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## Fire and persistence of montane chaparral in mixed conifer forest landscapes in the northern Sierra Nevada, Lake Tahoe Basin, California, USA<sup>1</sup>

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NAGEL, T. A. AND A. H. TAYLOR (Department of Geography, The Pennsylvania State University, 302 Walker Building, University Park, PA 16802). Fire and persistence of montane chaparral in mixed conifer forest landscapes in the northern Sierra Nevada, Lake Tahoe Basin, California J. Torrey Bot. Soc. 132: 442–457. 2005.—Tree cover in the mixed conifer zone in the Sierra Nevada is often interrupted by large shrub fields, or stands of montane chaparral. Chaparral stands are thought to be associated with either poor site conditions, or locations that have experienced severe fire. Fires have been excluded from mixed conifer forests for nearly a century because of a management policy of suppressing fire. This study quantifies the intervals between fires, and the response of chaparral shrubs and trees to fire and fire exclusion in six montane chaparral stands. *Quercus vaccinifolia* and *Arctostaphylos patula* were the dominant shrubs on all sites and the last fires burned in the six sites between 1861 and 1882. The mean point fire return interval before fire suppression was 28 yr (range 16–40 yr), and fire frequency in chaparral was lower than in nearby forest. The age structure of shrubs and trees in the stands indicate that shrubs and trees regenerated immediately post-fire. Shrub and tree regeneration, however, were not confined to a brief post fire period, regeneration continued for at least another five decades. On our sites, exclusion of fire due to fire suppression has caused the average area of a chaparral stand to shrink by 62.4%. Chaparral has been replaced by forest and this vegetation change has reduced the heterogeneity of the mixed conifer forest landscapes in the Sierra Nevada.

Key words: forest dynamics, landscape ecology, mixed conifer forests, fire history, fire effects, restoration ecology, fire exclusion, heterogeneity

Species abundance patterns in forested landscapes are influenced both by site conditions (i.e., soil characteristics, temperature, moisture) and the type, severity, and extent of disturbances (Whittaker 1956, Romme and Knight 1981, Harmon et al. 1983). In forested landscapes, high severity disturbances such as fires (Romme 1982), debris flows (Hupp et al. 1987), windstorms (Forest and Boose 1982), and logging (Bormann and Likens 1979) have all been documented to affect landscape vegetation patterns. For example, in California, tree cover in the montane zone is often interrupted by large shrub fields, or stands of montane chaparral (hereafter

referred as chaparral). The location and extent of these chaparral stands are associated with both harsh site conditions that inhibit tree growth, and areas that have experienced severe, stand-replacing forest fire(s) (Show and Kotok 1924, Rundel et al. 1977, Biswell 1974, Bolsinger 1989). Chaparral shrubs are fire-adapted and establish rapidly after fire, either by sprouting or by germinating from seed stored in the soil (Weatherspoon 1985, 1988; Kauffman 1990, Keeley 1991, 2000). The structure of surface and aerial fuels, and the low rate of fuel production, predisposes chaparral to crown fire, and recurring fires in chaparral have been observed to perpetuate shrub cover on sites otherwise edaphically suited for trees (Wilken 1967, Biswell 1974, Bock and Bock 1977).

Despite the widespread occurrence of chaparral in mixed conifer forest landscapes in the Sierra Nevada, little is known about their fire regimes. Fire frequency is thought to be lower and more variable, and fire severity is thought to be higher, than in surrounding mixed conifer forests (Skinner and Chang 1996). In mixed conifer forests, surface fuel structure and high rates of fuel production historically supported a regime of frequent (i.e., every 3–20 years) low and moderate severity surface fires (Kilgore and Taylor 1979, Parsons and DeBenedetti 1979, Ca-

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prio and Swetnam 1995, Taylor 2000a, Beaty and Taylor 2001, Bekker and Taylor 2001, Taylor and Skinner 2003). Yet, in the southern Cascade Range and Klamath Mountains, there is evidence that mixed conifer forests burned at high severity and that high severity burns were important for maintaining chaparral and even-aged forest patches in the landscape mosaic (Taylor and Skinner 1998, Beaty and Taylor 2001, Bekker and Taylor 2001). Chaparral and even-aged forest stands in these landscapes are proportionately more abundant on upper slope positions (Skinner and Taylor 1998, 2003; Beaty and Taylor 2001) where topographic controls on fire behavior favor higher fire line intensities and severe fire (Rothermel 1983, Weatherspoon and Skinner 1995). Where topography strongly influences the spatial pattern of severe fire, the location of chaparral stands in the mixed conifer forest matrix may be relatively fixed. In other types of terrain, however, the location of chaparral may shift in the landscape as a high severity burn generates chaparral from long lived seed buried in the soil and it is then replaced by forest (Conard and Radosevich 1982b, Weatherspoon 1988). In either case, the highly competitive shrub cover appears to greatly reduce the rate at which forest may replace chaparral. In the Sierra Nevada, the role of recurring high severity fire in the establishment and maintenance of chaparral, and in mixed conifer forests dynamics is not well documented or understood, particularly during the period before logging and other human caused disturbances altered the pre-EuroAmerican forest landscape in the mid to late 19<sup>th</sup> century. In many parts of the Sierra Nevada, contemporary shrub fields are thought to have developed after heavy 19<sup>th</sup> century logging and slash fires removed the forest cover, and nearby seed sources, leading to long term persistence of chaparral shrubs on many sites (Sudworth 1900, Leiberg 1902, Biswell 1974).

Species distribution and abundance patterns in mixed conifer forests have also been influenced by fire exclusion. Nearly a century of fire suppression has caused an increase in forest density, a compositional shift to more fire-sensitive species, and a shift from coarser to finer scale forest mosaics (Vankat and Major 1978, Parsons and DeBenedetti 1979, Skinner 1995, Taylor 2000a). Fire exclusion may also have affected chaparral stands. Repeat photographs of 19<sup>th</sup> century scenes of forested landscapes that were never logged or heavily disturbed by Euro-Americans often show an expansion of trees and forest into

shrub fields (Vankat and Major 1978, Gruell 2001). Forest encroachment into chaparral may have occurred gradually during the fire suppression period, as infilling of trees has in mixed conifer forest (Parsons and DeBenedetti 1979, Taylor 2000a), or trees may have established immediately post-fire, having only recently emerged from beneath the shrub canopy. Low soil moisture and low light levels beneath the shrub canopy greatly inhibits the establishment and growth of tree seedlings (Conard and Radosevich 1982a, Conard and Sparks 1993). Moreover, little is known about shrub regeneration except that chaparral species sprout or seed in prolifically immediately after severe fire (Bock and Bock 1977, Biswell 1974). Chaparral shrubs do regenerate episodically, after fire, but they may also regenerate more continuously promoting long term site occupation by shrubs.

The goal of this study is to better understand the role of fire and fire suppression in the dynamics of vegetation patterns in mixed conifer forest landscapes in the Sierra Nevada. We hypothesize that naturally recurring severe fires maintained chaparral and that replacement of shrub fields by forest is associated with fire regime changes caused by fire suppression. Our specific objectives were to: 1) determine if fire frequency in chaparral stands was lower than in surrounding mixed-conifer forests; 2) determine if shrub stems were of similar age, reflecting episodic establishment only after fire, or multi-aged suggesting a pattern of more continuous regeneration; 3) determine if the ages of trees growing in shrub fields were similar reflecting simultaneous establishment with shrubs after fire, or variable and multiple-aged, suggesting continuous establishment during a period with shrub dominance; and 4) determine the extent to which chaparral has been replaced by forest and whether forest expansion is associated with fire suppression.

**Study area.** Chaparral in the Sierra Nevada occurs within the mixed conifer forest zone, where any of six conifer species (*Pinus ponderosa* Laws.; *Calocedrus decurrens* (Torrey) Florin; *Pinus lambertiana* Douglas; *Pinus jeffreyi* Grev. & Balf.; *Abies concolor* (Gord. & Glend.) Lindley; and *Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco may co-occur and share dominance in a stand depending on site conditions, latitude, and stand history (Barbour 1988). In our study area, chaparral was dominated by *Quercus vaccinifolia* Kellogg and *Arctostaphy-*

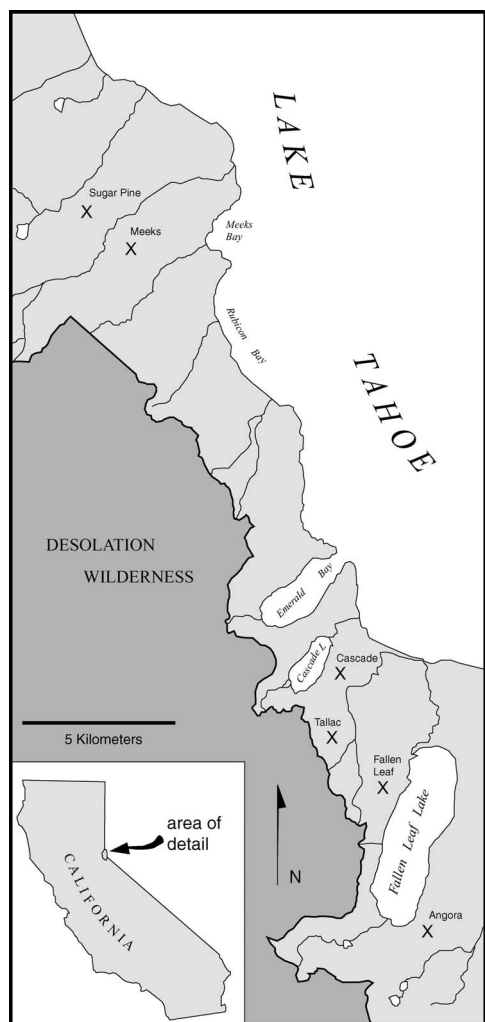


FIG. 1. Location of the six montane chaparral stands studied in the northern Sierra Nevada, Lake Tahoe Basin, California.

*los patula* E. Greene, but several other shrub species, including *Ceanothus velutinus* Hook., *C. cordulatus* Kellogg, *Castanopsis sempervirens* (Kellogg) Hjelmq., *Prunus emarginata* (Hook) Walp., and *Amelanchier alnifolia* (Nutt) Nutt were present. These shrub species are present in chaparral throughout the Sierra Nevada (Vankat and Major 1978, Conard and Radosevich 1982, Bolsinger 1989, Skinner and Chang 1996).

We studied chaparral stands in the northern Sierra Nevada on the west side of the Lake Tahoe Basin, California (Fig. 1). Elevations range from 1930 m to 2220 m and the terrain is steep and complex. Forest and chaparral grow on shal-

low (< 1m), excessively drained, medium acidity soils derived from Mesozoic aged granite developed in glacial till (Rogers 1974, Hill 1975). The climate is characterized by warm, dry summers and cold, wet winters. Mean annual precipitation at Tahoe City (1890m) is 98.4 cm, 86% of which falls as snow between November and April. Mean monthly temperatures range from 1 °C in January to 21.8 °C in July.

People have influenced vegetation in the Lake Tahoe Basin for at least 9,000 years (Lindström 2000). The Lake Tahoe Basin was used by Native Americans (Washoe) seasonally, and their use may have modified local vegetation patterns. Washoe people burned forests to drive game and to increase production of certain plants for food and fiber (Lindström 2000). Euro-Americans first arrived in the basin in 1844 but settlement was limited until the 1860s. Forests in large parts of the basin were cut heavily between 1873 and 1900 to meet demand for wood in mines in Virginia City, Nevada (Lindström 2000, Taylor 2004).

Although logging was extensive, there are tracts of uncut forest on the west shore of the Lake and intermixed in these forests are large patches of chaparral. Examination of 19<sup>th</sup> century historical documents (i.e., written and photographic records; Lindström 2000), early aerial photographs (1939), and field reconnaissance indicate that these shrub fields did not establish after logging and that they had been present on the landscape for > 100 years. We selected all large (> 40 ha) shrub fields ( $N = 6$ ) on the west shore of the lake that were surrounded by uncut forest for intensive study.

**Methods.** COMMUNITY STRUCTURE AND COMPOSITION. The structure and floristic composition of each chaparral stand was determined by estimating species canopy cover in six to nine systematically placed  $5 \times 50$  m belt transects (Fig. 2). Transects were placed in the middle, right edge, and left edge, at the top, middle, and bottom of each stand. This plot placement was used to detect any spatial differences in tree establishment dates within the shrub fields that might be related to seed dispersal distance from the forest edge (Greene and Johnson 2000). The elevation, slope aspect, slope pitch, and location (UTM) of each transect in each stand was also recorded (Table 1). Canopy cover of trees ( $\geq 5$ cm dbh; diameter at breast height) and shrubs in each belt transect was estimated, by species, in contiguous 5 m x 5 m quadrats in one of six

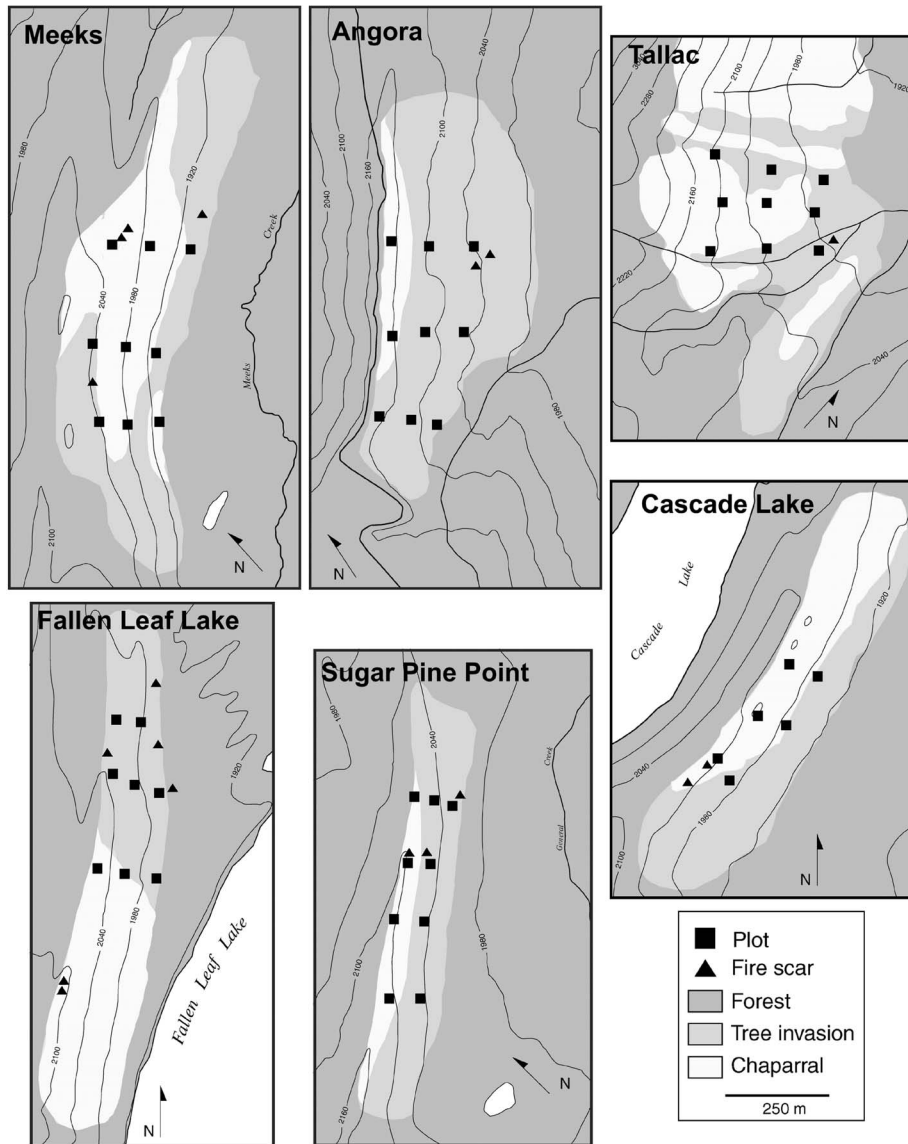


FIG. 2. Location of plots, fire scar samples, and area of forest encroachment between 1939 and 2000 in six montane chaparral stands in the northern Sierra Nevada, Lake Tahoe Basin, California.

cover classes (<1%, 1–5%, 5–25%, 25–50%, 50–75%, 75–100%). We also counted all seedlings (0.5 m–1.4 m tall) and saplings (>1.4 m tall < 5.0 cm dbh), and measured the diameter of each live and dead tree, and height of the tallest shrub, in each quadrat.

**FIRE HISTORY.** Since stands of chaparral establish after high severity fire, it is difficult to determine how often fires burn in them because evidence of earlier burns (i.e., fire scars, age structure) is usually consumed by the fire. Yet, older trees scattered in or along the edges of

brush fields that survived the last fire are sometimes present and their tree rings may contain records of earlier fires (Skinner and Chang 1996). We used trees with external fire scars that were growing in or on the edges of shrub fields to estimate the history of fire in each chaparral stand. Partial wood cross-sections from the fire scarred trees were removed with a chainsaw (Arno and Sneek 1977) and sample locations were then determined with a GPS, and recorded on a topographic map (Fig. 2). Fire years recorded in each sample were determined by first

Table 1. Mean ( $\pm$  S.E.) cover of shrubs and trees, mean maximum shrub height, and environmental characteristics of six montane chaparral stands in the northern Sierra Nevada, Lake Tahoe, California.

	Angora		Cascade		Fallen Leaf		Meeks		Sugar Pine		Tallac	
	Cover (%)	Height (m)	Cover (%)	Height (m)	Cover (%)	Height (m)	Cover (%)	Height (m)	Cover (%)	Height (m)	Cover (%)	Height (m)
Shrubs												
<i>Quercus vac-</i>	17 $\pm$ 3	1.1 $\pm$ 0.07	64 $\pm$ 4	1.1 $\pm$ 0.04	61 $\pm$ 3	1.2 $\pm$ 0.04	38 $\pm$ 4	1.2 $\pm$ 0.06	55 $\pm$ 3	1.3 $\pm$ 0.05	49 $\pm$ 4	1.2 $\pm$ 0.05
<i>cinifolia</i>												
<i>Arctostaphy-</i>	9 $\pm$ 2	1.3 $\pm$ 0.06	5 $\pm$ 1	0.6 $\pm$ 0.09	5 $\pm$ 1	1.1 $\pm$ 0.06	19 $\pm$ 3	1.2 $\pm$ 0.03	7 $\pm$ 1	1.1 $\pm$ 0.06	9 $\pm$ 1	1.2 $\pm$ 0.04
<i>los paula</i>												
<i>Ceanothus</i>	0.5 $\pm$ 0.3	1 $\pm$ 0.09	0.09 $\pm$ 0.06	0.3 $\pm$ 0	1.2 $\pm$ 0.8	0.9 $\pm$ 0.8	3 $\pm$ 0.8	0.8 $\pm$ 0.05	1.2 $\pm$ 0.4	0.9 $\pm$ 0.06	0.09 $\pm$ 0.05	0.7 $\pm$ 0.2
<i>cordulatus</i>												
<i>Ceanothus</i>	4 $\pm$ 0.9	1.2 $\pm$ 0.07	1.4 $\pm$ 0.8	1 $\pm$ 0.1							5 $\pm$ 1	1.2 $\pm$ 0.06
<i>Prunus emar-</i>												
<i>ginata</i>	0.6 $\pm$ 0.3	1.6 $\pm$ 0.3			0.7 $\pm$ 0.3	1.7 $\pm$ 0.2					1 $\pm$ 0.5	1.7 $\pm$ 0.3
<i>Amelanchier</i>												
<i>alnifolia</i>	0.04 $\pm$ 0.04	0.7			1 $\pm$ 0.4	1.6 $\pm$ 0.2					0.9 $\pm$ 0.5	0.8 $\pm$ 0.06
<i>Chrysolepis</i>												
<i>sempervi-</i>												
<i>rens</i>	0.04 $\pm$ 0.04	0.3									0.3 $\pm$ 0.2	0.9 $\pm$ 0.1
Total shrub-												
cover	30 $\pm$ 4		70 $\pm$ 3		69 $\pm$ 3		60 $\pm$ 4		64 $\pm$ 4		66 $\pm$ 4	
Dead <i>Arcto-</i>												
<i>staphylos</i>												
<i>patula</i>	12 $\pm$ 2		0.11 $\pm$ 0.06		2 $\pm$ 0.50		3 $\pm$ 1		2 $\pm$ 0.4		6 $\pm$ 0.8	
Dead <i>Quer-</i>												
<i>cus vaccin-</i>	4 $\pm$ 1		0.7 $\pm$ 0.4		0.8 $\pm$ 0.4		0.4 $\pm$ 0.2		0.7 $\pm$ 0.4		5 $\pm$ 2	
<i>ifolia</i>												
Trees												
<i>Abies con-</i>	48 $\pm$ 4		11 $\pm$ 3		28 $\pm$ 3		22 $\pm$ 4		31 $\pm$ 4		32 $\pm$ 3	
<i>color</i>												
<i>Abies magni-</i>												
<i>fica</i>	1.3 $\pm$ 0.7		14 $\pm$ 2		16 $\pm$ 3		14 $\pm$ 3		15 $\pm$ 2		1.6 $\pm$ 0.7	
<i>Pinus jeffreyi</i>	7 $\pm$ 2										6 $\pm$ 1	
<i>Pinus lam-</i>			0.9 $\pm$ 0.7									
<i>bertiana</i>												
<i>Calocedrus</i>							1.6 $\pm$ 0.9					
<i>decurrens</i>												
Total tree	55 $\pm$ 4		26 $\pm$ 3		44 $\pm$ 4		37 $\pm$ 4		46 $\pm$ 4		39 $\pm$ 4	
cover												
Site characteristics												
Elevation (m)	2170		2055		2010		2080		2010		2115	
Slope (°)	18		25		18		21		18		19	
Aspect (°)	115		130		135		95		135		130	



sanding each specimen to a high polish and then cross-dating the sample's annual growth rings using standard dendrochronological techniques (Stokes and Smiley 1968). The year of each tree ring with a fire scar lesion in it was then recorded as the fire date.

To determine if fire was less frequent and intervals between fires were more variable in chaparral than forest, we compared fire frequency and fire return intervals from samples in chaparral and forest in several ways. First, we calculated mean point fire return intervals (FRI) for all fire scar samples in each chaparral stand and compared them to mean point FRI for samples ( $n = 45$ ) from adjacent or nearby mixed conifer forest (Taylor 2000b). We chose to compare point FRIs, rather than composite FRIs, because point FRI estimates are less affected by variation in sample size than composites of multiple samples (Arno and Petersen 1983). Next, we compared the fire frequency for all chaparral samples ( $n = 17$ ) to an estimate of fire frequency for 17 of the 45 forest samples. This was done using program SSIZ (Holmes 1995) which computes an estimate of fire frequency for different sized, randomly selected subsets of sampled trees using Monte Carlo techniques (Swetnam and Baisan 2002). Finally, we compared the fire interval distribution of FRI for fires recorded in all point samples from chaparral and forest.

**CHAPARRAL AGE STRUCTURE.** We sampled the largest diameter stems of *Q. vaccinifolia* and *A. patula* in each transect by removing at least two stem cross-sections of each species as close to the ground as possible with a chainsaw. We assumed that the largest stems (basal diameter) were the oldest stems in the stand, an assumption that holds for other chaparral species (Keeley 1992). *Quercus vaccinifolia* and *A. patula* were chosen for the age sampling because they were dominant species on all sites. Stem cross sections were prepared in the laboratory by making a radial cut to the pith and shaving the cut edge with a razor blade. White chalk was then applied to the cut to accentuate ring boundaries and the rings were counted beneath a binocular microscope to estimate stem age. Stem ages were then grouped into 10-year age-classes to infer temporal variation in patterns of shrub establishment in each stand. Annual growth rings of *Q. vaccinifolia* could not be consistently distinguished even on full stem cross sections so these samples were not included in the age structure analysis.

**TREE ENCROACHMENT.** The ages of trees growing in each chaparral stand were estimated by coring all trees to the pith 30 cm above the ground surface in each transect. Cores were sanded to a high polish, their annual growth rings were cross-dated (Stokes and Smiley 1968), and a tree age was assigned based on the calendar year of the inner most ring. The date of establishment of each tree was then estimated by adding a correction factor to each core to account for the number of years a stem needs to grow to a height of 30 cm. The correction factor for *A. concolor* ( $N = 131$ ), and *P. jeffreyi* ( $N = 49$ ) was determined by removing two stem cross sections from seedlings and saplings, one at the soil surface and the other at 30 cm. The cross sections were sanded to a high polish and the average difference between the stem age at the soil surface and at 30 cm was then subtracted from the core date to estimate the tree establishment date. The average ( $\pm$  S.D.) difference for *A. concolor* was  $29.2 \pm 12.6$  yr and for *P. jeffreyi* it was  $19.2 \pm 9.7$  yr.

To identify the conditions of initial tree establishment in chaparral stands we measured variation in the temporal pattern of radial growth by counting the number of rings/cm along the length of each tree core. Presumably, trees with fast initial growth established immediately after fire along with shrubs while those with slow initial growth established in the low resource environment beneath the shrub canopy.

After established trees overtop the shrub canopy they may begin to reduce shrub vigor. To assess this effect, we examined the relationship between total tree cover (%) and live and dead shrub cover (%) for all transects in all sites using correlation analysis.

Tree encroachment into chaparral was also quantified at the landscape scale using repeat aerial photography. First, the forest-chaparral boundary in the year 1939 was identified and delineated for each study site by using variation in the tone and texture of the vegetation cover evident on 1939 aerial photographs, and it was then transferred to a topographic map (Scale 1:24,000). Second, forest-chaparral boundaries were identified again for the year 2000 on aerial photographs taken in 2000, and these boundaries were also transferred to topographic maps. Third, the change in the area of forest and chaparral was identified for each site by measuring forest and chaparral cover on each date using a dot-grid overlay. Additionally, change in the area of forest and chaparral at one site (Fallen

Leaf) was qualitatively assessed by rephotographing an early landscape photograph that included the chaparral stand. The initial photograph was taken in 1915 and the repeat photograph was taken in 2001.

**Results.** COMMUNITY STRUCTURE AND COMPOSITION. Mean shrub cover on the study sites exceeded 60% except at Angora (mean=30%) (Table 1). *Quercus vaccinifolia* had the highest cover of all shrubs on each site, followed by *A. patula* (Table 1). *Ceanothus cordulatus* was also present on all sites, but it had low mean cover (0.5—to 3 %). The shrubs *C. velutinus*, *Prunus emarginata*, *Amelanchier alnifolia*, and *Chrysolepsis sempervirens* each occurred on two or three sites but they always had low mean cover ( $\leq 5\%$ ). Mean maximum shrub height was similar among sites ( $P > 0.05$ , Kruskal-Wallis H-test) and ranged from 0.3 m to 1.7 m (Table 1). Trees were growing among chaparral shrubs on each site and *A. concolor* had the highest mean cover followed by *P. jeffreyi*, *A. magnifica*, *C. decurrens* and *P. lambertiana* (Table 1). Mean tree cover ranged from 26 to 55%, and in some individual transects tree cover exceeded 75%.

Density and basal area of trees growing in the chaparral varied by species and among sites (Table 2). The mean tree density was 784 trees  $\text{ha}^{-1}$  (range, 516–1139 trees  $\text{ha}^{-1}$ ) and most trees were *A. concolor* and *P. jeffreyi*. *Abies concolor*, on average, was more abundant than *P. jeffreyi* but *P. jeffreyi* was more abundant than *A. concolor* at Cascade and Meeks. Average basal area was 40.1  $\text{m}^2 \text{ha}^{-1}$  (range 27.7–66.4  $\text{m}^2 \text{ha}^{-1}$ ) and *A. concolor* basal area, on average, was much higher than that of *P. jeffreyi*. However, *P. jeffreyi* basal area was higher than that of *A. concolor*'s at Cascade and they were similar at Meeks and Fallen Leaf.

Tree seedlings and saplings were also present, and they had average densities of 121.2 (range 57–173 stems  $\text{ha}^{-1}$ ) and 107.3 stems  $\text{ha}^{-1}$  (55–301 stems  $\text{ha}^{-1}$ ), respectively (Table 2). Seedlings and saplings of *A. concolor* were more abundant than those of *P. jeffreyi* and other species, except at Cascade and Meeks. At Cascade and Meeks, *A. concolor* and *P. jeffreyi* saplings were present in about equal proportions.

**FIRE HISTORY.** Thirty-two fires were recorded in the fire scar samples ( $N = 17$ ) between 1714 and 1882 (Table 3). The last fire in each of the chaparral stands occurred between 1861 and 1882. The grand mean point FRI was 28 yr and

the mean site FRI ranged from 16 to 40 yr (Table 3). There was a wide range in the minimum (6–40 yr) and maximum (20–77 yr) interval between fires among the fire scar samples. For forest, in contrast, the grand mean point FRI was 14 yr, the range of minimum FRI was narrower (1–12 yr), but the range of maximum FRI was wider (16–81 yr). The mean point FRI was longer in chaparral than forest ( $P < 0.05$ , Mann Whitney U-test). The FRI distributions for chaparral and forest were also different. There were more short than long fire intervals in forest than chaparral ( $P < 0.05$ , Kolmogorov-Smirnov two sample test), the chaparral distribution was more skewed (1.52 vs. 1.09) to the right, and more dispersed (kurtosis) (3.04 vs. 0.98). Finally, the composite fire frequency for chaparral (10.1 fires per century) ( $N = 17$ ) was lower than the estimate (99% CI) for forest ( $16.5 \pm 4.4$  fires per century) for the same number of samples ( $N = 17$ ).

**CHAPARRAL AGE STRUCTURE.** The age structure of *A. patula* stems in the six stands was quite variable but they had certain common characteristics (Figure 3). First, a pulse of recruitment was associated with the date of the last fire on most sites. Second, *A. patula* stems were present in a wide range of younger age-classes suggesting that recruitment was not limited to the immediate post-fire period. Moreover, on three of the sites, the ages of some *A. patula* stems pre-dated the last fire. Finally, the lack of recruitment in the last 50 yr may be, in part, a sampling artifact. Small diameter stems in the transects were not aged and these stems may have established during the last 50 yr.

**TREE ENCROACHMENT.** There were similarities in the temporal patterns of tree establishment among sites (Fig. 4). Most trees growing in the chaparral stands established after the last fire and the age-class distributions for both *A. concolor* and *P. jeffreyi* were broadly unimodal. Tree recruitment into the chaparral stands was highest during the first two or three decades after the fire, but tree establishment continued for at least five decades after the last fire in all of the stands. The apparent lack of recent recruitment is a sampling artifact since seedlings and saplings were not aged and they represent trees that probably established during the last 50–75 yr. Finally, in three of the study sites (Meeks, Cascade, Tallac) establishment dates for some trees pre-date the year of the last fire.

The timing of tree establishment within the



Table 2. Density (Den; stems ha<sup>-1</sup>) and basal area (BA; m<sup>2</sup> ha<sup>-1</sup>) of trees (≥ 5 cm dbh), and density of saplings (>1.4 m tall < 5.0 cm dbh) and seedlings (0.5 m–1.4 m tall) growing in six montane chaparral stands in the northern Sierra Nevada, Lake Tahoe, California.

Species	Angora		Cascade		Fallen Leaf		Meeks		Sugar Pine		Tallac	
	Den	BA	Den	BA	Den	BA	Den	BA	Den	BA	Den	BA
Live trees												
<i>Abies concolor</i>	931	35.8	221	10.2	321	34.3	419	14.9	421	25.9	625	24.4
<i>Abies magnifica</i>	81	2.4	0	0	0	0	0	0	0	0	39	2.7
<i>Pinus jeffreyi</i>	121	4.6	359	16.5	184	30.7	481	12	331	13.8	99	7.7
<i>Pinus lambertiana</i>	6	0.03	7	1.03	11	1.4	0	0	0	0	0	0
<i>Calocedrus decurrens</i>	0	0	0	0	0	0	44	2.2	0	0	0	0
Total	1139	42.83	587	27.73	516	66.4	944	29.1	752	39.7	763	34.8
Saplings												
<i>Abies concolor</i>	122		36		57		57		67		155	
<i>Abies magnifica</i>	27		0		0		0		0		9	
<i>Pinus jeffreyi</i>	24		33		0		81		32		5	
<i>Pinus lambertiana</i>	0		0		0		0		0		0	
<i>Calocedrus decurrens</i>	0		0		0		22		0		0	
Total	173		69		57		160		99		169	
Seedlings												
<i>Abies concolor</i>	61		53		78		61		49		264	
<i>Abies magnifica</i>	0		0		0		0		0		37	
<i>Pinus jeffreyi</i>	5		20		0		10		6		0	
<i>Pinus lambertiana</i>	0		0		0		0		0		0	
<i>Calocedrus decurrens</i>	0		0		0		0		0		0	
Total	66		73		78		71		55		301	

Table 3. Fire return interval (FRI) statistics for six montane chaparral stands in the northern Sierra Nevada, Lake Tahoe, California.

Parameter	Angora	Cascade	Fallen Leaf	Meeks	Sugar Pine	Tallac	All sites
Number of samples	3	2	4	4	3	1	17
Total number of fires	6	8	8	5	3	2	32
Mean point FRI (yr)	30	24	29	16	27	40	28
Minimum sample FRI (yr)	10	6	13	12	16	40	6
Maximum sample FRI (yr)	48	77	46	20	32	40	77
Year of last fire	1882	1872	1861	1872	1861	1881	

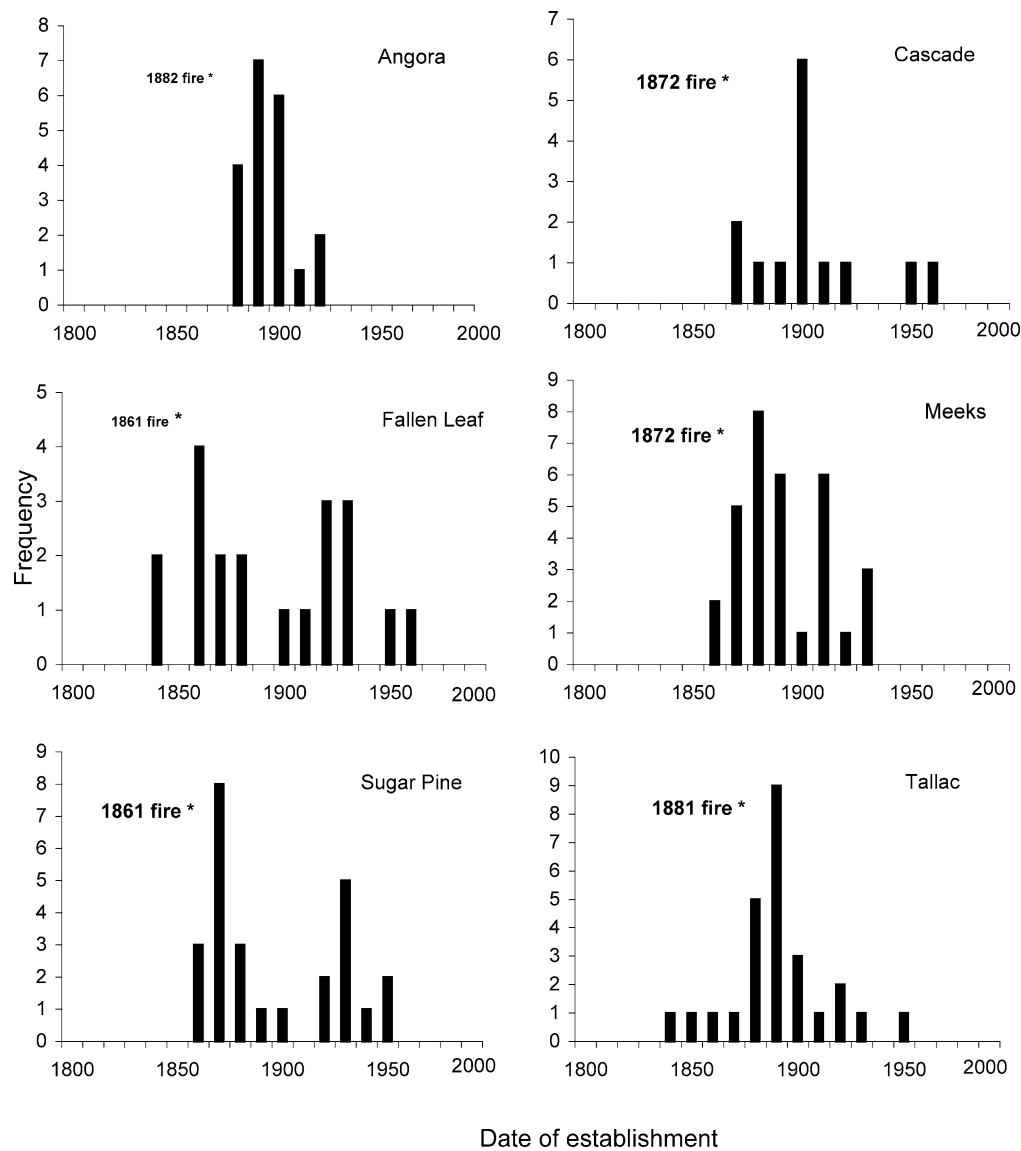


FIG. 3. Dates of establishment of *A. patula* in six montane chaparral stands in the northern Sierra Nevada, Lake Tahoe, California. The year of the last fire in the stand is indicated by an \*.

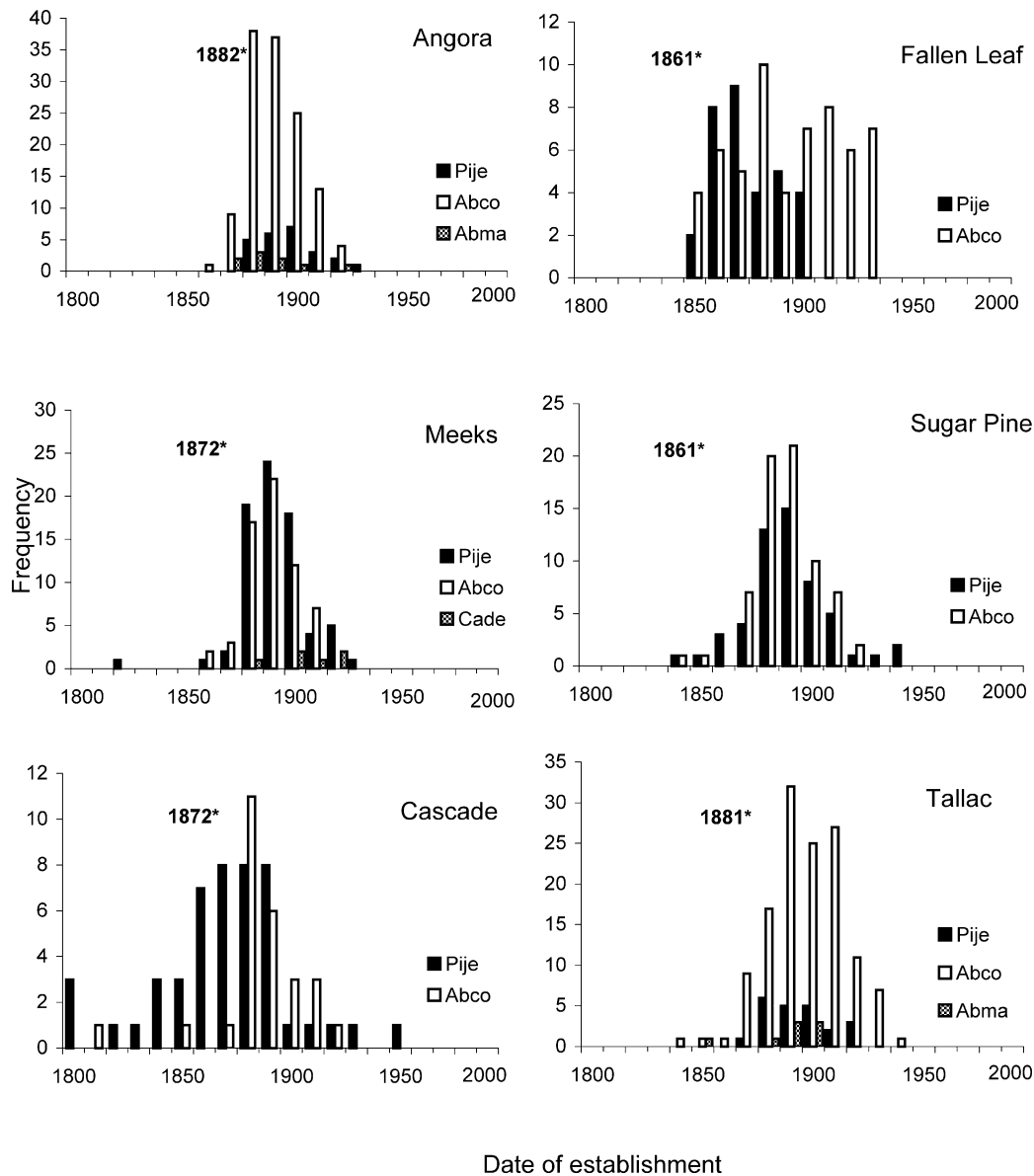


FIG. 4. Dates of establishment of *Abies concolor* (Abco), *Abies magnifica* (Abma), *Calocedrus decurrens* (Cade), and *Pinus jeffreyi* (Pije), trees ( $\geq 5$  cm dbh) in six montane chaparral stands in the northern Sierra Nevada, Lake Tahoe Basin, California. The year of the last fire in the stand is indicated by an \*.

chaparral stands at each site was not clearly related to distance of transects from the forest edge. The average difference in the median age of trees in the transects within each site was only 27 yr (range 13–47 yr). In some stands (e.g., Tallac), median tree ages near the forest edge were older than in the center of the shrub field (edge = 112 yr, range 107–116 yr; center = 90 yr, range 87–92 yr). Yet in other stands (e.g., Angora), median tree ages near the forest edge

were not older than in the center of the shrub field (edge = 108 yr, range 106–112 yr; Angora center = 99.5 yr, range 90–106 yr).

Trees that established in chaparral had slow initial growth (Fig. 5). Initial growth rates for *A. concolor* and *P. jeffreyi* trees were 10–20 rings/cm. The period of slow initial growth lasts for 30–50 yr and then radial growth doubles as trees reach a diameter of 8–10 cm (at 30 cm) and emerge from the shrub canopy (Fig. 5).

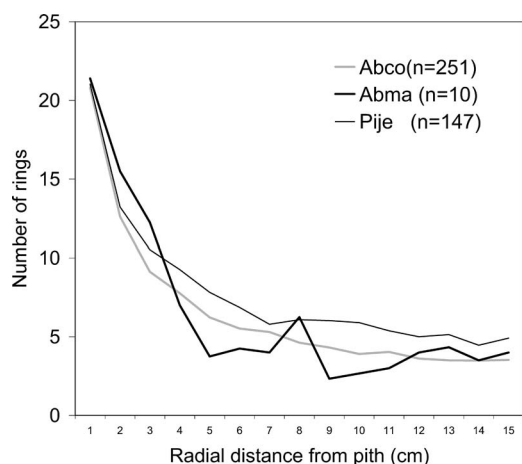


FIG. 5. Mean number of annual growth rings for *Abies concolor* (Abco), *Abies magnifica* (Abma), and *Pinus jeffreyi* (Pije) per cm of tree core counted from the pith for trees ( $\geq 5$  cm dbh) growing in six montane chaparral stands in the northern Sierra Nevada, Lake Tahoe Basin, California.

Once trees emerge from the chaparral canopy they compete with shrubs for light which may reduce shrub vigor and growth (Conard and Radosevich 1982a,b). There was a negative association between tree cover and shrub cover (Spearman's  $r_s = -0.61$ ,  $P < 0.01$ ) in the chaparral stands (Fig. 6). In transects with no tree cover, the average shrub cover was 89 %, while in transects with  $> 75\%$  tree cover mean shrub cover was only 28%. Moreover, the shrub response to high tree cover seemed to vary by species. *Arctostaphylos patula* cover declined continuously as tree cover increased, whereas *Q. vaccinifolia* appears to be only affected by high tree cover (Fig. 6).

Replacement of chaparral by forest was evident on the 1939 and 2000 aerial photographs (Table 4). On average, the area of chaparral in each stand decreased by 55.9 ha (range 30.3–80.8 ha) which represents an average decrease of 62.4% (range, 41.8–89.3%) in chaparral on each site. The replacement of chaparral by forest was also evident in the repeat photo pair of the Fallen Leaf landscape. Since 1915, forest has replaced much of the chaparral stand at Fallen Leaf (Fig. 7).

**Discussion.** The species composition of chaparral stands on the west shore of Lake Tahoe was similar to chaparral stands elsewhere in the Sierra Nevada (Vankat and Major 1978, Conard and Radosevich 1982, Bolsinger 1989,

Skinner and Chang 1996). On our sites, chaparral was dominated by *Q. vaccinifolia* and *A. patula*, which both have life history traits that promote rapid establishment and site dominance after high severity fire. *Quercus vaccinifolia* resprouts vigorously from a root crown when aboveground parts of the plant are damaged and *A. patula* sprouts from underground lignotubers (Biswell 1974, Keeley 1988). *Arctostaphylos patula* also establishes from fire-triggered germination of dormant seeds stored in a soil seed bank (Keeley 1988). Species of *Ceanothus* were also present in our stands and their long-lived ( $> 200$  yr) seeds also germinate after heat scarification by high severity fire. Great seed longevity may be particularly important for the persistence of *Ceanothus* sp. during long fire free periods (Geier-Hayes 1989, Conard et al. 1985, Weatherspoon 1985, 1988) because they may be shorter lived than other chaparral species and chaparral shrubs such as *Q. vaccinifolia* may overtop them during chaparral canopy development (Keeley 1992).

Determining how often fires burn in chaparral is difficult because of the stand replacing nature of chaparral fires and this explains, in part, the scant fire-scar evidence found in or on the edges of our chaparral stands, a scarcity also noted for Arizona chaparral (Dietrich and Hibbert 1990). Yet, our limited sample does support the idea that fire frequency is likely to be lower, more variable, and more severe than in surrounding mixed conifer forests (Skinner and Chang 1996). The mean point FRI for chaparral was twice as long as that for nearby mixed-conifer stands (Taylor 2000b) and the FRI distribution for chaparral was more dispersed and skewed to the right than for forest. Our mean FRI estimate for chaparral from the point samples is probably an underestimate because fires recorded by some of the scarred trees on the edges of chaparral stands may have burned in the forest and not in the chaparral. A longer FRI for chaparral than adjacent forest is consistent with differences in how the structure and composition of fuels in these two vegetation types affect flammability, and the spread and behavior of fire. For example, low intensity fires burning in surface fuels in mixed conifer forests under average weather conditions have been observed to stop spreading when they reach chaparral because of changes in the structure and abundance of surface fuels, and the high live fuel moisture in chaparral shrubs (Weatherspoon and Skinner 1995). The rate of fuel recovery after fire in chaparral is also

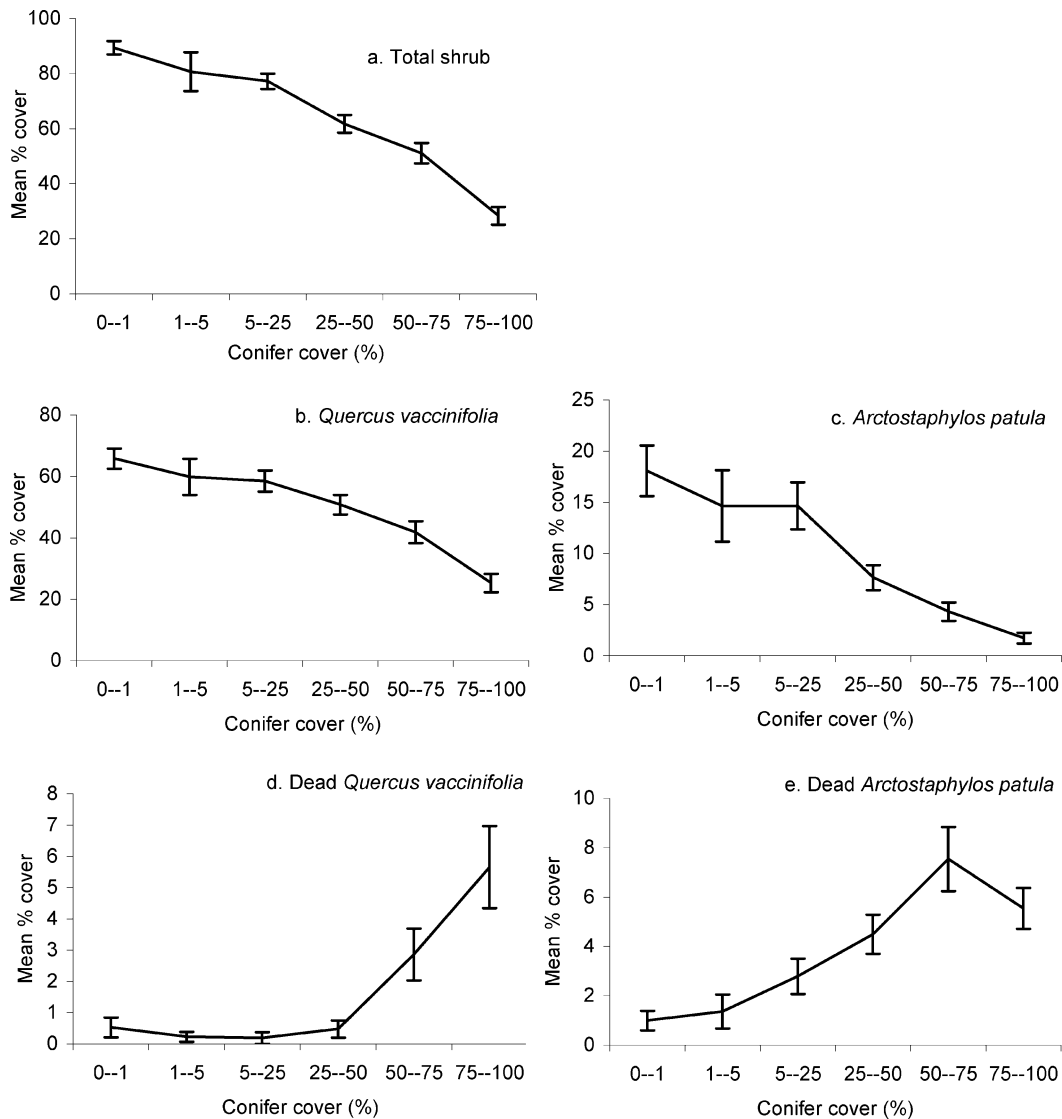


FIG. 6. Mean ( $\pm$  SE) shrub cover (%) by abundance class of conifer canopy cover for all transects at all sites ( $N = 50$ ).

Table 4. Area of montane chaparral at sample sites in 1939 and 2000 in the northern Sierra Nevada, Lake Tahoe, California. The reduction in chaparral at each site was caused by forest encroachment.

Study site	Year/area (ha)		Area change	Percent change
	1939	2000		
Angora	90.5	9.7	-80.8	89.3
Fallen Leaf	68.3	38.0	-30.3	44.4
Meeks	94.8	29.6	-65.2	68.8
Sugar Pine	49.1	12.1	-37.0	75.4
Tallac	161.2	93.8	-67.4	41.8
Cascade	100.1	45.2	-54.9	54.8

slower than in mixed conifer forest (Skinner and Chang 1996).

The coincidence of fire dates in fire scarred trees with the onset of establishment of most shrubs and trees is a strong indicator that high severity fires initiated the chaparral stands in our study in the mid to late 19<sup>th</sup> century. In the northern Sierra Nevada and southern Cascades, there are many chaparral stands that established in this period after heavy early-day logging (Sudworth 1900, Leiberg 1902, Biswell 1974, McKelvey and Johnson 1992). Chaparral shrubs respond vigorously to removal of the forest can-



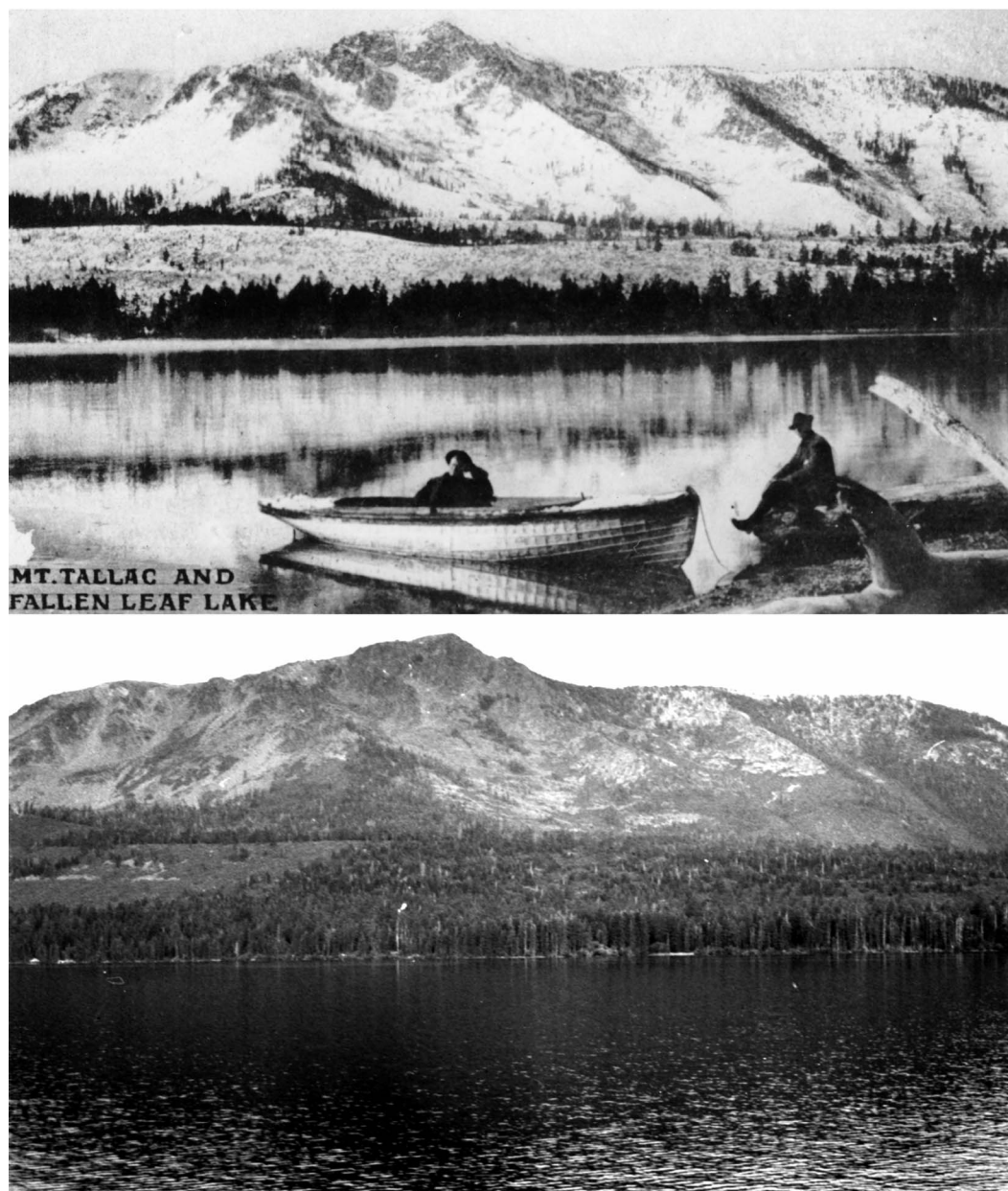


FIG. 7. Photo pair showing conversion of chaparral to forest at the Fallen Leaf site between the period 1915 (top) and 2000 (bottom).

opy by heavy logging and if subsequent wild-fires remove surviving trees, return of trees to these sites can be very slow (Biswell 1974, Walstad et al. 1987). In fact, there are large chaparral stands elsewhere in the Lake Tahoe Basin that were initiated by 19<sup>th</sup> century logging (Lindström 2000). However, there was no logging on our sites and chaparral dominance is not restricted to sites that have experienced logging. High

severity fires in the late 19<sup>th</sup> and early 20<sup>th</sup> century in old growth forest landscapes in the southern Cascades (Bekker and Taylor 2001, Beaty and Taylor 2001), Klamath Mountains (Taylor and Skinner 1998, 1993) and Sierra Nevada (Gruell 2001) generated large chaparral stands. Moreover, in deeply incised terrain (Taylor and Skinner 1998, 2003; Beaty and Taylor 2001) chaparral stands appear to be relatively

fixed in place due to feedbacks between terrain characteristics and fire behavior (Rothermel 1983). Our chaparral stands were predominantly on more xeric south and southeast facing slopes and conditions on these slopes may have predisposed them to recurring high severity fire rather than the low severity surface fires typical of surrounding forest. Thus, our chaparral stands may have been relatively fixed in the landscape due to recurring high severity fire on the same sites. Yet, data to support an interpretation of chaparral as being fixed in position in our landscapes is scarce because stand replacing fires erase the evidence of earlier fires.

Recurring fire in the same chaparral stand, however, has been observed to maintain shrub dominance and prevent replacement of chaparral shrubs by trees elsewhere in the Sierra Nevada, since at least the mid 19<sup>th</sup> century. An analysis of historical records (i.e., GLO survey notes, newspaper articles, USDA Forest Service fire records) has documented repeated fires in a large (>800 ha) chaparral stand that established sometime before 1866 (Wilken 1967). Since 1911, burns >40 ha occurred six times and burns tended to be patchy, but there were some areas of repeat burning during the 1911–1963 analysis period. In three of our chaparral stands, there were some trees and shrub stems that had establishment dates well before the last fire. The areas occupied by these older trees and shrubs were probably not affected by the last fire and suggests that the burns were patchy, a finding similar to Wilken's (1967).

Fires in the chaparral stands we studied initiated new cohorts of shrubs and trees and this large post-fire pulse of regeneration was a conspicuous feature of shrub and tree age structures in the chaparral stands. Yet, shrub and tree establishment was not confined to the immediate post fire period. In each chaparral stand, on average, shrub and tree recruitment occurred in seven different 10-yr age-classes. Thus, both tree and shrub populations in the stands are not even-aged but multi-aged. The multi-aged structure of the *A. patula* populations indicates that recruitment of *A. patula* is not limited to the immediate post-fire period but that it continues during fire free periods. Similar, multi-aged populations of chaparral shrubs have been identified in lower elevation stands of foothills chaparral that have not burned in over a century (Keeley 1992). In foothills chaparral, the shrub canopy is rejuvenated continuously via sprout recruitment (Keeley 1992). Similarly, sprout recruit-

ment by *A. patula* and *Q. vaccinifolia* may be an important regeneration mechanism that contributes to shrub dominance in our chaparral stands.

Tree encroachment was conspicuous in our chaparral stands. *Abies concolor* was the most frequent colonizer followed by *P. jeffreyi* and the density and basal area of invading trees is similar to reported values for other post-fire mixed conifer stands with chaparral in the northern Sierra Nevada (Conard and Radosevich 1982b). *Abies concolor* is highly shade tolerant and can establish and grow slowly for long periods beneath a shrub canopy (Conard and Radosevich 1982a). In our chaparral stands it took nearly 30 yr, on average, for an *A. concolor* seedling to grow to a height of 30 cm. Once trees grow tall enough to emerge from the shrub canopy they increase growth dramatically, cast shade, and reduce the vigor of shrubs which leads to replacement of chaparral by forest. During the >120 yr fire free period in our stands the area of a chaparral stand declined, on average, by 62.4%.

Changes in the structure and composition of mixed conifer forests since the late 19<sup>th</sup> century have also been identified the Sierra Nevada (Vankat and Major 1978, Parsons and DeBenedetti 1979), the southern Cascades (Taylor 2000a), and the Klamath Mountains (Skinner 1995, Taylor and Skinner 2003). In general, nearly a century of fire exclusion has caused an increase in forest density, a shift in composition from more fire-resistant to more shade tolerant or fire-sensitive species, and a reduction in forest heterogeneity. In our chaparral stands, no fires have occurred since the mid to late 19<sup>th</sup> century (i.e., 1861–1882). The >120 yr fire free period in our chaparral stands exceeds the longest interval between fires identified in the chaparral fire scar samples by several decades. This unusually long fire free period is probably the most significant factor leading to replacement of chaparral by forest in our study sites. Similar encroachment of trees into chaparral has been observed in mixed conifer forest landscapes elsewhere in the Sierra Nevada (Bock and Bock 1977, Conard and Radosevich 1982b), the southern Cascades (Bekker and Taylor 2001, Beaty and Taylor 2001), and the Klamath Mountains (Skinner 1995). Our data suggest that the well documented effects of fire suppression on mixed conifer forest structure and composition also apply to the forest-chaparral mosaic. Forests have expanded into chaparral and reduced the coarse

grained structural heterogeneity of mixed conifer forest landscapes.

Our data indicate that stands of chaparral were a conspicuous feature of the mixed conifer forest landscape in the northern Sierra Nevada at or near the time of Euro-American settlement and that they were maintained mainly by fire. However, the extent and spatial pattern of chaparral in the pre-EuroAmerican mixed conifer forest landscape is uncertain because contemporary chaparral stands originated after both fire and early-day logging. Historical records, either natural (i.e., trees and shrubs) or documentary (i.e., written, photographic) are insufficient in most areas to assess, for example, what proportion of the landscape in chaparral might have been. Nevertheless, after a century or more of fire exclusion trees have established in chaparral stands and they are converting to forest. In the Lake Tahoe Basin resource managers and citizen stakeholders are seeking ways to restore forests to a condition more like those at the time of Euro-American settlement (Christopherson et al. 1996). Our study suggests that maintenance of chaparral should be an integral part of ecosystem restoration plans for mixed conifer forest landscapes in the Lake Tahoe basin and northern Sierra Nevada.

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