RESEARCH ARTICLE

AGE AND STRUCTURE OF MATURE KNOBCONE PINE FORESTS IN THE NORTHERN CALIFORNIA COAST RANGE, USA

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ABSTRACT

An understanding of current structural conditions and disturbance history is a requisite for optimal management of forest ecosystems, especially for serotinous species such as knobcone pine (*Pinus attenuata* Lemmon). Knobcone pine is widely distributed in California, yet little is known regarding age and forest structure patterns. In this study, we quantify forest conditions of 21 mature knobcone pine stands in the northern Mayacmas Mountains, north Coast Range, California, USA. Characterized by complex terrain, knobcone pine forests occur in small patches interspersed with chaparral and mixed evergreen forests. Stands displayed unimodal, bimodal, and diffuse age distributions with predominant stand ages ranging from 42 yr to 70 yr, although trees ranged from 17 yr to 98 yr old. Knobcone pine stands appear to have been maintained by stand replacing fires. However, stands with uneven-aged structures were produced through the persistence of residual trees and low intensity fires that created secondary cohorts. Stands varied in density, ranging from 503 stems ha^{-1} to 2986 stems ha^{-1}, with snags comprising 12% to 40% of total density. Wildfires that occurred from the 1930s to the 1960s, in addition to a large wildfire in 1981, created a heterogeneous landscape of knobcone pine forests. Older stands have lower canopy cover, high snag densities, and many trees with evidence of western gall rust (*Peridermium harknessii*) infections—signs that they are approaching their expected life spans. Risks and constraints associated with using stand replacing prescribed fire pose a challenge for managers of knobcone pine forests, and research may be needed to explore feasible treatment alternatives.

Keywords: closed cone pine, fire dependent, serotiny, tree age, tree density, wildfire

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INTRODUCTION

Many plant species that occupy Mediterranean environments possess character traits that couple them to periodic disturbances such as fire (Trabaud 1987, Bond and Wilgen 1996, Stephens and Libby 2006). One variant is cone serotiny, the protection of seeds in sealed woody structures (i.e., closed cones; Lamont *et al*. 1991) that open and disperse seeds after being exposed to elevated temperatures from wildfires. This adaptation allows species to exploit the favorable conditions of the post-fire environment for recruitment of offspring. Among all conifers in California, the habit of serotiny is most strongly expressed in knobcone pine (*Pinus attenuata* Lemmon) (Vogl *et al*. 1977, Keeley and Zedler 1998). Additionally, knobcone pine does not vegetatively resprout and intra-fire interval seedling establishment is rare; thus, it is fire dependent (Vogl 1973, Keeley *et al*. 1999).

There is little research on demography and management of knobcone pine forests. This is due in part to assumptions about fire regime characteristics of serotinous species (Schwilk and Ackerly 2001, Davis and Borchert 2006, Mallek 2009), as well as physiognomic characteristics (i.e., small, discontinuous stands; lack of self-pruning in trees; dense shrub understory), which make accessibility and study of knobcone pine forests challenging. Research has mainly focused on general forest descriptions (e.g., Imper 1991, Johnson 1995, Lanner 1999), genetic relationships (Millar 1986, Strauss and Conkle 1986, Millar *et al*. 1988, Burczyk *et al*. 1997) and evolutionary adaptations to fire (Linhart 1978, Lamont *et al*. 1991, Schwilk and Ackerly 2001). Only two studies have investigated the effects of wildfire and these were in central (Keeley *et al*. 1999) and southern California (Vogl 1973).

Research related to fire regimes of closed cone conifer forests in California usually have to do with fire frequencies and lifecycle risks (Zedler 1995). For these species, geographic databases and age structures of stands are used to assess current forest conditions and determine recent fire intervals. Despite fire suppression efforts in California (Sugihara *et al*. 2006, Syphard *et al*. 2007), fire-free periods have been too short to allow a sufficient seed banks to accumulate for the next regeneration, posing a risk of local extinction in some serotinous pine and cypress populations (Zedler 1981, Keeley *et al*. 1999). Conversely, some mature pine forests with long fire-free intervals show signs of senescence (i.e., high snag densities, older trees with reduced vigor) (Vogl 1973, Imper 1991, Storer *et al*. 2001). Yet others have shown a low risk for either situation (Ne'eman *et al*. 1999, Mallek 2009).

Presence of a serotinous species such as knobcone pine usually implies a spatially uniform, stand-replacing fire regime (Davis and Borchert 2006). Few studies, however, have examined age structures across multiple stands. As managers continue to implement treatments that closely resemble natural disturbance patterns to maintain or restore forest health or mitigate fire hazard (Stephens *et al.* 2009), current forest conditions and disturbance histories are key components to informing management decisions. Furthermore, implementing forest treatments at the appropriate spatial and temporal extent adherent to sound forest management is critical (Turner and Romme 1994, Turner *et al*. 1997).

The purpose of this study was to assess current forest structural and stand age distributions, and to describe the stand histories in mature knobcone pine forests in the northern Mayacmas Mountains, located in the northern Coast Range, California, USA. Specifically, we used plot data and modern fire records to address the following questions: 1) What is the current structure (i.e., canopy cover, species composition, density, and age) of mature stands?; 2) Are stands even-aged or uneven-aged, and how much variation is there across the landscape?; 3) What is the disturbance histories of the stands?; and 4) Are the older stands showing signs of senescence (i.e., higher snag density or shrub cover, lower canopy cover)? A better understanding of the historical context of the present forest conditions may help direct long-term management planning.

METHODS

Study Area

This study was conducted at the Bureau of Land Management (BLM) South Cow Mountain Recreation Area (COW; 39˚4´N, 123˚22´W) and the University of California Hopland Research and Extension Center (HOP; 39˚0´N, 123˚4´W), located in the interior Coast Ranges of northern California, USA. These sites are in the northern Mayacmas Mountains, a range that straddles the southeastern Mendocino and western Lake county boundaries. The elevations of COW and HOP range from 244 m to 1220 m and 153 m to 915 m above sea level, respectively. The climate is Mediterranean with cool, wet winters and hot, dry summers. Average winter and summer maximum temperatures are 16 ˚C and 32.5 ˚C, respectively. Average precipitation, depending on elevation, ranges from 94 cm to 144 cm, falling mostly as rain, with snowfall occurring occasionally at the upper elevations.

The sites are composed of a variety of vegetation types (Barbour and Major 1988). In the valley bottoms and lower slopes, grasslands and oak woodlands prevail, while mixed evergreen forests are found on mesic, north-facing slopes. Knobcone pine forests are found in small, relatively pure stands interspersed in chaparral (Figure 1), primarily on ridge tops and north-facing slopes. Associated tree species include Pacific madrone (*Arbutus menziesii* Pursh), California bay (*Umbellularia californica* [Hook. & Arn.] Nutt.), canyon live oak (*Quercus chrysolepis* Liebm.), California black oak (*Q. kelloggii* Newb.), and California nutmeg (*Torreya californica* Torr.). Typical understory shrub species include shrub oaks (*Quercus* spp. L.) and manzanita (*Arctostaphylos* spp. Adans.).

The BLM acquired COW (21 654 ha) in 1958. Prior to this date, the land was in various private ownerships, utilized for grazing, hunting, and recreation. The University of California purchased HOP (2110 ha) in 1951, and the property is currently managed for scientific research. Recent management and research activities on COW and HOP have included prescribed burning, primarily in grasslands and chaparral (Stephens *et al*. 2008, Potts and Stephens 2009, Potts *et al*. 2010).

Forest Measurements

We selected stands from a pool of mature knobcone pine stands initially identified from

Figure 1. Knobcone pine forests in the northern Macyacmas Mountains, north Coast Ranges, occur in small, isolated stands (left, stand A) often surrounded by chaparral. Moderate shrub cover consisting of several species of manzanita and oak are common in stands (right, stand F).

aerial photos. Suitable stands were verified through field reconnaissance and tree-ring cores to estimate the age of overstory trees. Stands were selected according to the following criteria: accessibility to roads or trails, size (≥0.5 ha), presence of a relatively continuous overstory canopy of knobcone pine, and a stand age of at least 25 yr. In 1981, a wildfire burned a large portion of the eastern side of COW; stands in these areas were eliminated from selection (Figure 2). Descriptions of forest stand characteristics were not from a random sample bur represent older knobcone pine forests in the northern Mayacmas Mountains.

Forest structure and tree age data were collected in 10 m radius circular inventory plots. Within each stand, five plots were installed at intersections of a 50 m grid in 2004 and 2005; the starting point was chosen randomly. Slope and aspect were measured at the plot center using a compass and clinometer, respectively. Canopy cover was measured using a sight tube on a 5 m × 5 m grid around the plot center at a 5 m spacing. At each point on the grid, the sight tube was used to determine if a tree crown was directly overhead; the species of the tree was recorded if the grid point was under canopy. Percent canopy cover was estimated by the total number of points under canopy divided by the total number of grid points sampled (25). It's noteworthy that grid points considered under the canopy included not only knobcone pines, which were the tallest trees in the stand, but mid-story species such as Pacific madrone, canyon live oak, and black oak.

For all knobcone pines and stems of other species >10 cm diameter at breast height (dbh; 1.4 m above the ground) in each plot, we recorded the following: dbh, species, status (live or dead), maximum height, and height to live crown base. Plots were also surveyed for any knobcone pine seedlings and saplings (stems <1.4 m tall). Identification, percent cover (six modified Daubenmire percent cover classes, Barbour *et al*. 1999), and height (0.5 m intervals) of all shrub species were recorded in each plot by two observers. Cover class mid-point values were used for summaries, assuming that actual values were symmetrically dispersed about midpoints.

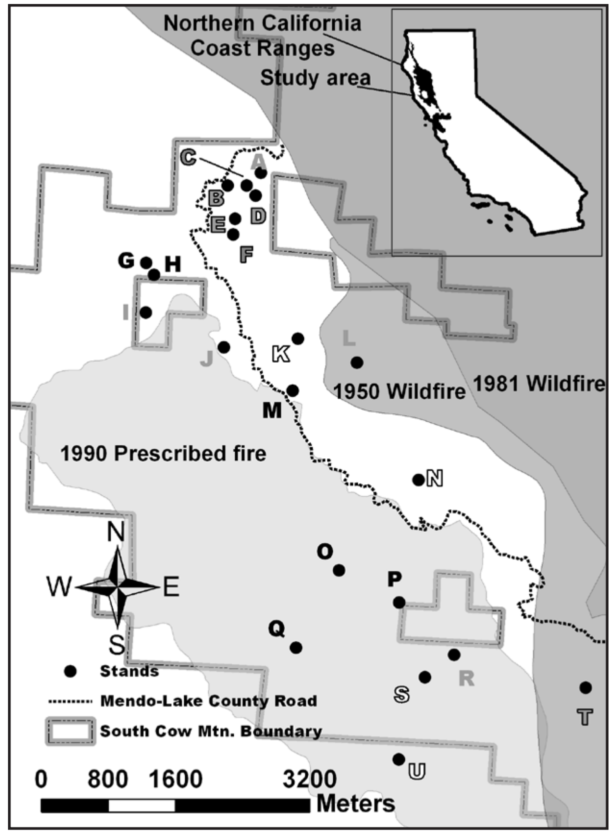

Figure 2. Map of study area showing locations of the 21 knobcone pine stands on the northern Mayacmas Mountains, northern California. The southernmost plot (U) is located in the University of California Hopland Research and Extension Center. Patterned letters refer to four groupings identified from a cluster analysis using tree age data. Cluster 1 has gray letters with black borders, and represents the oldest even-aged stands; Cluster 2 has black letters, and represents stands established ca. 1943; Cluster 3 has gray letters and represents uneven-aged stands; and Cluster 4 includes the youngest stands (see Figures 3 and 5).

Age Structure and Fire History

To determine stand age structures, tree age distributions for each plot were produced from tree-ring data. Live knobcone pines in each plot were hand bored using an increment corer approximately 30 cm above the ground surface. Trees were re-cored up to 3 times if the pith was missed, and the best core was used. For stands that were treated for a separate experiment, tree rings were counted from partial cross-sections cut from stumps 20 cm to 30 cm above the ground surface. A total of 1215 increment core samples were sanded to a smooth finish so that annual rings could be counted microscopically. For cores that failed to include the pith (52.8 %), or when the pith was rotten, the number of rings from the innermost ring to the pith was estimated with a pith locator (mean number of rings estimated to pith = 2.96 yr, SD = 1.78 yr). Young knobcone pines grow rapidly in the first several years post disturbance (see Keeley *et al*. 1999); therefore, age estimates do not include adjustments for the time required for seedlings to reach core- or cross-section height (30 cm). For each plot, we evaluated frequency distributions of tree pith dates to identify an age structure type (even- or uneven-aged).

To supplement the interpretation in stand age data, we collected fire scars found on knobcone pine trees in and around plots and dated them by ring counts along two separate radii. Additionally, dates and perimeters of past fires in the study area were obtained from the CALFIRE (California Department of Forestry and Fire Protection 2008) geodatabase and merged with mapped knobcone pine stands in a geographic information system (GIS) database. Summary statistics of forest structure and tree age were calculated from the five plots in each knobcone pine stand. Changes in stand structure, such as decreased canopy cover in older stands, may indicate tree senescence. Relationships between stand structure variables (percent canopy cover, shrub cover, and snag density) and stand age were analyzed using linear regression. When stands had more than one establishment date, the predominant year (i.e., estimated year when most of the trees were established) was used. Normal probability plots and residual plots were examined for non-normality, nonlinearity, and heteroscedasticity, which violate assumptions of linear regression. Statistical tests were considered significant when P values were less than 0.05.

To categorize the variation in tree age distributions of the 21 stands across the study area, a multivariate technique commonly referred to as cluster analysis was employed. Using input variables, cluster analysis classifies the stands into mutually exclusive groups, maximizing within-group similarity while minimizing between-group similarity (McGarigal *et al*. 2000). An agglomerative hierarchical clustering technique was used in which, initially, each stand was identified as an individual cluster. Similar stands were grouped into clusters in a hierarchy of larger clusters as the distance coefficient increased. One output of this technique was a dendrogram, or cluster tree, depicting the agglomeration sequence and the degree of similarity between clusters containing stands. Three variables were used in the analysis describing tree age distributions: mean, median, and standard deviation of the mean. All analyses were performed using SYSTAT 10 (Systat Software, Evanston, Illinois, USA).

RESULTS

Stand and Age Characteristics

The 21 knobcone pine stands ranged from 0.75 ha to 1.5 ha and were dispersed over an area of approximately 2600 ha (Figure 2). Vegetation survey plots were located on all aspects, but in this area knobcone pine stands were found primarily on level ridge tops and mesic slope positions (drainages, north and east aspects). Of the 2651 trees measured, 89 % were knobcone pine, followed in abundance by canyon live oak (3.6 %), Pacific madrone (3.0 %), California nutmeg (1.4 %), California black oak (1.2 %), and California bay

(0.9%). Three of the stands were monotypic knobcone pine. Of the 105 plots surveyed (approximately 3.4 ha), only three knobcone pine saplings were found. Stand average shrub cover was 41.8% (SD = 14.7%, range = 14.3% to 83.6%) and was dominated by shrub oaks (Table 1, Figure 1).

The largest (54.1 cm) and tallest (32.5 m) knobcone pines were found in stand N and were approximately 46 yr and 44 yr old, respectively. The youngest stand, S, had the smallest average tree dbh at 9.6 cm (SD = 5.5 cm), less than half the overall average for the 21 stands (Table 2, Figure 3). This stand also had the highest total tree density (2986 stems ha^{-1}) and snag density (573 stems ha^{-1}) in the study area. The average total tree density for all stands was 817 stems ha^{-1} (SD = 113 stems ha^{-1}), although the range was large (503 stems ha^{-1} to 2986 stems ha^{-1}).

Combined with the few seedlings found in the survey area, age distributions show that knobcone pine trees were established in almost every decade of the twentieth century (Figure 4A). Fourteen of the 21 stands surveyed exhibited tree age distributions that were unimodal, or even-aged (e.g., stands C, G, and N; Figure 3). Most of these stands also had smaller, younger trees (e.g., stands D, O, and Q), indicating that recruitment continued for several years after initial stand establishment. Tree age patterns within the remaining seven stands were mixed, with either bimodal or diffuse distributions (e.g., stands L, R, and T), with recruitment appearing either continuous or episodic. In examining the variation in tree ages at the plot level, even-aged distributions were apparent for stands I and U, whereas the other five stands had mixed ages throughout.

The average standard deviation for tree ages within even-aged stands was 4.6 years (range = 1.6 yr to 7.2 yr), whereas for the uneven-aged stands it was 10.2 years (range = 7.3 yr to 12.4 yr). The oldest trees (86 yr to 96

Table 1. List of shrub species, including frequency, mean cover, and height surveyed in 21 mature knobcone pine stands. Frequency is the percentage of plots in which the species was found. Cover is the mean percent cover of the species in plots in which it was found. SE is one standard error of the mean.

Species	Frequency (%)	Cover (%)	Cover SE	Height (m)	Height SE
Adenostoma fasciculatum Hook. & Arn.	47.6	3.6	2.5	1.3	0.3
Aesculus californica (Spach) Nutt.	4.8	25.0	-	1.3	-
Arbutus menziesii Pursh	57.1	2.7	2.7	1.8	1.2
Arctostaphylos canescens Eastw.	28.6	10.6	11.8	2.0	0.5
A. glandulosa ssp. *glandulosa* Eastw.	95.2	11.3	1.6	2.0	0.3
A. standfordiana ssp. *standfordiana* Parry	33.3	3.0	1.2	1.7	0.7
Ceanothus integerrimus Hook. & Arn.	9.5	2.5	-	1.7	0.4
Chrysolepis chrysophylla var. *minor* (Benth.) Munz	9.5	18.1	13.8	2.5	1.0
Garrya fremontii Torr.	14.3	2.5	-	1.4	0.5
Heteromeles arbutifolia (Lindl.) M. Roem.	38.1	3.5	3.0	1.4	1.0
Pickeringia montana Nutt. ex Torr. & A Gray	38.1	2.5	-	1.5	0.6
Quercus berberidifolia Liebm.	81.0	21.3	18.7	1.8	0.6
Q. chrysolepis Liebm.	61.9	12.9	12.0	4.2	1.7
Q. durata Jeps.	33.3	4.9	4.7	1.3	0.4
Q. kelloggii Newberry	23.8	3.0	1.1	2.6	2.0
Q. wislizeni A. DC. var. *frutescens* Engelm.	100.0	43.7	13.3	2.6	0.4
Rhamnus californica Eschsch.	42.9	3.6	3.3	1.4	1.0
Torreya californica Torr.	76.2	5.0	4.0	2.2	1.2
Umbellularia californica (Hook. & Arn.) Nutt.	71.4	3.6	1.6	2.6	1.4

Table 2. Summary of forest characteristics measured in 21 mature knobcone pine stands in the northern Mayacmas Mountains, north Coast Range. SE is one standard error of the mean.

	Mean	SE	Median	Range
Slope (%)	37.2	2.1	37.8	18.6 to 56.8
Canopy cover (%)	59.7	2.2	61.6	34.4 to 77.6
Dbh (cm)	20.4	0.8	20.6	9.6 to 25.9
Height (m)	14.7	0.9	16.0	9.8 to 17.4
Height to live crown base (m)	8.5	0.8	9.6	5.5 to 11.5
Age (yr)	55.4	1.9	56.4	34.8 to 66.5
Live basal area (m^2 ha^{-1})	16.6	1.5	16.4	5.8 to 27.2
Live density (trees ha^{-1})	450.5	103.2	311.2	139.5 to 2412.8
Snag basal area (m^2 ha^{-1})	3.6	0.3	3.3	1.5 to 6.1
Snag density (trees ha^{-1})	191.0	24.5	183.0	87.5 to 573.0

yr) were in stand T, which had a diffuse age distribution and the largest knobcone pine age range (60 years). The youngest trees (17 yr to 19 yr) were located in stand S, which had an even-aged distribution and an age range that was the approximate overall average (32 yr).

The relationship between stand age and canopy cover, snag density, and shrub cover was tested for significance using linear regression. Percent canopy cover ranged from 34.4% to 77.6% and was positively related to stand establishment date ($F_{1,19}$ = 8.697, P = 0.009; Figure 4B), with younger stands having higher cover. Snag density accounted for 10.7% to 39.6% of total tree density (Figure 4C); although the highest percentages were in older stands (B and R), the relationship to stand establishment date was not statistically significant ($F_{1,19}$ = 2.071, P = 0.166). Shrub cover was not significantly related to stand establishment date ($F_{1,19}$ = 0.848, P = 0.369; Figure 4D).

Fire History

Stand-level tree age distributions showed that knobcone pine stands were established between the 1930s and 1960s (Figure 3), although individual tree recruitment has occurred over the last 100 yr (tree establishment range *ca.* 1908 to 1988; Figure 4A). Five of the even-aged stands (B, C, D, E, and F) and five uneven-aged stands (A, I, J, L, and T) were established *ca.* 1931, although some stands (especially stand T) had trees that were established prior to that date. Six other even-aged stands (G, H, M, O, P, and Q) and two uneven-aged stands (R and U) were established *ca.* 1943. The five stands (A, I, J, L, and T) initially established in *ca.* 1931 had a second cohort of trees established in *ca.* 1943, resulting in a multi-aged distribution. Live trees sampled in stands D and I had fire scars that dated to 1940 and 1944, respectively. These two periods, *ca.* 1931 and *ca.* 1943, were the primary establishment dates for nine and eleven of the 21 stands, respectively, and covered a large portion of the study area. Neither of these tree-age derived dates was in the state fire perimeter geodatabase, but the city newspaper reported on large wildfires on COW in August 1931 (Ukiah Republican Press 1931).

Two uneven-aged stands (L and T) that were established in *ca.* 1931 were within the perimeter of a 1950 wildfire (2090 ha, Figure 2) identified in the state fire geodatabase. Although not within the mapped perimeter, this wildfire was associated with subsequent knobcone pine establishment in two even-aged stands (K and N) and scarred live trees in four other stands (A, D, G, and M) (Figure 3); how-

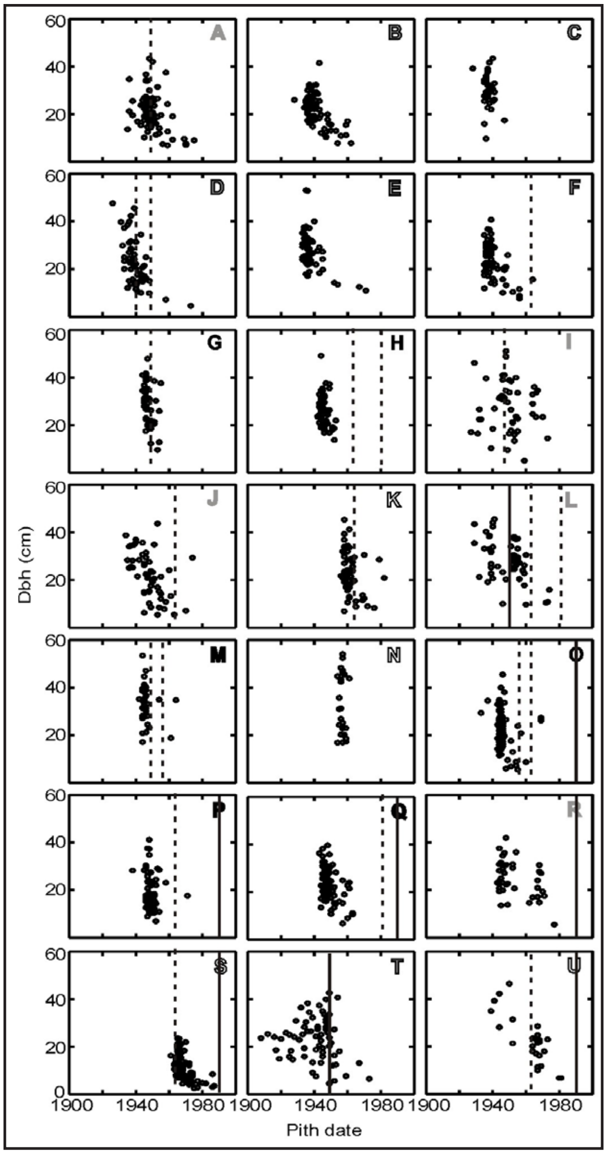

Figure 3. Tree age and diameter distributions of 21 knobcone pine stands from the northern Mayacmas Mountains. Vertical lines represent years of fires identified from the California digital database of fire perimeters (California Department of Forestry and Fire Protection 2008; continuous lines) and fire scars found on live knobcone pines (dash lines). See Figure 2 for plot locations within the study area. Patterned letters refer to groupings identified from a cluster analysis using tree age statistics (see Figure 5).

ever, tree recruitment was not initiated in all of these stands. An apparently large fire, not identified in the geodatabase but reported in the Ukiah Daily Journal (1962), was associated with subsequent establishment in stand S on the southern end of the study area in *ca.* 1962. This fire apparently also burned through three other uneven-aged stands (I, R, and U) that were established *ca.* 1943 and scarred live knobcone pines in many plots throughout the study area. Finally, in spring of 1990, a 2362 ha prescribed fire conducted by local agencies burned through several stands (O, P, Q, R, S, and U) at the southern end of the study area (Figure 2). While there was evidence of fire (e.g., fire scarred trees, burned shrub stems, and shrub regeneration), this fire did not induce a new cohort of knobcone pines in these stands.

Cluster analysis grouped stands according to tree age patterns (Figure 5). After the initial grouping of similar stands with distance coefficients less than three, stands were sorted into four distinct clusters. Cluster 1 consisted of the five oldest, even-aged stands (established ca. 1931) and all were located in the northern part of the study site (gray letters with black borders; Figure 2). Stand T, an uneven-aged plot in the southern portion of the study area, was an outlier joining cluster 1 at distances exceeding those required to group clusters 2 and 3. The six stands in cluster 2 (black letters), located throughout the study area, were established ca. 1943 and exhibited even-aged distributions. Cluster 3 (gray letters) consisted of five uneven-aged stands located throughout the study area. The four youngest plots in the study area with both even and uneven-aged distributions formed cluster 4 (white letters with black borders).

DISCUSSION

Mature knobcone pine forests varied in structural characteristics across the study area, but only a few studies have provided comparable information. Generally, the averages in tree age, diameter, density, and height in the northern Mayacmas Mountains were similar to those described in northern (Imper 1991, Johnson 1995), central (Keeley *et al*. 1999), and

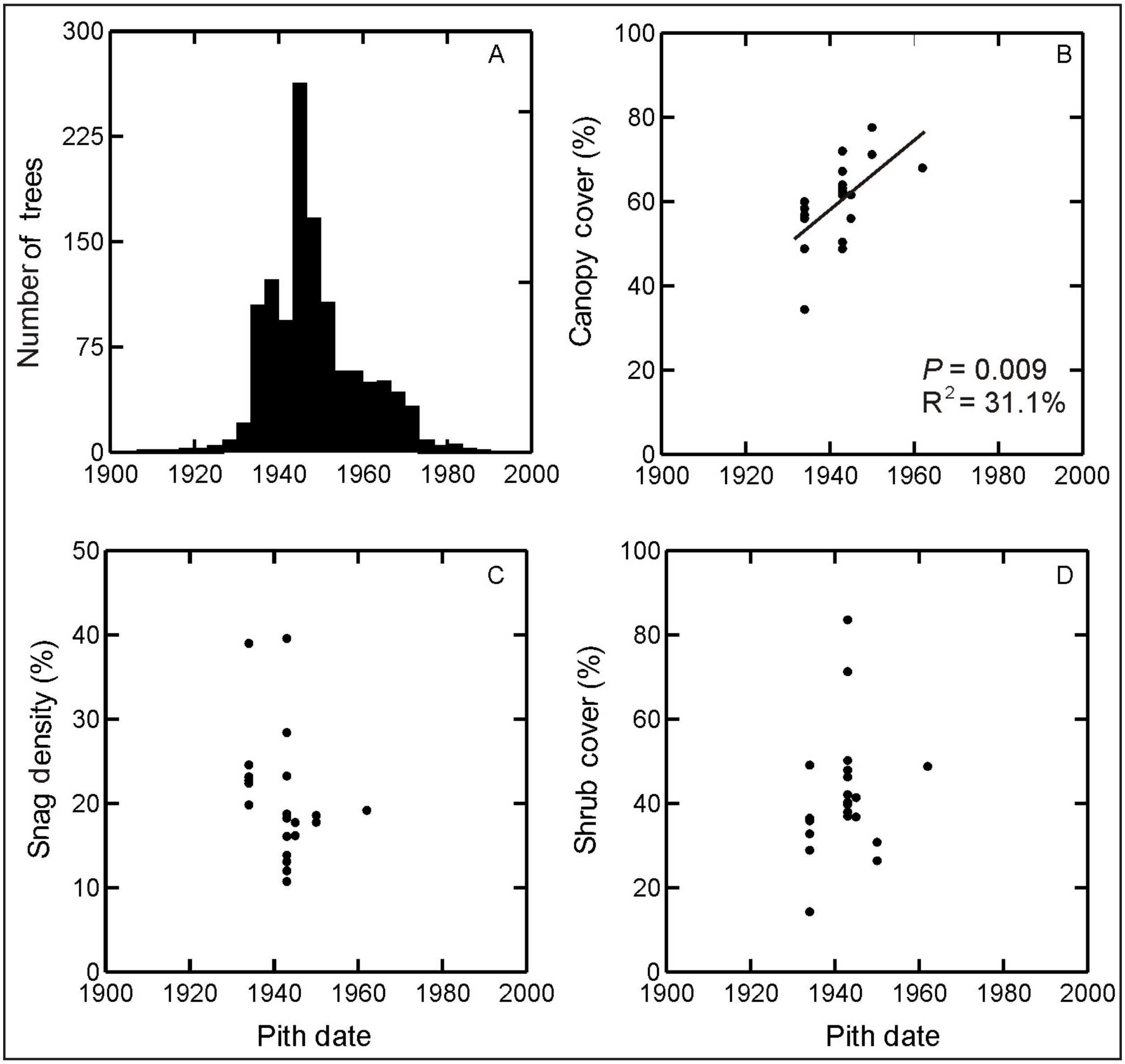

Figure 4. Tree age distribution (A) and average percent canopy cover (B), snag density (C), and shrub cover (D) by stand age collected from 21 plots in mature knobcone pine forests.

southern California (Vogl 1973). The range of site conditions includes marginal sites that dramatically hinder growth (thickets of short, small diameter trees; e.g., Imper 1991) to more favorable sites such as in this study where many trees grow to greater than 30 m in height and 50 cm in diameter. The discontinuous distribution, growth patterns, and numerous tree and shrub species associates reflect the ability of knobcone pine to exist in a variety of conditions that are distinct and uncommon (Sawyer and Keeler-Wolf 1995, Lanner 1999).

The combination of even-aged stands (two thirds of stands), fire records, and fire scarred trees provides evidence that knobcone pine forests in the study area were primarily established after stand-replacing fires. High intensity fires dramatically alter environmental conditions and create recruitment opportunities for knobcone pine by inducing an intense seed rain from newly opened serotinous cones; by consuming canopy fuels, which improves light penetration to the forest floor; by consuming surface fuels; and by eliminating competition

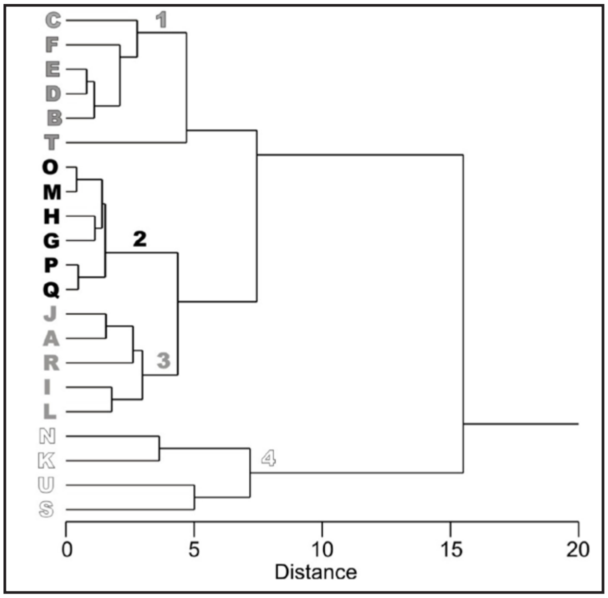

Figure 5. Tree age grouping through hierarchical cluster analysis using summary statistics (mean, median, and standard deviation) of stand age calculated from 21 knobcone pine plots in the northern California Coast Range. See Figure 2 for plot locations within the study area. Age class distribution within each stand is shown in Figure 3.

from understory vegetation (Lamont *et al.* 1991). These conditions for successful recruitment persisted for several years post-fire since most stands had trees that were much smaller and younger than average. Stands with uneven-aged distributions suggest that conditions for recruitment occurred repeatedly. For some stands, this was due to the location of plots overlapping multiple fire perimeters (despite our efforts to place them within homogeneous stands). For the other uneven-aged stands, adjacent stands with corresponding tree ages and dates of fire scars provided evidence that stands ranging from 7 yr to 19 yr were burned by surface fires. Under these conditions, many overstory trees were scarred but not killed—an unusual occurrence in a species with fire sensitive morphological characteristics (Schwilk and Ackerly 2001)—and some cones were heated sufficiently to open, releasing seeds that resulted in a new cohort.

Fine scale mechanisms that control fire behavior involve complex interactions of topography, weather, and fuels (Turner and Romme 1994), and contribute to the variation in tree ages between stands and even within some stands. This variation was illustrated in two ways from the cluster analysis: stands with similar age structures were located throughout the study area, and stands with multi-aged structures were added to groups at larger distances compared to other stands. Fires that occurred from the 1930s through the 1960s, as well as the large 1981 wildfire that burned the eastern portion of the range, have created a heterogeneous landscape pattern of knobcone pine forests. Interestingly, in several instances, fires that burned through our plots did not induce a new cohort. This included the large management prescribed fire in 1990, although there were some patches of shrub regeneration within the larger burn perimeter. There is a minimum heat threshold for seed dispersal from serotinous cones, and age structures in this study show that some knobcone pine stands have been maintained with fires that have varied in intensity. For many serotinous species, stand-replacing fires not only create opportunities for recruitment within the stand, but potential for population expansion into adjacent plant communities (Lamont *et al*. 1991, Ne'eman *et al.* 1999). Conditions following low intensity fires at this site in the past were sufficient for recruitment within the stand. In this study, we measured structural patterns within stands and therefore cannot infer past changes at forest boundaries. But given the changing fire regimes in California (Syphard *et al*. 2007), relationships between current age structures, disturbance intensities, and impacts on landscape distributions is an important research need for these forests (e.g., Turner and Romme 1994, Ne'eman *et al.* 1999).

For other serotinous conifer species in California, regeneration may not depend exclusively on large, uniform, stand-replacing fire (Stephens *et al*. 2004); other processes such as canopy gap formation may play a role (Storer *et al*. 2001, O'Brien *et al*. 2007, Mallek 2009). Gaps in the forest canopy develop from fallen branches and mortality of one to several mature trees. As new trees become established in these gaps adjacent to older trees, mixed-age structures result at small spatial scales (e.g., Storer *et al*. 2001). Given the serotinous habit of knobcone pine, the overall lack of regeneration in the 21 stands we surveyed (especially in older stands), and the suspected low incidence of western gall rust-caused mortality, regeneration via canopy gaps currently is not evident at this site. However, it is unclear how western gall rust influences young, developing knobcone pine stands since most research has focused on commercially important species. Perhaps as knobcone pine stands age and snag densities increase in the absence of fire, this type of regeneration will become more important, resulting in a higher proportion of mixed-age stands across the landscape.

Stands established prior to 1950 are composed of snags (accounting for 11 % to 40 % of total tree density) and large trees showing abundant evidence of infection by western gall rust (D. Fry, Department of Environmental Science, Policy and Management, University of California, Berkeley, unpublished data). In the Cascades, up to 50 % of the trees in older knobcone pine stands (65 yr to 80 yr) were snags (Imper 1991). Vogl's (1973) study in southern California reported 55 % of trees were snags in a 65 yr stand, with trees over 50 yr showing abundant signs of deterioration, indicating that these forests may be approaching the 'senescence risk' stage of their lifecycles (Zedler 1995). The lower percentages found in this study may be due to favorable climatic and edaphic conditions that lead to longer life spans. Cone production and seed bank viability in older stands is important when considering risk to populations. Seed viability in older knobcone pine trees is not well known, but limited information suggests that seeds remain viable for many decades (Vogl 1973, Warren and Fordham 1978).

Management Implications

The majority of knobcone pine stands (18 of 21) surveyed were established in the 1930s and 1940s, prior to the acquisition of the study area by BLM and HOP. In recent decades, both institutions have implemented fuel treatments in several vegetation types to achieve both research and management goals (e.g., Stephens *et al*. 2008, Potts and Stephens 2009, Potts *et al*. 2010). While not critical when considered at the landscape scale, the need for effective treatments to regenerate knobcone pine forests is evident in some stands as indicated by stand age and decreased canopy cover. However, there is little research in support of using prescribed burning to regenerate knobcone pine stands.

Managers have the dual role of suppressing wildfires to protect property and natural resources, and maintaining ecosystem function and integrity. Managers have the dual role of suppressing wildfire to protect property and natural resources, while maintaining ecosystem function and integrity. Prescribed burning programs face local operational and weather constraints, and larger scale constraints associated with air quality and social pressures against the use of fire (Stephens and Ruth 2005). Chamise (*Adenostoma fasciculatum* Hook & Arn.) dominated chaparral, which is found primarily on dry, south-facing slopes, can be prescription burned across multiple seasons (Potts and Stephens 2009, Potts *et al.* 2010). Knobcone pine stands have a shorter prescription window for burning, and the range of stand age structures shows that both low- and high-intensity burning have been a part of the natural history of the species. The local variability in fire severity allows managers to burn at small spatial scales, but unit costs will increase. Possible alternative treatments, such as mastication, cut and pile, or biomass removal, might be tested for effectiveness, but improvements in predictions of crown fire behavior (e.g., Cruz *et al.* 2003) might allow for the expanded use of prescribed fire. Maintaining or simulating the role of fire for perpetuation of serotinous-coned species like knobcone pine will remain a real challenge in coming decades.

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