

Fire disturbance and forest structure in an old-growth *Pinus ponderosa* forest, southern Cascades, USA

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Abstract

Questions: Did fire regimes in old-growth *Pinus ponderosa* forest change with Euro-American settlement compared to the pre-settlement period? Do tree age structures exhibit a pattern of continuous regeneration or is regeneration episodic and related to fire disturbance or fire-free periods? Are the forests compositionally stable? Do trees have a clumped spatial pattern and are clumps even- or mixed-age? How might information from this old-growth forest inform current restoration and management practices?

Location: A 235-ha old-growth forest in the Ishi Wilderness, southern Cascade Mountains, California.

Methods: Age, size, and spatial pattern of trees were quantified in seven stands. Fire history was reconstructed using fire scar dendrochronology. The influence of fire on stand structure was assessed by comparing fire history with age, size, and spatial structure of trees and identifying and measuring trees killed by two recent fires.

Results: Species composition in plots was similar but density and basal area of tree populations varied. Age structure for *P. ponderosa* and *Quercus kelloggii* showed periods of episodic recruitment that varied among plots. Fire disturbance was frequent before 1905, with a median period between fires of 12 years. Fire frequency declined after 1905 but two recent fires (1990, 1994) killed 36% and 41% of mostly smaller diameter *P. ponderosa* and *Q. kelloggii*. Clusters of similar age trees occurred at scales of 28–1018 m² but patches were not even-aged. Interactions between tree regeneration and fire promoted development of uneven age groups of trees.

Conclusions: Fire disturbance strongly influenced density, basal area, and spatial structure of tree populations. Fire exclusion over the last 100 years has caused compositional and structural changes. Two recent fires, however, thinned stands and created gaps favorable for *Q. kelloggii* and *P.*

ponderosa regeneration. The effects of infrequent 20th century fire indicate that a low fire frequency can restore and sustain structural characteristics resembling those of the pre-fire suppression period forest.

Keywords: Fire effects; Fire return interval; Fire; Forest Structure; Ishi Wilderness; *Quercus kelloggii*; Spatial autocorrelation; Stand dynamics.

Nomenclature: Hickman (1993).

Introduction

Recurring fire is a key disturbance process that influences the structure and dynamics of pine forests in the United States (White 1985; Mast et al. 1999; Taylor 2004; Brown & Wu 2005), Mexico (Fulé & Covington 1998; Skinner et al. 2008) and Europe (González-Martínez & Bravo 2001; Wirth et al. 2002; Fulé et al. 2008). The importance of fire as an agent that controls pine forest structure and dynamics changed in much of western North America with Euro-American settlement in the mid- to late 19th century, particularly in the most fire prone pine forests. For example, Californian *Pinus ponderosa* forest structure and composition was dramatically altered through fire suppression, logging, and grazing (Vankat & Major 1978; McKelvey & Johnston 1992; van Wagendonk & Fites-Kaufmann 2006). These land-use changes have limited our understanding of how fire regimes shaped ponderosa pine forest structure and influenced forest dynamics. They have also increased the susceptibility of these forests to high severity stand-replacing fire (Skinner & Chang 1996; Schmidt et al. 2008).

Post-fire regeneration of *P. ponderosa* is related to the presence of a mineral soil seedbed exposed by fire (Oliver & Ryker 1990), favorable climatic conditions, and a good seed crop (Oliver & Ryker 1990; Savage et al. 1996). The regeneration of non-serotinous pines (*P. nigra*, *P. sylvestris*, *P. pinea*) in European pine forests is influenced by the same factors (Kuuluvainen & Rouvinen 2000; González-Martínez & Bravo 2001; Castro et al. 2004; Pausas et al. 2004). In *P. ponderosa* forests, the interactions

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between fire effects, climate, and seed production are thought to maintain a forest comprised of small groups of even-aged trees (Cooper 1960), but uneven-aged groups of similar sized trees have been identified in some forests (White 1985). Differences in growth rates among trees may create a size hierarchy within a patch and lead to small groups of trees that differ in size (Mast & Veblen 1999), and tree size differences may be interpreted as differences in tree age groups (Duncan & Stewart 1991; Veblen 1992).

The spatial analysis of trees can provide important insights into the formation and maintenance of pattern during stand development (Nakashizuka & Numata 1982; Rebertus et al. 1989; Duncan & Stewart 1991; Beaty & Taylor 2007). Although several studies have quantified the spatial patterns of trees in *P. ponderosa* forests (e.g., Cooper 1960; Biondi et al. 1994; Harrod et al. 1999; Youngblood et al. 2004; Sánchez et al. 2009), few have examined the spatial patterns of tree size and age to evaluate the even-aged tree group model of stand development (White 1985; Mast & Veblen 1999; Mast & Wolf 2004).

This study examines how fire disturbance influences stand structure and dynamics in an old-growth *P. ponderosa* forest in California, where logging has dramatically altered most *P. ponderosa* forests (Beardsley et al. 1999). Particular emphasis is given to the spatial analysis of tree populations to elucidate the spatial structure and development of tree groups within stands. Specific questions addressed are: 1. Did fire regimes change with Euro-American settlement compared to the pre-settlement period? 2. Do tree age structures exhibit a pattern of continuous regeneration or is regeneration episodic and related to fire disturbance or fire-free periods? 3. Are the forests compositionally stable? 4. Do trees have a clumped spatial pattern and are clumps even-age or mixed-age? 5. How might information from this old-growth forest inform current restoration and management practices?

Methods

Study Area

Old-growth *P. ponderosa* forests were studied in the Ishi Wilderness in the Lassen National Forest, in the southern Cascades of California in the summer of 2000 (Appendix S1). Forest stands in Beaver Creek (BC) (40°5′N, 121°43′W) and Devils Pinery

(DP) (40°5′N, 121°41′30″W) cover 210 ha and 25 ha, respectively. BC and DP occupy the surface of a remnant volcanic peneplain underlain by Tertiary pyroclastic flows of the Tuscan formation (Oakeshott 1971) and are on opposite banks of Deer Creek, a perennial stream. Elevations range from 790 to 910 m. Soils are Cohasset Gravelly Loam (Miles & Goudey 1997). The climate is Mediterranean, and average annual precipitation and temperature in Red Bluff (elevation 104 m) 70 km northwest of the study area are 59.7 cm and 17.1°C, respectively. Average annual precipitation in Cohasset (elevation 800 m), 20 km southwest is 145 cm. Most (85%) precipitation falls between November and April.

People have influenced fire regimes in the study area in known and unknown ways. The area was used and inhabited by Native Americans (Yana) before widespread Euro-American settlement in 1849. Yana are known to have used fire for hunting and to encourage growth of certain plants for food and fiber (Schulz 1954). Ishi, the last known Yana living in a native environment, lived in the study area until 1911, when he emerged in poor condition near Oroville, California (Schulz 1954). Livestock grazing and forest burning by herders and miners influenced vegetation and fire regimes in nearby areas (McKelvey & Johnston 1992) and may have affected vegetation in the study site. In 1905, the Lassen Forest Reserve was established and a policy of fire suppression was implemented (Strong 1973).

Field sampling, sample processing, and analysis

Old-growth stands were selected for sampling in BC and DP using several criteria: (1) presence of large diameter trees (≥ 1.0 -m diameter at breast height [dbh]); (2) homogenous site conditions and stand structure; and (3) selected stands should include the range of variation in old-growth structure (age, size, horizontal pattern) observed in BC and DP.

A total of seven forest stands (BC, $n = 6$; DP, $n = 1$) were sampled with a single large (0.9-1.0-ha) plot (Appendix S1). The location (GPS), elevation, slope aspect, slope pitch, slope configuration, and topographic position of each plot were recorded (Appendix S2). Plot size does impose limits on the maximum scale of inference for spatial structure (Upton & Fingleton 1985). Groups of trees in the same age class among plots, however, do permit inference on the potential contribution of larger scale events or processes on stand structure and development (Brown & Wu 2005).

Fire history

Fire history (return interval, frequency, season, relative extent) was reconstructed using fire scars in wood samples identified in logs, and in live and dead standing trees. Samples were collected with a chainsaw (Arno & Sneek 1977) at multiple locations across both sites (BC, $n = 27$; DP, $n = 10$), and sample location was determined with a GPS then recorded on a topographic map (Appendix S1).

Fire years were determined by first polishing each sample to a high polish and then cross-dating annual growth rings of each sample (Stokes & Smiley 1968). The calendar year of each tree ring with a fire scar lesion in it was then recorded as the fire date.

The season of burn for a fire was determined from the position of the fire scar lesion within the annual growth ring (Baisan & Swetnam 1990). Fire scar positions were classified as: (1) early (first 1/3 of early-wood); (2) middle (second 1/3 of early-wood); (3) late (last 1/3 of early-wood); (4) late-wood (in late-wood); (5) dormant (ring boundary). Dormant season scars in this strongly winter-wet, summer-dry climate probably represent fires that burn in late summer or fall after radial growth has ceased for the year, and not in winter or early season burns, as in the southwestern USA (Caprio & Swetnam 1995). High fuel moisture in winter and spring reduces the likelihood of early growing season burns, except in very dry years.

Fire extent was estimated using an index of fire extent based on the percentage of samples that recorded a fire. Composite fire scar chronologies were calculated for fire return intervals (FRI) for fire years recorded by any, 25% or more, and 50% or more of the samples. FRI statistics were also calculated for each sample as a point recording fire (PFRI). The FRI analysis was performed using FHX2 software (Grissino-Mayer 2001).

Forest structure and composition

Forest structure and composition were determined by mapping and measuring live and dead trees (> 5 -cm dbh) in a $10\text{ m} \times 10\text{ m}$ grid established in each plot. Stem location in each grid cell (x, y) in each plot was determined by recording stem distance from the cell origin (0,0) with a metric tape. The species, dbh, and relative height class of each tree (suppressed, intermediate, lower main canopy, upper main canopy, emergent) were then recorded. Saplings (> 1.4 -m tall and ≤ 5 -cm dbh) and seedlings (0.2-m-1.4-m tall) were also mapped

and classified by origin (sprout, seed) in each cell. *P. ponderosa* only establishes from seed. For *Quercus kelloggii*, seed or sprout origin was inferred as stems emerging from the base of top-killed trees or stumps (sprouts) or those growing individually (seed). Canopy openings are often sites for tree regeneration, and canopy cover of trees above each cell was estimated in one of three cover classes: open ($< 33\%$ cover), intermediate (33-66% cover), and closed ($> 66\%$ cover). The number of contiguous cells of $< 33\%$ cover in a plot was used to estimate the size range (m^2) for gaps in each plot.

Stand dynamics and fire effects were interpreted from the age structure of tree populations and recent post-fire tree mortality. Tree age structure was determined by coring all live *P. ponderosa* ($n = 567$) and *Q. kelloggii* ($n = 189$) in each plot 30 cm above the soil surface. Cores were sanded to a high polish, their growth rings were cross-dated (Stokes & Smiley 1968), and tree age was assigned using the calendar year of the innermost tree ring for cores that hit the pith. An age correction was added to cores that missed the pith using the method described by Duncan (1989) based on measurements of the innermost rings. Cores from *Q. kelloggii* were often incomplete (46%) because of rot, and the annual growth rings of *Q. chrysolepsis* (canyon live oak) could not be consistently distinguished so this species was excluded from the age structure analysis ($< 1\%$ of trees). Ages for *P. ponderosa* (6%) and *Q. kelloggii* trees with incomplete cores were estimated using a least squares regression of age on dbh using cores from all plots (*P. ponderosa* $r^2 = 0.46$, $P < 0.0001$, $n = 516$; *Q. kelloggii* $r^2 = 0.44$, $P < 0.001$, $n = 101$).

There was considerable variation in the rate of early radial growth (first 5 years) of *P. ponderosa* (0.4 - 4.7 mm yr^{-1} , $n = 126$) and *Q. kelloggii* (0.4 - 2.6 mm yr^{-1} , $n = 11$). Consequently, an age correction factor was not added to tree core ages to estimate dates of tree establishment. Tree ages are reported as the center date at coring height.

The effects of two recent burns in BC (1990, 1994) on tree mortality were inferred from the population of dead standing and downed trees with scorched bark in each plot. The dbh and location (x, y) of each scorched dead tree was recorded in each cell of each plot.

Spatial analysis

The spatial autocorrelation of tree ages and tree sizes (dbh) was identified using Moran's I (Moran 1950). Moran's I measures the property that entities

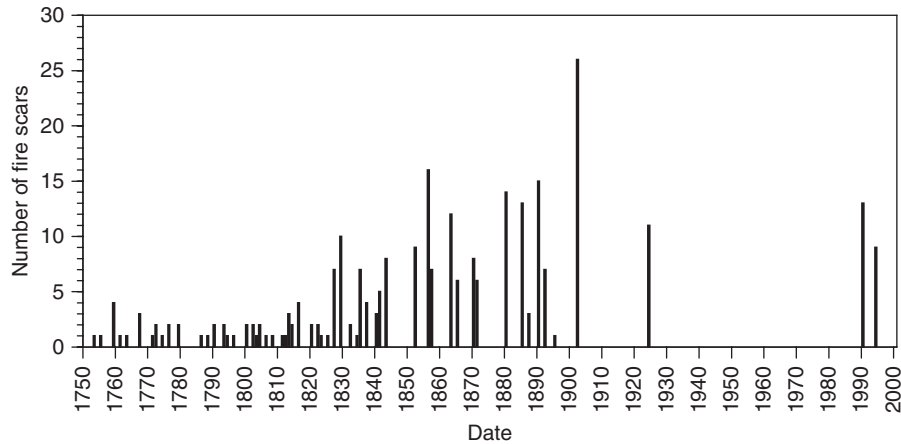


Fig. 1. Number of fire scar samples ($n = 37$) that recorded fires between 1750 and 2000 in old-growth *P. ponderosa* forests in the southern Cascades Range, California.

(trees) that have similar characteristics (age or dbh) are found closer to each other than entities that have different characteristics (Upton & Fingleton 1985). Values of Moran's I were calculated for age and dbh for all trees and for trees > 100 years old in successive 3-m distance classes (d) up to 48 m to identify spatial autocorrelation over a range of spatial scales; significance was identified using two-tailed tests (Upton & Fingleton 1985). The frequency of significant values of Moran's I was then summarized for all plots. Finally, tree ages were mapped to visually interpret and confirm the spatial autocorrelation analysis.

Results

Fire record

A total of 59 fire dates were recorded in the fire scars in the 27 samples from BC, while 11 fire dates were recorded in the fire scars from 10 samples in DP. Few of the fire dates ($n = 9$) in the study area were recorded before 1750, so the period after 1750 was selected for the fire disturbance analysis (Fig. 1).

Fire return intervals

The fire interval distributions for fires of any extent were positively skewed, with more short than long intervals, and the median FRI was shorter than mean FRI (Table 1). Fire extent varied among fire years and the median composite FRI for fires of small to intermediate extent was shorter (2 years) than for widespread fires that scarred 50% or more (5 year) of the recorder trees (Table 1; Fig. 1). The

Table 1. Statistical characteristics of composite and point fire return intervals for 37 fire scar samples in old-growth *P. ponderosa* forests in the southern Cascades, California.

Composite FRI	Mean	Median	Range	SD
<i>Fire return interval (years)</i>				
All scarred	4.2	2.0	1-66	8.7
> 25%	4.8	2.0	1-66	9.4
> 50%	8.1	5.0	2-69	12.4
Point FRI	16.0	12.0	7-19	7.1

number of samples scarred by fires increased after 1825, in part because of the increase in sample depth or the number of trees able to record a fire. Only two of 11 fires recorded in DP also burned in BC. Deer Creek probably impeded fire spread between sites in most years.

PFRI were longer than the composite FRI (Table 1). The median point FRI for all samples was 12 years.

There was also temporal variation in the composite FRI (Table 2, Fig. 1). Mean composite FRI was shorter in the pre-Euro-American ($P < 0.05$, t -test) than in the settlement or fire suppression period. There was no statistical difference in the mean composite FRI between the settlement and fire suppression period ($P > 0.05$, t -test), but only four fires were recorded in the fire suppression period.

Season of fires

The position of fire scars in annual growth rings indicated that fires burned mainly late in the growing season (late-wood = 40.4%) and after trees had stopped growth for the year (dormant = 36.7%). Growing season fires were less frequent, with 21.1%

Table 2. Composite fire return interval statistics (FRI) (years) for the pre-Euro-American (1750-1849), settlement (1850-1904), and fire exclusion (1905-2000) periods in old-growth *P. ponderosa* forests in the southern Cascades, California. Mean values with the same letter are different ($P < 0.05$, *t*-test). *n* is the number of intervals.

Time period	<i>n</i>	Mean	SD
1750-1849	40	2.3 ^{ab}	1.2
1850-1904	13	3.9 ^{ab}	2.4
1905-2000	3	24.3 ^a	36.1

in the last third of early-wood and 1.8% in the middle third of early-wood.

Stand characteristics

The density and basal area of trees varied among plots (Table 3). *P. ponderosa* was the most abundant species in all plots, with an average density of 104 trees ha⁻¹ (range, 58-146 trees ha⁻¹) and an average basal area of 23.1 m² ha⁻¹ (range, 13.9-30.8 m² ha⁻¹). *Q. kelloggii* abundance was more variable among plots and it had an average density and basal area of 31.4 trees ha⁻¹ (range, 1-106 trees ha⁻¹) and 4.0 m² ha⁻¹ (range, 0.9-10.2 m² ha⁻¹), respectively. *Q. kelloggii* trees were confined mainly to the suppressed and intermediate height classes (Table 3). In contrast, *P. ponderosa* was present in all height classes, and emergent and main canopy trees were common in some plots. *Q. chrysolepsis* trees (*n* = 10) were present in two plots.

Recent fire effects on forest structure

The 1990 and 1994 fires in BC changed forest structure. On average, these fires killed 69 *P. ponderosa* ha⁻¹ (range 3-134 trees ha⁻¹) and nine *Q. kelloggii* trees · ha⁻¹ (range, 0-28 trees ha⁻¹), or 36% and 41% of the trees of each species in each plot, respectively (Table 3; Fig. 2). More small (<35-cm dbh) than large (≥ 35-cm dbh) diameter trees were killed by the fire, and some small diameter trees may not have been measured because they were consumed by the fires. The 1990 and 1994 fires, on average, reduced basal area of *P. ponderosa* and *Q. kelloggii* in the plots by 4.4 m² ha⁻¹ (range 0.5-7.0 m² ha⁻¹) and 0.6 m² ha⁻¹ (range 0-1.3 m² ha⁻¹), respectively.

Seedlings, saplings, and canopy density

P. ponderosa seedlings were present in all plots, and the average density of seedlings in a plot was

Table 3. Characteristics of live and dead (in parentheses) trees (> 5-cm dbh), density of seedling (0.2-1.4-m tall) and saplings (> 1.4-m tall ≤ 5-cm dbh) and average gap size (contiguous 10 m × 10 m cells with <33% canopy cover) and range in plots of old-growth *P. ponderosa* forests in the southern Cascades, California. Species acronyms are *P. ponderosa* (Pipo) and *Q. kelloggii* (Quke).

Plot	BC1		BC2		BC3		BC4		BC5		BC6		DP	
	Pipo	Quke	Pipo	Quke	Pipo	Quke	Pipo	Quke	Pipo	Quke	Pipo	Quke	Pipo	Quke
Basal area (m ² ha ⁻¹)	13.9 (5.8)	0.9	28.1 (7.0)	1.78 (0.9)	23.5 (0.5)	9.0 (0.4)	26.8 (3.0)	3.0 (1.0)	22.5 (4.0)	16.0 (6.1)	30.8 (3.2)	2.1 (1.3)	136 (21)	10.2 (1.5)
Total density (ha ⁻¹)	81 (121)	1	102 (55)	26 (19)	58 (3)	57 (10)	138 (46)	20 (6)	146 (132)	64 (43)	136 (21)	7 (7)	106 (26)	
Height class (ha ⁻¹)														
Emergent	10		19 (2)		6	1	(1)		6 (2)	5	13 (1)			
Upper main canopy	5 (3)		39 (10)		18		27 (4)		24 (2)	16 (9)	22 (1)			
Lower main canopy	22 (15)	1	21 (18)	2	16 (1)		35		47 (3)	12 (3)	25 (5)	4		
Intermediate	23 (33)		15 (10)	6 (1)	11 (1)	32 (1)	33 (8)	4 (3)	41 (38)	13 (6)	21 (3)	30 (3)		
Suppressed	21 (70)		8 (15)	18 (18)	7 (1)	24 (9)	43 (33)	16 (3)	28 (87)	18 (25)	55 (11)	72 (23)		
Seedlings (ha ⁻¹)	675	60	691	342 (74)	37	229 (1)	121	61	1408 (2)	730	84	73 (15)	7 (294)	
Saplings (ha ⁻¹)		1		70 (7)		25	3	4	450 (100-2000)	0 (1)	3 (3)	1 (14)		
Average gap size (m ²)	1000 (600-2400)		450 (100-900)		350 (100-800)		313 (100-500)		450 (100-2000)	1300 (500-2000)	233 (200-400)			

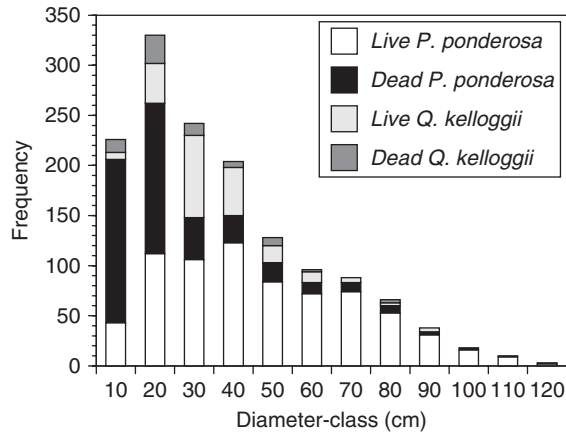


Fig. 2. Size class distribution of live and dead (standing and down) *P. ponderosa* and *Q. kelloggii* trees (stems > 5-cm dbh) in seven old-growth forest plots in the southern Cascades Range, California. Values on the x-axis are the mid-point of a 10-cm dbh class. Not shown is one stem in the 150-cm dbh class.

535 stems ha^{-1} (range, 37-1408 stems ha^{-1}). Saplings were only present in one plot (Table 3). *P. ponderosa* seedlings were concentrated in open (67%) or intermediate (19%) forest canopy conditions rather than in closed conditions (14%).

Q. kelloggii regeneration was also concentrated in open (49%) and intermediate (26%) canopy conditions, compared to closed canopy conditions (25%). Overall, average *Q. kelloggii* seedlings density in the plots was 133 stems ha^{-1} , lower than for *P. ponderosa* (Table 3). *Q. kelloggii* saplings were present in six of seven plots, although most (> 90%) were only in two plots. *Q. chrysolepsis* seedlings and saplings were most abundant in DP; they were only present in three plots in BC.

The average size of a gap was 585 m^2 , but there was considerable variation in average gap size among plots, and the average gap size was smallest in DP (Table 3). Individual gaps in the plots ranged in size from 100 to 2400 m^2 .

Forest age structure

P. ponderosa and *Q. kelloggii* were present in a wide range of age classes, and the pattern of regeneration in the plots was episodic (Fig. 3). In four of the plots (BC1, BC3, BC4, BC6), there were two distinct pulses of regeneration between 1870-1930 and 1710-1770, separated by a nearly 100-year period with little recruitment. In BC5, there was also a pulse of recruitment between 1710 and 1770, but the second cohort was younger, with regeneration concentrated in 1900-1930. Regeneration in DP was

high in 1875-1920 and 1800-1830, but the intervening period of low recruitment was shorter and less distinct than in the other plots. Tree recruitment in BC2, in contrast, was concentrated in the 1820-1880 period with some older and younger trees in the plot. The dearth of young trees in the age-class histograms is, in part, a sampling artifact. Saplings and seedlings were not aged.

Spatial patterns of trees

The spatial autocorrelation analysis for age shows a pattern of significant ($P < 0.05$) positive autocorrelation for both *P. ponderosa* and *Q. kelloggii*, indicating patchiness in the spatial distribution of tree ages (Table 4). Both *P. ponderosa* tree populations (all trees, trees > 100 years old) exhibited a frequent pattern of positive spatial autocorrelation ($P < 0.05$) at distances from 3 to 21 m (28-1385 m^2). This pattern is evident on two representative maps of tree ages (Appendix S3). Positive spatial autocorrelation in tree age was also evident for *P. ponderosa* and *Q. kelloggii* at longer distances in several plots. Negative values of Moran's *I* at 30-42 m ($P < 0.05$) in several plots represent distances between groups of trees of different age.

The Moran's *I* for tree dbh indicates that spatial autocorrelation of *P. ponderosa* occurs less frequently than for tree age (Table 4). The difference in spatial autocorrelation between *P. ponderosa* tree dbh and age is most evident at distances < 24 m and for trees > 100 years old. Positive or negative spatial autocorrelation was infrequent for *Q. kelloggii*, indicating little tendency for similar sized trees to occur near each other.

Discussion

Fire disturbance was frequent in old-growth *P. ponderosa* forests before Euro-American settlement. The median PFRI of 12 years for the pre-fire exclusion period is within the range of values for the drier east side *P. ponderosa* forests in the southern Cascades (Taylor 2000; Norman & Taylor 2005), and pine-dominated mixed conifer forest in the Klamath Mountains (Taylor & Skinner 2003; Fry & Stephens 2006) and the Sierra Nevada (Taylor 2004; Beaty & Taylor 2007, 2008; Scholl & Taylor 2010) of California. Clearly, frequent fire was a key disturbance regulating development of pre-settlement *P. ponderosa* forests on the Pacific Slope, as also in interior *P. ponderosa* forests elsewhere in western

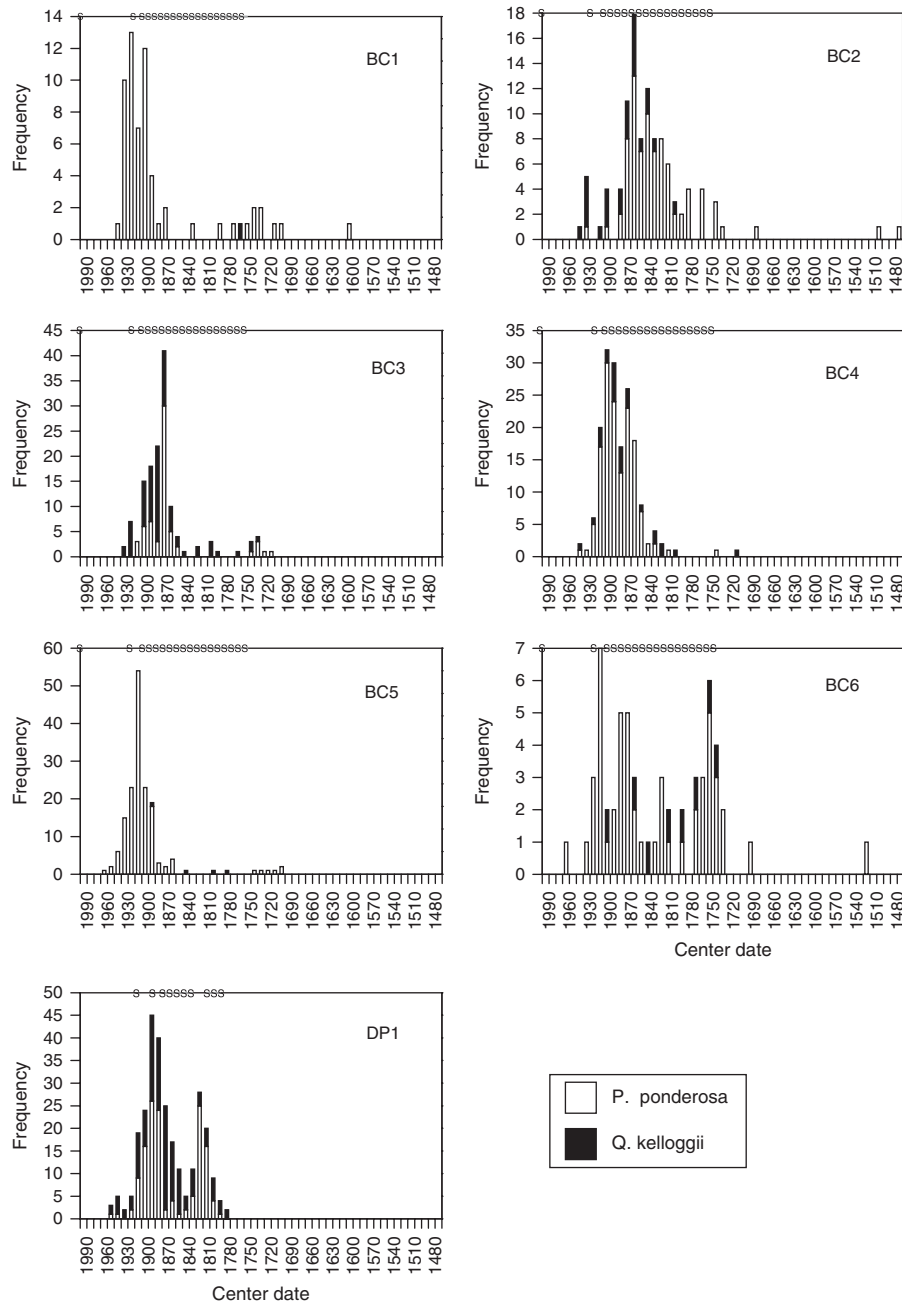


Fig. 3. Fire occurrence and age structure of *P. ponderosa* and *Q. kelloggii* trees (stems > 5-cm dbh) in old-growth forests in the southern Cascades Range, California. Note that only every third class is labeled and that the scale of the vertical axis is different on each graph. The occurrence of fires in a decade that scarred 50% or more of the fire scar samples in the study area is indicated by the letter s.

North America (Veblen et al. 2000; Heyerdahl et al. 2001; Brown & Wu 2005).

Fire regimes changed in California when large numbers of Euro-Americans arrived in 1849 during the gold rush (Holliday 1999). Fire frequency declined nearly two-fold in the Ishi Wilderness after 1850. Demise of the local Native American population (Cook 1955) and the introduction of livestock

grazing would have reduced ignitions and continuity of fine fuels, reducing the potential for fire spread across the landscape (Caprio & Swetnam 1995). Reductions in fire frequency coincident with the onset of the gold rush have been reported for other sites in California (Norman & Taylor 2005; Fry & Stephens 2006) but a later 19th century or early 20th century decline in fire frequency is more common

Table 4. Spatial autocorrelation of *P. ponderosa* and *Q. kelloggii* trees (> 5-cm dbh) in old-growth *P. ponderosa* forests in the southern Cascades, California. Values are the frequency of plots ($n = 7$) with positive or negative (in parentheses) spatial autocorrelation ($P < 0.05$) as identified by Moran's I in 3-m distance classes for tree diameter (a) and tree age (b) for two categories of trees (all trees; trees > 100 years old).

Population	Distance class (m)															
	3	6	9	12	15	18	21	24	27	30	33	36	39	42	45	48
Diameter																
<i>P. ponderosa</i>	4	6	6	4	6	4	5	2	2	2(1)	2	1(1)	1(1)	1(2)	1	0(1)
<i>P. ponderosa</i> > 100 years old	2	5	4	5	6	5	5	1	1	2	2(1)	1(1)	1	2(3)	1	0(2)
<i>Q. kelloggii</i>	2	2	2	1	1	0	1	0	0	0	0	0	2	0(1)	0(1)	0
<i>Q. kelloggii</i> > 100 years old	1	1	1	1	1	1	0	0	0	0	0	0	1(1)	0	1	0(1)
Age																
<i>P. ponderosa</i>	4	5	0	4	2	2	2	0(1)	2(2)	1(1)	2	2	2	1	1	2(1)
<i>P. ponderosa</i> > 100 years old	1	1	2	1	1	2	2	1(1)	1(1)	1	1	2	0	1	0	0
<i>Q. kelloggii</i>	1	0	1	0	0	0	0	0	0	1	0	1(1)	1(1)	0	0	0
<i>Q. kelloggii</i> > 100 years old	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0

and related to a federal policy of fire exclusion that began on National Forest Lands in 1905 (Caprio & Swetnam 1995; Taylor 2000; Beaty & Taylor 2001; Scholl & Taylor 2010). Fire frequency also declined in the Ishi Wilderness after 1905. Only five fires burned in *P. ponderosa* stands in the 20th century, a six-fold reduction in fire frequency compared to the settlement period with a maximum interval between fires of 66 years.

The 1990 and 1994 fires reduced basal area and forest density and shifted forest structure (Photo S1). The thinning effects of fire were concentrated (79%) on smaller diameter stems (<35-cm dbh) in the shortest height classes. Thinning of smaller trees by fire is a hallmark of pine forests in North America (Keyser et al. 2006; Schwilk et al. 2006; Youngblood et al. 2006; Fulé & Laughlin 2007) and Europe (e.g., *P. sylvestris*) (Wirth et al. 1999) that experience low- and moderate-intensity surface fires. However, the 1990 and 1994 wildfires had severe effects in some areas. The 1990 fire killed or top-killed virtually all understory and overstory trees in old-growth *P. ponderosa* stands in the nearby Graham Pinery.

The fires also promoted regeneration of *P. ponderosa* and *Q. kelloggii* (Photo S1). Post-fire regeneration of *P. ponderosa* was abundant on the mineral soil seedbeds created by fire, especially in canopy openings (Photo S2). Conditions created by fire and canopy openings are favorable for *P. ponderosa* establishment (Oliver & Ryker 1990) as they are for non-serotinous pines in Europe (e.g., *P. nigra*, *P. sylvestris*, *P. pinea*) (Kuuluvainen et al. 1998; Pausas et al. 1999; Kuuluvainen & Rouvinen 2000; González-Martínez & Bravo 2001; Castro et al.

2004) and Mexico (*P. arizonica*, *P. durangensis*, *P. engelmannii*) (Fulé & Covington 1998). Precipitation in the study area was also above normal for 3 of 4 years (1995-1998) (WRCC 2007) after the 1994 fire, and moist spring conditions increased *P. ponderosa* seedling establishment and subsequent survival (Oliver & Ryker 1990). *P. ponderosa* produces medium seed crops every 2 to 3 years so the coincidence of fire, wet years, and a medium cone crop would be conducive to *P. ponderosa* regeneration. *Q. kelloggii* also regenerates after fire, particularly from sprouts (McDonald 1990). Sprouting was frequent (34% of seedlings and saplings) but establishment from seed was more common, especially where the forest canopy was open.

The age structure of *P. ponderosa* and *Q. kelloggii* trees show periods of high or low recruitment during the last 250+ years that lasted several decades. Peaks of establishment in the pre-settlement period were not clearly related to individual widespread fires or to long fire-free periods, as in some other *P. ponderosa* forests (Brown & Wu 2005). However, a large pulse of establishment occurred after fire frequency declined with initial Euro-American settlement in the 19th century. The wetter than average conditions in northern California between 1854 and 1916 (Graumlich 1987) may also have contributed to this pulse.

Old-growth *P. ponderosa* forests have a complex spatial structure that results from the interaction between fire and seedling establishment and survival (Cooper 1960; White 1985). Intense surface fires following the death of a canopy tree(s) that create a mineral soil seedbed would be favorable to ponder-

osa pine establishment. Given adequate seed and moisture, seedlings would establish in this burned patch. Repeated over a wide area, this patch formation process would result in a forest comprised of small even-aged groups of trees (Cooper 1960).

The positive spatial autocorrelation of *P. ponderosa* and *Q. kelloggii* trees > 100 years old at small to intermediate scales (78-1385 m²) supports this view of structural development. Moreover, clump sizes of similar-aged trees fall within the range of gap sizes identified in the plots (0.01-0.24 ha) and those reported (0.02-0.64 ha) for other ponderosa pine forests (Cooper 1960; White 1985; Moore et al. 1993; Harrod et al. 1999; Taylor 2004; Youngblood et al. 2004). Yet, trees in individual clumps frequently had a wide range of ages, suggesting a more complex pattern of tree group development (Photo S3). Variation in fire intensity related to spatial variability in fuel loads that kill some seedlings in a patch but not others would promote development of uneven-aged group development (White 1985; Stephens & Fry 2005). A wide range of ages in small groups of *P. ponderosa* trees that established before fire exclusion has been identified in Arizona forests (White 1985), and in closely related mixed conifer forests in California (Beatty & Taylor 2007). Similar uneven aged patch development caused by partial mortality of groups of understory trees by surface fire and then post-fire regeneration is also characteristic of *P. sylvestris* forests in Europe (Wirth et al. 1999). Moreover, spatial autocorrelation of tree size was less frequent than for tree age, suggesting that after an even-aged group of trees establishes a size hierarchy develops, with eventual dominance of one or several trees (Mast & Veblen 1999). Asymmetric competition among trees in a patch has also been observed in European *P. sylvestris* forests, and leads to stands composed of small groups of even-sized trees (Kuuluvainen et al. 1998). It may be that tree groups in *P. ponderosa* forests are commonly uneven-aged (Photo S4). Cooper (1960) did not include spatially explicit data on tree age structure in developing his model of old-growth *P. ponderosa* forest development.

Old-growth *P. ponderosa* pine-*Q. kelloggii* forest are rare in California because of forest harvest and other unharvested stands have changed dramatically in structure and composition because of a century or more of fire exclusion (Vankat & Major 1978; McKelvey & Johnston 1992). In forests where fire has been excluded for a century or more, *P. ponderosa* is replacing *Q. kelloggii* (Vankat & Major 1978). *P. ponderosa* is capable of establishing beneath *Q. kelloggii* and *P. ponderosa* can overtop *Q. kelloggii* as they mature (McDonald 1990). This

tendency was evident in stands in the Ishi Wilderness. The 1990 and 1994 burns thinned stands and created gaps that were favorable for *P. ponderosa* and especially for *Q. kelloggii* regeneration. This suggests that fire is a key disturbance that promotes persistence of fire-dependent *Q. kelloggii* in these mixed forests. Similarly, low to moderate intensity surface fire appears critical to the maintenance of mixed *Pinus-Quercus* in other dry forests in the American southwest (Barton 1999), northern Mexico (Fulé & Covington 1998), and northeastern Spain (Garcia et al. 2002; Retana et al. 2002). The structure of *P. ponderosa* forests in the Ishi Wilderness, which experienced two late 20th century fires, also demonstrates that even infrequent use of wildland or prescribed fire, under specified burning conditions, could be used to restore and sustain structural features (composition, density, basal area, spatial pattern) resembling those of the pre-fire suppression forest.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Location of study area, plots ($n = 7$), and fire scar samples ($n = 37$) in old-growth *P. ponderosa* forest in the southern Cascades, California.

Appendix S2. Plot and site characteristics in old-growth *P. ponderosa* forests in the southern Cascades, California.

Appendix S3. Spatial distribution of tree (>5-cm dbh) ages of *P. ponderosa* and *Q. kelloggii* in old-growth forests in the southern Cascades, California. Plot dimensions are 100 m × 100 m (BC6) and 130 m × 70 m (BC3). Circle size is scaled to tree age.

Photo S1. Aerial view of the clumped nature of *Pinus ponderosa* trees and seedlings in 2005 in the Beaver Creek Pinery, Lassen National Forest, Southern Cascades, USA. Fires burned through this old-growth forest in 1990 and 1994 killing smaller diameter trees which reduced tree density and basal area. Photo by E. Knapp

Photo S2. Even aged patch of *P. ponderosa* pine seedlings that established on bare mineral soil beneath a standing dead tree that was consumed by fire in either 1990 or 1994 in the Beaver Creek Pinery, Lassen National Forest, Southern Cascades, USA. Photo by A. Taylor.

Photo S3. Group of *P. ponderosa* trees with small clumps of different age trees forming a multi-aged patch at small to intermediate spatial scales in the Beaver Creek Pinery, Lassen National Forest, Southern Cascades, USA. Note the *Q. kelloggii* in the background that are being over-topped by *P. ponderosa*. Fires burned through this old-growth forest in 1990 and 1994. Photo by C. Skinner.

Photo S4. Mosaic of *P. ponderosa* and *Q. kelloggii* tree groups in an old-growth forest in the Beaver Creek Pinery, Lassen National Forest, Southern Cascades, USA. Fires burned through this forest in 1990 and 1994. Photo by M. Beaty.

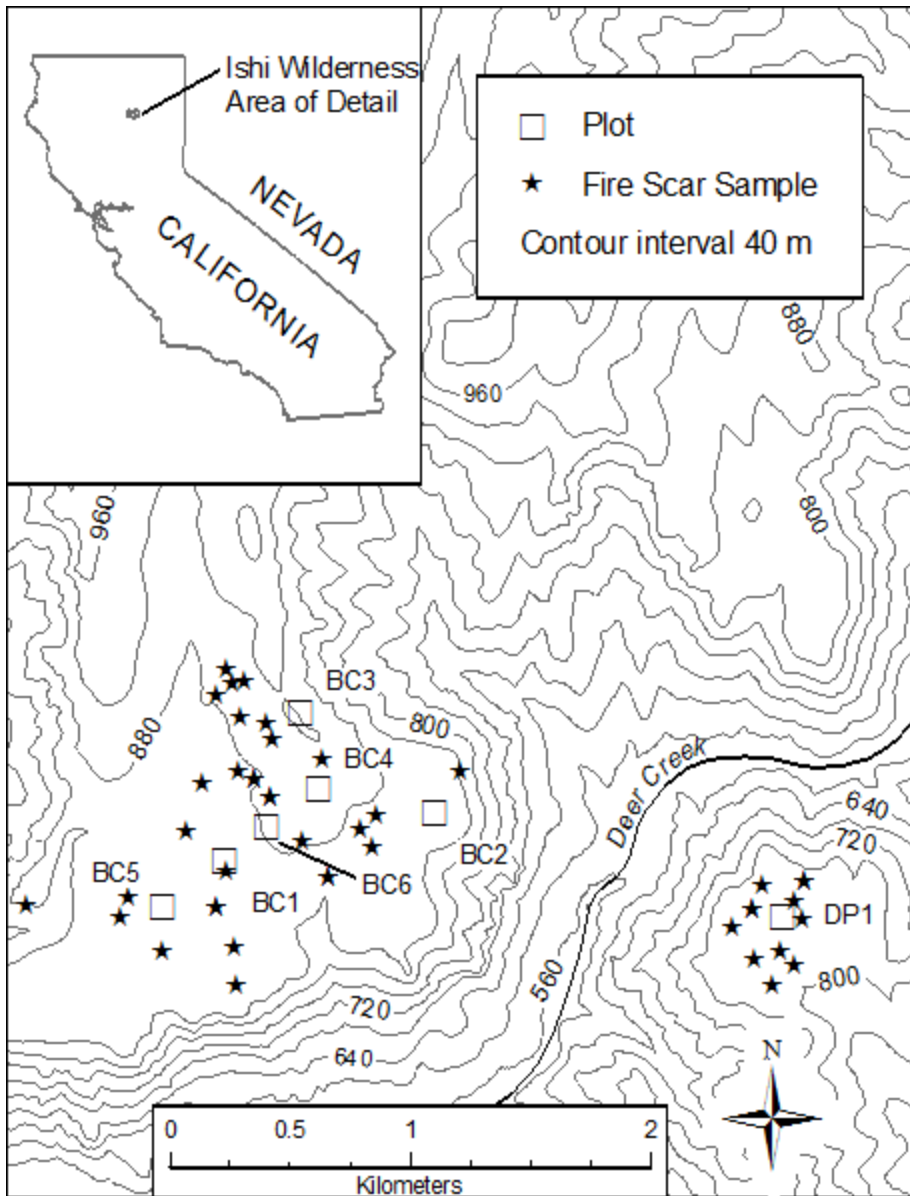
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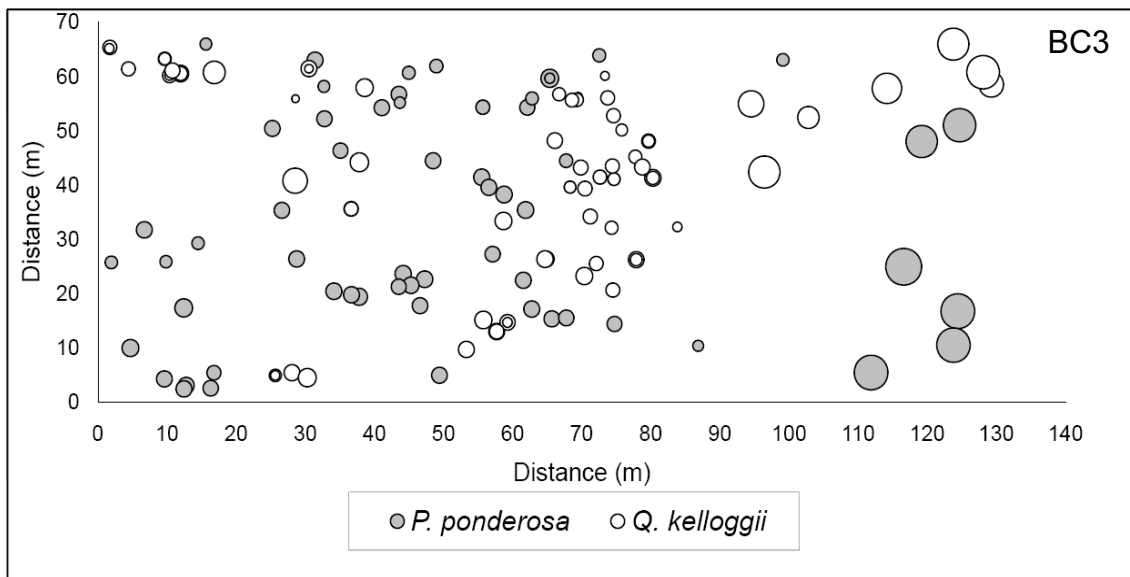
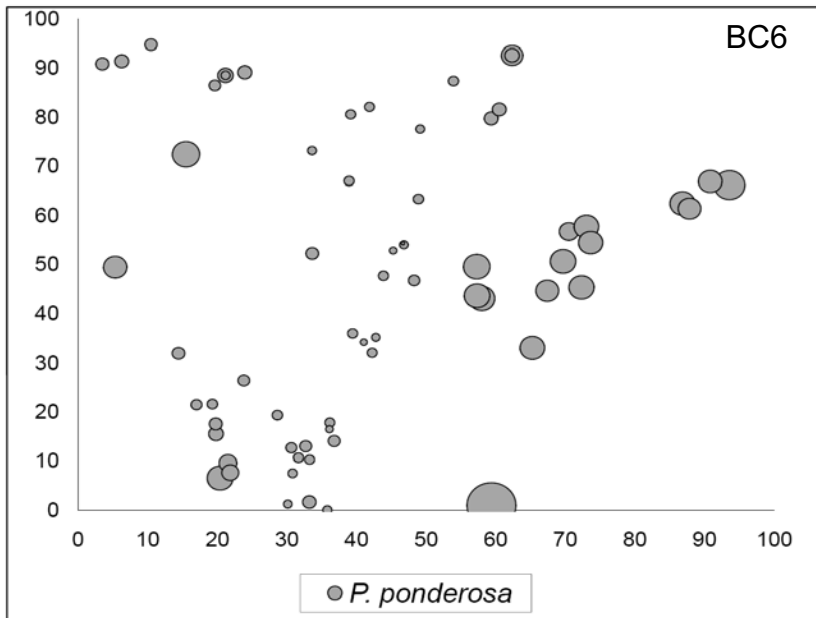
Appendix S1 Location of study area, plots (n=7), and fire scar samples (n=37) in old-growth *P. ponderosa* forest, in the southern Cascades, California.



Appendix S2. Plot and site characteristics in old-growth *P. ponderosa* forests in the southern Cascades, California.

Plot	Plot dimensions	Elevation	Aspect (°)	Slope pitch (°)
BC1	100 m x 100 m	870 m	130	2
BC2	100 m x 100 m	840 m	167	6
BC3	130 m x 70 m	870 m	84	8.5
BC4	100 m x 100 m	875 m	140	10
BC5	100 m x 100 m	860 m	270	3
BC6	100 m x 100 m	850 m	292	4
DP1	100 m x 100 m	775 m	78	3

Appendix S3. Spatial distribution of tree (>5 cm dbh) ages of *P. ponderosa* and *Q. kelloggii* in old-growth forests in the southern Cascades, California. Plots dimension are 100 m x 100 m (BC6) and 130 m x 70 m (BC3). Circle size is scaled to tree age.



Captions

Photo 1. Aerial view of the clumped nature of Pinus ponderosa trees and seedlings in 2005 in the Beaver Creek Pinery, Lassen National Forest, Southern Cascades, USA. Fires burned through this old-growth forest in 1990 and 1994 killing smaller diameter trees which reduced tree density and basal area. Photo by E. Knapp

Photo 2. Even aged patch of P. ponderosa pine seedlings that established on bare mineral soil beneath a standing dead tree that was consumed by fire in either 1990 or 1994 in the Beaver Creek Pinery, Lassen National Forest, Southern Cascades, USA. Photo by A. Taylor.

Photo 3. Group of P. ponderosa trees with small clumps of different age trees forming a multi-aged patch at small to intermediate spatial scales in the Beaver Creek Pinery, Lassen National Forest, Southern Cascades, USA. Note the Q. kelloggii in the background that are being over-topped by P. ponderosa. Fires burned through this old-growth forest in 1990 and 1994. Photo by C. Skinner.

Photo 4. Mosaic of P. ponderosa and Q. kelloggii tree groups in an old-growth forest in the Beaver Creek Pinery, Lassen National Forest, Southern Cascades, USA. Fires burned through this forest in 1990 and 1994. Photo by M. Beaty.







