Forest Composition, Structure, and Change in an Old-Growth Mixed Conifer Forest in the Northern Sierra Nevada

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Forest composition, structure, and change in an old-growth mixed conifer forest in the northern Sierra Nevada.[1]

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ANSLEY, J.S. AND J.J. BATTLES (Department of Environmental Science, Policy, and Management, University of California-Berkeley, 151 Hilgard Hall, Berkeley, CA 94720-3110.) Forest composition, structure, and change in an old-growth mixed conifer forest in the northern Sierra Nevada. J. Torrey Bot. Soc. 125:297–308. 1998.—We documented current forest conditions and 39 years of change in community composition and structure in an old-growth, mixed conifer forest in the northern Sierra Nevada. In 1996, we remeasured and mapped a 4-ha stand, originally established by F.S. Baker between 1954 and 1961. For trees ≥ 9.5 cm dbh in 1996, total tree density was 721 stems/ha, and total basal area was 75.3 m^2/ha. *Pseudotsuga menziesii* (Mirbel) Franco var. menziesii and *Abies concolor* (Gordon & Glend.) Lindley codominated the plot. *A. concolor* was the most abundant tree species, 420 stems/ha, but *P. menziesii* had the highest basal area, 31.3 m^2/ha. A retrospective analysis of trees ≥ 24 cm in dbh showed that in the last 39 years, stand density increased 39% from 157 to 219 stems/ha, and stand basal area increased 15% from 57.9 to 66.7 m^2/ha. These increases were due largely to the canopy recruitment of *A. concolor* (60% of new recruits) and the continued growth and low mortality (0.3%/yr) of *P. menziesii*. Overall stand mortality of trees originally measured by Baker was 0.6%/yr. Regeneration size classes were dominated (in order of frequency) by *A. concolor*, *P. menziesii*, and *Calocedrus decurrens* (Torrey) Florin. There was little regeneration of the less shade-tolerant pine species, *Pinus lambertiana* Douglas and *Pinus ponderosa* Laws.

Key words: mixed conifer, old-growth, Sierra Nevada.

The mixed conifer forest covers 10% of the vegetated area in the Sierra Nevada of California (Sierra Nevada Ecosystem Project 1996), and forms the dominant community of the lower montane zone (Rundel et al. 1995). This commercially valuable forest type has been extensively disturbed by both logging and decades of fire suppression. Currently, less than 15% of the mixed conifer forest retains old-growth or late-successional structural features; much of this remaining old-growth is found in the national parks of the southern Sierra Nevada (Franklin and Kaufmann-Fites 1996). Although categorized as a single community, the composition, structure, and history of the mixed conifer forest varies with latitude.

In 1954, Frederick S. Baker, Professor of Silviculture at the University of California, Berkeley, established a 4.7-ha (11.5 ac) plot in a "virgin, all-aged" mixed conifer stand on the Plumas National Forest in the northern Sierra Nevada near the University's forestry camp in Meadow Valley, California. Professor Baker's original intention was to measure in detail the productive capacity of the stand. Towards this end, he measured and tagged all trees on the study plot ≥ 24 cm diameter at breast height (dbh, breast height equal to 1.37 m). Professor Baker died before completing his analysis.

By remeasuring the plot and recovering Baker's original data, we were able to document current stand conditions and to perform a retrospective analysis of mortality, canopy recruitment, and growth through time for a cohort of canopy-sized trees. Most of what is known about temporal dynamics in the mixed conifer forests comes from studies using indirect, inductive methods (Minnich et al. 1995) conducted primarily in the southern Sierra Nevada. To understand pattern and process, long-term, repeated measurements on permanent plots are essential (e.g., Hunter 1997; Volk and Fahey 1994). The Baker plot is a rare scientific resource: it is an old-growth mixed conifer stand in the northern Sierra Nevada with a legacy of stand measure-

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ment that can be used to assess forest dynamics. Fire prevention throughout the 20th century in the Sierra Nevada forests (Husari and McKelvey 1996) has acted as a long-term manipulation of the natural disturbance regime in this stand. Fire suppression in the mixed conifer forests has led to an increase in the density of shade-tolerant species at the expense of the shade-intolerant but more fire-resistant trees (Rundel et al. 1995). While there is broad consensus on this general pattern of community change, the details of the pattern, as well as the demographic processes (e.g., mortality and growth) that drive these patterns, remain largely undocumented.

The main goal of this paper is to document the changes in forest composition and structure that have occurred over the 39 year interval including species-specific mortality and canopy recruitment rates. Despite the commercial importance of the mixed conifer forest, no direct observations of these demographic parameters from permanently marked plots have been reported in the ecological or forestry literature. Such information is crucial to understanding the vegetation dynamics of this forest type under an altered disturbance regime. As a necessary first step, we also describe the current composition and structure of the Baker plot, and compare our results to other old-growth and late-successional mixed conifer stands in the Sierra Nevada.

Study Area. The research was conducted on the main 4-ha (100 m × 400 m) section of Baker's original study plot. The plot is situated on an east-facing slope of Little Schneider Ridge in the Plumas National Forest of California (N39°55′ W121°02′). Located on moderate terrain, plot elevation ranges from 1,158 to 1,219 m. The climate is characteristically Mediterranean with warm, dry summers and mild winters. Annual precipitation averages 1046 mm/yr with 84% of precipitation falling during the winter months (November–April; NCDC 1995). The basic igneous bedrock of the study area has weathered to a relatively fine loamy soil classified as an Ultic Haploxeralf. These soils are well-drained with depths ranging from 1 to 2 m (Laacke 1979). Site productivity of the plot is estimated to be high for the region (P. Zinke, pers. comm.).

Baker described the plot as an old-growth, all-aged mixed conifer stand (F.S. Baker, unpublished notes). Earlier silvicultural studies conducted in nearby mixed conifer forests showed that age of the average canopy tree in virgin stands ranged from 140 to 290 years old, with the oldest trees > 400 years old (F.S. Baker, unpubl.). The Sierra Nevada mixed conifer forest is composed of variable proportions of five coniferous and one hardwood tree species (Tappeiner 1980). Constituent tree species include *Abies concolor* (Gordon & Glend.) Lindley (white fir), *Pseudotsuga menziesii* (Mirbel) Franco var. menziesii (Douglas-fir), *Pinus lambertiana* Douglas (sugar pine), *Pinus ponderosa* Laws. (Pacific ponderosa pine), *Calocedrus decurrens* (Torrey) Florin (incense-cedar), and *Quercus kelloggii* Newb. (California black oak). Nomenclature follows Hickman (1993). In the interval between Baker's original inventory and our remeasurement, the only activity on the study area was the removal of < 10% of the large dead trees for firewood. For most of the twentieth century, the Plumas National Forest has employed an aggressive fire suppression policy (Husari and McKelvey 1996). There is no record of a large fire occurrence on the plot in the time since Baker's study (J. Hurley, Fire Management Officer, Mt. Hough Ranger District, Plumas National Forest, pers. comm.).

Data Collection. The study area was resurveyed in 1996 using the few surviving plot markers as references. To ensure complete sampling, we divided the plot into a systematic grid of 20 × 20 m quadrats. All live and standing dead trees ≥ 9.5 cm in dbh were tagged, measured for dbh, and identified to species. We took care to determine the fate of all trees in the original study using Baker's hand-drawn tree maps and surviving tree tags.

Canopy height and tree regeneration were sampled at each of the 76 interior corner stakes of the quadrat grid. Only interior points were sampled to avoid edge effects. At each of these points, two 10-m transects were established running north-south and east-west. In each of the four resulting quadrants, the height of the nearest tree not currently suppressed by overhead shade was measured. Mean canopy height at each sample point was calculated by averaging the height of the four measured trees. Trees smaller than 9.5 cm were divided into three size classes: poles were defined as stems ≥ 2 and < 9.5 cm dbh; saplings were stems < 2 cm dbh and ≥ 1 m tall; seedlings were stems <1 m tall. The number of trees in each size class was tallied by species. Poles were counted in the entire 10-m diameter plot (79.5 m^2); saplings within 1 m of either side of the 10-m transects were counted (36.0 m^3 total); seedlings were counted in a 2-m diameter plot (3.1 m^2) centered on the point. To describe overall canopy architecture, we measured the height of 98 trees (dbh ≥ 5 cm) located at random in the Baker plot. These 98 trees included both suppressed and unsuppressed trees.

To estimate the light available to the understory trees in the Baker plot, we measured the fraction of diffuse light (DIFN) penetrating to a height of 1 m above the ground at each of the 76 interior points with a Li-Cor Plant Canopy Analyzer (Li-Cor Incorporated, Lincoln, Nebraska). DIFN values range from 0% for no sky visible to the sensor, to 100% for no vegetation visible to the sensor. Thus, DIFN is inversely correlated to canopy closure. All light measurements were made at dawn or dusk to best approximate isotropic skylight conditions. The above canopy measurements of light were made with a separate instrument placed in a large opening just north of the Baker plot.

Data Analysis. Change through time was documented by comparing the subset of the tree community measured by Baker (i.e., trees ≥ 24 cm in dbh) to the comparable 1996 subset of trees. Baker measured the main area of the study plot over a seven-year period. He measured half the plot in 1954, another hectare in 1957, and the last hectare in 1961. For simplicity, we made comparisons of density and basal area using the median age of the original sample, 1957. However, annual mortality, which is more dependent on the time between sampling, was calculated for the exact number of years since measurement. Annual mortality was calculated after Sheil et al. (1995). Canopy recruitment was defined as the number of new trees found in the 1996 inventory within the Baker size class (i.e., new trees ≥ 24 cm dbh).

A challenge to any long-term study is to minimize the bias introduced by the inevitable errors that occur during sampling occasions. This study was no exception. We encountered three types of problems: differences in the exact location of the plot boundaries, "missed" trees in the original Baker inventory, and "lost" trees absent from the 1996 inventory.

To account for boundary differences, we simply narrowed the plot size by 5% to ensure an accurate stand comparison between sampling dates. Correcting for missed and lost trees was more involved. Missed trees were large trees that were measured for the first time in 1996, but were likely to have been at least 24 cm in dbh when Baker first measured the plot. Lost trees were trees in the original Baker survey that could not be relocated in 1996. There were 4 lost trees in the 1996 survey. To identify missed trees, we calculated species-specific regression equations to estimate 1957 dbh as a function of 1996 dbh. We used the data from the surviving Baker trees to generate these equations. We took a conservative approach to identifying missed trees. Only trees whose predicted 1957 dbh exceeded 30 cm were considered to be missed. This conservative screening identified 27 missed trees. Two of these missed trees matched the species, size, and general location of 2 out of 4 lost trees. The remaining two lost trees were presumed dead in 1996. The remaining 25 missed trees and their estimated 1957 dbh were then added to the 1957 original inventory. These "problem" trees represent only 3% of the total number of trees in the Baker's original inventory and our results reported in Table 3 for 1957 closely match the stand summary included in Baker's notes.

From our sample of unsuppressed trees, we developed species-specific regression equations to estimate the height of all other trees in the 1996 inventory as a function of dbh. Sugar pine and ponderosa pine trees were pooled due to small sample size. Statistical corrections for log-transformation were incorporated when predicting tree height from these equations (Sprugel 1983). Heights of the infrequent black oak trees on the plot were predicted using coefficients developed by Biging et al. (1994).

Results. For all trees ≥ 9.5 cm dbh, total tree density was 721 stems/ha, and total basal area was 75.3 m^2/ha (Table 1). White fir was the most abundant tree species on the plot with a density of 420 stems/ha. Douglas-fir was the dominant tree species with a basal area of 31.1 m^2/ha. Linear equations on log transformed values used to predict height as a function of dbh were significant (p values of all slopes < 0.001) and provided good fits to the data (R^2 values ranged from 0.82 to 0.97; Table 2). Ponderosa and sugar pine were the largest trees on the plot: ponderosa pine had a quadratic mean diameter of 94.5 cm and a mean height of 42.6 m; sugar pine had a quadratic mean diameter of 104.7 cm and a mean height of 40.2 m (Table 1). The tallest individual was a Douglas-fir 176.2 cm in dbh and 77.1 m tall.

The diameter class distribution of all trees fol-

Table 1. Current (1996) composition of trees ≥ 9.5 cm dbh by species in an old-growth mixed conifer forest in the northern Sierra Nevada. Numbers in parentheses are ± one standard deviation.

	Density (stems/ha)	Basal area (m^2/ha)	Quadratic mean diameter (cm)	Mean height (m)
Douglas-fir	200	31.1	44.5	20.1 (13.4)
White fir	420	20.9	25.2	14.1 (8.1)
Sugar pine	12	10.6	104.7	40.2 (17.2)
Ponderosa pine	7	4.9	94.5	42.6 (14.1)
Incense-cedar	76	7.6	35.6	14.2 (9.3)
Black oak	5	0.2	23.7	18.3 (6.5)
Mountain dogwood	1	0.0	10.4	not estimated
All species	721	75.3	36.5	16.5 (11.4)

lowed a reverse J-shaped curve (Fig. 1A). White fir and Douglas-fir were the most abundant and frequent (Fig. 1B, Table 3) tree species in all size classes. This codominance was evident in the intermediate size class (trees 9.5 to 24 cm in dbh). However, the relative density of intermediate white fir, 64%, was more than twice that of Douglas-fir, 25%. With the exception of sugar pine seedlings, regeneration of both pine species was infrequent on the study plot (Table 3). Although pine trees in the smaller size classes were more abundant than in larger size classes, the diameter distribution of the pine species tended to be more irregular in the size classes ≥ 9.5 cm dbh (Fig. 1C). Incense-cedar regeneration was frequent in all size classes (Table 3).

Based on the average unsuppressed tree height at the 76 interior points, mean canopy height was 29.3 m (std = 8.8 m). The distribution of canopy heights at the interior points was bimodal (Fig. 2A). Half of the points had a canopy that was between 30 and 45 m tall; 43% had a height between 15 and 30 m tall. Points with either a tall canopy (> 45 m) or a short canopy (< 15 m) were infrequent (Fig. 2A). The fraction of diffuse radiation (DIFN) that reached the understory varied from a minimum of 2% to a maximum of 31% with a median of 8% of above-canopy radiation (Fig. 2B). More than two thirds of the points received between 3% and 12% DIFN.

The height distribution of the randomly located, individual trees demonstrated a multilayered canopy architecture (Fig. 2C). Tree heights ranged from 3.1 m to 55.9 m. More than 65% of the trees sampled were shorter than 15 m, yet 5% of the trees were taller than 45 m. The remaining 30% of the trees fell within the bimodal range of canopy heights noted above (i.e., between 15 and 45 m in height, Fig. 2C).

For trees ≥ 24 cm dbh, stand density increased 39% from 157 to 219 stems/ha between 1957 and 1996. Stand basal area increased 15% from 57.9 to 66.7 m^2/ha (Table 4). Of the original 555 trees measured by Baker (not including the 25 missed trees added to the 1957 inventory), 119 died by 1996 giving an annual mortality of 0.6 %/yr. Using size classes defined by 1957 dbh, the highest mortality occurred in the 24–32 cm diameter class (16% of total mortality), and approximately 50% of total mortality occurred in the size classes between 24 and 56 cm dbh. Recruitment into the Baker size class (trees ≥ 24 cm dbh) during the same time period was 348 trees with 69% of new recruitment occurring in the 24–32 cm diameter class in 1996. Due to the ingrowth of smaller diameter trees, the average height of the canopy decreased from 34.4 m (std = 11.53) to 29.7 m (std = 12.54) and quadratic mean diameter decreased from 68.5 cm to 62.3 cm between 1957 and 1996. However, the re-

Table 2. Species-specific linear equations generated to predict height as a function of dbh in an old-growth mixed conifer forest in the northern Sierra Nevada. Equation follows the formula: $\ln(y) = a + b[\ln(\text{dbh})]$ with dbh in centimeters and the intercept already corrected for log transformation using the standard error. P values of all slopes were <0.001.

	Slope constant	Intercept	Standard error	R^2
Douglas-fir	0.748	0.479	0.020	0.93
White fir	0.874	0.016	0.022	0.92
Sugar and Ponderosa pine	0.588	1.146	0.051	0.82
Incense-cedar	0.869	−0.022	0.030	0.97

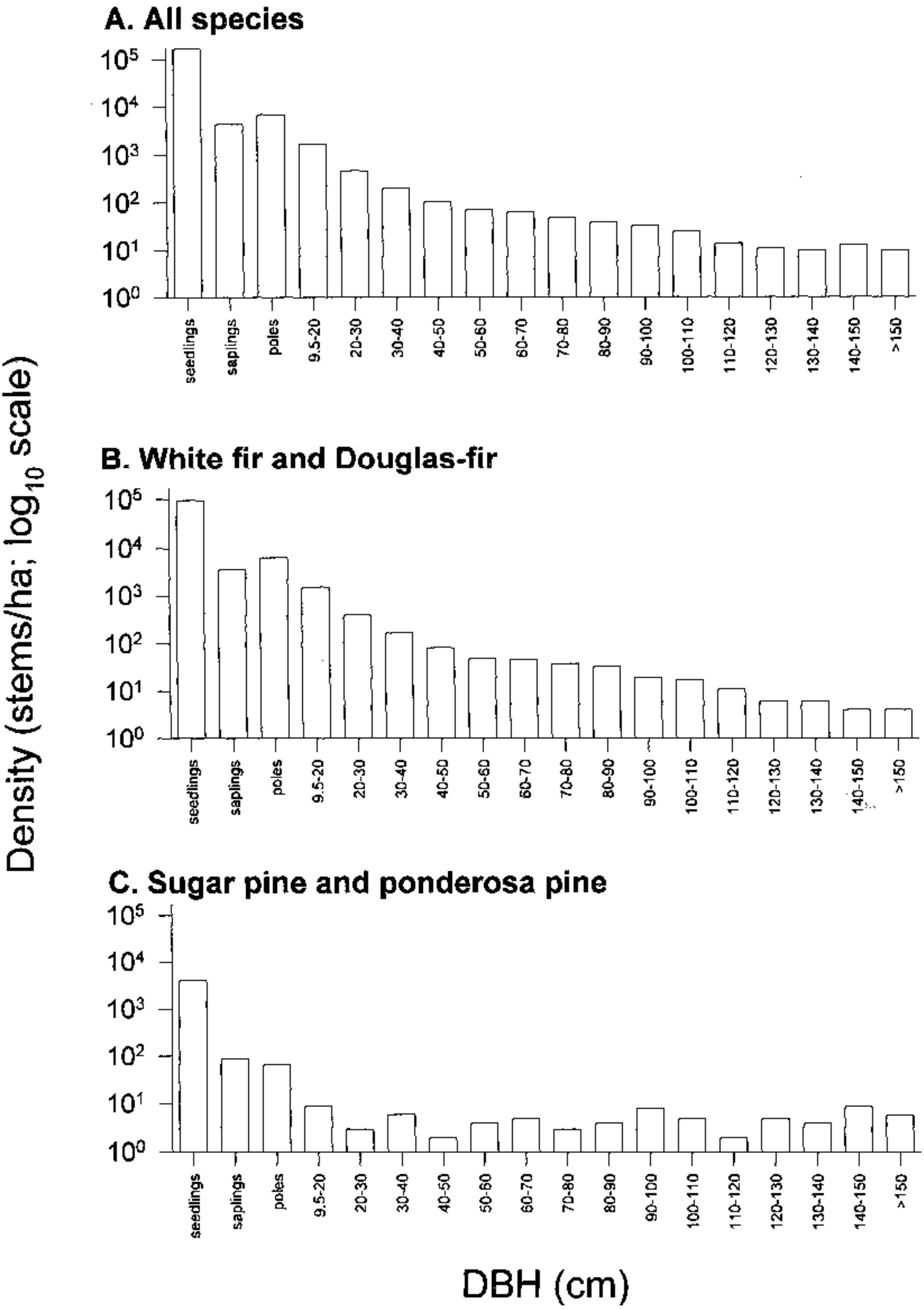

Fig. 1. Diameter distribution of trees in an old-growth mixed conifer forest in the northern Sierra Nevada. A. all species, B. Douglas-fir and white fir, C. sugar pine and ponderosa pine.

Table 3. Contribution of each species to regeneration in the seedling (< 1 m ht.), sapling (< 2 cm dbh and > 1 m ht.), pole (2 to < 9.5 cm dbh) and intermediate (9.5–24 cm dbh) size classes in an old-growth mixed conifer forest in the northern Sierra Nevada.

		Frequency (%)		Relative density (%)
	Seedlings	saplings	Poles	intermediate
Douglas-fir	92[a]	54	68	25
White fir	—	58	97	64
Sugar pine	22	4	5	<1
Ponderosa pine	3	3	1	<1
Incense–cedar	34	20	33	9
Black oak	14	0	1	1
Mountain dogwood	8	8	3	<1
No Regeneration	1	25	0	—

[a] White fir and Douglas–fir seedling counts were pooled.

verse J-shaped diameter distribution curve that was present in 1957 remained in 1996 (Fig. 3).

In contrast to the large changes in stand structure, the relative contribution of tree species to stand density and basal area remained nearly constant from 1957 to 1996 (Table 4). For trees $\geq$ 24 cm dbh, species rank by density and by basal area remained the same between 1957 and 1996, except that incense-cedar replaced ponderosa pine as the fourth largest contributor to basal area. White fir made the largest contribution to canopy tree recruitment, 60%, but also had the highest annual mortality 1.4 %/yr (Table 5). In contrast, Douglas-fir had moderate canopy tree recruitment, 27%, and relatively low annual mortality, 0.3 %/yr. Only small changes in density and basal area of both pine species occurred during the 39 year interval (Table 4).

Discussion. CURRENT COMPOSITION. The Baker plot is representative of old-growth mixed conifer forests in the Sierra Nevada. The overall species composition (SAF Type 243; Tappeiner 1980) and the observed codominance of Douglas-fir and white fir (Table 1) on the Baker plot is typical for many mixed conifer stands in the northern Sierra Nevada (Rundel et al. 1995). Compared to other late-successional mixed conifer stands throughout the Sierra Nevada (Table 6), the Baker plot with a basal area of 75 m^2/ha fell near the median (median = 70 m^2/ha). The Baker plot in 1996 met the current definitions for old-growth mixed conifer forests in the Sierra Nevada (Fites et al. 1992; Franklin and Kaufmann-Fites 1996) based on the density of large live trees (> 6 large live trees/ac) and snags (> 2 large snags/ac); the presence of large down wood (> 2 logs/ac; J. Ansley pers. obs.); and the existence of a multilayered canopy (Fig. 2C).

The reverse J-shape of the diameter distribution on the Baker plot (Figs. 1A, 3) is typical for old forests (McCarthy and Bailey 1996) and indicative of a potentially self-replacing, uneven-aged stand (Harcombe 1986). While age distribution is more commonly used to make such projections, for long-lived species like those that comprise the mixed conifer forest, size distribution is often a better predictor of future forest composition (Veblen 1992). Despite this indication of forest continuity, there was a dichotomy in species composition between large and small trees. A mix of the five conifer species comprised the larger trees (dbh > 100 cm), while Douglas-fir and white fir dominated trees < 100 cm dbh.

The height of the canopy in the Baker plot varied, with an abundance of low canopy points between 15–30 m tall and high canopy points between 30–45 m tall (Fig. 2A). The low canopy corresponded to points in or near canopy gaps where there were one or more short trees growing unsuppressed in an opening. The high canopy was formed by codominant trees growing in undisturbed areas of the canopy.

The canopy of the Baker plot was more closed, 92% (median DIFN 8%), than other mixed conifer stands in the Sierra Nevada which typically exhibit 50–80% canopy closure (Barbour 1988). For example, a mature mixed conifer stand at the Blodgett Forest Research Station in the Central Sierra Nevada had a median DIFN of 21% (J. Battles unpubl. data) and understory light levels in comparable lower montane stands in Sequoia-Kings Canyon National Park also were commonly greater than 10% (Kern 1997). However, compared to an old-growth Douglas-fir—hemlock forest in the Pacific Northwest where only 0.6% of overstory light reached the understory (Canham et al.

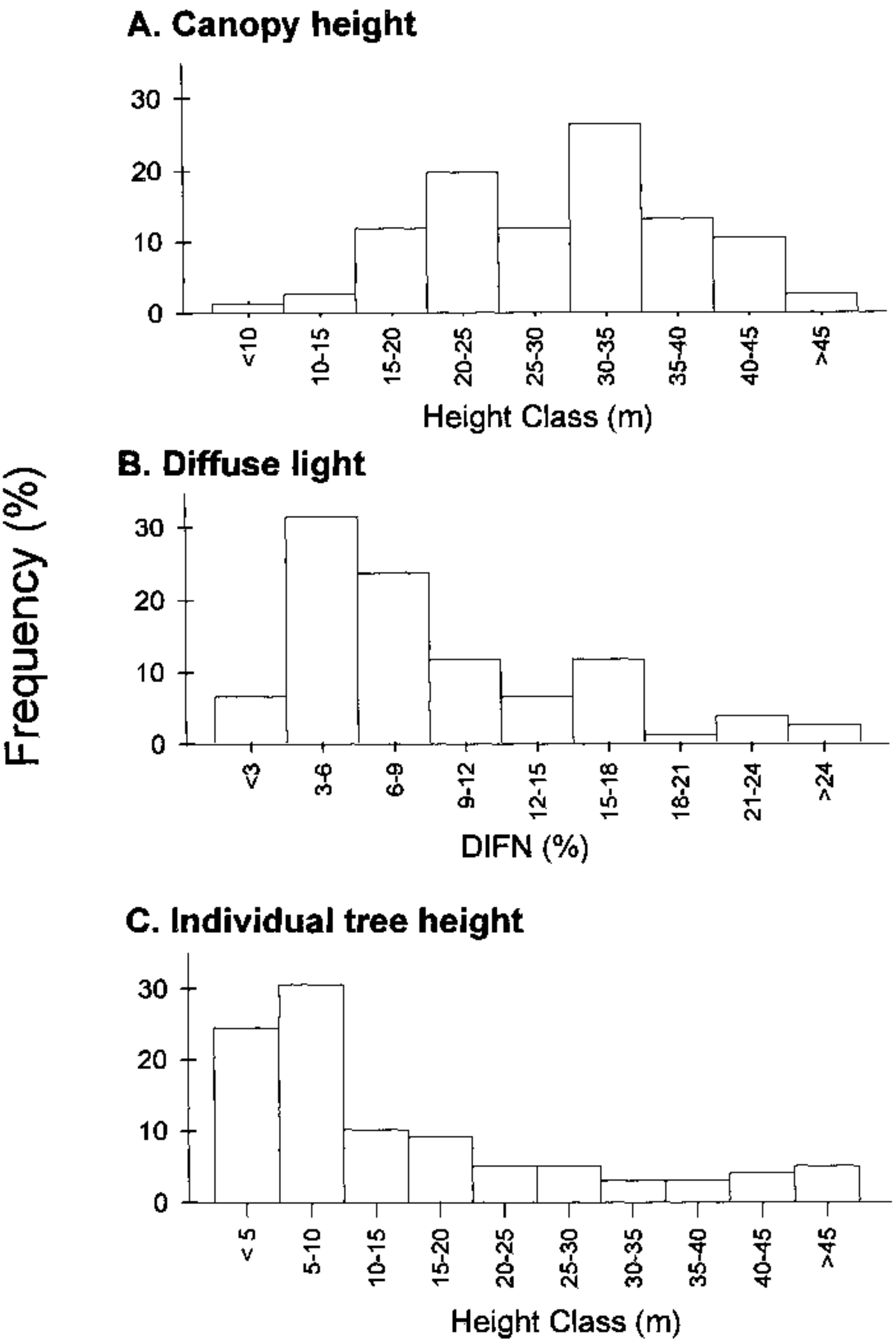

Fig. 2. Canopy structure in an old-growth mixed conifer forest in the northern Sierra Nevada. A. Frequency distribution of canopy heights. B. Frequency distribution of diffuse light reaching a point in the understory 1 m above the ground. Measurements for figures A and B were made from 76 interior sample points (see methods). C. Frequency distribution of tree heights from a random sampling of 98 suppressed and unsuppressed trees.

Table 4. Composition in 1957 and 1996 of trees ≥ 24 cm dbh in an old-growth mixed conifer forest (4-ha) in the northern Sierra Nevada.

	Number		Density (stems/ha)		Basal area (m²/ha)	
	1957	1996	1957	1996	1957	1996
Douglas-fir	201	275	54	75	23.6	29.6
White fir	227	355	61	96	13.1	14.8
Sugar pine	43	38	12	10	10.7	10.7
Ponderosa pine	28	23	8	6	5.4	5.0
Incense-cedar	81	111	22	30	5.1	6.5
Black oak	0	7	0	2	0.0	0.1
All species	580	809	157	219	57.9	66.7

1990), a relatively large fraction of above canopy radiation reached the understory in the Baker plot.

Retrospective Analysis. For trees ≥ 24 cm dbh on the Baker plot, canopy recruitment rate exceeded the mortality rate during the last 39 years. As a result, canopy tree density increased 39% between 1957 and 1996. This density increase was due to the high recruitment rate of white fir and to a lesser extent, Douglas-fir and incense-cedar (Table 5). For both pine species, mortality and recruitment were low; the slightly higher mortality rate led to minor decreases in pine density (Table 4, Table 5). In addition to increases in density, a 15% increase in basal area of trees ≥ 24 cm dbh was observed on the Baker plot. All conifer species increased in total basal area except ponderosa pine. More than half the increase in basal area was associated with Douglas-fir growth, and 19% with white fir (Table 5).

The increases in density and basal area have been related to the changes in the Sierra Nevada disturbance regime, specifically fire suppression. The pattern of fire in the presettlement mixed conifer forest consisted of frequent (12 year median fire return interval; Sierra Nevada Ecosystem Project 1996), moderate-to-low intensity ground fires (Skinner and Chang 1996). Minnich et al. (1995) found increases in tree density similar to ours in their 60 year comparison of vegetation change in the San Bernadino Mountains. They attributed the 41% increase in tree density in the mixed conifer association to 60 years of fire suppression. Other studies in the southern Sierra Nevada have reported similar results and have reached the same conclusion—stand density increases in the absence of periodic fire (McKelvey and Johnston 1992; Parsons and DeBenedetti 1979; Vankat and Major 1978). The apparent explanation for this change is that the mortality of understory trees decreases without fire; consequently, more trees reach the canopy.

Table 5. Relative contributions of tree species to canopy recruitment, basal area increase and annual mortality in the ≥ 24 cm dbh size class in an old-growth mixed conifer forest in the northern Sierra Nevada.

	Recruitment (%)	Basal area increase (%)	Annual mortality (%/yr)
Douglas-fir	27	65	0.3
White fir	60	19	1.4
Sugar pine	1	0	0.7
Ponderosa pine	0	—	0.4
Incense-cedar	10	15	0.2
Black oak	2	1	—

The increase in observed basal area on the Baker plot contradicts the general expectation for old-growth forests. Conceptual models of stand biomass accumulation predict that biomass and characteristics related to biomass (i.e., basal area) should fluctuate around a steady-state endpoint once old-growth status is reached (Bormann and Likens 1979; Peet 1992). However, such models assume a constant disturbance regime. Considering the fire suppression policy of the Plumas N.F. (Husari and McKelvey 1996), it is not surprising that even this old-growth remnant of the mixed conifer forest does not approximate steady-state or equilibrium conditions.

Despite substantial mortality and recruitment over the 39 year interval, the relative species composition of the stand in terms of both density and basal area remained similar. Comparisons made by McKelvey and Johnston (1992) of data from the Plumas National Forest in 1913 to recent inventory data also indicate that current species composition has remained similar to that observed at the turn of the century. In contrast, studies on the effects of fire suppression in the southern Sierra Nevada have, in most cases, documented a compositional shift towards in-

Table 6. Summary of reported basal area for comparable forest stands throughout the Sierra Nevada. Standard deviations, when available, are reported in parentheses following basal area values.

Location	Stand history	Basal area (m^2/ha)	Source
Northern Sierra Nevada			
Plumas N.F.	Old-growth stand–no disturbance in the last 70 years.	75	This study[a]
Northern Sierra Nevada	Stands > 70 years	84 (26)	Fites 1993[b]
Central Sierra Nevada			
Blodgett Forest Research Station	Old-Growth Reserve Compartments	65	Olson and Helms 1996[c]
Placer County	"Virgin mixed conifer forest"	49	Rundel et al. 1995[d]
Central Sierra Nevada	Data collected by George Sudworth in 1899.	165 (58)	Olson *unpublished manuscript*[3]
Southern Sierra Nevada			
Southern Sierra Nevada	Data collected by George Sudworth in 1900.	264 (67)	Olson *unpublished manuscript*
Sequoia-Kings Canyon N.P.[j]	Mixed conifer–white fir forest type	70	Vankat and Major 1978[f]
Sequoia-Kings Canyon N.P.	Mixed conifer–ponderosa pine forest type	48	Vankat and Major 1978
Sequoia-Kings Canyon N.P.	No significant fire since approximately 1875	129	Parsons and DeBenedetti 1979[g]
Sequoia-Kings Canyon N.P.	Ponderosa-mixed conifer forest type. No significant fire since approximately 1875	54	Parsons and DeBenedetti 1979
Sequioa-Kings Canyon N.P.	"A mosaic of large old trees"	67	Riegel et al. 1988[h]
Sequoia-Kings Canyon N.P.	63 years since last recorded wildfire	98	McBride and Sugihara 1990[i]
Sequoia-Kings Canyon N.P.	140 years since last recorded wildfire	52	McBride and Sugihara 1990

[a] Includes all trees ≤ 9.5 cm dbh on the 4-ha. Baker Plot

[b] Mean basal area for 22 plots specifically in the PSME-MCN-CONU2-ADBI plant association that matches the Baker plot.

[c] Weighted mean of 3 old-growth compartments. The old-growth reserves of the Blodgett Forest Research Station consist of stands that were not clearcut before 1933, and then not actively managed from 1933 until the present.

[d] All woody stems ≥ 3 cm measured on 80 plots scattered over several hectares.

[e] Reported values consist of mean basal area values form 1/4 acre plots, 9 in the central and 8 in the southern Sierra Nevada. Means and standard deviations calculated by authors from data in Olson *unpublished manuscript*.

[f] A compilation of stand surveys and belt transects in the mixed conifer–white fir forest type and mixed conifer–ponderosa pine forest type.

[g] All woody stems measured for dbh [assume all woody stems greater than 1.37 m tall measures] on 5 replicate randomly placed 0.04-ha plots in the mixed conifer type.

[h] All woody stems ≥ 1.37 m tall measured and mapped on a 1.1-ha stand in the mixed conifer.

[i] Data was collected in each stand using 20, 100-m^2 circular plots to measure the dbh of all stems 0.5 m tall to 10 cm dbh. Trees greater than 10 cm dbh were sampled in each stand using the point quarter method.

[j] The western portion of Sequoia National Park was protected as a national park in 1890. The remainder of the park was declared a reserve in 1893 and officially included in the park in 1926. (Vankat and Major, 1979)

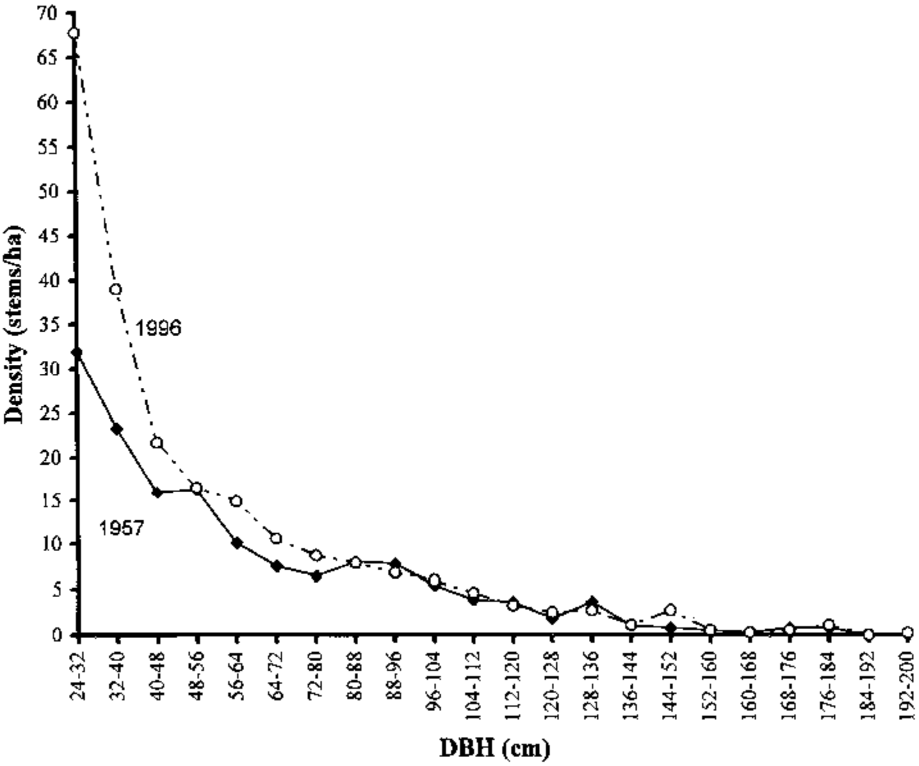

Fig 3. Diameter distribution of canopy trees (trees ≥ 24 cm dbh) in 1957 and 1996 in an old-growth mixed conifer forest in the northern Sierra Nevada.

creased abundance of shade-tolerant trees that tend to be fire-intolerant, primarily white fir, at the expense of the shade-intolerant, but more fire-resistant species such as ponderosa pine and giant sequoia (*Sequoiadendron giganteum* (Lindley) Buchholz) (McKelvey and Johnston 1992; Parsons and DeBenedetti 1979; Vankat and Major 1978).

We attribute the continued presence of ponderosa and sugar pine on the Baker plot to the moderate mortality of these long-lived species. However, both pine species showed little recruitment into the canopy (< 1% of total recruitment). Even under moderate shading of 47% of full sun, ponderosa pine seedling height growth is only half that of its mixed conifer associates (Oliver and Ryker 1990). The brightest area of the Baker plot receieved only 31% of diffuse light. There seems to be inadequate amounts of understory light on the Baker plot for robust ponderosa pine regeneration. The scarcity of bare mineral soil in the absence of fire may be another factor contributing to the lack of ponderosa pine regeneration. The amount of sugar pine regeneration in all but the smallest regeneration size class was low despite a seemingly adequate seed source of approximately 11 adult trees/ha. Sugar pine seedlings are moderately shade tolerant and have been found to respond to small canopy gaps (Oliver and Dolph 1992). In the southern Sierra Nevada, Parsons and DeBenedetti (1979) reported considerable increases in relative density of sugar pine in the mixed conifer forests in the absence of periodic fire. We do not know why sugar pine was failing to regenerate on the Baker plot, but the presence of white pine blister rust (*Cronartium ribicola*) (Kinloch and Scheuner 1990) in the Sierra Nevada may be a factor.

The continued codominance of white fir and Douglas-fir in the Baker plot was due to different mechanisms of persistence. The ability of white fir to regenerate under a closed canopy (Minore 1979) and the absence of fire from the Baker plot led to vigorous white fir regeneration and recruitment to the canopy. This recruitment was offset by a high mortality rate. Compared to its other mixed conifer associated species, white fir has a shorter life span and a greater susceptibility to pathogens (Minore 1979). In contrast, Douglas-fir had a moderate rate of recruitment coupled with low mortality.

Although species composition remained relatively constant over the 39 year period, the current size structure suggests that changes in the canopy composition of the Baker plot will occur in the future under a continued policy of fire suppression (Fig. 1, Table 3). With density in the canopy increasing and the low amount of diffuse radiation presently reaching the understory, the shade-intolerant ponderosa pine can be expected to slowly drop out of the stand. The scarcity of sugar pine advance regeneration in the sapling and pole size classes indicates that this species also may be in long-term decline on the Baker plot. The low numbers of pines in nearly all understory size classes supports this conclusion (Fig. 1C). On the Baker plot, the moderate recruitment and low mortality of incense-cedar over the 39 year interval has maintained its secondary presence in the canopy. Throughout the Sierra Nevada, the moderately shade-tolerant incense-cedar occurs primarily as a canopy subdominant due to its slower height growth relative to its mixed conifer associates (Powers and Oliver 1990). The current mortality, canopy recruitment rates and regeneration of Douglas-fir and white fir suggests that these species will increase their codominance of the Baker plot into the future.

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