Influence of Fire and El Niño on Tree Recruitment Varies by Species in Sierran Mixed Conifer

Malcolm North, Matthew Hurteau, Robert Fiegener, and Michael Barbour

Abstract: The influence of fire and climate events on age structure of different species was examined in old-growth mixed conifer in the southern Sierra Nevada. Within a 48-ha stem-mapped sample area, after a mechanical thinning, all stumps were examined for fire scars and 526 stumps were cut to ground level and aged. Before 1865, which was the last widespread fire event, the mean interval between scars for an individual tree was 17.3 years and the mean fire return interval for the period with the greatest number of recording trees was 11.4 years. A significantly greater than expected number of fires occurred in dry La Niña years, but these fires were not significantly larger in size than fires in other years. The response of mixed-conifer recruitment to climate and fire events varied by species. Before 1865, Jeffrey pine and sugar pine recruitment were correlated with wet El Niño years, but only sugar pine establishment was associated with fire. Red fir recruitment did not follow fire events but was associated with El Niño years before and after 1865. Most white fir and incense cedar (84%), including many large-diameter trees (>76 cm dbh), recruited after the last widespread fire in 1865. Although tree distribution is clustered in the southern Sierra Nevada, mixed-conifer groups are not age cohorts because species have different recruitment patterns relative to climate and fire events. In mixed conifer, top-down effects of fire and weather on recruitment are mediated by different species responses to these effects and within-stand differences in where species are located. FOR. SCI. 51(3):187–197.

Key Words: *Abies concolor*, *Abies magnifica*, *Calocedrus decurrens*, climate, microclimate, old-growth, Palmer Drought Severity Index, *Pinus jeffreyi*, *Pinus lambertiana*, Sierra Nevada, Teakettle Experimental Forest.

SPECIES DISTRIBUTION AND ABUNDANCE in forests can be influenced by the interaction of local site conditions with the history and severity of disturbance events (Miller and Urban 1999a, Brown and Hebda 2002). For any particular forest, tree composition and age structure can be affected by regional events such as large-scale fire and drought (Swetnam and Betancourt 1990), a stand's particular disturbance history (Barton et al. 2001), and site-specific conditions such as microclimate and seedbeds (Gray and Spies 1997). Some recent fire studies have suggested that burn patterns result from both top-down influences such as regional climate patterns, and bottom-up influences such as local topography (Kitzberger et al. 1997, Hyerdahl et al. 2001). Few studies, however, have used this approach to examine how regional influences such as particular weather years, local events such as fire, and stem location may interact to influence age demographics within a mixed-species stand. We were interested in examining how climate and fire events may affect tree recruitment in a stand with a mix of species with different fire and drought tolerances, and preferred microsites.

Fire and weather should significantly influence age and species composition of Sierra Nevada mixed conifer. Before the 1860s, mixed-conifer forests had a frequent low-intensity fire regime, which has shifted with fire suppression to the equivalent of 644 years (McKelvey and Busse 1996). These forests also have prolonged summer droughts and high temperatures (Major 1988). Soil surface temperatures often exceed 55° C during May to Oct. when less than 2 cm of precipitation occurs (North et al. 2002). Plants rely almost exclusively on soil moisture from the winter snowpack (Barbour et al. 1991). California's winter snowpack is significantly affected by El Niño/La Niña events, between which snow depth may vary sixfold or more. Although El Niño/La Niña events are extremes of the cycle, the El Niño Southern Oscillation (ENSO) is probably more accurately viewed as a continuous variable, which in any year, can significantly influence annual weather patterns. ENSO fluctuations have been linked to outbreaks of the western spruce budworm and tree regeneration patterns in the Southwest (Swetnam and Betancourt 1998), widespread fire years in the western US (Westerling et al. 2003), and variability in stream flows, flood events, and salmon productivity (Redmond and Koch 1991, Mantua et al. 1997, Cayan 1999).

These top-down effects on tree demography, however, are likely moderated by how different species respond to fire and weather, and within-stand differences in growing conditions. Substrate conditions in mixed conifer are patchy

Malcolm North, USFS Sierra Nevada Research Center, 2121 2nd Ave., Suite A-101, Davis, CA 95616—Phone: (530) 754-7398; mnorth@ucdavis.edu. Matthew Hurteau, Department of Environmental Horticulture, University of California, Davis, CA 95616—mdhurteau@ucdavis.edu. Robert Fiegener, Department of Environmental Horticulture, University of California, Davis, CA 95616—Current address: 435 NW 8th St., Corvallis, OR 97330. Michael Barbour, Department of Environmental Horticulture, University of California, Davis, CA 95616—mgbarbour@ucdavis.edu.

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with deep, moist soils near creeks and in depressions, and shallow, dry soils near exposed rock and on ridge tops (North et al. 2002) (Figure 1). Deeper, moist soils often have more fir and cedar, whereas upslope conditions are more open, xeric, and support more pine. Because of this high site heterogeneity and patchy spatial structure, some researchers have suggested that fire and site conditions interact to produce trees grouped by age cohorts (Kilgore and Taylor 1979, Bonnicksen and Stone 1981, 1982, Stephenson et al. 1991). Managers attempting to restore mixed-conifer ecosystems need a better understanding of how weather, fire, and site conditions influence tree establishment, and how these influences may have changed with fire suppression.

We examined the fire, climate, and tree-establishment history of an old-growth mixed-conifer area. Using a thinning treatment employed in the Teakettle Experiment, we located and sampled all fire scars, and aged 526 trees from stump cross sections cut at the root collar. We evaluated tree ages by location against extensive data gathered on species

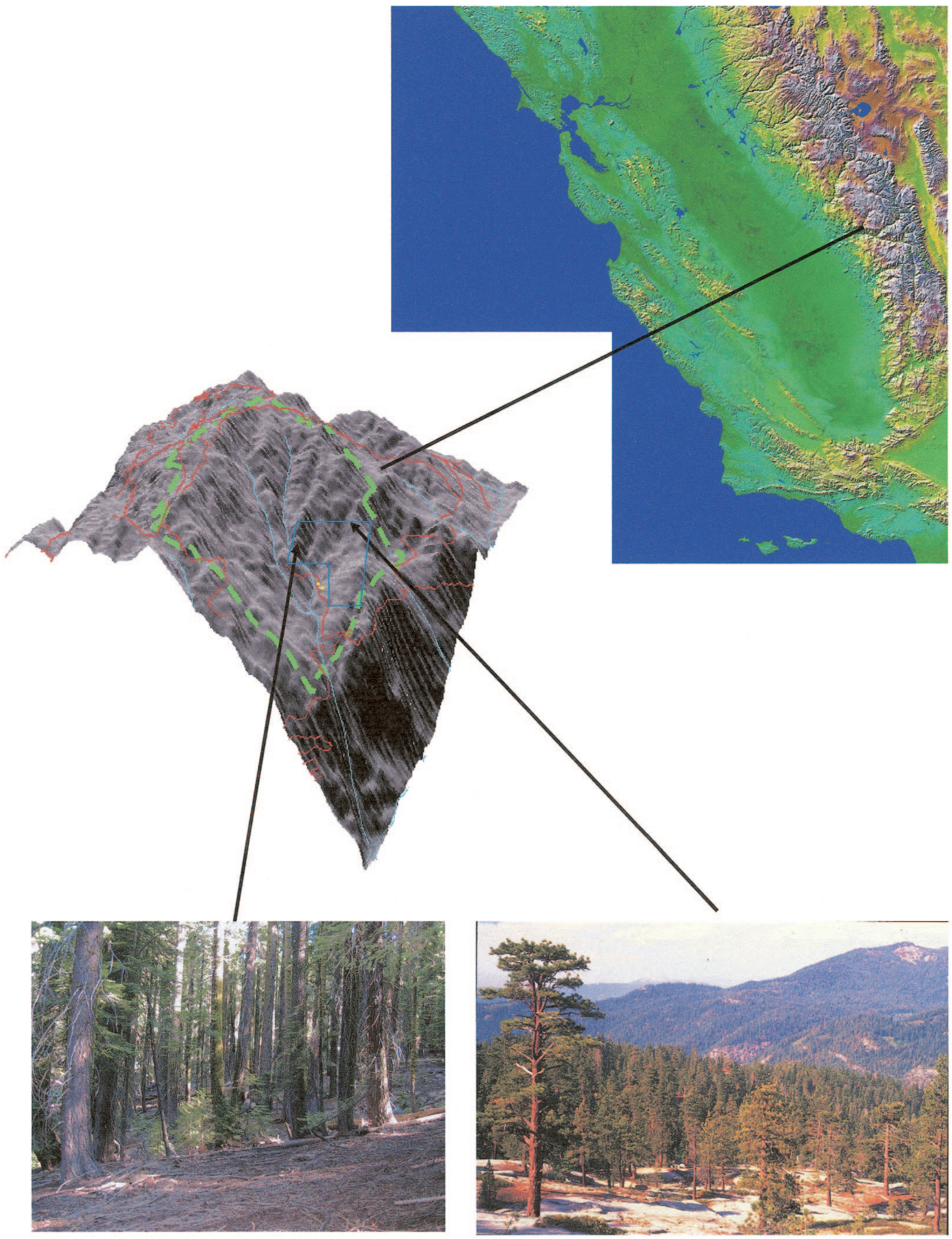

Figure 1. A shaded relief map of southern California indicating the location of the Teakettle Experimental Forest. The 30-m DEM image of Teakettle shows the boundary of the Experimental Forest (dashed line), two research buildings and the study area (solid line). The two photos and their location show the difference between open shallow soil areas dominated by Jeffrey pine and deeper soils with a mix of all species.

distribution and microsite conditions developed over the course of mapping all trees and sampling soils on 72 ha of forest. Our objectives were to: 1) identify the fire history and spatial extent of burns; 2) compare tree establishment by species to historic fire and El Niño/La Niña events; and 3) evaluate age structure in relation to mixed-conifer stem distribution. We focused on examining how broad-scale factors such as fire and weather interact with local topography and different species to help explain age structure in a mixed-conifer stand.

Methods

The study was conducted in old-growth forest at the 1,300-ha Teakettle Experimental Forest, elevation 1,900–2,600 m, located 80 km East of Fresno, CA on the north fork of the Kings River (Figure 1). Teakettle's most common soil is a well-drained, mixed, frigid Dystric Xeropsamment, formed from decomposed granite, typical of many southern Sierra forests (Giger and Schmitt, 1993). The annual precipitation of 125 cm falls almost entirely as snow between Nov. and Apr. (North et al. 2002).

Within the experimental forest, forest type varies by elevation, grading from mixed-conifer on lower benches to red fir (*Abies magnifica*) on mid-slope, and to red fir and lodgepole pine (*Pinus contorta*) at higher elevations. Our study occurred in mixed conifer, which contains white fir (*Abies concolor*), red fir, sugar pine (*Pinus lambertiana*), incense-cedar (*Calocedrus decurrens*), Jeffrey pine (*Pinus jeffreyi*), and small amounts of black oak (*Quercus kellogii*). As is characteristic of the mixed-conifer forest type throughout California (Rundel et al. 1988), white fir dominates stem density and basal area at Teakettle. However, sugar pine and Jeffrey pine are the largest-diameter and tallest trees.

Our research focused on a 200-ha contiguous block of mixed-conifer forest, within which eighteen 4-ha plots were established for a long-term experiment. Within these plots, a surveyor's total station was used to tag and map the locations of all trees (≥5 cm dbh), snags (≥2 m tall), logs (≥2 m long) and shrubs (≥4 m^2 area). Of these 18 plots, we focused on 12 (Figure 2), which were thinned in the summers of 2000 and 2001, providing stumps used to identify fire scars and to age trees. Two thinning prescriptions were used in the experiment: a thinning from below followed guidelines developed for the California Spotted Owl (Verner et al. 1992), leaving all trees ≥76 and ≤25 cm dbh, and a thinning from above followed shelterwood guidelines leaving 22 evenly spaced trees/ha and all trees ≤25 cm dbh. With incidental logging damage and large tree cutting in the shelterwood, available stumps ranged from 5 to 180 cm. in diameter.

Fire-Scar Collection

Before logging, the study area was surveyed, and all visible fire scars on dead material were sampled. Postharvest, every stump was examined for fire scars, and potential scars were examined after brushing clean the stump surface. Scars were scrutinized to determine the causative agent. Scars resulting from beetle attack, root rot, and treefall were dismissed (Mitchell et al. 1981, Gara et al. 1986), and fire scars and scars of unknown origin were flagged and recorded. Wedge-shaped or full cross-sections were removed, depending on the size, shape, and quality of the stump (Arno and Sneck 1977). All samples were processed and crossdated according to standard dendrochronological procedures (Stokes and Smiley 1968), and fire-history data were analyzed with FHX2 software (Grissino-Mayer 1995).

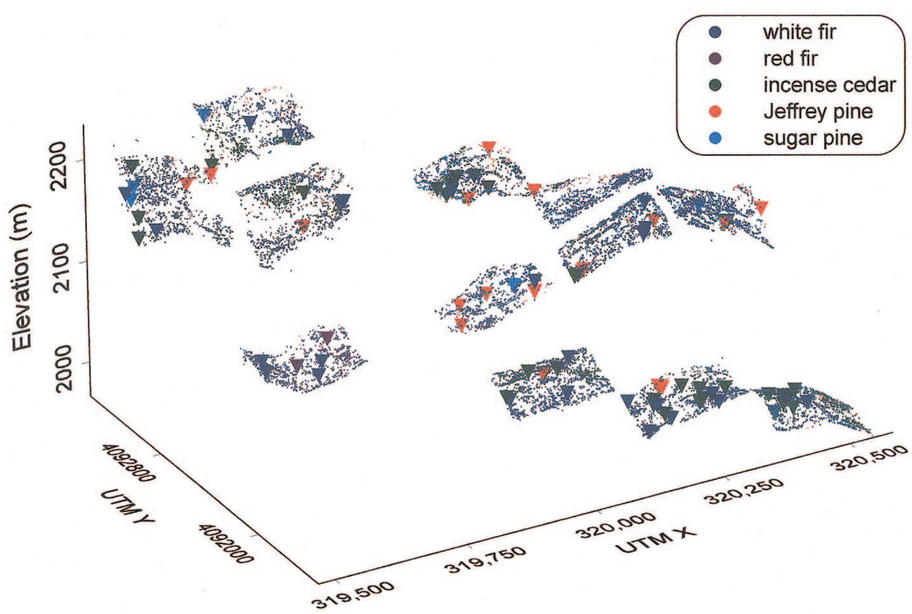

Figure 2. The shape and location of the twelve 4-ha plots used in this study. All prethinning live trees ≥5 cm dbh are plotted and colored by species (N = 19,360). The large triangles are the location of the 61 trees with fire scars.

For each year with a fire scar, maps were created showing the spatial relationship of scarred and unscarred samples. There are no major barriers to fire spread across the study area, although small islands (0.01–0.25 ha) of bare ground, typically decomposed granite or rock outcrops, do occur. We calculated the size of the study area and estimated the area burned for individual fire years with the program SPANFIRE (Swetnam and Holmes 1994). Area was calculated as the size of the polygon that connects the samples on the perimeter with a convex hull, for both the area burned and the total study area. The area burned should be viewed as an approximation because it assumes that all area within the polygon was burned.

To collect tree ages, we used a stratified and opportunistic sampling scheme. Within the twelve 4-ha sites, we surveyed for groups of adjacent stumps with intact heart wood that also contained at least one large-diameter (>76 cm) stump. We also stratified these sample areas into one of three topographic categories: ridgetop, midslope, and riparian. Previous analysis indicated that soil moisture, depth to bedrock, and microclimate vary among these topographic categories affecting local species composition (North et al. 2002). Jeffrey pine are more abundant on ridge tops, and red fir more common in riparian areas, however both species are intermixed with white fir, incense cedar, and sugar pine throughout the sample area. In addition to this stratified sampling, we opportunistically sampled large stumps adjacent to skid roads. This sampling was designed to increase our information on older tree establishment while factoring in a reasonable haul distance for large-stump cross sections (many >1 m in diameter). Litter and dirt were removed from around stumps and a cross section was cut at the root collar. Cross sections were transported to a bench site with a generator, sanded, crossdated, and independently aged by two trained technicians using standard procedures (Stokes and Smiley 1968).

Weather Records

Because our focus is on a particular location while weather events are general regional trends, we wanted to accurately assess local conditions as best as possible. Winter snowfall is highly variable across the Sierra Range depending on a storm's tracking pattern. To determine past El Niño/La Niña years at Teakettle, we used a nested calibration approach. First, we collected data from Grant Grove, the closest weather station (20 km South at the same elevation) with the longest snow records (back to 1930) (California Department of Water Resources, http://cdec.water.ca.gov/). Next we collected annual precipitation records for Fresno (80 km away) back to 1878 (Western Regional Climate Center, http://www.wrcc.dri.edu). For each data set we standardized each water year's total precipitation (July 1 through June 30) by subtracting the mean and dividing by the standard deviation calculated from each station's complete recorded values. There is no single list of El Niño/La Niña years, so we consulted three widely cited sources and identified El Niño/La Niña events that all three agreed on over the last 30 years (Kiladis and Diaz 1989, Smith and Sardeshmukh 2000, National Oceanic and Atmospheric Administration (NOAA) Climate Prediction Center, http://www.cpc.ncep.noaa.gov/). We compared this list with Grant Grove snow records and found years that were greater than one standard deviation above and below the mean that matched all listed El Niño and La Niña events, respectively. We then compared Grant Grove snow and Fresno precipitation records to determine high and low precipitation thresholds in the Fresno data that matched every El Niño/La Niña year in the Grant Grove data. We used these thresholds to identify potential El Niño/La Niña years between 1878 and 1929 using the Fresno precipitation data.

These records were compared to the North American Drought Variability Reconstructions (PDSI) data for the gridpoint nearest to Teakettle (119.5° longitude, 37° latitude: only 25 km away), which had values for 1700–1978. PDSI is a relative measure of moisture stress calculated from a network of 425 tree ring data sets (Cook et al. 1999). The mean PDSI is zero, and most values range between plus 6 (very wet) and minus 6 (very dry). We used the end year in the water year snow and precipitation records (i.e., 1890 is used for the precipitation total from July 1, 1889 through June 30, 1890) from Grant Grove and Fresno to evaluate calendar year PDSI values. Comparing the Grant Grove (1930–1978) and Fresno (1878–1929) records to the years with PDSI values (i.e., 1700–1978), we calculated PDSI threshold values that correlated with every El Niño/La Niña year in the Fresno and Grant Grove records.

Analysis

To evaluate whether fires occurred significantly more often than expected in La Niña, neutral, or El Niño years, we used chi-square analysis comparing fire years to the overall frequency of weather events over the 1700–1865 period covered by PDSI and our record of fire events. To compare fire size in La Niña years to other years, we used a Student's t-test. Fire size is biased by time period because the size of the sample area increases toward the present as more recording trees "come online." To standardize for this change in study area through time, we used the percentage of the study area burned instead of total hectares burned.

We evaluated snowpack, precipitation, and PDSI records for normality using the Shapiro-Wilk test. Because all three data sets were distributed normally, we used Pearson's correlation analysis to compare the fit among the three weather data sets.

Although tree ages determined from root collar cross sections avoid some of the problems with estimating age from aboveground increment cores (Villalba and Veblen 1997a, Wong and Lertzman 2001), underestimation errors can still occur (e.g., Desrochers and Gagnon 1997). To reduce the effects of any underestimation errors, we used a range of years when comparing establishment age to fire and El Niño/La Niña events. To estimate potential recruitment response of different species to fire, we calculated the percentage of trees that became established between 1 and 4 years after a burn event. We used this length of postfire time because it covers a period before extensive shrub sprouting and significant litter deposition is likely to occur (Tappeiner and McDonald 1996). Using the fire and stem maps, we only included a tree in this tally if it was located within the fire perimeter. Comparing tree age to weather, we averaged PDSI values for a 2-year period: the year of estimated establishment and the year after. We took this approach because moist years may be important during both establishment and initial growth (Fowells and Stark 1965, Stark 1965). For each tree, we calculated a mean PDSI value by averaging the tree's establishment year and following year PDSI value. We summed and averaged these mean PDSI values by species.

To examine whether a cohort age structure was present, we used two areas, 0.7 and 0.9 ha in size, where we had collected the ages on all adjacent trees. For each area, we fit an empirical variogram and than applied either a spherical or Gaussian model (Kaluzny et al. 1998). We evaluated and selected a model for each area based on the smallest residual sum of squares between the theoretical and empirical variogram. For each theoretical model, we calculated the relative nugget effect as the ratio of the nugget to the sill (Rossi et al. 1992). The relative nugget effect provides a measure of spatial autocorrelation in the data, with greater values corresponding to a lack of spatial dependence (Bailey and Gatrell 1995). All statistical analyses were performed using SPLUS software (S-Plus 2001).

Results

Over Grant Grove's 70-year record, annual snow accumulation averaged 132.8 cm, and all years higher than 203 and lower than 63 cm corresponded to El Niño and La Niña years agreed upon by the three published sources. From 1930 to 2001, Fresno precipitation and Grant Grove snow accumulation were significantly correlated ($r^2 = 0.92$, $P < 0.01$) and Fresno years higher than 40.5 and lower than 15.3 cm of rain corresponded to all El Niño and La Niña years. From 1878 to 1978, PDSI and Fresno precipitation were correlated significantly ($r^2 = 0.81$, $P < 0.01$) and PDSI values above 1.74 and below -1.74 corresponded to all putative El Niño and La Niña years in the Fresno record. We selected ± 1.74 as thresholds in the PDSI record for potential El Niño and La Niña years.

Within the 48 ha of cut plots, nearly 8,000 stumps and snags were examined for fire scars, and sections of 149 scarred trees were crossdated successfully. Of these, scars on 61 tree cross sections were attributed conclusively to fire and represent the samples used for all fire interval analyses (Figure 2). Many trees recorded multiple fire events. Of the 88 trees with potential fire scars, 35 contained scars in years that were identified as fire years by the 61 trees. We included these trees only in the analysis of potential burn area for a given fire event.

Fire was detected in 76 years from 1614 to 1917. Mean point (individual tree) fire interval was 17.4 years. The shortest fire interval on a single sample was three years, and the longest was 115 years. Using a criterion of three or more fire scars to establish a fire event (Dieterich 1980), the mean fire return interval for the study area was 11.4 years from 1692 to 1865. Based on the conservative interpretation of the plotted fire scar data, there were ten widespread (>15% of the study area) fires: 1795, 1800, 1814, 1823, 1829, 1840, 1843, 1845, 1856, and 1865 (Table 1). After 1865, only two fires occurred (1897 and 1917) and both were highly localized.

Between 1700 and 1865, there were 30 La Niña events (18%), 28 El Niño events (17%) and 107 neutral years (65%). During this period, Teakettle had 19 fires that scarred ≥3 trees, with 10 in La Niña years (53%), 7 in neutral years (37%) and 2 in an El Niño year (10%) (Table 1). The number of fires in La Niña years was greater significantly than expected ($\chi^2 = 15.94$, $P < 0.001$). The proportion of the study area burned in La Niña years (44%), however, was not different significantly than in other years (39%) (Student's *t*-test, $P = 0.774$). The average elapsed time between a previous El Niño event and a fire was 5.4 years.

Ages were collected on 526 trees with establishment dates ranging from 1593 to 1939 (Table 2). There was little correlation between diameter and age typified by comparing the youngest tree, a 61-year-old, 62-cm dbh white fir, with the twelfth oldest tree, a 287-year-old, 10-cm dbh sugar pine. Of trees sampled, 77% became established after the last widespread fire in 1865.

The relationship between tree establishment, and fire and climate varied by species. Before fire suppression, sugar

Table 1. Fire events with ≥3 scarred trees at the Teakettle Experimental Forest from 1700 through 1865

Year	Recorder trees scarred[a] (%)	Study area burned (%)	PDSI value[b]	Years since previous El Niño[c]
1707	25	14.1	−3.563	2
1755	18	1.0	−1.872	8
1757	13	0.1	−2.482	10
1771	11	3.7	1.679	2
1783	10	2.8	−4.989	14
1785	19	70.7	3.177	16
1795	51	85.3	−8.342	3
1800	19	53.6	−2.665	1
1807	22	79.4	0.572	3
1809	8	0.9	−0.775	5
1814	24	65.1	0.551	3
1823	40	81.5	−2.629	12
1829	59	81.1	−4.581	3
1836	7	0.2	−0.725	3
1840	28	58.4	2.69	2
1843	24	17.3	−4.002	5
1845	30	56.6	−0.209	7
1856	11	15.9	−5.469	1
1865	61	92.8	−0.838	3
Mean	25	41.1	−1.814	5.4

[a] Recorder trees are trees that had been scarred previously.
[b] Positive values in the Palmer Drought Severity Index (PDSI) are associated with wetter years and negative values with drier years.
[c] Years since previous El Niño is the time between a fire event and an earlier year with a PDSI ≥ 1.74.

Table 2. Characteristics of the 526 age samples collected at Teakettle by species

	White fir	Red fir	Incense cedar	Jeffrey pine	Sugar pine
No. of samples	33.6	30	107	28	25
Percent of sample	63.9	5.7	20.3	5.3	4.8
Percent of live stems at Teakettle[a]	66.3	2.8	18.7	4.9	7.2
Mean dbh (cm)	38.4	43.0	36.7	68.6	52.9
dbh range (cm)	6–160	13–101	5–140	13–142	11–162
Median age	111	165	114	197	152
Age range	61–397	92–332	77–403	103–407	98–354
Mean PDSI[b]	−0.08	1.93	0.16	2.36	1.54
Percent established 1–4 yrs after a fire event	42	13	20	17	96

[a] The live stem species composition is calculated from all trees ≥5 cm dbh in the twelve 4-ha plots.
[b] The mean PDSI is calculated by multiplying the number of trees established in a particular year by the mean of the establishment and following years' PDSI values. Values are than summed and averaged by species. For each species, the percentage of trees established 1–4 yrs after a fire is calculated only for trees located within the burn perimeter of each fire event between 1755 and 1865.

pine was the only species (96%) that established consistently 1–4 years after a fire (Table 2). Both shade-tolerant species, however, were associated positively with the cessation of fire. In our age sample, 84% of the white fir and incense cedar became established after 1865 (Figure 3).

Jeffrey pine, red fir, and sugar pine recruitment were associated with wetter years (Figure 3). Average PDSI values for Jeffrey pine, red fir, and sugar pine establishment were 2.36, 1.93, and 1.54. Average PDSI values for both white fir and incense cedar were close to the mean PDSI of zero (Table 2).

Although trees are highly clustered (Figure 2), adjacent tree ages are not autocorrelated (Figure 4). The best fit theoretical variogram (not shown) for the 0.7- and 0.9-ha areas had a relative nugget effect of 78% and 72%, respectively.

Discussion

The association of mixed-conifer recruitment with fire and El Niño/La Niña events varied by species. White fir and incense cedar had high recruitment starting 13 years after the last widespread fire in 1865. Almost all Jeffrey pine and most sugar pine established before 1865 in wet years. Most sugar pine established within 1–4 years after a fire. Red fir recruitment was not associated with fire events, did not change with fire suppression, and was associated consistently with wet El Niño events. The distinct responses of

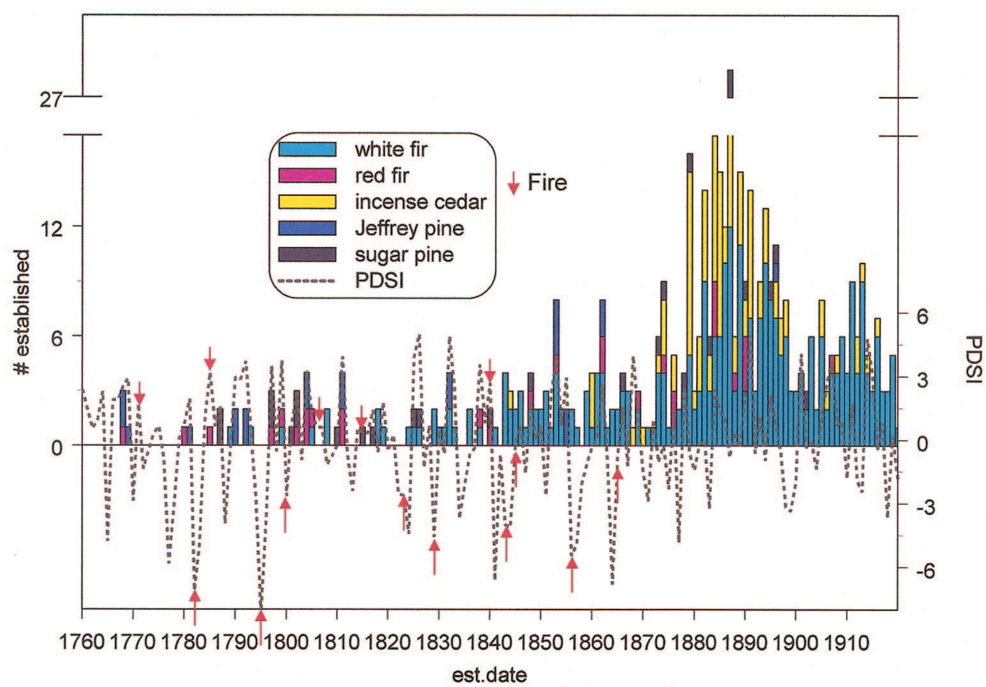

Figure 3. A graph of the number of trees established each year between 1760 and 1920 by species. The dashed line is the Palmer Drought Severity Index for the same period and plotted against the second *y* axis. Positive and negative values correlate to wet and dry years, respectively. The years when a fire occurred that scarred ≥3 trees are indicated by red arrows.

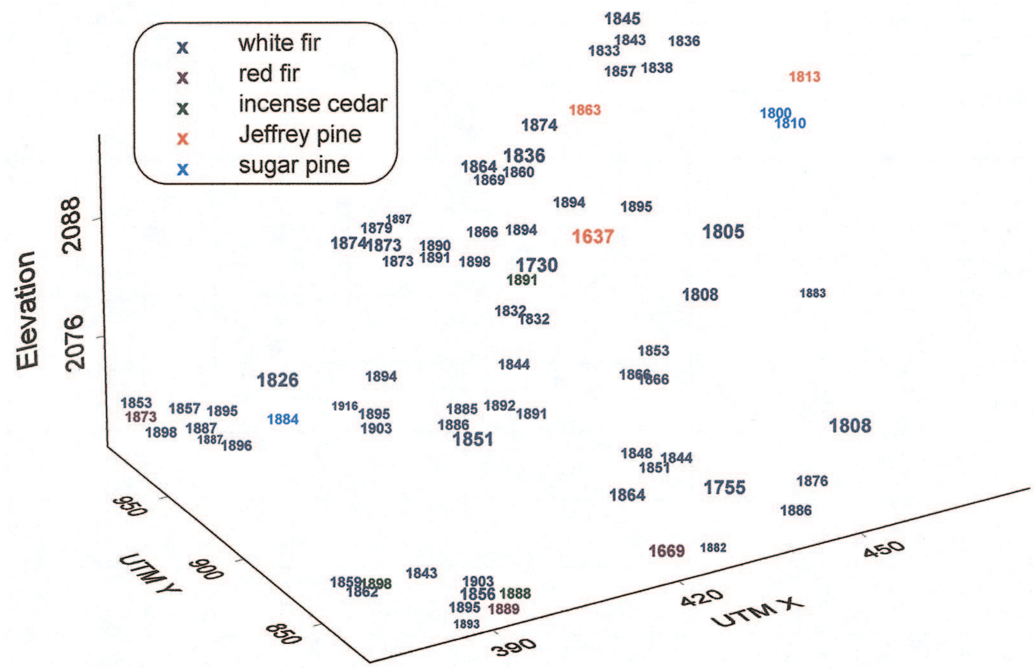

Figure 4. Location and establishment age for all trees sampled in one 4-ha plot. Trees are color coded by species and the size of the establishment date is in proportion to the tree's diameter.

mixed-conifer species to climate and fire may result from species differences in seedling requirements and favored microsite distribution.

Several studies have found a relationship between local fires and regional climate patterns, particularly in areas where ENSO patterns exert a strong influence on annual precipitation (Swetnam and Betancourt 1990, Veblen et al. 1999). Our study agrees with these patterns, finding a greater than expected proportion of fires in La Niña years. Dry fuels during La Niña events may increase the likelihood of a fire growing to a size or burning with enough intensity to show up in the fire scar record. Although regional climate patterns may increase the probability of fire, many factors influence fire size (Agee 1993). In our study area, fires did occur in neutral and El Niño years. Furthermore, many of these fires burned a large percentage of the sample area and there was no significant difference in size between La Niña and non-La Niña fires. Regional climate patterns may set the stage by increasing the probability of occurrence, but fire size is influenced by local fuel and current weather conditions (Miller and Urban 1999b), which a mean annual drought-severity index cannot assess.

Studies in the Southwest (Swetnam and Betancourt 1990, Grissino-Mayer and Swetnam 2000) and Patagonia (Kitzberger et al. 1997, Veblen et al. 1999) have suggested a 1–3-year lag between an El Niño event and widespread fires, possibly resulting from increased grass and forb biomass after years with abundant precipitation. Examining El Niño and fire dates, we did not find this pattern at Teakettle, possibly because grass and herb cover is sparse (<2% cover) and distribution is patchy (North et al. 2002). Current sparse understory cover could be less than it was before 1865 when the forest was more open because of frequent fires. However, in the southern Sierra Nevada, soil moisture is a more important influence on understory cover than light mediated by the overstory canopy (North et al. in press). Studies in Yosemite and Sequoia National Parks suggest that mixed-conifer fuels are influenced mostly by the accumulation of tree needle cast and coarse woody debris over time (Parsons and DeBenedetti 1979, van Wagtendonk 1998).

Although the last widespread fire at Teakettle occurred in 1865, fire cessation may not be because of active suppression. Teakettle is fairly remote, and until the 1940s, the nearest road and settlement were 30 km away. Most of the area, including lower elevations that could carry a fire up to Teakettle, would have been difficult to access before the era of smoke jumpers. An 1860s decrease in fire frequency has been widely observed in many western forests and at least two alternate explanations have been suggested. Native American ignitions may have decreased during this period because of disease or resettlement (Anderson and Moratto 1996). This period also coincides with a period of abrupt climate change with an increase in warmer and wetter conditions in the Sierra (Millar and Woolfenden 1999). Although European settlement and active fire suppression could have influenced this change in Teakettle's fire regime, it is unlikely to be its only cause.

The establishment of three species, Jeffrey pine, sugar pine, and red fir, was significantly associated with wet El Niño years. The Sierra Nevada has a prolonged summer drought characteristic of Mediterranean climates. Deep snow packs resulting from El Niño weather may play an important role for seedlings by providing more moisture over a longer time period during the critical early stages of establishment. Studies in the Southwest have found a similar pattern of greater ponderosa pine recruitment in wet years (Cooper 1960, White 1985). A limitation with some studies is that decadal approximations of tree recruitment patterns were used (Swetnam 1993, Barton et al. 2001) because exact establishment dates could not be determined from the aboveground increment cores used to age trees. We tried to reduce this uncertainty by calculating establishment age from stump cross sections cut at the root collar. Some researchers have also noted that, for the Southwest, PDSI values do not distinguish between winter–spring moisture and the potentially more important summer monsoon precipitation (Barton et al. 2001). This problem of seasonal precipitation is less of an issue in the Sierra Nevada because almost all soil moisture is produced by the winter snowpack (Major 1990). Although we attempted to locally calibrate the PDSI to our study site at Teakettle, the accuracy of its predictions of past drought conditions should be treated with caution.

Although we may have reduced these two problems, our inferences are limited by at least three other challenges inherent in this type of data (Barton et al. 2001). Periods of abundant moisture and infrequent fires are confounded, making it difficult to isolate the effect of each on tree establishment (Villalba and Veblen 1997b, Mast et al. 1998). A second limitation is that past recruitment events can be wiped out by subsequent mortality events leaving only a selective record of age structure (White 1985). This may produce significant bias when analyzing recruitment patterns from current static age structure (Johnson et al. 1994). Coupled with this selective record of age structure is the problem that many of the younger individuals in our sample were established after fire cessation, further reducing the available data for determining the effect of fire events on recruitment. We attempted to have our age sample composition be representative of live tree composition with a high percentage of white fir and incense cedar (Table 2). Unfortunately most of these trees, even many large-diameter stems, proved to be young, providing little information on presuppression establishment for shade-tolerants. A third problem is that many factors influence successful recruitment, including annual cone crop, preparation of favorable seed beds, and seed predation, to name but a few (Barbour et al. 1990, Mutch and Parsons 1998). All of these confounding factors limit inferences that can be drawn from current conditions because the age distribution has been filtered by mortality and recruitment factors over a stand's development (Johnson et al. 1994). With these limitations, we consider our results as hypotheses that require more rigorous testing using controlled experimentation and tree radial growth analysis. Although our age sample has been filtered by these factors, establishment patterns suggest an association with fire events and wet years. These patterns may be explained by within-stand differences in where each species is distributed and seedling requirements.

Jeffrey pine recruitment did not follow fire, but became established during or shortly before an El Niño year. This may result because Jeffrey pine is located on mixed conifer's driest sites, often on ridge tops and in areas with shallow soils (Vasek 1976). These areas have sporadic canopy cover (<40%) with little or no litter layer, and sparse understory fuels (Figure 1) (North et al. 2002). Fire may not significantly change seedbed conditions or understory light in these open forests. In dry, shallow soil conditions, deep root development is probably essential to survival and may be affected significantly by greater soil moisture conditions, which occur in El Niño years (Arkley 1981). In southern California, in conditions similar to Teakettle, Jeffrey pine was found to extract a significant portion of its water from fractures in the granitic bedrock (Hubbert et al. 2001). Surface soils dry rapidly and Jeffrey pine is less efficient at extracting soil moisture than greenleaf manzanita (*Arcostaphylus patulas*), a competing shrub on shallow soil sites (Royce and Barbour 2001). A constraint on Jeffrey pine establishment may be seedling survival until roots grow deep enough to gain access to bedrock water. El Niño events could provide establishing seedlings with a buffer for this root development. At Teakettle, during the 1998 El Niño year, high soil moisture (>20%) persisted on most sites throughout the summer into Oct. (Andrew Gray, USFS PSW Forest Inventory and Analysis, Portland, OR, May 2003).

Sugar pine recruitment followed fire events in years with above-normal precipitation. Sugar pine is intermixed typically with white fir and incense cedar in closed-canopy patches with deeper litter layers. Sugar pine is less shade tolerant, and seedling survival rates are lower in thick litter layers than for white fir and incense cedar (Fowells and Stark 1965, Stark 1965). Increased sugar pine recruitment after fire events may be the result of fire's effect of killing competing seedlings, reducing litter depth, or increasing understory light availability. Although mature sugar pines are more drought tolerant than white fir and incense cedar (Minore 1979), sugar pine seedlings may require high soil moisture until they reach sapling or older age stages (Tappeiner and McDonald 1996).

Red fir recruitment was not associated with fire events and did not change with fire suppression, but establishment was associated consistently with El Niño events. Red fir is the dominant tree and forest type at higher elevations (2,400–2,800 m) in the Teakettle Experimental Forest. At the lower elevation of our mixed-conifer study area, it usually occurs in riparian and cold drainage areas where it replaces white fir. Several studies found that white fir and red fir seedlings have similar ecophysiological requirements during the growing season, but that the transition to red fir dominance relates to snowpack tolerance (Barbour et al. 1990, Pavlik and Barbour 1991). The ecotone between mixed-conifer and red fir forest types corresponds to the mean freezing level during Dec. to Mar. storms, which is the elevation at which snowpack depth increases substantially over small-elevation increases (Barbour et al. 1991). Royce and Barbour (2001) have suggested that the red fir ecotone can be modeled based on timing of snowpack melt, slope aspect, and soil moisture-storage capacity. In the spring of 1998, after an El Niño year, Teakettle's riparian areas and slope depressions had a deep, persistent snowpack, typical of the higher elevations favored by red fir. The consistent cool, damp conditions may also limit fire extent and severity in mixed-conifer's red fir microsites. Only three fire-scarred red fir were located in our study area and its recruitment rate did not change significantly after fire cessation. In the mesic microsites favored by red fir, fire may be more infrequent and have lower intensity.

The most significant impact on our mixed-conifer age structure was the dramatic increase in white fir and incense cedar after fire cessation in 1865. Within our age sample, 84% of white fir and incense cedar were <136 years old. Current age structure suggests that establishment of white fir and incense cedar was not associated with El Niño events, and that recruitment did not follow fire. This assessment, however, is probably biased because white fir and incense cedar are more susceptible to fire damage than pines (Kilgore and Taylor 1979, Stephens and Finney 2002). Given Teakettle's fire frequency, any postfire pulses of white fir and incense cedar recruitment probably would have been eliminated from the record by subsequent fires. The largest pulse of white fir and incense cedar recruitment occurs between 1878 and 1897 (Figure 3), starting 13 years after the last widespread fire. The 1865–1877 period has a range of wet and dry years, but does not show a prolonged drought that might limit establishment. We do not know what may have caused this lag in recruitment.

Despite a highly clustered distribution of trees in mixed conifer (North et al. 2004), tree ages were not correlated spatially. Some studies (Bonnickson and Stone 1981; 1982; Stephenson et al. 1991) have suggested that mixed conifer's pattern of tree groups is an age cohort produced by gaps created when low-intensity fire locally crowns out. Cohort structure has been an important issue in managing Sierra Nevada forests as group selection (removing all trees in a group within an area of 0.8 ha) has been suggested as a means of restoring historic age structure and spatial pattern (Anonymous 2004). In our study area, however, none of the tree groups, even those with similar diameter sizes, had a synchronized age structure. Diameter was a poor indicator of age, and many large trees were actually less than 135 years old. The rapid growth of some trees (up to 0.018 m^2 basal area/yr) was a surprise given Teakettle's elevation and hot, dry summers. Although a post-1865 age cohort did occur across Teakettle, at a finer scale, discrete tree groups had a diverse age structure.

In mixed conifer, top-down effects of fire and weather on recruitment are mediated by different species' response to these effects and within-stand differences in species location. Annual climate alone is synchronous with recruitment patterns of two species: Jeffrey pine recruiting on shallow droughty soils and red fir, which requires a deeper, persistent snowpack. Fire had little effect on Jeffrey pine and red fir recruitment, possibly because it has lower severity in the rock-dominated and riparian areas favored by the two species. Fire cessation is synchronized with the main white fir and incense cedar recruitment pulse. Any effect of climate on white fir and incense cedar recruitment could not be detected in our data because of fire's overriding effect on their recruitment record. Sugar pine is the one species synchronized with both fire and climate. This may be because it often occupies the same midslope sites as white fir and incense cedar, and its seedlings have a high moisture requirement. Frequent fire on these sites may have provided favorable seedbed conditions while reducing competition.

Conclusion

Several studies focusing on pine recruitment, fire, and climate have emphasized that regional weather and its influence on fire can generally synchronize tree recruitment, but that local disturbance also influences age structure (Swetnam 1993, Villalba and Veblen 1997b, Barton et al. 2001). Sierran mixed-conifer stands have a complex species distribution influenced by fine-scale differences in soil depth and microclimate conditions. In our study, age structure is highly varied because fire, climate, and microsite conditions may have differentially affected species recruitment. We found that potential fire and weather influences on tree recruitment patterns varied by species, and this variance may be explained by within-stand-distribution and seedling-requirement differences between species. If warmer years and more frequent fires occur with future climate change, species responses in mixed conifer may be asynchronous, making future forest composition difficult to predict.

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