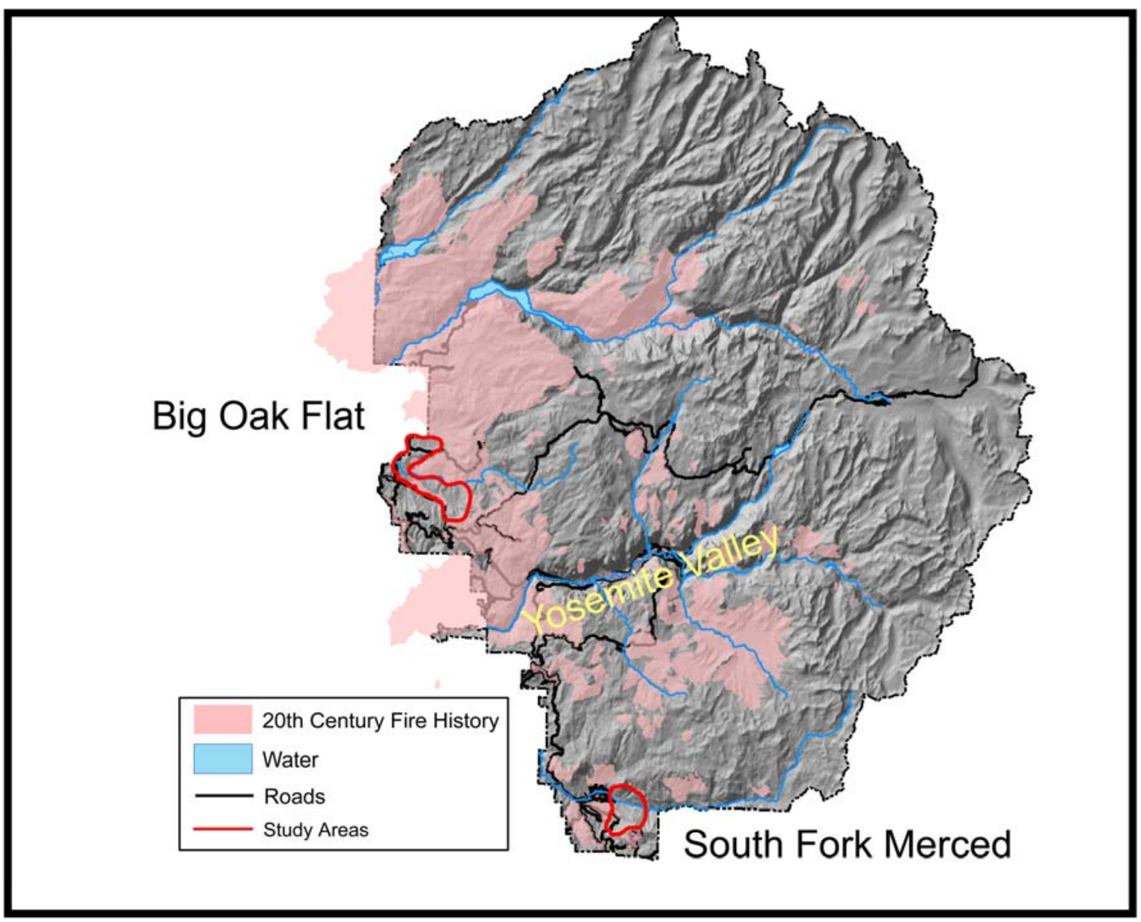


Figure 1. Location of the Big Oak Flat and South Fork Merced mixed conifer forests, Yosemite National Park, California.

Forest Structure and Composition

Forests were sampled on a systematic 500 m X 500 m sampling grid placed over each study site (Figure 2a, b). At each grid point (BOF n = 85, SFM n = 64) forest structure and composition were characterized in nested circular plots. Conifers >35.0 cm dbh and hardwoods >15.0 cm dbh were measured (dbh) on the entire plot (1000 m^2) and trees 10-35 cm dbh (conifers) or 5-15 cm dbh (hardwoods) were measured (dbh) in the intermediate plot (250 m^2), and saplings (1.4 m tall – 5.0 cm dbh) and seedlings (0.5 m – 1.4 m tall) were tallied by species in the small plot (100 m^2). The position (x,y coordinates) of all trees, either live or dead, in each plot was determined from measurements of distance and direction from the plot center. The dbh, species, direction of fall, and decay class (Maser et al. 1979) of all logs (>35 cm dbh) rooted in the plot were also recorded in the large plots. Environmental variables recorded for a plot included elevation, slope pitch, slope aspect, slope configuration, and topographic position. The last four variables were combined to estimate the Topographic Relative Moisture Index (TRMI) for each plot. TRMI is an index of relative potential soil moisture based on topographic variables with values that range from 0 (xeric) to 60 (mesic) (Parker 1982).

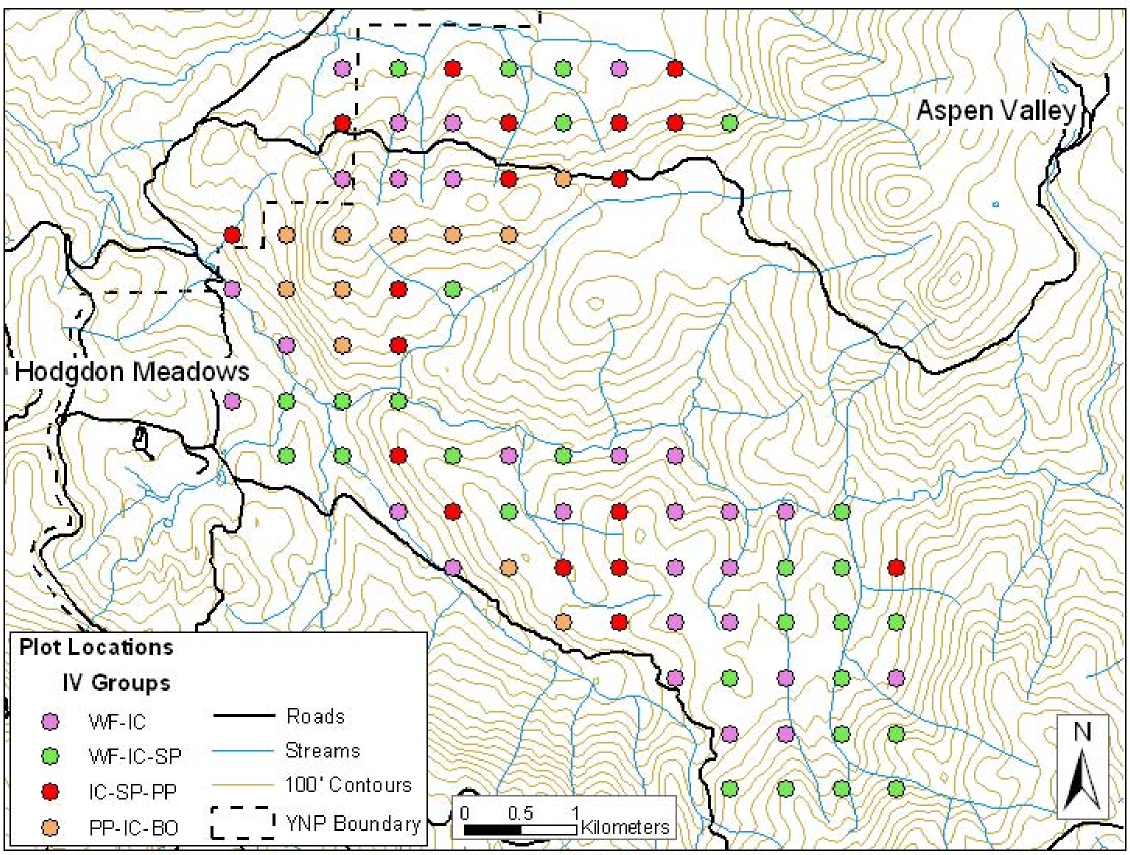


Figure 2a. Location of sample points and the type of forest at each point identified by cluster analysis of species importance values in the Big Oak Flat mixed conifer forests, Yosemite National Park, California.

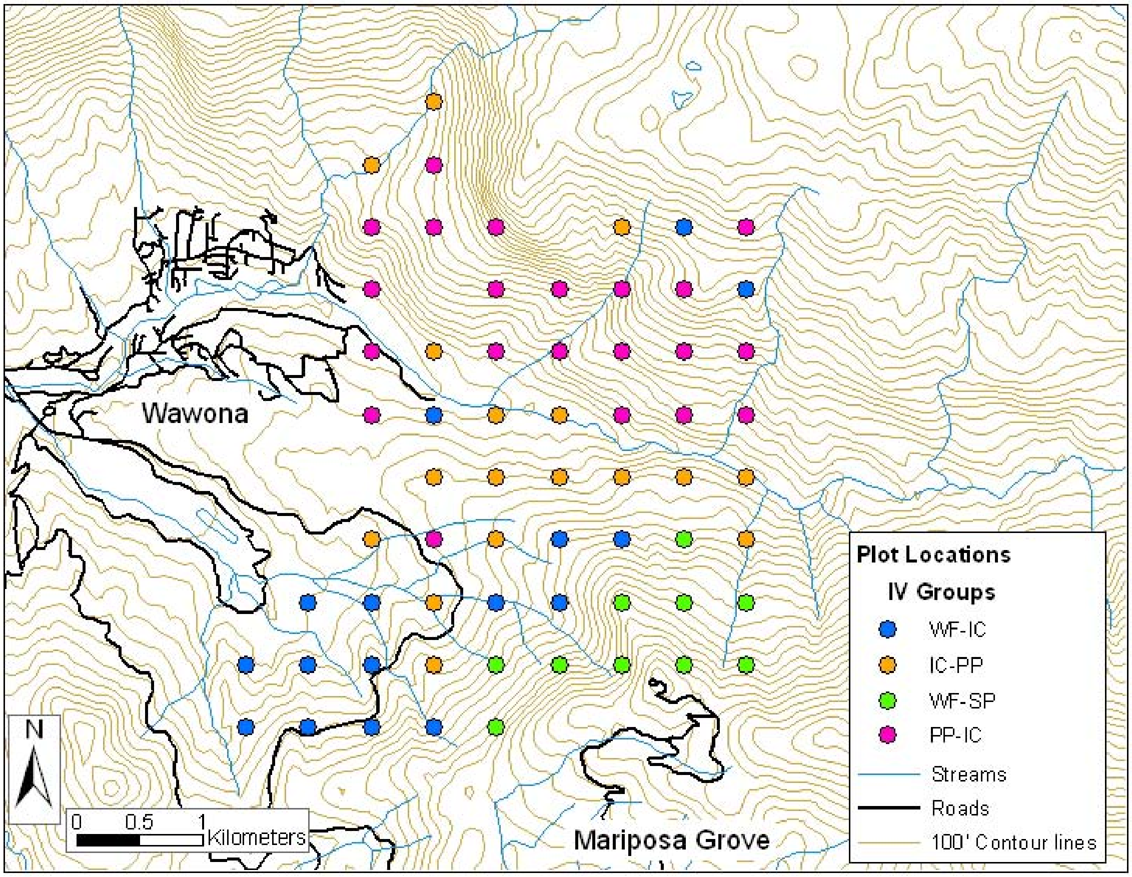


Figure 2b. Location of sample points and the type of forest at each point identified by cluster analysis of species importance values in the South Fork Merced mixed conifer forests, Yosemite National Park, California.

Forest age structure was determined by coring all live trees in a plot 30 cm above the ground. Cores were sanded to a high polish, their annual growth rings were cross-dated (Stokes and Smiley 1968), and the date of the innermost ring was used as the estimate for tree age. Species' specific regression equations (range of r^2= 0.61-0.92, $P<0.001$) were used to estimate tree ages for trees with incomplete cores (BOF = 19%, SFM = 15%).

<u>Variation in Forest Composition</u>

Variation in species composition across each study area was identified by using cluster analysis and ordination. Compositional groups were identified by clustering species' importance values (IV) or the sum of relative basal area (BA) and relative density for each plot (maximum value = 200). Species importance values were also ordinated using detrended correspondence analysis (DCA). DCA is a modified reciprocal averaging technique that simultaneously arranges species and stand scores along orthogonal axes that explain the largest amount of variation among samples (Gauch 1982). Environmental conditions associated with forest composition were then identified by group and across the study areas using the IV, DCA axis scores, and environmental variables collected in each plot.

Forest Reference Conditions

Forest reference conditions (density, basal area, diameter) for the pre-fire suppression period were reconstructured using dendroecological methods (cf. Fule et al. 1997). The reference point for the forest reconstruction was 1899, the year of the last widespread fire in each study area. Reconstruction for an earlier date would be less precise because woody material would have been consumed by the 1899 fires.

Forest reference conditions in 1899 were reconstructed using measurements of the contemporary forest using the following procedure. First, we eliminated stems for live trees that established after 1899 (i.e., stems ≤103 yrs old). Second, we determined the diameters of trees (stems >10 cm dbh) that were alive in 1899 by subtracting radial growth since 1899 from each tree core.

Trees that died since 1899 must also be included in the forest reference condition estimate if they established before 1899. The date of death for snags and downed trees measured in the contemporary forest was estimated using measurements of dbh and decay class, and estimates of decomposition rate, following the method developed by Fule et al. (1997). Once death dates for snags and downed trees were determined, the dbh of trees alive in 1899 but dead today were determined using tree death dates and average annual radial growth rates for each species from the trees cores.

Decomposition rates can vary depending on cause of death or climate conditions (Harmon et al. 1987), affecting tree death date estimates. A sensitivity analysis was performed to assess the influence of different decomposition rates on the characteristics of the reconstructed reference forest in 1899. Death dates were estimated for trees using three decomposition rates; the 25^{th} (slowest), 50^{th} (middle), and 75^{th} (fastest) percentile. Structural characteristics (basal area, density, quadratic mean diameter) for the reference forest were then calculated and compared for each decomposition rate.

The accuracy of the forest reference reconstruction was evaluated using independent measurements of forest conditions in 1911. In 1911, a forest inventory was conducted in the Stanislaus National Forest and inventory plots were measured in and adjacent to the BOF study site. Density, basal area, and dbh were calculated for trees in the 1911 forest and the values were compared to those for the reference forest that were reconstucted using the dendroecological reconstruction method.

Changes in forest conditions since 1899 were determined by comparing reference and contemporary forest characteristics using distribution free Kruskal-Wallis H-tests.
Comparisons were made for density, basal area, and quadratic mean diameter for each species. Furthermore, structural diversity was compared by calculating the standardized Shannon's diversity index (Turner et al. 2001) of the density of trees for each species in each size class in each plot.

Fire Regimes

Fire regime characteristics (i.e., frequency, fire return interval, severity, extent, seasonality, and rotation) were reconstructed in BOF and SFM using four types of data: (1) written fire records on file at Yosemite National Park; (2) fire dates from partial cross-sections removed from live and dead fire scarred trees; and (3) radial growth patterns observed in cored trees. Fire scarred trees within a 9 ha circular plot centered on each grid point were located and an average of two fire scar samples (range, 1-5) were collected at each grid point. Partial wood cross sections were removed from fire scarred trees using a chainsaw (Arno and Sneck 1977) and the calendar date each fire scar was formed was determined using standard dendrochronological techniques (Stokes and Smiley 1968).

Fire occurrence at a grid point was also inferred from variation in the radial growth patterns of cored trees. Fires that burn through a stand may affect tree growth, but not scar the tree. A tree damaged, but not scarred, by fire often exhibits a sudden decrease (suppression) in radial growth for several years post-fire, and the fire date corresponds with the year before the onset of suppressed growth. Conversely, a fire may kill a tree or group of trees and improve local growing conditions for surviving tree(s) resulting in an increase (release) in radial growth. In this case, the fire date corresponds with the onset of a sudden increase in radial growth. Dates of growth suppression or release in trees in plots were used to infer fire occurrence at a grid point if the date was coincident with a fire scar date in samples from an adjacent grid point.

Fire season-Season of burn was inferred from the relative position of each fire scar within an annual growth ring (Baisan and Swetnam 1990). Seasons were: 1) early (first one-third of earlywood); 2) middle (second one-third); 3) late (last one-third); 4) latewood (in latewood); 5) dormant (at ring boundary). In this strongly winter wet, summer dry climate, dormant season fires occur in late summer or fall after seasonal growth has stopped for the year, rather than in early spring (Caprio and Swetnam 1995).

Spatial variation in fire return intervals - Spatial variation in fire return intervals (FRI) related to slope aspect and forest composition was identified by comparing mean FRIs for different slope aspect and forest compositional types. Mean composite fire intervals (CFI) and mean point fire interval (PFI) were calculated for each slope aspect and compositional group and compared using a distribution free Kruskal-Wallis H test.

Temporal variation in fire return intervals - Temporal variation in fire return intervals that may be related to land use changes was identified by comparing composite FRIs for three time periods: (1) pre-settlement (pre-1850), (2) settlement (1850-1904), and (3) fire suppression (1904-2002). A composite fire record for each study area was used for temporal comparisons because composite records are more sensitive to changes in ignitions or burning conditions that might influence fire occurrence at landscape scales than are point FRIs (Dieterich 1980). Differences in the frequencies of fire between time periods were determined using a t-test.

Fire Extent – Fire extent was estimated from the frequency of fire dates in each study area in several ways. First, the extent of burning each year was estimated using a ratio method (Morrison and Swanson 1990, Taylor and Skinner 1998) which estimates fire extent using the number of grid points that recorded a fire in a given year and the total number of grid points with samples old enough to record a fire in that year. Using this method fire extent is estimated as:

$$A_i = (AT \times NS_i)/(NST - NRE)$$

Where, A_i is the extent burned in the *i*th year, AT is the size of the study area (in hectares), NS_i is the number of grid points with a record of the fire in the *i*th year, NST is the total number of grid points, and NRE is the number of sites without samples present to record the fire in the *i*th year. Since the accuracy of this method decreases as NRE increases we chose a cutoff for the fire extent analysis of 1575 to reduce the influence of small sample size on fire extent estimates. In each study area, >15% of the grid points were recording fire on this date.

Second, fire extent was also assessed using the percentage of grid points that recorded a fire in a given year. This measure was used to infer the relative importance of small *vs*. widespread fires. Composite fire chronologies were developed for fires recorded by any grid point, 10% or more, or 25% or more of the grid points. FRI statistics were then calculated for the different composite fire chronologies for each study area.

Fire Rotation - Fire rotation is the number of years needed to burn an area equal in size to the study area given the frequency and extent of burning during that period (Heinselman 1973). For a given period, some parts of the study area may have burned more than once, and others not at all. Fire rotation was calculated using the ratio method estimates of annual fire extent and fire rotation was calculated separately for the pre-settlement (pre-1850), settlement (1850-1904), and fire suppression (1905-present) periods.

Fire Severity – Fire severity was assessed indirectly by analyzing the age structure of tree populations in the plots. Since fires burn with variable severity across a landscape, their impact on forest structure can vary from place to place, killing many trees in some stands and few trees in others. Stands that have experienced high severity fires that killed most or all trees are usually even-aged, while stands with a multi-aged structure develop under a regime of moderate severity fires that kill only portions of a stand. In contrast, forests that experience mainly low severity fires are multi-aged, but they may have no distinct age classes related to fire events (Agee 1993). Consequently, the number of 20 year age-classes occupied by trees in a plot was used as an index of fire severity in the plot. Presumably, plots with few age-classes experienced more severe fire than plots with a large number of occupied age-classes. The number of 20 yr age-classes occupied by each species was tallied for each plot for both all age-classes, and for age-classes during the pre-fire suppression period (>100 yrs).

<u>Fuel Limitations and Fire Occurrence</u>

Fires consume fuel on the forest floor and lack of fuel in a burn patch can influence the pattern of subsequent burns. Fires can re-burn a patch again when enough fuel has accumulated to carry fire. The potential influence of reduced fuels on the location of a subsequent fire was identified by calculating the frequency that successive fires burned the same grid point, a different grid point, or the same and a different grid point. Moreover, the influence of previous burns on area burned by subsequent fires was assessed by calculating the frequency of grid points that were burned by only the first fire, only the second fire, and by both fires.

SUMMARY OF RESULTS

Forest Structure and Composition

Big Oak Flat

Four forest compositional groups were identified by cluster analysis of species importance values for BOF: 1) white fir/ incense-cedar; 2) white fir/ incense-cedar/ sugar pine; 3) incense-cedar/ sugar pine/ ponderosa pine; and 4) ponderosa pine/ incense-cedar/ California black oak (Table 1; Figure 2a).

1) The white fir/ incense-cedar (WF/IC, n=28) group is dominated by white fir and incense-cedar, with lesser amounts of sugar pine and ponderosa pine. On average, white fir had a higher density and IV than incense-cedar but their basal areas were similar. Ponderosa pine had a high basal area and low density in this group. This group occupies relatively mesic north and northwest-facing slopes at low to mid elevations.

2) The white fir/ incense-cedar/ sugar pine group (WF/IC/SP n =28) is strongly dominated by white fir and with lesser and nearly equal amounts of sugar pine and incense-cedar. The average density of white fir is 10-fold greater than that for incense-cedar or sugar pine and mean basal area for white fir is higher too. This group occupies relatively mesic north-facing slopes from low to high elevation.

3) The incense-cedar/ sugar pine/ ponderosa pine group (IC/SP/PP, n=18) is dominated by incense-cedar, and sugar pine and ponderosa pine are important associates. White fir is also common. Although sugar pine and ponderosa pine IV are similar, ponderosa pine basal area is higher but its density is lower than sugar pines'. This group occupies mid-slope positions on south-facing slopes at low to mid elevation.

4) The ponderosa pine/ incense-cedar/ California black oak group (PP/IC/BO, n=11) is the smallest group, and is dominated by ponderosa pine with lesser amounts of incense-cedar and California black oak. California black oak achieved its highest abundance in this group. This group is restricted to xeric south and west-facing slopes at mid-elevation.

South Fork Merced

Four compositional groups were identified from the cluster analysis of species importance values for SFM: 1) white fir/ incense-cedar; 2) incense-cedar/ ponderosa pine; 3) white fir/ sugar pine; and 4) ponderosa pine/ incense-cedar (Table 2, Figure 2b).

1) The white fir/ incense-cedar group (WF/IC, n=16) has characteristics similar to the white fir/ incense-cedar group in BOF and occupies sites with similar characteristics.

2) The incense-cedar/ ponderosa pine group (IC/P, n=17) is dominated by incense-cedar with lesser amounts of ponderosa pine. This group occupies mesic sites at low to mid-elevation on north and northwest-facing slopes.

3) The white fir/ sugar pine group (WF/SP, n=10) is the smallest group and is dominated by white fir with lesser amounts of sugar pine. This group occupies higher elevations on mesic north-facing slopes.

4) The ponderosa pine/ incense-cedar group (PP/IC, n=21) is the most widespread group and is strongly dominated by ponderosa pine which is two-fold more abundant than incense-cedar. This group occupies xeric south-facing slopes at all elevations.

Species distributions in both study areas were influenced by topographically related variation in environmental conditions (Table 1, 2 and DCA-not shown).

Table 1. Mean importance value (maximum 200), basal area (m2 ha-1) and density (ha-1) of trees (>10 cm dbh) in forest types identified by cluster analysis of species importance values in the Big Oak Flat mixed conifer forest, Yosemite National Park, California. Forest types are white fir/ incense-cedar (WF/IC), white fir/ incense-cedar/ sugar pine (WF/IC/SP), incense-cedar/ sugar pine/ ponderosa pine (IC/SP/PP), and ponderosa pine/ incense-cedar/ California black oak (PP/IC/BO). n= number of samples in each forest type. Elevation and relative soil moisture (TRMI) varied among forest groups (P<0.001, Kruskal Wallis H-test). TRMI varies between 0 (xeric) and 60 (mesic).

	Forest Types											
	WF/IC *n=28*			WF/IC/SP *n=28*			IC/SP/PP *n=18*			PP/IC/BO *n=11*		
Species	IV	BA	Density	IV	BA	Density	IV	BA	Density	IV	BA	Density
White fir	76.2	18.7	307.1	126.1	30.5	399.6	22.9	6.3	75.6	1.4	0.2	4.5
Incense Cedar	45.2	18.4	151.4	29.3	14.3	38.2	83.2	26.6	275	47.8	12.1	75.5
Ponderosa pine	38.7	12.2	25.6	9.9	17.1	36.8	33.3	8.1	131.7	99.4	0.5	8.2
Sugar pine	20.6	24.2	50.4	25.6	5.6	5.7	34.9	14.3	64.4	2.6	30.8	93.6
Douglas-fir	8	3.8	20.7	3.3	0.9	6.4	8.7	5.1	15	1.6	0.4	3.6
California black oak	7.7	1.9	28.9	3.4	0.9	9.3	17.1	6.1	56.7	47.3	6.2	112.7
	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.
Elevation	1532	1312	1738	1576	1334	1920	1526	1372	1653	1550	1426	1657
TRMI	34	12	53	35	17	54	28	15	51	19	12	28

Table 2. Mean importance value (maximum 200), basal area (m2 ha-1) and density (ha-1) of trees (>10 cm dbh) in forest types identified by cluster analysis of species importance values in the South Fork Merced mixed conifer forest, Yosemite National Park, California. Forest types are white fir/ incense-cedar (WF/IC), incense-cedar/ ponderosa pine (IC/PP), white fir/ sugar pine (WF/SP), and ponderosa pine/ incense-cedar (PP/IC). n= number of samples in each forest type. Elevation and relative soil moisture (TRMI) varied among forest groups (P<0.001, Kruskal Wallis H-test). TRMI varies between 0 (xeric) and 60 (mesic).

	Forest Types											
	WF/IC *n=16*			IC/PP *n=17*			WF/SP *n=10*			PP/IC *n=21*		
Species	IV	BA	Density	IV	BA	Density	IV	BA	Density	IV	BA	Density
White fir	72.5	18.2	331.9	9.2	1.7	44.7	103.9	24.7	425	2.5	12.9	8.1
Incense Cedar	63	20.7	319.4	83.1	22	468.8	14.8	6.8	53	40.6	12.7	126.2
Ponderosa pine	31.7	10	28.8	35.9	7.2	44.7	-	-	-	127.3	5.7	18.1
Sugar pine	15.7	18.6	33.1	18.3	16.7	98.2	58.7	33.2	78	6.7	37.4	218.1
Douglas-fir	4	1.4	11.9	24.1	5.8	94.7	17.9	21.1	39	1.6	2	2.4
California black oak	13.2	4.4	38.8	29.5	8.1	97.6	4.8	1.7	13	21.3	4.8	47.6
	Mean	Min.	max.	Mean	Min.	max.	Mean	Min.	max.	Mean	Min.	max.
Elevation	1524	1314	1977	1466	1302	1885	1780	1597	1967	1567	1262	2058
TRMI	33	18	46	34	14	55	30	19	42	25	12	51

Ponderosa pine and California black oak were concentrated on drier sites at lower elevations, and on southerly aspects, whereas white fire was the dominant at higher elevations and on mesic, north facing slopes. On the other hand, sugar pine and incense cedar were most abundant on intermediate sites. Each of the five mixed conifer species in both study areas had overlapping distributions, however, and each species occurred in each forest compositional group.

Forest Reference Conditions

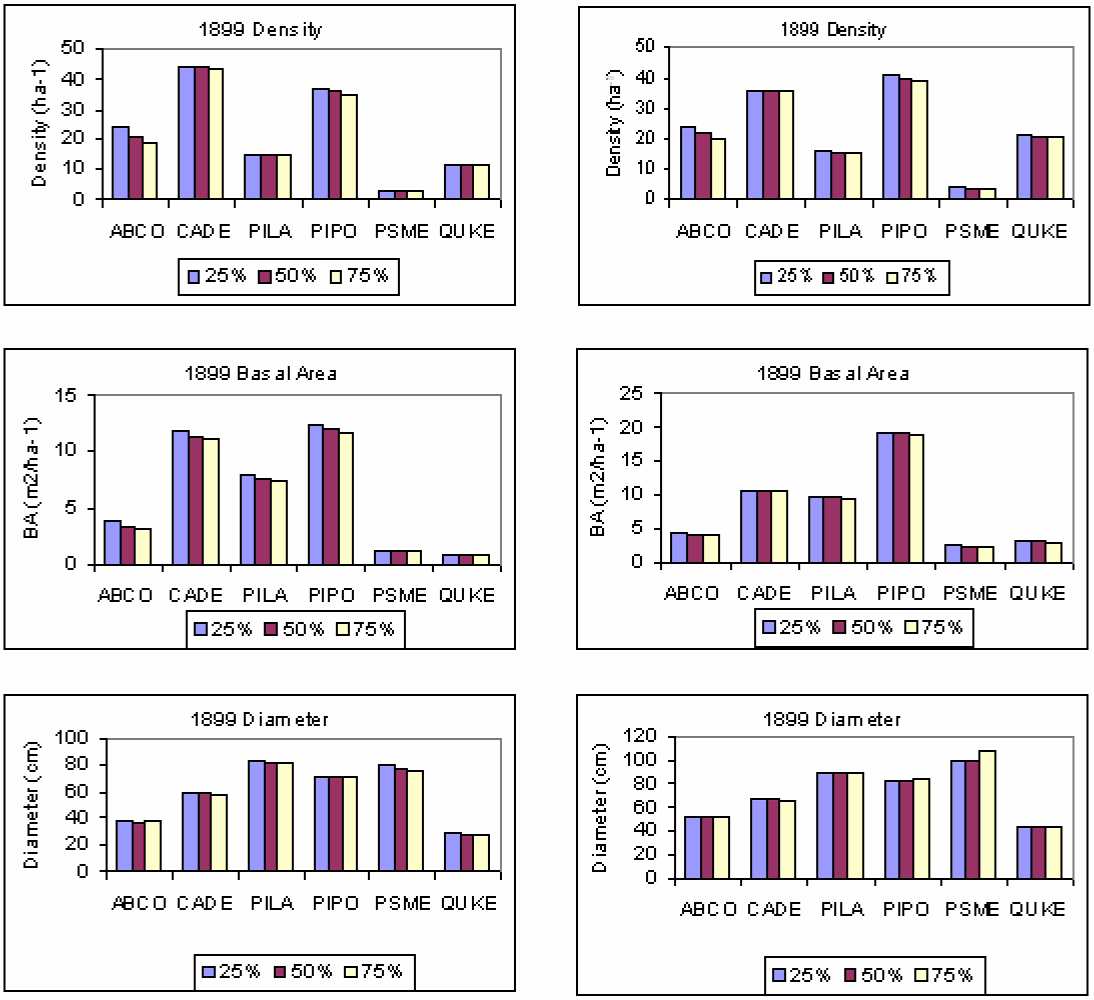
Sensitivity analysis and comparison with forest inventory

The sensitivity analysis indicates that estimates of forest reference conditions are not strongly influenced by variation in decomposition conditions used to estimate tree death date (Figure 3a, b). No trees dead in 2002 were assigned death dates before 1899 using any of the modeled decomposition rates. Differences in reference forest characteristics predicted by the different decomposition condition models (25^{th}, 50^{th}, 75^{th}) were greater for tree density than for basal area or tree diameter. In BOF, the difference for tree density was 34 trees ha^{-1} with a 25^{th} percentile estimate 13.2% higher, and a 75^{th} percentile estimate 4.4% lower than for the 50^{th} percentile model. The tree density difference was smaller in SFM (21 trees ha^{-1}). For basal area, both the 25^{th} and 75^{th} percentile models estimate small differences for BOF (2.9-3.8%) and SFM (1.6%-3.2%) from the 50^{th} percentile estimate. Similarly, for tree diameter, the 25^{th} and 75^{th} percentile model estimates for BOF (-8.8%-0.5%) and SFM (-0.5%-0.5%) were close to the 50^{th} percentile estimate. Sensitivity analyses for individual species gave results similar in magnitude to the forests as a whole, and inter-specific differences were greatest for white fir. Given the small differences in reconstructed forest characteristics and the wide range of differences in decomposition rate percentiles and tree death dates (1930-2002), the reconstruction method is relatively insensitive to imprecision in the decomposition rate models. Consequently, only the reference forest characteristics using the 50^{th} percentile decomposition model are reported.

Comparison of reference and contemporary forest conditions

Forest comparisons

The reference mixed conifer forests in BOF and SFM were, on average, different than the contemporary forest (Table 3a, b). Contemporary forests had more trees and basal area, and the average diameter of trees was smaller ($p<0.01$, Kruskal Wallis H-test). On an individual species basis, contemporary forests have, on average, a two or more-fold increase in white fir and incense-cedar than the reference forest in both study areas. Moreover, in BOF and SFM, white fir and incense cedar basal area was larger in the contemporary forest ($p<0.01$), while the average diameter decreased for both species.
The change in density, basal area, and tree size since 1899 altered the shape of tree diameter distributions for incense-cedar, sugar pine and Douglas-fir. In both BOF and SFM, the average shape of incense-cedar diameter-class distribution in the reference and contemporary forest were significantly different ($p<0.01$, Kolmogorov-Smirnov two sample test), while sugar pine was only different in BOF and Douglas-fir was only different in SFM (Figure 4a, b).



a) **b)**

Figure 3. Mean density, basal area, and quadratic mean diameter of the reference forest using the three different decomposition condition models (25th, 50th, 75th) to estimate the death date of trees that were dead in 2002 in the Big Oak Flat (a) and South Fork Merced (b) mixed conifer forests, Yosemite National Park, California. Species acronyms are Abco (<u>Abies concolor</u>), Cade (<u>Calocedrus decurrens</u>), Pila (<u>Pinus lambertiana</u>), Pipo (<u>Pinus ponderosa</u>), Psme (<u>Pseudotsuga menziesii</u>), Quke (<u>Quercus kelloggii</u>). Values are for trees >10 cm dbh.

Site and forest group comparisons

Big Oak Flat

White fir/ incense-cedar – Reference and contemporary forest conditions were different and the contemporary forest has more trees, more basal area, and smaller diameter trees ($p<0.001$) (Table 4). The overall difference is mainly due to significant increases in density, and basal area for white fir and incense-cedar ($P<0.05$). These

Table 3. Mean (SD) density (ha^{-1}), basal area (m^2 ha^{-1}), and quadratic mean diameter (cm) of trees (>10 cm dbh) of the reference (AD 1899) and contemporary forest in the Big Oak Flat (a) and South Fork Merced (b) mixed conifer forests, Yosemite National Park, California. Species acronyms are Abco (Abies concolor), Cade (Calocedrus decurrens), Pila (Pinus lambertiana), Pipo (Pinus ponderosa), Psme (Pseudotsuga menziesii), Quke (Quercus kelloggii). Reference forests that are significantly different from 2002 forests, * = p<0.05; ** = p<0.01; *** = p<0.001.

	Density (# trees/ha)			Basal area (m2/ha)			Quadratic Mean Diameter (cm)		
	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
Abco									
2002	248.9	196.7	0-750	17.5	13.8	0-53.9	32.1	11.9	15.3-70.2
1899	20.9***	27.9	0-140	3.4***	6.5	0-32.5	37.1	23.6	10.1-117.4
Cade									
2002	128.1	152.2	0-800	18	14.8	0-69	56.8	31.8	12.2-118.7
1899	43.6***	43.3	0-290	11.4**	10.8	0-52.9	59	25.2	12.9-118.1
Pila									
2002	48.7	89.3	0-400	11.4	15.5	0-70.5	80.8	59.1	10.2-215
1899	14.5*	19.3	0-100	7.6	12.2	0-61.3	81.6	48.9	12.1-208.7
Pipo									
2002	44.2	75.1	0-470	16.8	18.4	0-84.9	86.2	33.1	22-159.5
1899	35.8	38.9	0-160	11.9	10.9	0-39.7	71.1**	30.2	17.5-157.9
Psme									
2002	12.6	33.4	0-200	2.7	9.7	0-60.2	45.9	25.3	14.5-111.3
1899	3.1	13.4	0-110	1.2	4.8	0-37.9	77.7	42.4	16.3-134.1
Quke									
2002	33.5	67.2	360	2.9	6.4	0-43.5	31.9	12.8	13.4-72.9
1899	11.8	24.7	0-140	0.8	1.7	0-9.1	28.4	12.2	10.8-65.6
All Trees									
2002	516.1	242.4	90-1220	69.4	25.9	20.7-150.8	43.5	11.3	19.2-80.6
1899	129.6***	75.5	30-450	36.3***	20.4	4.9-103.7	62.5***	20.9	28.3-131.2

a)

	Density (# trees/ha)			Basal area (m2/ha)			Quadratic Mean Diameter (cm)		
	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
Abco									
2002	162	228.4	0-1140	9.3	12.4	0-46.6	28.9	15	14.4-92.8
1899	21.6***	36.4	0-150	4.1*	7.6	0-36.2	51.4***	26.7	13-102.2
Cade									
2002	249.1	321.5	0-1470	15	12.9	0-60.6	35.9	21.9	11.3-121.3
1899	35.6***	42.4	0-200	10.6*	11.5	0-56.6	66.5***	28.4	17.3-153.7
Pila									
2002	37.2	49.1	0-170	9.6	13.4	0-52.7	67.9	44.6	11.1-177
1899	15.6*	24.7	0-130	9.6	14.8	0-51	90.7*	35.7	17.6-140.9
Pipo									
2002	104.7	153.5	0-750	21.3	17.4	0-63.8	72	39.3	18.1-221
1899	40.2	49	0-340	19.1	17	0-62.5	82.8*	30.7	14-170.7
Psme									
2002	34.4	96.3	0-580	3.3	7.2	0-34.2	45.2	30.2	16.5-141
1899	3.3	10.5	0-70	2.4	6.9	0-37.5	99.3**	49.7	10.6-177
Quke									
2002	50.2	65.3	0-300	4.3	6	0-29.5	33.4	11.7	14.8-64.3
1899	20.8*	30.3	0-120	3.1	4.6	0-20.3	44.4**	17.8	11.5-82.3
All Trees									
2002	637.5	412.4	90-2060	62.9	21.2	29.1-120	40.7	14.3	19.3-84
1899	137***	88.7	10-520	49***	22.8	5.9-99	72.6***	22.2	36.3-129.8

b)

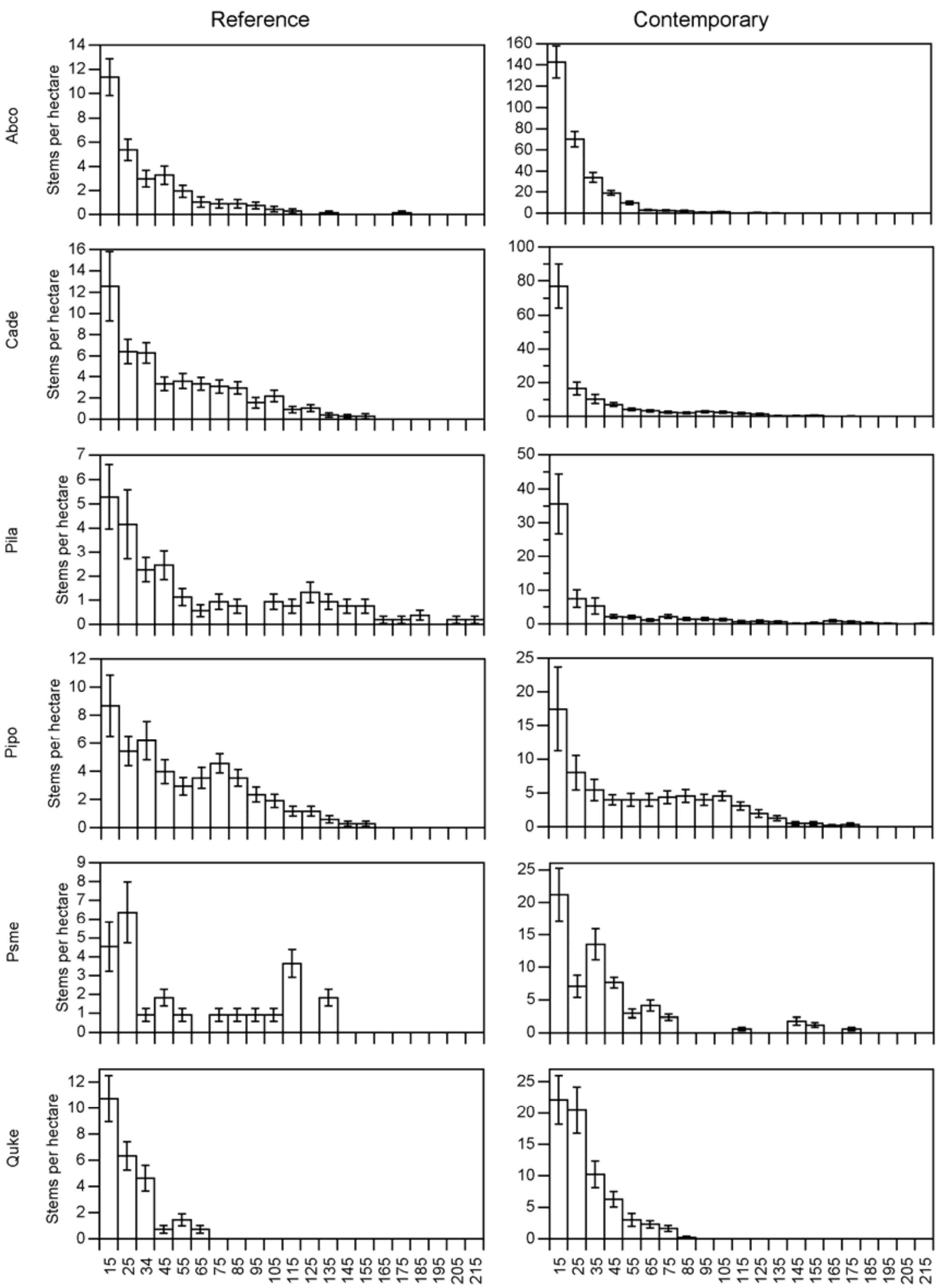


Figure 4a. Mean (± SE) density of trees (>10 cm dbh) in 10 cm diameter classes in the reference (AD 1899) and contemporary Big Oak Flat mixed conifer forest, Yosemite National Park, California. Note that the y-axis scale is different on each graph. Species acronyms are Abco (Abies concolor), Cade (Calocedrus decurrens), Pila (Pinus lambertiana), Pipo (Pinus ponderosa), Psme (Pseudotsuga menziesii), Quke (Quercus kelloggii). Values are for trees >10 cm dbh on each date. Size-class distributions were significantly different between 1899 and 2002 for incense-cedar and sugar pine (p<0.01).

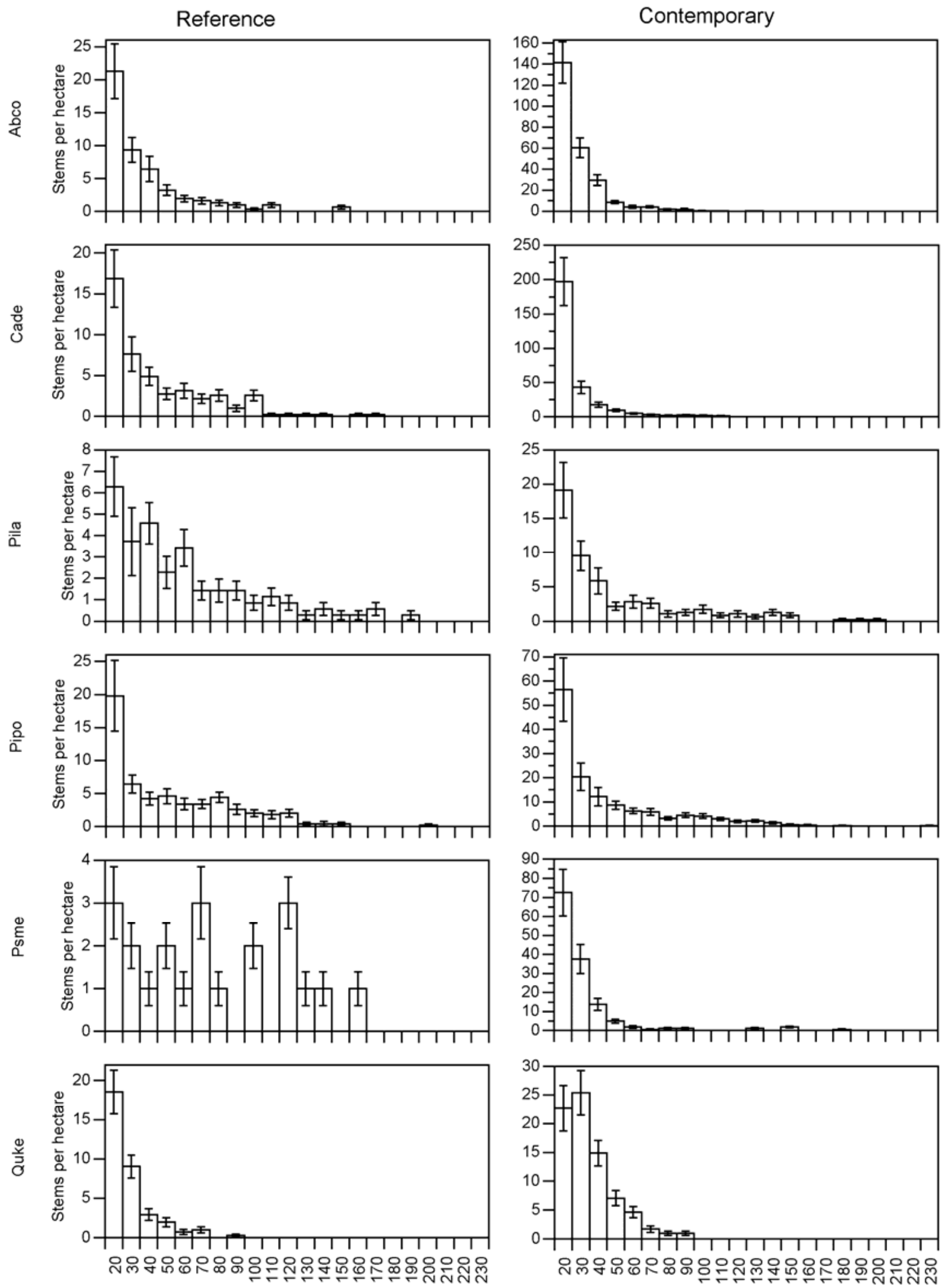


Figure 4b. Mean (± SE) density of trees (>10 cm dbh) in 10 cm diameter classes in the reference (AD 1899) and contemporary South Fork Merced mixed conifer forest, Yosemite National Park, California. Note that the y-axis scale is different on each graph. Species acronyms are Abco (Abies concolor), Cade (Calocedrus decurrens), Pila (Pinus lambertiana), Pipo (Pinus ponderosa), Psme (Pseudotsuga menziesii), Quke (Quercus kelloggii). Values are for trees >10 cm dbh on each date. Size-class distributions were significantly different between 1899 and 2002 for incense-cedar and Douglas-fir (p<0.01).

Table 4. Mean, standard deviation and range of density (ha^{-1}), basal area (m^2 ha^{-1}), and quadratic mean diameter (cm) of trees (>10 cm dbh) in the reference (AD 1899) and contemporary forest, in forest types identified by cluster analysis of species importance values in the Big Oak Flat mixed conifer forest, Yosemite National Park, California. Forest types are white fir/ incense-cedar (WF/IC), white fir/ incense-cedar/ sugar pine (WF/IC/SP), incense-cedar/ sugar pine/ ponderosa pine (IC/SP/PP), and ponderosa pine/ incense cedar/ California black oak (PP/IC/BO). n= number of samples in each forest type. Species acronyms are Abco (<u>Abies</u> <u>concolor</u>), Cade (<u>Calocedrus</u> <u>decurrens</u>), Pila (<u>Pinus</u> <u>lambertiana</u>), Pipo (<u>Pinus</u> <u>ponderosa</u>), Psme (<u>Pseudotsuga</u> <u>menziesii</u>), Quke (<u>Quercus</u> <u>kelloggii</u>). Reference forest types that are significantly different from 2002 forests, * = p<0.05; ** = p<0.01; *** = p<0.001.

	Forest Types											
	WF/ IC n=28						WF/ IC/ SP n=28					
	1899			2002			1899			2002		
Species	Density	BA	QMD	Density	BA	QMD	Density	BA	QMD	Density	BA	QMD
White fir	27.9 (33)***	5.5 (8.6)***	39.9 (28.2)	307.1 (154.7)	18.7 (7.5)	32 (14.4)	23.9 (23)***	3.8 (6.3)***	38.2 (23.8)	398.2 (153.1	30.5 (11.1	32.5 (9)
Incense Cedar	40 (30.8)***	11.3 (11)	58.9 (23.5)	147.1 (122.7)	18.4 (16.6)	48.3 (26.1)	40.7 (29.6)	13.4 (11.1)	63.9 (24.3)	38.2 (41.7)	14.3 (12.8	79.1 (31.6)
Ponderosa pine	37.9 (35.5)	13.3 (10.3)	71.9 (28.5)*	50.4 (72.5)	24.2 (22.6)	92.2 (32.8)	12.5 (15.8)	5.8 (9.1)	72.5 (33.5)*	5.7 (9.2)	5.8 (9.8)	111.4 (31.9)
Sugar pine	14.3 (15.5)	7.1 (11.1)	71 (42.9)	24.1 (23.7)	12.2 (13)	92 (54.5)	15 (18)	9.1 (14.7)	87.3 (60.1)	36.8 (83.5)	17.7 (20.9	113.7 (59.3)
Douglas-fir	4.6 (20.8)	0.8 (3)	62.2 (62.3)	20.7 (49.9)	3.8 (11.9)	42.8 (21)	0.7 (2.6)	0.3 (1.4)	56.2 (56.4)	6.4 (19.5)	1 (2.9)	44.6 (12.5)
California black oak	8.6 (16.9)	0.7 (1.7)	29.4 (14.2)	24.6 (72.4)	1.9 (4.3)	36.7 (15.2)	5.4 (10.7)	0.3 (0.7)	25.5 (10.1)	9.3 (22.4)	0.9 (2.4)	32 (16.6)
Total	133.2 (70.4)*	38.6 (20.7)**	61.4 (16.1)**	573.2 (247.4)	79.2 (26.6)	44.2 (10.8)	98.2 (45.1)**	32.6 (19.3)**	66.3 (23.4)***	494.6 (181.3	69.2 (26)	43.3 (10.6)

	Forest Types											
	IC/ SP/ PP n=18						PP/ IC/ BO n=11					
	1899			2002			1899			2002		
Species	Density	BA	QMD	Density	BA	QMD	Density	BA	QMD	Density	BA	QMD
White fir	16.7 (30.5)***	1.3 (2.5)***	27.6 (8.7)	75.6 (54.6)	6.3 (6.9)	32.2 (12.2)	2.7 (6.5)	0.3 (0.8)	35.3 (6)	4.5 (15.1)	0.2 (0.6)	23 (0)
Incense Cedar	70.6 (70.5)***	12 (12)**	49.2 (25.6)	270.6 (215.7)	26.6 (13.8)	41.6 (20.3)	16.4 (13.6)*	5.7 (5.6)	65.5 (30.2)	75.5 (82.7)	12.1 (11)	56.1 (38.9)
Ponderosa pine	40.6 (32.4)	15.3 (11.1)	75 (35.3)	64.4 (111.4)	14.3 (15.2)	69.5 (28.9)	81.8 (54.2)	18.8 (9.7)**	59.9 (19.9)	93.6 (64.7)	30.8 (9.8)	74.4 (25.9)
Sugar pine	21.2 (29.3)*	8.4 (12.4)	85 (37.4)**	131.7 (132.7)	8.1 (9)	30.9 (22.7)	4.5 (5.2)	3.7 (7.3)	88.3 (56.7)	8.2 (16)	0.5 (1.3)	32.5 (36.1)
Douglas-fir	5.6 (12.5)	3.6 (9.2)	88.4 (29.7)	15 (25.5)	5.1 (14.4)	51.5 (37.4)	0.9 (3)	0.9 (3)	113.3 (0)	3.6 (12.1)	0.4 (1.4)	38.1 (0)
California black oak	25 (43.6)	1.3 (2.3)	26.1 (7.8)	52.2 (77.7)	5.7 (11)	31.4 (10.7)	14.5 (19.2)**	1.2 (1.8)*	35.1 (17.8)	87.3 (80.6)	6.1 (5.7)	27.7 (10)
Total	178.3 (99)***	41.9 (25.6)**	57 (22.7)**	609.4 (272.8)	66 (23.8)	39.3 (11)	120.9 (71.8)	30.6 (9.3)**	64.6 (22.9)	272.7 (147.9	50.1 (14.7	52 (12.5)

structural characteristics did not increase ($p>0.05$) for other species between 1899 and 2002. The shape of species' size-class distribution in 1899 and 2002 was different for white fir and incense-cedar ($p<0.05$).

White fir/ incense-cedar/ sugar pine – Reference and contemporary forest conditions were different and the contemporary forest has more trees, more basal area, and smaller diameter trees ($p<0.01$) (Table 4). The overall difference is mainly due to significant increases in density, and basal area for white fir ($p<0.01$) and not for other species ($p>0.05$). Size-class distributions were different between 1899 and 2002 for only Douglas-fir and ponderosa pine ($p<0.05$).

Incense-cedar/ sugar pine/ ponderosa pine – Reference and contemporary forest conditions were different and the contemporary forest has more trees and more basal area ($p<0.01$) but not larger diameter trees ($p>0.05$) (Table 4). The overall differences in density and basal area are due to increases ($p<0.05$) for white fir, incense-cedar, and sugar pine and not for other species ($p>0.05$); white fir and black oak diameter were also larger in 2002 ($p<0.01$). Size-class distributions were different between 1899 and 2002 for all species except white fir ($p<0.05$).

Ponderosa pine/ incense-cedar/ California black oak – Reference and contemporary forest conditions were different and the contemporary forest has more trees and more basal area ($p<0.01$) but not larger diameter trees ($p>0.05$) (Table 4). The overall differences in density and basal area are due to increases ($p<0.05$) for black oak and incense-cedar, and not for other species ($p>0.05$). In fact, sugar pine and Douglas-fir basal area were lower in the contemporary forest ($p<0.01$). Size-class distributions were different between 1899 and 2002 for white fir, incense-cedar, sugar pine and Douglas-fir ($p<0.05$).

South Fork Merced

White fir/ incense-cedar – Reference and contemporary forest conditions were different and the contemporary forest has more trees that are smaller in diameter ($p<0.05$) but basal areas were similar ($p>0.05$) (Table 5). The overall differences in density and tree diameter are due to increases ($p<0.05$) in the density of small diameter white fir and incense-cedar ($p<0.05$); white fir basal area was also higher in 2002 ($p<0.01$). Size-class distributions were different between 1899 and 2002 for incense-cedar, Douglas-fir, and California black oak ($p<0.01$).

Incense-cedar/ ponderosa pine – Reference and contemporary forest conditions were different and the contemporary forest has more trees that are smaller in diameter ($p<0.05$) but basal areas were similar ($p>0.05$) (Table 5). The overall differences in density and tree diameter are due to increases ($p<0.05$) in the density of small diameter incense-cedar ($p<0.01$), there were no increases for other species ($p>0.05$). Size-class distributions were different between 1899 and 2002 for white fir, incense-cedar, Douglas-fir, and California black oak ($p<0.05$).

White fir/ sugar pine – Reference and contemporary forest conditions were different and the contemporary forest has more trees that are smaller in diameter ($p<0.05$) but basal areas were similar ($p>0.05$) (Table 5). The overall differences in density and tree diameter are due to increases ($p<0.05$) in the density of small diameter white fir ($p<0.01$), there were no increases for other species ($p>0.05$). Size-class distributions were

Table 5. Mean (SD) density (ha^{-1}), basal area (m^2 ha^{-1}), and quadratic mean diameter (cm) of trees (>10 cm dbh) in the reference (AD 1899) and contemporary forest, in forest types identified by cluster analysis of species importance values in the South Fork mixed conifer forest, Yosemite National Park, California. Forest types are white fir/ incense-cedar (WF/IC), incense-cedar/ ponderosa pine (IC/PP), white fir/ sugar pine (WF/IC), ponderosa pine/ incense-cedar (PP/IC). n= number of samples in each forest type. Species acronyms are Abco (<u>Abies concolor</u>), Cade (<u>Calocedrus decurrens</u>), Pila (<u>Pinus lambertiana</u>), Pipo (<u>Pinus ponderosa</u>), Psme (<u>Pseudotsuga menziesii</u>), Quke (<u>Quercus kelloggii</u>). Reference forest types that are significantly different from 2002 forests, * = p<0.05; ** = p<0.01; *** = p<0.001.

	Forest Types											
	WF/ IC n=16						IC/ PP n=17					
	1899			2002			1899			2002		
Species	Density	BA	QMD	Density	BA	QMD	Density	BA	QMD	Density	BA	QMD
White fir	35.6 (44.4)***	4.6 (5.8)***	42.1 (23.7)	326.9 (129.3)	18.2 (8.3)	27.2 (9.4)	12.4 (29.7)	1.7 (3.3)	56.9 (34.3)*	44.7 (66.5)	1.7 (3.1)	22.4 (9.2)
Incense Cedar	45.6 (52.3)***	15.3 (15.3)	74.5 (34.7)**	314.4 (264.9)	20.7 (13.5)	39 (25)	44.7 (39.9)***	14.6 (9.9)	69.3 (27.9)**	461.8 (461.3)	22 (12.7)	30.1 (14.3)
Ponderosa pine	30.6 (22.6)	18.3 (13)	92.3 (32.5)	33.1 (28)	18.6 (12.2)	96.2 (34.9)	28.8 (21.5)*	15.1 (15.2)	77.3 (37.7)	93.5 (124.4)	16.7 (14.2)	69.1 (50.2)
Sugar pine	11.9 (15.2)	8.3 (11.4)	88.7 (37.4)	28.8 (33.2)	10 (10.2)	79.3 (45.5)	10.6 (15.2)	5.1 (8)	85.9 (46.4)	44.7 (50)	7.2 (8.7)	57 (48.2)
Douglas-fir	1.9 (7.5)	1.3 (5.2)	94.2 (0)	11.9 (36.4)	1.4 (4.2)	44.2 (28)	7.6 (18.2)	3.2 (9.4)	53.6 (32.2)	92.4 (164)	5.8 (8.2)	32.7 (13.9)
California black oak	21.9 (30.2)	3.8 (4.7)	51 (15.4)	36.3 (39.8)	4.4 (5.3)	37.6 (12.4)	37.1 (41.3)	5.4 (6.4)	42 (11.4)	90.6 (94.2)	8 (8.9)	33.9 (10.8)
Totals	147.5 (82.6)***	51.6 (24.1)	68.7 (19.2)***	751.3 (298.2)	73.3 (18.7)	37.2 (8.9)	141.2 (82.8)**	45 (24.3)*	68.6 (23.6)**	827.6 (510.1)	61.4 (23.1)	33.7 (8.8)

	Forest Types											
	WF/ SP n=10						PP/ IC n=21					
	1899			2002			1899			2002		
Species	Density	BA	QMD	Density	BA	QMD	Density	BA	QMD	Density	BA	QMD
White fir	55 (40.9)	14.4 (12.3)	58.9 (25.7)*	421 (350.7)	24.7 (15.5)	29.5 (12.2)	2.4 (7.7)*	0.8 (3)	63.6 (41.2)	8.1 (32.8)	1.2 (3.9)	62.5 (42.7)
Incense Cedar	20 (43.5)***	4.2 (7)	56.4 (24.4)***	49 (53.4)	4 (7)	26.5 (17.1)	28.1 (34)	7 (8.6)	59.1 (23.5)*	122.4 (151)	10.3 (9.1)	42.2 (25.4)
Ponderosa pine	-	-	-	-	-	-	75.7 (67.1)***	32.1 (14.9)	80.5 (23.2)**	218.1 (195.2)	37.4 (12.6)	58 (23.6)
Sugar pine	54 (34.7)*	36.2 (13.8)	102.6 (30.6)	78 (60.7)	29.8 (17.4)	86.5 (42.1)	4.3 (11.2)	1.6 (4.4)	68.4 (5.3)	18.1 (42.4)	1.6 (3.8)	40.7 (23.6)
Douglas-fir	5 (5.3)	7.7 (9.1)	136.9 (30.4)	39 (71.4)	8.4 (12)	74.9 (46.4)	-	-	-	2.4 (8.9)	0.2 (0.6)	36.5 (12.3)
California black oak	8 (15.5)	0.6 (1.2)	28.2 (14.4)	13 (18.3)	0.9 (1.3)	27.9 (6)	12.9 (18.7)*	2 (2.8)	47.5 (23.7)	45.7 (52.2)	3 (3.2)	31.5 (13.4)
Totals	142 (89.8)***	63.1 (23.3)	82.3 (23.1)***	600 (311.2)	67.9 (22)	41.4 (15.6)	123.3 (101.4)*	43.6 (18.3)	74.2 (22.8)**	414.8 (351.2)	53.7 (18)	48.7 (17.2)

different between 1899 and 2002 for white fir, incense-cedar, Douglas-fir, and California black oak (p<0.05).

Ponderosa pine/ incense-cedar – Reference and contemporary forest conditions were different and the contemporary forest has more trees that are smaller in diameter (p<0.05) but basal areas were similar (p>0.05) (Table 5). The overall differences in density and tree diameter are due to increases (p<0.05) in the density of small diameter ponderosa pine and incense-cedar (p<0.05), there were no increases for other species (p>0.05). Size-class distributions were different between 1899 and 2002 for white fir and sugar pine (p>0.05).

Structural diversity

Despite differences in the density, size, and basal area of the reference and contemporary forest the average shape of species' diameter-class distributions were only different for incense-cedar, sugar pine, and Douglas-fir at the study area scale. There was more variation in diameter-class distributions at the forest group scale. However, the reference forests were structurally similar to the contemporary forest (Table 6). In both study areas, the average Shannon's diversity index of forest size structure for all plots was similar (p>0.05) for the reference (BOF = 2.0, SFM = 1.8) and the contemporary forest (BOF = 1.9, SFM = 1.9). Moreover, reference forest structure was similar (p>0.05) to the contemporary forest structure in all forest groups except for the ponderosa pine/ incense-cedar/ California black oak group in BOF (p<0.05) and the ponderosa pine/ incense-cedar group in SFM (p<0.05). The structural changes are clearly evident in visualizations of the reference forest and contemporary forest in BOF at plot (Figure 5) and study area scales (Figure 6).

Table 6. Shannon's diversity of the density of trees (>10 cm dbh) for each species in 10 cm diameter classes in the reference (AD 1899) and contemporary forest in the Big Oak Flat (a) and South Fork Merced (b) mixed conifer forest, Yosemite National Park, California. Species acronyms are Abco (Abies concolor), Cade (Calocedrus decurrens), Pila (Pinus lambertiana), Pipo (Pinus ponderosa), Psme (Pseudotsuga menziesii), Quke (Quercus kelloggii). * = Compositional groups with different structural diversity between 1899 and 2002 (p<0.05).

BOF	Shannon's Diversity Index		
		1899	2002
Entire Study Area		2	1.9
Compositional Group			
	WF/ IC	2.1	1.9
	WF/ IC/ SP	1.9	1.7*
	IC/ SP/ PP	2.1	2
	PP/ IC/ BO	1.9	1.9

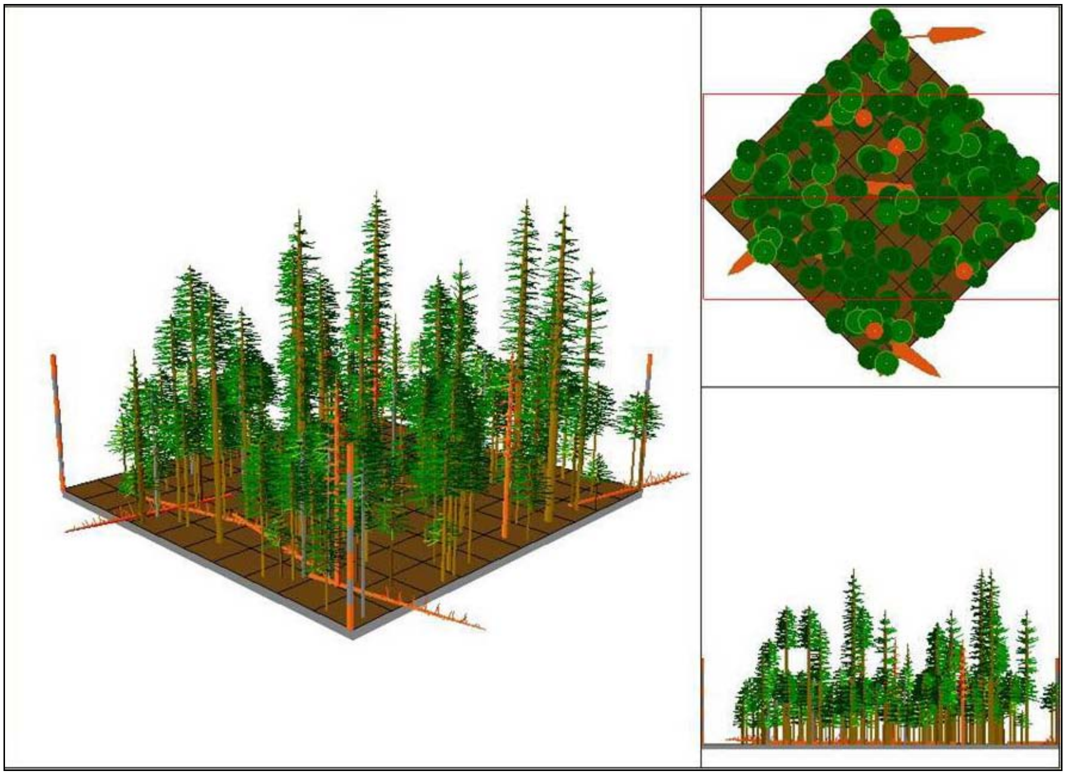
a)

SFM	Shannon's Diversity Index		
		1899	2002
Entire Study Area		1.8	1.9
Compositional Group			
	WF/ IC	1.9	1.9
	IC/ PP	1.8	1.9
	WF/ SP	2	1.9
	PP/ IC	1.7	1.9*

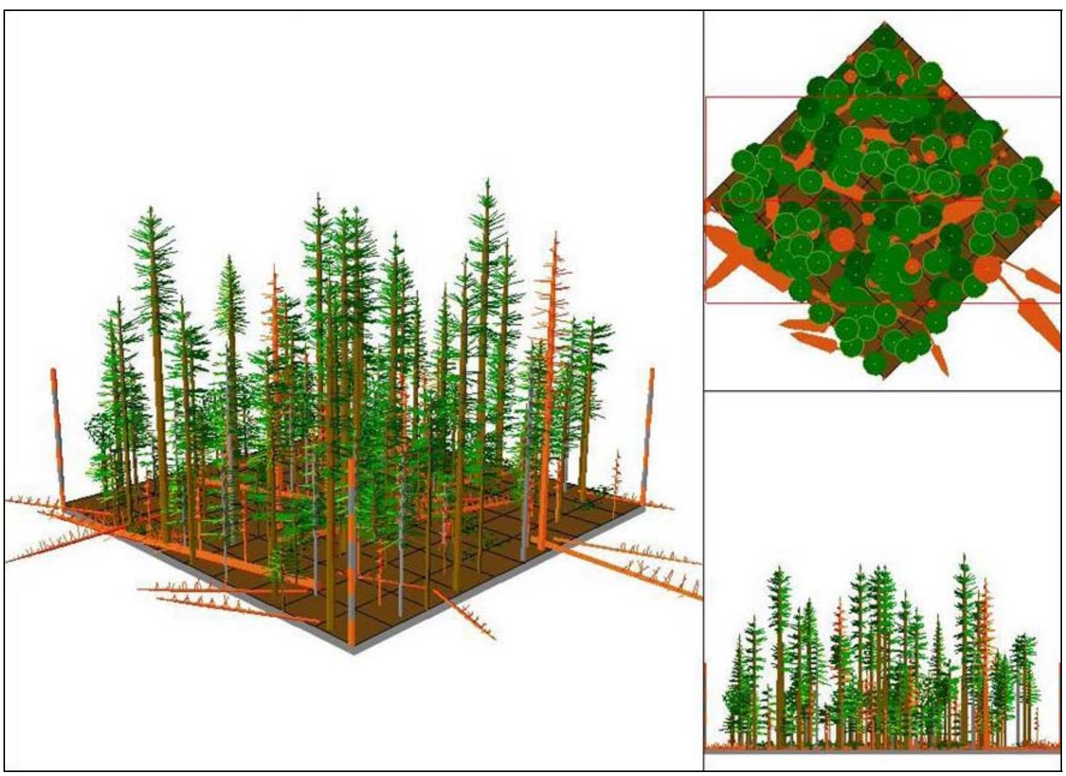
b)

Reference conditions and 1911 forest survey

There were similarities and differences in the reconstructed characteristics of the BOF forest and the 1911 inventory data within the BOF study area (Table 7). Overall, the reconstructed and 1911 forest had a similar density (p>0.05) but the reconstructed

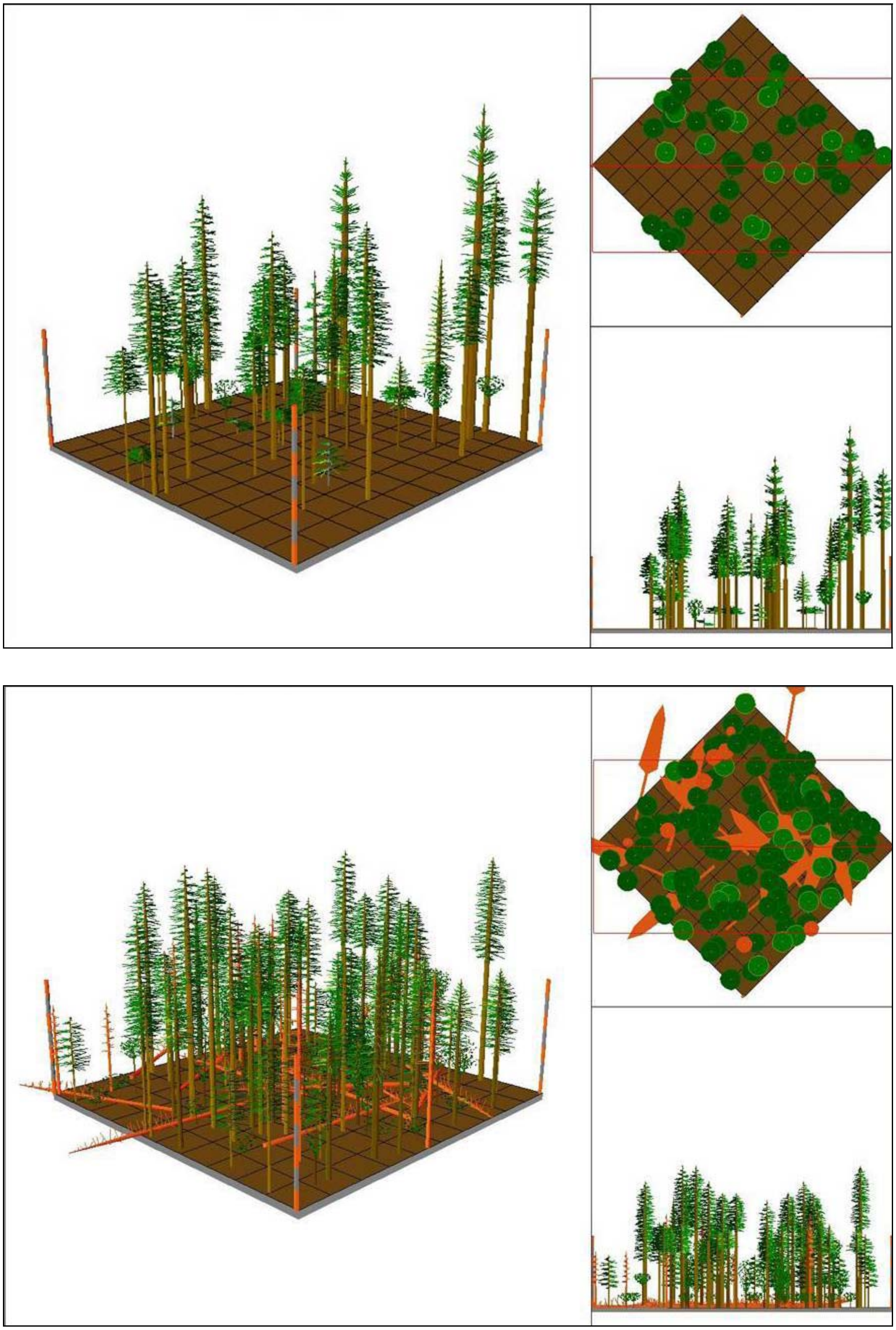


a)



b)

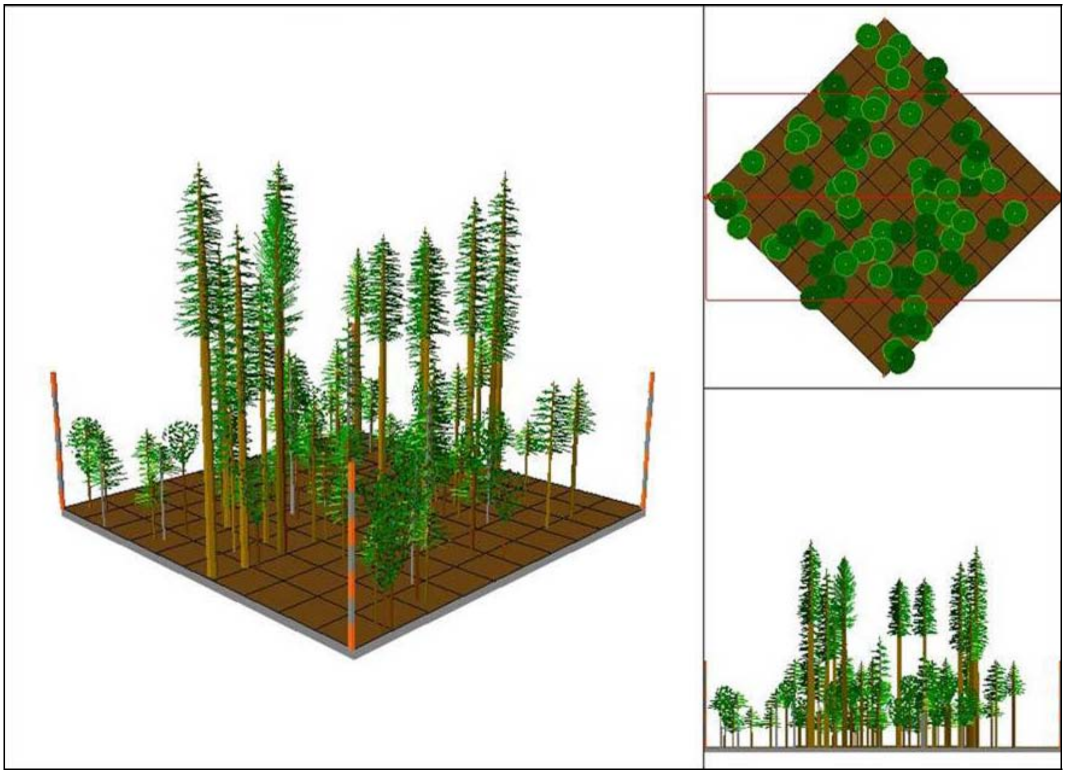
Figure 5a. Visual representations of reference (AD1899) (a) and contemporary (b) forest structure in selected plots representative of a low degree of structural change in the Big Oak Flat mixed conifer forest. Visualizations were developed using FVS software and represent 1 acre of forest.



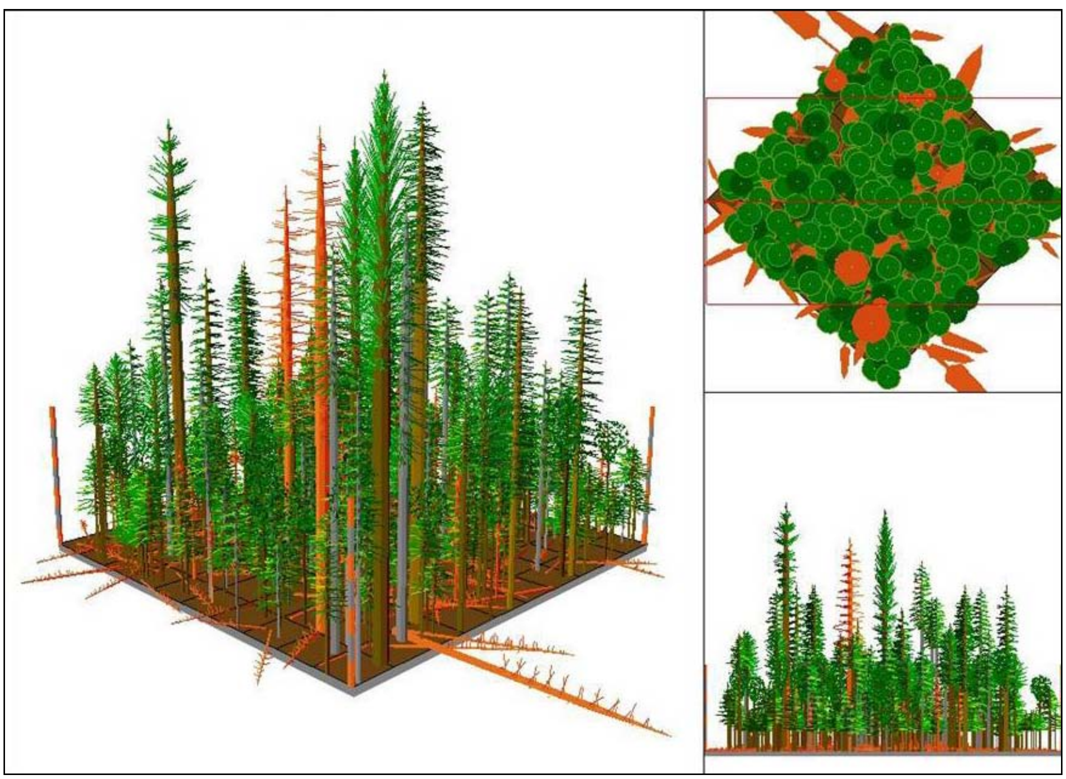
a)

b)

Figure 5b. Visual representations of reference (AD1899) (a) and contemporary (b) forest structure in selected plots representative of a medium degree of structural change in the Big Oak Flat mixed conifer forest. Visualizations were developed using FVS software and represent 1 acre of forest.

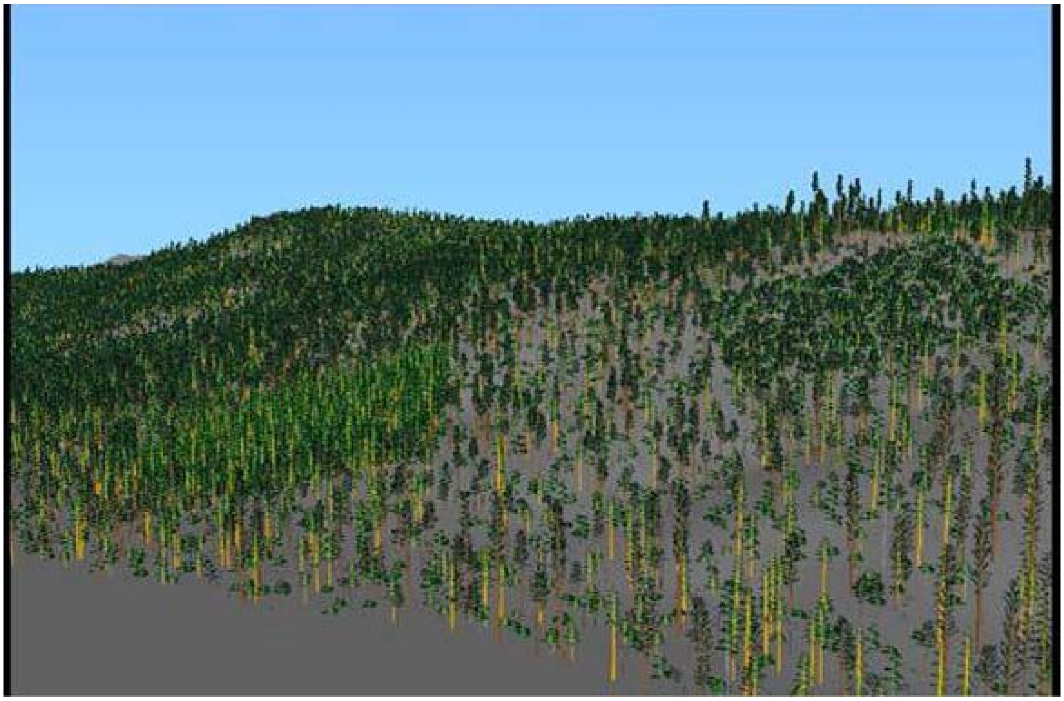


a)

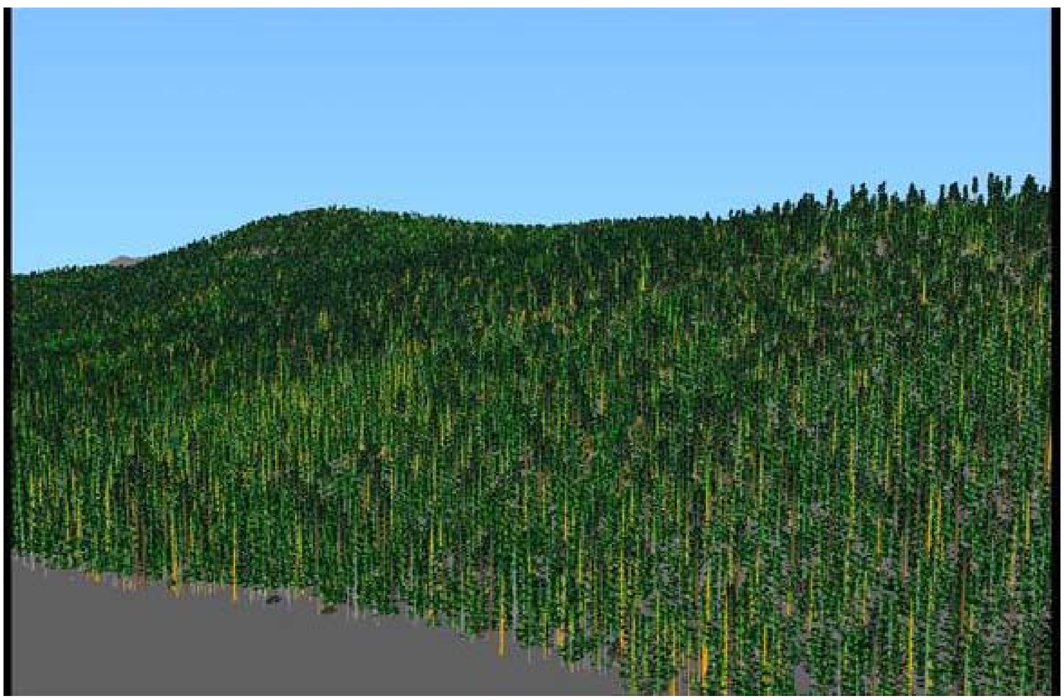


b)

Figure 5c. Visual representations of reference (AD1899) (a) and contemporary (b) forest structure in selected plots representative of a high degree of structural change in the Big Oak Flat mixed conifer forest. Visualizations were developed using FVS software and represents 1 acre of forest.

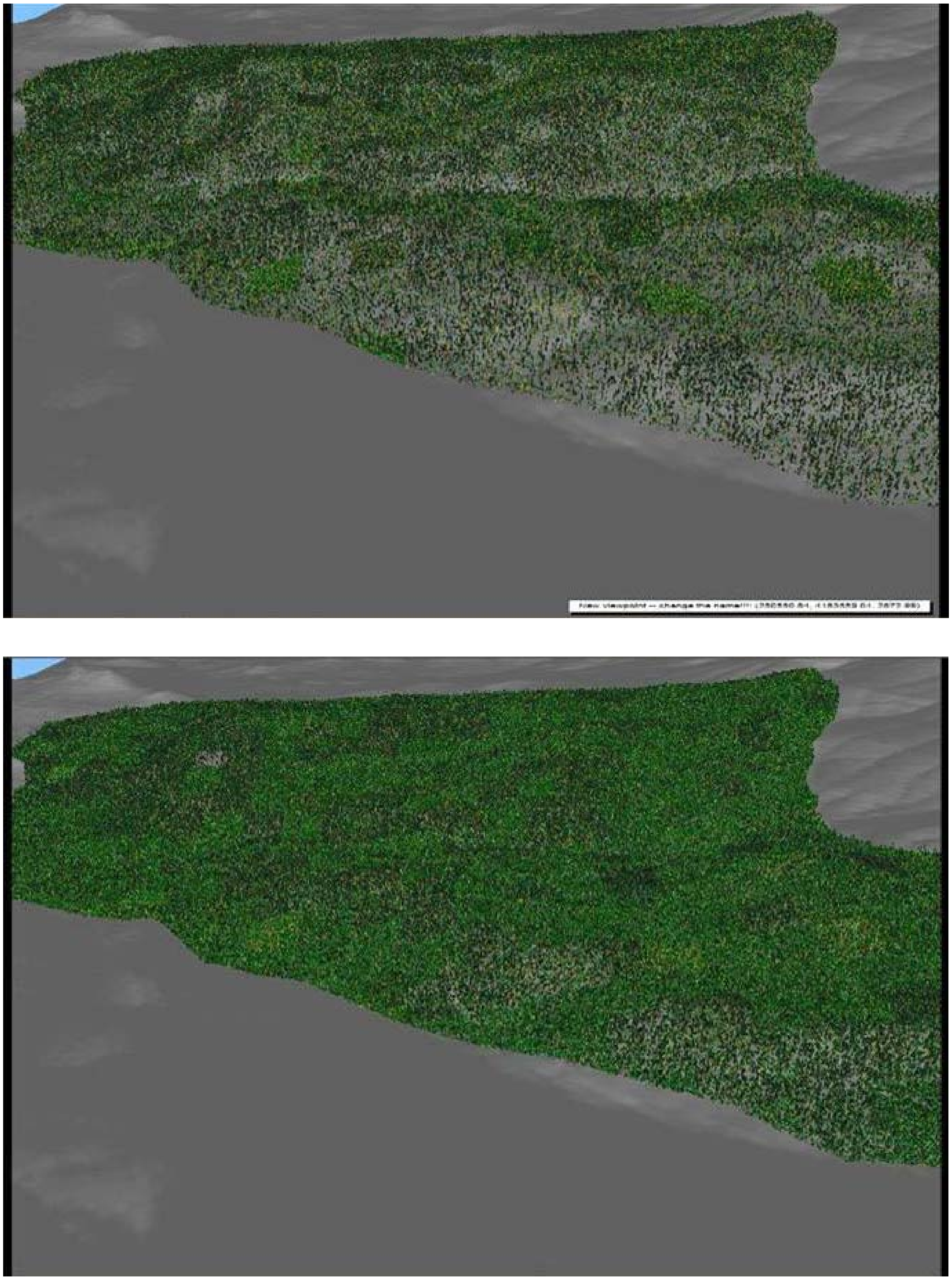


a)



b)

Figure 6a. Visual representation of the reference (AD1899) (a) and contemporary (b) forest landscape in the Big Oak Flat mixed conifer forest. The landscape visualization was developed by: 1) predicting the location (grid) of each forest type using topographic data and discriminant function analysis; and 2) placing average forest structure (tree size and density) of each forest type group in each grid cell on the landscape using FVS software. The view of the Big Oak Flat study area is from the southeast side looking northwest.



a)

b)

Figure 6b. Visual representation of the reference (AD1899) (a) and contemporary (b) forest landscape in the Big Oak Flat mixed conifer forest. The landscape visualization was developed by: 1) predicting the location (grid) of each forest type using topographic data and discriminant function analysis; and 2) placing average forest structure (tree size and density) of each forest type group in each grid cell on the landscape using FVS software. The view of the Big Oak Flat study area is from the southeast side looking northwest.

forest had a higher basal area and larger average sized trees (p<0.01). On a species basis, only incense-cedar and white fir had characteristics in the reconstructed forest that were different than in the 1911 forest. Incense-cedar had a greater reconstructed basal area (p<0.01) and white fir had a smaller average diameter (p<0.01) than in the 1911 forest.

Table 7. Mean (SD) density (ha^{-1}), basal area ($m^2\ ha^{-1}$), and quadratic mean diameter (cm) of trees (>15 cm dbh) in the reference (AD 1899) and contemporary forest, and in the forest inventory plots (1911) in the Big Oak Flat study area. Species acronyms are Abco (Abies concolor), Cade (Calocedrus decurrens), Pila (Pinus lambertiana), Pipo (Pinus ponderosa), Psme (Pseudotsuga menziesii). Black oak (Quercus kelloggii) was not sampled in the inventory plots and is not included. Reference forest characteristics that are significantly different from 1911 survey forest forests, ** = p<0.01; *** = p<0.001.

		Density (# trees/ha)			Basal area (m^2/ha)			Quadratic Mean Diameter (cm)		
		Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
Abco										
	2002	181.2	140.8	0-500	17.7	14.1	0-57.3	36.9	11.2	22.8-70.5
	1911	13.1	19.6	0-63.8	3.4	6.1	0-27.8	72.7	24.5	22.3-122.1
	1899	15.8	22.8	0-110	3.4	6.6	0-34.1	44.8**	24.3	22.9-120.3
Cade										
	2002	74.5	90.7	0-480	17.8	15	0-69.4	67.1	27.8	22.8-118.9
	1911	31.8	39.8	0.5-158.6	4.6	3.9	0-13.8	54.9	22.2	22.5-104.4
	1899	35.4	28.3	0-140	11.3**	10.8	0-52.4	62.5	24.3	22.9-120.7
Pila										
	2002	31.8	52.6	0-210	11.4	15.6	0-67.4	87.4	57.1	22.8-220.9
	1911	8.5	9	0-38.6	2.8	3.2	0-10.2	68.5	32.1	13.9-130.1
	1899	12.9	17.6	0-100	7.6	12.4	61.8	85.5	48.1	22.9-205.7
Pipo										
	2002	38.1	56.6	0-330	16.8	18.5	0-86.1	87.9	31.8	22.8-160
	1911	42.9	42.6	0-145.2	8.9	7.9	0-25.8	62	23.1	21.3-105.9
	1899	32.4	35.2	0-160	11.9	10.9	39.6	72.7	29.7	22.9-160
Psme										
	2002	9.8	25.8	0-150	2.8	9.9	0-60.7	54.7	35.8	22.8-160.5
	1911	1.6	6.1	0-31	0.9	3.7	0-19.3	77.2	7.9	71.9-89
	1899	2.6	9.8	0-70	1.2	4.6	0-35.2	78.6	40.1	22.9-129.5
All Trees										
	2002	335.3	146.4	30-750	66.6	27.8	18.1-142	53.1	14	25.4-100.8
	1911	97.9	68	8.3-216.3	20.6	10.1	0.7-34.4	56.7	17.2	32.6-98.4
	1899	99.1	53.2	10-330	35.3***	20.8	4.5-101	69.7***	22.2	34.7-132.3

Tree Spatial Patterns

There was a high incidence of spatial autocorrelation in the ages of trees in the reference forests. Tree ages were spatially autocorrelated in 74% and 50% of the plots in BOF and SFM, respectively. In BOF, the highest frequencies of positive spatial auto correlation were in the 1-9 m and 18-27 m distance classes while in SFM positive frequencies were distributed more equally among distance classes (Table 8). Thus, Moran's I indicates that small and intermediate sized patches of similarly aged trees were a conspicuous structural feature of the reference forest. For both study areas, significant negative spatial autocorrelation was most frequent in intermediate distance classes (15-24 m). This suggests that different aged patches are most frequently separated by distances of 15-24 m.

Spatial autocorrelation of tree ages was also evident in the contemporary forest but the scale of analysis was confined to distances <10 m. Trees that established after

1899 were only sampled in intermediate sized plots (250 m^2) at each grid point. At these distances, 44.8% and 43.5% of the tree ages in the plots in BOF and SFM exhibited spatial autocorrelation, respectively. The frequency of spatial autocorrelation in the reference forest in the same distance classes (i.e. < 10 m) was lower (BOF 32.9 %, SFM 18.8%). The higher frequency of positive spatial autocorrelation in the contemporary forest is probably the result of patchy post fire suppression tree establishment.

Table 8. Frequency of plots in the Big Oak Flat (BOF, n=85) and South Fork Merced (SFM, n=64) mixed conifer forests with values of Moran's I that indicate spatial autocorrleation (P<0.05) by 1 m distance classes for the reference (AD 1899) and contemporary forest (AD 2002). Positive spatial autocorrelation represents distances between similar aged trees, while negative values represent distances between trees of dissimilar age.

BOF

Year		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
2002	"+"	4	4	1	4	3	4	2	1		2																				
	"-"		4	1		2	4	6	2	2	6																				
1899	"+"	3	6	2	8	3	9	6	3	5	3		1			2	1	2	1	1	3	2	4	5	4	6	5	4	4	5	5
	"-"				3	3	3	3	3	3	2	1	4	6	3	5	5	8	7	7	3	5	3	1		3	1	2	1		2

SFM

Year		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
2002	"+"	2	4	6	4	3	4	3	2	3	4																				
	"-"		3	2	2	1	5	3	3	4	5																				
1899	"+"	2		2		3	4	2	1		3	1	2	2	1	3	2		1	1	4	1	1		1	1	3	2			2
	"-"					1	1	2		2		4		1			2	1	5	1	1	1	3	6	1	2	1			1	2

Fire Regimes

Fire record – A long record of fire was recorded in fire scar samples in both study sites. In BOF, a total of 288 fires were identified in the 209 samples between 1379 and 2002. In SFM, the fire record spanned the period 1499-2002 and a total of 153 fires were identified in 156 samples. The period 1575 to 2002 was selected as the period for the fire disturbance analysis to ensure adequate sample depth. Samples depths >10% are generally adequate to analyze temporal variation in fire occurrence in short fire return interval ecosystems (Caprio and Swetnam 1995) and sample depth at both sites exceeded 10% after 1575.

Fire Season – The position of fires within annual growth rings indicate that fires burned mainly late in the growing season (latewood BOF = 38.7%, SFM = 54.2%) or after trees had stopped growth for the year (dormant BOF = 39.8%, SFM = 37.6%). Earlier season fires were recorded by the samples, but infrequently (Table 9).

Fire return intervals – Statistical description of fire-return intervals for grid points in each study area includes the mean fire interval (MFI, average number of years between fires), median fire interval, and the Weibull median probability interval (WMPI) as measures of central tendency. The WMPI is a measure used to describe central tendency in asymmetrical distributions, like fire interval distributions (Grissino-Mayer 2001). The composite fire interval distributions for both study areas were positively skewed, they had more short than long FRI, and they had similar mean, median, and WMPI FRI (P>0.05) (Table 10). The mean composite FRI of all fires was 1.5 years (range 1-16 yrs) in BOF and 1.7 years (range 1-12 years) in SFM. More widespread burns recorded by 10% or more and 25% or more of the grid points occurred at longer intervals. In BOF and

SFM, the mean FRI for 10% burns were 2.6 years (range 1-11 years) and 2.5 years (range 1-12 years) and for 25% burns were 10 years (range 2-28 years) and 6.9 years (range 1-48 years), respectively. As expected, mean point FRI were longer than the mean FRI for the composite records. The mean point FRI was 12.4 years (range 2-84 years) for BOF and 9.9 years (range 1-60 yrs) for SFM. There was no spatial variation in mean composite or point fire return intervals related to forest composition ($p>0.05$) or slope aspect ($p>0.05$) in either study area (results not shown). Consequently, fire regime statistics are reported for each study area as a whole.

Table 9. Seasonal distribution of fires recorded in tree ring samples in the Big Oak Flat (BOF) and South Fork Merced (SFM) mixed conifer forests, Yosemite National Park, California.

BOF

	Seasonality of Burn		Fire Scar position				
Total	Determined	Undetermined	Early	Middle	Late	Latewood	Dormant
Number	1700	1178	19	108	238	658	677
Percentage	59.1	40.9	1.1	6.4	14	38.7	39.8

SFM

	Seasonality of Burn		Fire Scar position				
Total	Determined	Undetermined	Early	Middle	Late	Latewood	Dormant
Number	1387	966	6	21	87	752	521
Percentage	58.9	41.1	0.4	1.5	6.3	54.2	37.6

Table 10. Composite and point fire return interval statistics (years) for the period 1575-2002 in the Big Oak Flat (BOF) and South Fork Merced (SFM) mixed conifer forest, Yosemite National Park, California.

BOF

Type of Sample	Mean	Median	WMPI	SD	Min.	Max.	Skewness	Kurtosis
Point	12.4	10	10.7	10.1	2	84	3.1	14.5
Composite								
Any scarred	1.5	1	1.2	1.6	1	16	5.5	34.5
>10% scarred	2.6	2	2.3	1.8	1	11	2	5.7
> 25% scarred	10	9	9.2	6.1	2	28	1	0.7

SFM

Type of Sample	Mean	Median	WMPI	SD	Min.	Max.	Skewness	Kurtosis
Point	9.9	8	8.7	7.4	1	60	2.3	7.8
Composite								
Any scarred	1.7	1	1.4	1.96	1	12	3.4	11.68
>10% scarred	2.5	2	2	2.34	1	12	2.23	4.91
> 25% scarred	6.9	4	5.2	8	1	48	3.32	12.94

Temporal patterns – Fire occurrence varied by time period (Table 11). The mean composite FRI was the same for the pre-Euro American and settlement periods in both study areas (BOF = 1.2 yrs, SFM 1.4 yrs). However, mean FRI were longer (BOF = 6.2 yrs, SFM = 5.3 yrs) during the fire suppression period ($p < 0.05$) and this temporal difference was also evident for more widespread fires. In both BOF and SFM, there was no difference in the mean FRI for either 10% or 25% burns for the pre-Euro American and settlement periods. Moreover, no burns of wider extent (10%, 25%) were recorded during the fire suppression period.

Fire Extent – In each study area, fires in most years (BOF, 81%; SFM 83%) intersected the edge of each sample area. This suggests that actual sizes for individual fires are larger than the reconstructed values.

Table 11. Composite fire return interval statistics (years) for the pre-Euro American, settlement, and fire suppression periods in the Big Oak Flat (BOF) and South Fork Merced (SFM) mixed conifer forest, Yosemite National Park, California. There was no difference in the median or mean fire return interval between the pre-Euro American and settlement period in either study area but both were longer (P<0.01, Kruskall Wallis H-test and t-test) during the fire suppression period.

BOF

All Fires	Time Period	Mean	Median	S.D.	Skewness	Range
All Years	1575-2000	1.4	1	1.5	5.8	1-16
Pre-EuroAmerican	1575-1849	1.2	1	0.7	8.3	1-10
Settlement	1850-1904	1.2	1	0.5	1.5	1-3
Fire Suppression	1905-2002	6.2**	5	4.2	0.9	2-16

10% scarred	Time Period	Mean	Median			Range
All Years	1575-2000	3.2	3	2.1	1.7	1-10
Pre-EuroAmerican	1575-1849	3	3	1.9	1.8	1-10
Settlement	1850-1904	3.7	3	2.6	1.3	1-9
Fire Suppression	1905-2002	-	-	-	-	-

25% scarred	Time Period	Mean	Median			Range
All Years	1575-2000	13.8	11	13.9	3	2-28
Pre-EuroAmerican	1575-1849	14.1	11	14.3	3.2	3-28
Settlement	1850-1904	14.7	9	16.3	0.5	2-16
Fire Suppression	1905-2002	-	-	-	-	-

SFM

All Fires	Time Period	Mean	Median	S.D.	Skewness	Range
All Years	1575-2000	1.7	1	1.8	3.5	1-12
Pre-EuroAmerican	1575-1849	1.4	1	1.4	5.5	1-12
Settlement	1850-1904	1.6	1	0.9	1.1	1-4
Fire Suppression	1905-2002	5.3**	5	3.2	0.04	1-10

10% scarred	Time Period	Mean	Median			Range
All Years	1575-2000	2.4	2	2.2	2.3	1-12
Pre-EuroAmerican	1575-1849	2.3	2	2.1	2.6	1-12
Settlement	1850-1904	3.7	3	2.8	0.8	1-10
Fire Suppression	1905-2002	-	-	-	-	-

25% scarred	Time Period	Mean	Median			Range
All Years	1575-2000	6.7	4	8.2	3.3	1-48
Pre-EuroAmerican	1575-1849	6.4	4	8	3.7	1-48
Settlement	1850-1904	11.7	6	11.6	0.6	4-25
Fire Suppression	1905-2002	-	-	-	-	-

Fire extent varied among years (Figure 7, 8) but most burns were small and half or more of the fires burned <10% (212 ha BOF, 160 ha SFM) of a study area in a given fire year (Figure 9). Large fires, however, burned in some years. Four fires in BOF and two fires in SFM burned areas > 1000 ha. The percentage of area burned by fires of different extent in BOF and SFM was similar. Burns <350 ha in size accounted for > 50% of the total area burned, while larger fires (i.e. >1000 ha) burned only 11% (BOF)

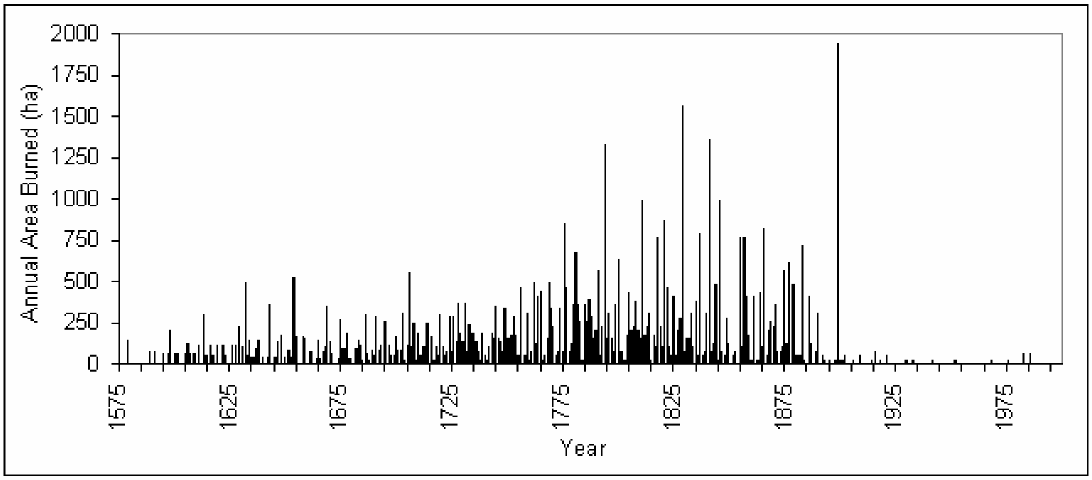


Figure 7. Annual fire extent between 1575 and 2000 in the Big Oak Flat mixed conifer forest, Yosemite National Park, California. Minimum fire extent is 25 ha.

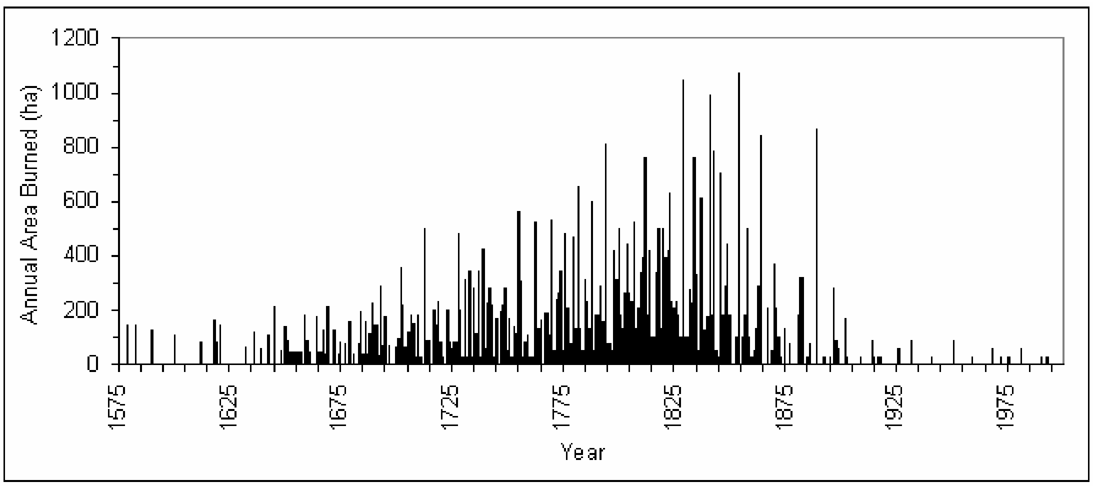


Figure 8. Annual fire extent between 1575 and 2000 in the South Fork Merced mixed conifer forest, Yosemite National Park, California. Minimum fire extent is 25 ha.

and 5% (SFM) of the total burned area, respectively. The median and mean extent of a fire was 205 ha and 115 ha in BOF, and 199 ha and 131 ha in SFM, respectively (Table 12). There was no statistical difference in the median or mean extent of a fire in the pre-Euro American and settlement periods ($P>0.05$), but the median and mean extent of a fire was smaller during the suppression period in both study areas.

Fire Rotation – The fire rotations for BOF (15 years) and SFM (16 years) for the entire study period (1575-2002) were similar, but fire rotations in each study area varied by time period (Table 13). Fire rotations for the pre-Euro American and settlement periods were much shorter in BOF (13 years, 10 years) and SFM (11 years, 13 years) than during the fire suppression period. Fire rotations for the fire suppression period were 378 years and 211 years in BOF and SFM, respectively.

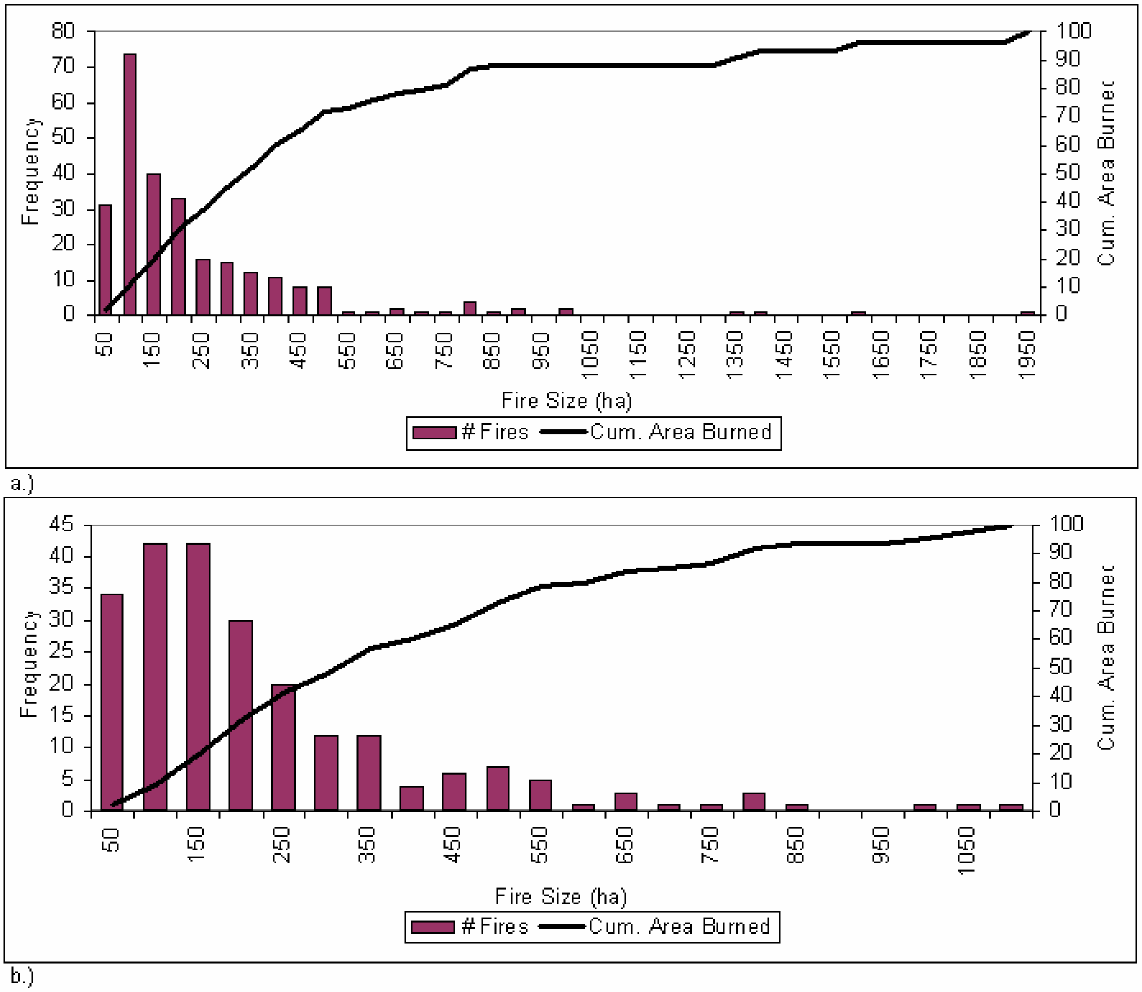


Figure 9. Frequency (50 ha fire extent classes) and cumulative area burned between 1575 and 2002 in the Big Oak Flat (a) and South Fork Merced (b) mixed conifer forest, Yosemite National Park, California.

Age Structure Patterns and Fire Severity

Six age-class groups were identified in each study area from the cluster analysis of stems >100 yrs old. All species were present in each group and tree density varied ($p<0.01$) among groups (Figure 10, 11). Ponderosa pine, incense-cedar and sugar pine were the species most widely distributed among age-classes and they were the oldest trees in the age-structural groups.

Big Oak Flat- Group 1 plots had the lowest density (for stems >100 years old) and ponderosa pine, incense-cedar, and sugar pine were present in a wide range of age-classes (Figure 10, Table 14a). White fir, Douglas-fir and California black oak were all < 300 years old. The large number of <100 year old white fir, incense-cedar and sugar pine established after fire suppression. On average, plots had trees in 5.5 age-classes >100 years (range 2-10) and they burned 27 times. Frequent tree establishment and high fire frequency suggest that fires were mainly of low severity with some moderate severity fire.

Table 12. Fire extent statistics during different time periods in the Big Oak Flat (BOF) and South Fork Merced (SFM) mixed conifer forests, Yosemite National Park, California.

BOF

	Period	Fire Extent (ha)			
		Mean	Median	S.D.	Range
All	1575-2000	205	115	246.3	25-1946
Pre-EuroAmerican	1575-1849	203	130	224.3	26-1562
Settlement	1850-1904	266	102	354.3	26-1946
Fire Suppression	1905-2002	39	28	17.9	26-80

SFM

	Period	Fire Size (ha)			
		Mean	Median	S.D.	Range
All	1575-2000	199	131	197.3	26-1075
Pre-EuroAmerican	1575-1849	209	148	189.6	26-1048
Settlement	1850-1904	214	118	254.2	26-1075
Fire Suppression	1905-2002	46	30	23.6	30-89

Table 13 Fire rotation (years) for different time periods in the Big Oak Flat (BOF) and South Fork Merced (SFM) mixed conifer forests, Yosemite National Park, California.

BOF

	Period	Fire rotation
All	1575-2002	16
Pre-EuroAmerican	1575-1849	13
Settlement	1850-1904	10
Fire Suppression	1905-2002	378

SFM

	Period	Fire rotation
All	1575-2002	15
Pre-EuroAmerican	1575-1849	11
Settlement	1850-1904	13
Fire Suppression	1905-2002	211

Group 2 plots had the highest density, most stems were <300 years old, and there were a large number of 80-180 year old trees. Older (>300 yrs) ponderosa pine, incense-cedar and sugar pine were present too. Douglas-fir was most abundant in this group. On average, plots had trees in 5.6 age-classes (range 3-9) and they burned 25.9 times. The frequent tree establishment and high frequency of fire suggest that fires were mainly low or moderate in severity.

Group 3 plots were moderately dense and distinguished by the wide range of age-classes occupied by ponderosa pine, incense-cedar, and California black oak. White fir, incense-cedar and sugar pine < 140 years old were abundant but few of their stems were > 300 years old. On average, plots burned 28.6 times and had trees in 5.9 age-classes (range 2-10). High fire frequency and frequent tree regeneration suggests that fires were mainly low and moderate in severity.

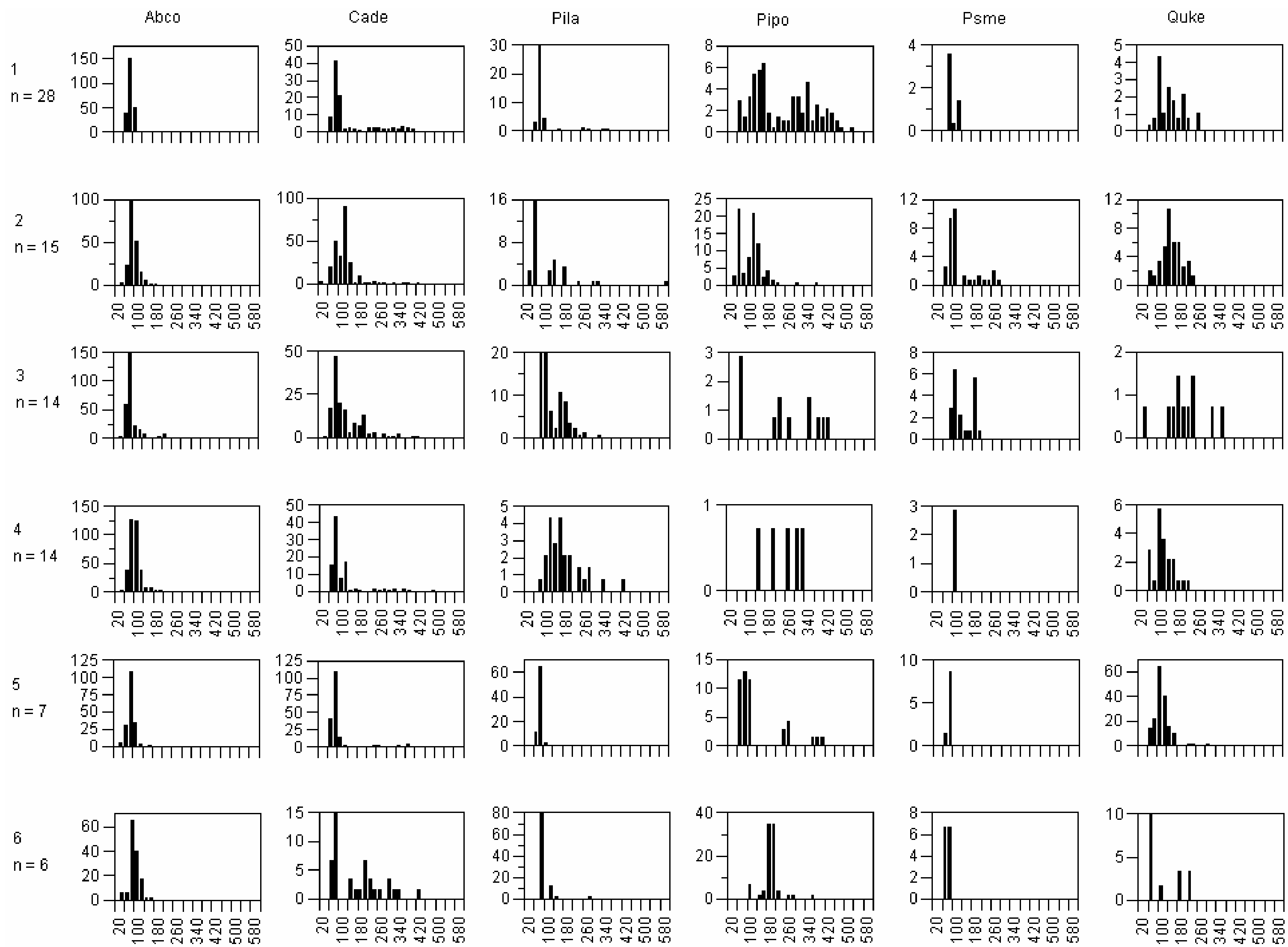


Figure 10. Mean age-class distribution for each species in the six age-class groups identified by cluster analysis of stems/ha >100 yrs old in 20 yr age-classes in Big Oak Flat mixed conifer forest, Yosemite National Park, California; n= number of plots. Species acronyms are Abco (<u>Abies concolor</u>), Cade (<u>Calocedrus decurrens</u>), Pila (<u>Pinus lambertiana</u>), Pipo (<u>Pinus ponderosa</u>), Psme (<u>Pseudotsuga menziesii</u>), Quke (<u>Quercus kelloggii</u>).

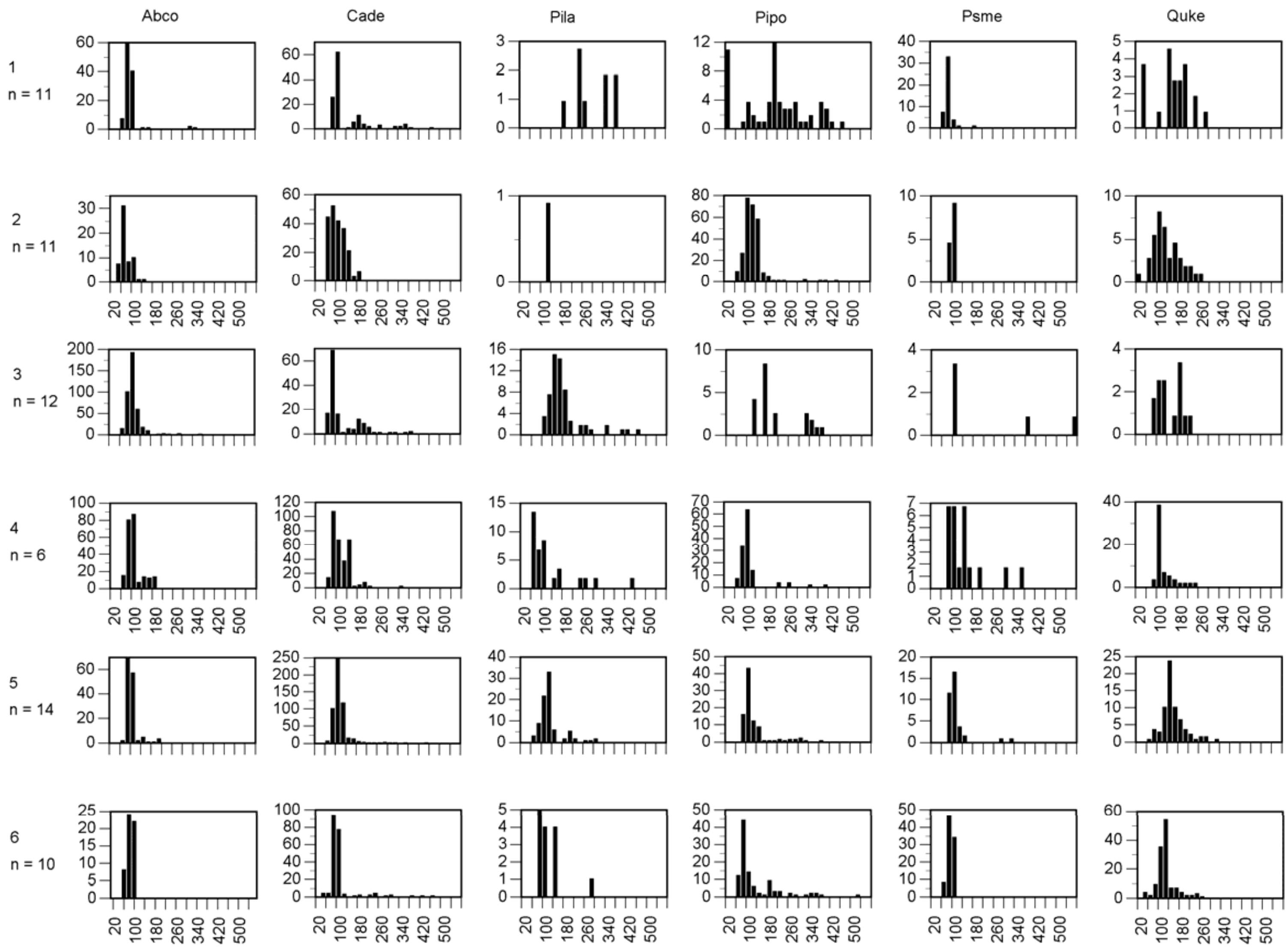


Figure 11. Mean age-class distribution for each species in the six age-class groups identified by cluster analysis of stems/ha >100 yrs old in 20 yr age-classes in South Fork Merced mixed conifer forest, Yosemite National Park, California; n= number of plots. Species acronyms are Abco (<u>Abies</u> <u>concolor</u>), Cade (<u>Calocedrus</u> <u>decurrens</u>), Pila (<u>Pinus</u> <u>lambertiana</u>), Pipo (<u>Pinus</u> <u>ponderosa</u>), Psme (<u>Pseudotsuga</u> <u>menziesii</u>), Quke (<u>Quercus</u> <u>kelloggii</u>).

Table 14. Mean density (stems/ha) of aged stems > 100 years old and all aged stems, mean number of occupied age-classes, and fire history characteristics for age-class groups identified by cluster analysis of stems >100 years old in plots in the Big Oak Flat (BOF) and South Fork Merced (SFM) mixed conifer forests, Yosemite National Park, California.

BOF

		Stems >100 yrs (ha^{-1})			All Stems (ha^{-1})			# 20 yr age-classes > 100 yrs		# 20 yr age-classes all stems		Mean #	Fires per
Group	n	Mean	Range	SD	Mean	Range	SD	Mean	Range	Mean	Range	Fires	age-class
1	28	92.5	20-300	57	459	90-960	236	5.5	2-10	7.9	4-12	27	4.9
2	15	257	30-680	187	622	110-1180	315	5.6	3-9	8.2	5-11	25.9	4.6
3	14	151	50-340	100	519	300-820	189	5.9	2-10	8.5	6-11	28.6	4.8
4	14	127	60-340	81	499	270-780	163	4.7	3-7	7.2	5-11	20.9	4.4
5	7	99	30-140	36	664	180-1040	353	4.4	3-6	7.4	6-10	26.7	6.1
6	6	153	90-200	46	405	220-600	161	6	4-7	7.8	5-10	11.3	1.9

a)

SFM

		Stems >100 yrs (ha^{-1})			All Stems (ha^{-1})			# 20 yr age-classes > 100 yrs		# 20 yr age-classes all stems		Mean #	Fires per
Group	n	Mean	Range	SD	Mean	Range	SD	Mean	Range	Mean	Range	Fires	age-class
1	11	109	40-230	68	366	90-810	261	4.6	3-7	6.5	3-8	22.8	5
2	11	240	20-1330	369	579	110-1420	417	3.8	2-5	6.4	4-9	14.3	3.7
3	12	217	20-380	108	636	190-1180	325	5.4	2-10	7.4	4-11	19.3	3.6
4	6	235	70-480	158	790	330-1130	369	5.3	3-8	7.7	6-10	19.2	3.6
5	4	315	50-630	187	924	190-2180	548	6	3-9	8.3	5-11	24.6	4.1
6	10	137	40-270	77	586	230-1330	332	5.8	1-8	8.6	5-10	12.8	2.2

b)

Group 4 plots were also moderately dense and they had few Douglas-fir or ponderosa pine, although the ponderosa pine ranged from 120-320 years old. The group was distinguished by the large number of 80-160 year old white fir, incense-cedar, sugar pine, and California black oak and few older trees. On average, plots in this group burned 20.9 times and had trees in 4.7 age-classes (range 3-7). Frequent tree regeneration and high fire frequency suggests plots experienced mainly low to moderate severity fires.

Group 5 plots were high density and trees 60-120 years old of all species were abundant. Older stems were present but only incense-cedar and ponderosa pine had trees > 300 years old. Plots burned an average of 26.7 times and had trees in 4.4 age-classes (range 3-6). Intermittent tree regeneration over a long period and the high frequency of fire suggest a regime of frequent low to moderate severity fire.

Group 6 plots were intermediate in density and 60-100 year old white fir, incense-cedar, and sugar pine were abundant. Douglas-fir and California black oak were concentrated in these age-classes and 160-200 year old ponderosa pines were abundant. The few black oak were <220 years old. Plots in this group, on average, had trees in 6 age-classes and burned 11.3 times. Peaks in the age-class distribution suggest that plots experienced a mix of both low and moderate severity fires.

South Fork Merced-Group 1 plots had the lowest density and ponderosa pine and incense-cedar were represented in a wide range of age-classes (Figure 11, Table 14b)). Douglas-fir and California black oak were < 300 years old and most white fir and Douglas-fir were < 100 years old. Plots in this group, on average, had trees in 4.6 age-classes (range 3-7) and they burned 23 times. Frequent tree regeneration and the high frequency of fire suggest plots experienced mainly low and moderate severity fire.

Group 2 plots are moderately dense, few trees are >300 years old, and trees 60-140 years old are abundant, especially ponderosa pine. Most white fir were < 100 years old. The oldest trees in this group are California black oak and ponderosa pine. Plots in this group, on average, had trees in 3.8 age-classes (range 2-5) and they burned an average of 14 times. Distinct peaks in the age-class distribution suggest that plots experienced a mix of both moderate and low severity fires.

Group 3 plots are also intermediate in density and all species have trees in a wide range of age-classes. Trees 100-180 years old are abundant, especially sugar pine, and most white fir are < 100 years old. Plots in this group burned an average of 19 times and had 5.4 age-classes (range 2-10). Peaks in the age-class distribution suggest that plots experienced a mix of both low and moderate severity fires.

Group 4 plots are dense and incense-cedar, sugar pine, ponderosa pine and Douglas-fir occur in a wide range of age-classes, but most stems are between 60-140 yrs old. There are few plots in this group. On average, plots had trees in 5.3 age-classes (range 3-8) and burned 19.2 times. Frequent tree regeneration and the high frequency of fire suggest plots experienced mainly low and moderate severity fire.

Group 5 plots are also dense and the form of the age-class distributions for species in this group was similar, except for California black oak. Most trees are < 320 years old and trees <120 years old are abundant; especially incense-cedar and white fir. Plots in this group, on average, burned 24.6 times and had trees in 6 age-classes (range 3-9).

Frequent tree regeneration and the high frequency of fire suggest plots experienced mainly low and moderate severity fire.

Group 6 plots are low density and are distinguished by incense-cedar and ponderosa pine in a wide range of age-classes. In contrast, white fir and Douglas-fir are all < 100 years old. Few stems are > 400 yrs, most are from 60-120 yrs old. On average, plots had trees in 5.8 age-classes (range 1-8) and burned 12.8 times. The presence of old trees and frequent fire suggests plots experienced mainly low and moderate severity fire.

Fire Occurrence and Fuel Limitation –The location and extent of burns in one year affected burn patterns in subsequent years in both study areas. Consecutive pairs of fires burned different grid points more often than the same point ($p<0.01$) during all time periods (Table 15). Most consecutive fires burned different points (BOF 57%, SFM 67%) or the same and different points (BOF 41%, SFM 33%). Few consecutive fires (BOF 2%, SFM 0%) only burned the same grid point. Burn extent was also affected by patterns of the previous burn. The extent of re-burn (BOF = 4350 ha, SFM = 3300 ha) for consecutive fires was 10-fold smaller than for areas not burned by the previous fire (BOF = 47100, SFM = 38875 ha) (Table 14). Moreover, this influence was evident during both the pre-Euro American and settlement period. As expected, no fires consecutively reburned the same points during the fire suppression period.

Table 15. Percentage of consecutive fires that burned the same, another, or the same and another areas burned by the previous fires in the Big Oak Flat (BOF) and South Fork Merced (SFM) mixed conifer forests, Yosemite National Park, California.

		BOF				SFM			
		Consecutive Fires				Consecutive Fires			
		Same	Another	Both	n	Same	Another	Both	n
Whole	n	5	130	92	227	0	129	64	193
	%	2	57	41	100	0	67	33	100
	Ha	4350	47100			3300	38875		
Pre-Settlement	n	2	107	78	187	0	105	55	160
	%	1	57	42	100	0	66	34	100
	Ha	3550	36650			2750	32375		
Settlement	n	3	18	14	35	0	18	9	27
	%	9	51	40	100	0	67	33	100
	Ha	800	10175			550	6125		
Suppression	n	0	5	0	5	0	6	0	6
	%	0	100	0	100	0	100	0	100
	Ha	0	275			0	375		

DISCUSSION

The distribution and abundance of tree species in the BOF and SFM mixed conifer forests were influenced by topographically controlled patterns of soil moisture and elevation. Ponderosa pine and California black oak were most abundant on dry south-facing slopes, particularly at low elevation while white fir was most abundant on mesic sites at higher elevations. Sugar pine and incense-cedar, on the other hand, were most abundant on intermediate sites. Douglas-fir, a minor forest component, was locally abundant on mesic sites. Overall, the species distribution and abundance patterns in BOF and SFM were similar to patterns identified elsewhere in the Sierra Nevada (Barbour 1988; Vankat and Major 1978; Vankat 1982; Barbour et al. 2002).

Variation in forest composition, elevation, and slope aspect affect the structure, production, arrangement, and moisture of fuels, which in turn, may influence the spatial patterns of fire frequency. For example, in some mixed conifer forests in the southern Cascades pre-fire suppression FRI are shorter on south-facing than other slopes (Beaty and Taylor 2001). Presumably, fuels dry out sooner each year on south aspects so the period fires can burn each year is longer than on other aspects. Yet, in other mixed conifer forests little variation in FRI is related to slope aspect (Bekker and Taylor 2001; Heyerdahl et al. 2001). In BOF and SFM, there was no spatial variation in FRI related to forest species composition, elevation, or slope aspect. In fact, the fire regimes for the two study areas were quite similar despite contrasting terrain. This suggests that the fire regime data are broadly representative of mixed conifer forests on modal sites in YNP and on adjacent lands in the Sierra and Stanislaus National Forests.

The response of species to fire is strongly influenced by the season of burn (Kauffman 1990). In YNP mixed conifer forests, the position of fire scar lesions within annual growth rings indicates that fires occurred when trees were nearly finished (latewood) or had finished (dormant) growing for the year. In the Stanislaus National Forest, the cessation of tree growth occurs in early to mid September for ponderosa pine (Oliver and Ryker 1990), and late August to early September for incense-cedar (Powers and Oliver 1990). (Few burns occurred early in the growing season. Similar seasonal patterns of burning have been reported from tree ring studies in other mixed conifer forests in the central and southern Sierra Nevada (Caprio and Swetnam 1995). Lightning ignitions are most frequent in YNP in July and August. The data for season of burn in YNP mixed conifer forests indicate that a predominance of burning (prescribed or wildland fire use) from mid-summer to fall period would be consistent with the seasonal pattern of burning during the pre fire suppression period.

Fire severity is an important cause of structural diversity in forested landscapes because burns can kill all trees in some stands and few in others. Post fire regeneration in stands that have experienced high severity fires is generally even-aged with stems concentrated in a few age-classes. On the other hand, stands that have experienced mainly low and moderate-severity fires have stems in a wider range of age-classes because fires kill few trees in the stand (Agee 1993). Stands in the mixed conifer forests in BOF and SFM were multi-aged and virtually all of the stands had trees >250 years old. A significant portion of these older trees were incense cedar and white fir and these species are fire sensitive compared to the pines or Douglas-fir. This suggests that the burns were often low and moderate in severity and patchy enough to permit white fir and incense cedar to grow to a fire-resistant size (e.g. Agee 1993). On average, plots in the BOF and SFM reference forests had stems in 5.3 different 20 year age-classes and 26% of the plots had stems in 7-10 different 20 year age-classes. Few plots had distinct cohorts of trees. Mixed conifer forests with multi-aged structures have been described in other parts of the mixed conifer zone in the Sierra Nevada (Parsons and DeBenedetti 1979; North et al. 2005), the southern Cascades (Taylor 2000), and the Klamath Mountains (Taylor and Skinner 2003). The lack of distinct cohorts is probably related to the high frequency of fire, and overlap in post-fire regeneration which makes cohorts indistinguishable in broad age-classes. Interannual variation in tree ages in southern Sierra Nevada mixed conifer forests suggests that post-fire recruitment patterns may vary by species with climate mediating the formation of distinct age cohorts (North et al. 2005).

Patterns of fire severity identified in BOF and SFM do not include the range of pre-fire suppression fire severity observed in some other California mixed conifer forests. Mixed conifer forests in the southern Cascades (Beaty and Taylor 2001; Bekker and Taylor 2001) the Klamath Mountains (Taylor and Skinner 1998), and northern Sierra Nevada (Nagel and Taylor 2005) have even-aged patches of trees and/or montane chaparral embedded within a matrix of multi-aged forest. This suggests that high-severity fire plays an integral role in shaping forest structure at least in some mixed conifer forests. Early photographs of mixed conifer forest landscape in YNP depict areas of chaparral and even-aged patches of trees (Gruell 2001). Chaparral shrubs are fire adapted and establish rapidly after fire, either by sprouting or by generating from seed stored in the soil (Kauffman 1990; Keeley 1991; Nagel and Taylor 2005). Prior to fire suppression, stands of chaparral were maintained or initiated by high severity fire at least in the northern Sierra Nevada (Nagel and Taylor 2005). Chaparral stands and even-aged patches initiated during the pre-fire suppression period covered up to 100 ha in these landscapes. The extent and spatial pattern of high severity burns and associated vegetation structures in the pre-fire suppression mixed conifer forest landscapes in California are still poorly known and insufficient to provide reliable estimates of the proportion of landscapes burned by high severity fire.

The median extent of a fire in each study area was similar, relatively small (i.e. 115-130 ha), and comparable to median and average fire extents in mixed conifer forests in the Klamath Mountains (128 h), and southern Cascades (100-170 ha) (Taylor 2000; Beaty and Taylor 2001; Bekker and Taylor 2001). Although the estimated extent of fires within a study area tended to be small, the full range of fire extent was probably larger. Most fires intersected sample area boundaries so the full extent of these fires was not detected. Moreover, many small fires <25 ha may not have been detected because of the 25 ha grid size used for sampling. However, >80% of the fires in both study areas burned two or more grid points suggesting that fires <25 ha were uncommon.

Both large and small burns were an important component of pre-fire suppression fire regimes. Smaller burns were much more frequent than large ones and >75% of the fires had an estimated extent ≤ 300 ha but these fires burned only 40% of the cumulative area burned over the study period. On the other hand, only 6% of the fires were >700 ha but they burned 10-20% of the cumulative area burned depending on the study area. The importance of larger burns in the fire regime appears to have increased recently. Larger burns became more frequent after 1775 in both study areas increasing the contribution of large fires to cumulative area burned. A similar increase in the importance of larger burns after 1775 has also been documented in pine dominated forests in the northern Sierra Nevada (Taylor and Beaty 2005) and this shift appears to be related to climatic changes. The frequency and strength of switching of the El Niño-Southern Oscillation is thought to have weakened for several decades at about this time altering fire regimes (Grissino-Mayer and Swetnam 2000; Swetnam and Baisan 2003). This fire regime shift may also have influenced forest structure and hence the forest reference conditions identified in this study. Forest reference conditions may more strongly reflect the effects of the post 1775 pattern of large burns rather than smaller burns that prevailed earlier.

Spatial patterns of burning in mixed conifer forests are thought to be strongly influenced by the time-dependent process of fuel accumulation (Bonnicksen and Stone 1982; Minnich et al. 2000). Both modeling studies and fire perimeter maps for 20th century fires suggest that burn patches influence the extent and location of subsequent fires (van Wagtendonk 1995; Miller and Urban 2000). There was evidence for this in the pre-fire suppression reconstruction of fire location and extent in both BOF and SFM. In BOF and SFM, consecutive fires burned mainly other sites and the extent of burns was also influenced by previous burns. Burn areas were ten-fold smaller in previously burned patches than at other locations in each study area. Yet, at times, large burns spread across the burn patch mosaic, especially during dry years. Between 1650 and 1900, Five-fold more area burned in the study areas during the 10 driest years than in the 10 wettest years (PDSI Grid point 047 Cook and Krusic 2004). This indicates that regional scale climate variation, specifically drought, also influenced fire extent in mixed conifer forests during the pre fire suppression period.

Fire regimes in the mixed conifer forests varied with historical time period and fire occurrence and area burned declined dramatically after 1905 when a national policy of fire suppression was implemented on national forest lands that surround YNP. The >15-fold increase in fire rotation from 10-13 years to 211-378 years is a strong indicator of the magnitude of the fire regime change associated with fire suppression. Similar declines in fire frequency and extent have been reported in mixed conifer forests in the Klamath Mountains (Taylor and Skinner 2003), the southern Cascades (Taylor 2000; Beaty and Taylor 2001), and the Sierra Nevada (Stephens and Collins 2004). In some Sierra Nevada and Klamath Mountain mixed conifer forests fire occurrence declined earlier during the settlement period, perhaps due to livestock grazing or declines in Native American populations (Caprio and Swetnam 1995; North et al. 2005; Fry and Stephens 2006). No settlement period decline in fire frequency was evident in the BOF or SFM study areas.

Mixed conifer forests changed after exclusion of fire. Forest density and basal area increased and forest composition shifted from more-fire resistant pines and black oak, which sprouts after fire, to fire-sensitive white fir and incense cedar. In both study areas the onset of these changes corresponds with the date of onset of fire suppression. Overall, these forest changes have reduced forest structural diversity at both the stand and landscape scale compared to forest structure at the end of the pre-fire suppression period. Similar changes in forest structure and composition have been described for other mixed conifer forests in the Sierra Nevada (e.g. Parsons and DeBenedetti 1979; Kilgore and Taylor 1979; Skinner and Chang 1996). The temporal coincidence of the fire frequency decline and a large increase in the establishment of fire sensitive trees implicate fire suppression as being the major cause of forest change over the last century in YNP mixed conifer forests.

The tree-ring based method used to estimate pre-fire suppression forest conditions in this study has limitations and assumes that evidence of the reference forest was present in the contemporary forest sample. Complete decay or consumption of wood by fire could eliminate the physical legacy of the original forest (Fule et al. 1997; Stephenson 1999). Decay resistance varies with tree size and by species. In California montane forests, fir decays more rapidly than pine associates and small trees decay and decompose faster than large ones (Kimmey 1955; Harmon et al. 1987). Therefore, the part of the estimate (33%) of pre fire suppression forest conditions contributed by trees that were dead in 2002 is probably more reliable for pines than fir and for large rather than small trees. The sensitivity analysis indicates that estimates of pre-fire suppression basal area and tree size did not vary much (<10%) under different decomposition conditions and that estimates for these variables are more robust than those for tree density. Moreover, inter-specific variation was greater for white fir than for the other species. This suggests that the reference condition estimates for density and for white fir are less precise than for other species. Yet, there was no statistical difference between the average tree density estimates determined using the reconstruction method and that using the 1911 forest inventory. Moreover, only incense cedar and white fir had statistically different reconstructed forest characteristics compared to the 1911 forest. Reconstructed incense cedar basal area was higher than in the 1911 forest as was overall basal area and tree diameter. The sensitivity analysis and the similarity of density, basal area, and tree size estimates from the tree ring reconstruction and 1911 forest inventory suggests the estimates reconstructed from the contemporary forest sample is sufficiently reliable to guide forest-restoration planning in the mixed conifer zone in YNP and in the adjacent Stanislaus and Sierra National Forest.

Reference forest conditions in YNP mixed conifer forests are different than reference forest conditions reconstructed for mixed conifer forests in the Lake Tahoe basin (Taylor 2004) or in contemporary Jeffrey pine-mixed conifer forests in the Sieera San Pedro Martir (SSPM) in northern Mexico that have not experienced 20th century fire suppression management (Minnich et al. 2000). Jeffrey pine is taxonomically similar to ponderosa pine, their ranges overlap, and they hybridize (Jenkinson 1990, Oliver and Ryker 1990). Reconstructed densities for mixed conifer forests in the Lake Tahoe basin averaged 68 trees ha^{-1}, lower than the 194 trees ha^{-1} and 263 trees ha^{-1} in YNP. Forest density in the SSPM (120 ha^{-1}) is higher than in Tahoe, but still lower than in YNP. Moreover, average reconstructed basal area for YNP (38.4-56 m^2 ha^{-1}) is greater than reconstructed average values for Lake Tahoe (25.5 m^2 ha^{-1}) or for SSPM forests (34 m^2 ha^{-1}). Higher tree density and basal area in YNP are probably related to higher precipitation and better site conditions in the west-central Sierra Nevada than in SSPM or the Carson Range, which are dryer. Differences in the characteristics of YNP forests and those in SSPM and Lake Tahoe suggest that locally developed reference conditions are more appropriate models for restoration than reference information from distant areas.

Conclusions

Restoring and maintaining the highly altered mixed conifer forests to a pre-fire suppression condition is a key objective of YNP fire and resource managers, and managers in the Sierra and Stanislaus National Forests, who have similar fire management goals for lands adjacent to YNP. An important limitation to developing restoration plans for mixed conifer forests has been a lack of quantitative reference data on forest structure and fire regimes. This study fills that gap and provides the necessary foundation for development of appropriate structural goals in restoration plans. Reference conditions reconstructed for mixed conifer forests in YNP suggest that restoration objectives should emphasize: 1) density and basal area reduction, primarily of smaller diameter fire intolerant trees (88% of fire intolerant trees <35 cm dbh established after fire suppression); 2) reintroduction of frequent fire as a process regulating forest structure and dynamics; and 3) increasing structural heterogeneity across the forest landscape. Measurements of stand structure indicate that there was a wide range of conditions on the pre-fire suppression landscape. Managers should use this information to develop plans that emphasize the variability in conditions across the landscape rather than average ones and they should integrate these data with other types of ecological information when developing restoration plans. For example, reference estimates for white fir are probably less precise than for other species and white fir was more abundant on mesic than xeric sites in our forests, and in the Sierra mixed conifer zone (Vankat 1982; Barbour 1988). To accommodate for this, prescriptions based on reconstruction estimates could be adjusted to include more white fir on mesic parts of the landscape. Moreover, there was little evidence of high severity fire in the pre-fire suppression forests of BOF and SFM. Yet, there is increasing evidence that limited areas of mixed conifer in the Sierra Nevada and southern Cascades forests experienced high severity fire during the pre fire suppression period and that montane chaparral once dominated these sites (Beaty and Taylor 2001; Bekker and Taylor 2001; Nagel and Taylor 2005). Consequently, maintenance of montane chaparral should be included as a goal in restoration plans although there was little evidence of montane chaparral in the pre-fire suppression landscape in the two areas sampled in this study. In short, the reference estimates for forest structure and fire regimes provided by this study should not be viewed as rigid targets that define an acceptable restoration treatment (Allen et al. 2002). Instead, they represent a strong foundation for articulating restoration plans and designs that can meet management objectives.

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