CANOPY STRUCTURE AND TREE CONDITION OF YOUNG, MATURE AND OLD-GROWTH DOUGLAS-FIR/HARDWOOD FORESTS[1]

Bruce B. Bingham[2] and John 0. Sawyer, Jr[3]

Abstract. *Sixty-two Douglas-fir/hardwood stands ranging from 40 to 560 years old were used to characterize the density; diameter, and height class distributions of canopy hardwoods and conifers in young (40 -100 yr), mature (101 - 200 yr) and old-growth (>200 yr) forests. The crown, bole, disease, disturbance, and cavity conditions of canopy conifers and hardwoods were also described. A series multivariate and univariate analyses were used to determine which tree conditions differed significantly among the age-classes. Stepwise discriminant analysis was used to identify variables with significant discriminatory power. Several conditions of canopy trees, including the percentage of trees with broken-topped crowns, the percentage with conks, the percentage with fire scars, and the percentage with basal cavities showed significant differences. Most conditions had their highest values in old-growth. The greatest difference among the age classes was in the percentage of canopy conifers with fire-blackened bark. An average of 68% of the canopy conifers had fire-blackened bark. A summary of the average canopy structure and tree condition of old-growth should provide additional criteria for defining old-growth Douglas-fir/hardwood forests.*

Introduction

Douglas-fir/hardwood forest, defined as a subdivision of the mixed evergreen forest (Sawyer *et al.,* 1977; wainwright and Barbour, 1984), forms the most extensive low elevation forest vegetation in northwestern California. Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is the dominant conifer, although other conifers including redwood (*Sequoia sempervirens* (D. Don) Endl.), Port-Orford-cedar (*Chamaecyparis lawsoniana* (A. Murr.) Pail.), western red-cedar (*Thuja plicate* Donn ex D. Don), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), sugar pine (*Pinus lambertiana* Dougl.), and incense cedar (*Calocedrus decurrens* (Torr.) Florin) may occur in low densities. One or more hardwoods share dominance with Douglas-fir. Familiar hardwoods include tanoak (*Lithocarpus densifiora* (H. & A.) Rehd.), madrone (*Arbutus menziesit* Pursh), chinquapin (*Chrysolepis chrysophylla* (Dougl. ex Hook.) Hjelmquist), California bay (*Umbellularia californica* (H. & A.) Nutt.), canyon live oak (*Quercus chrysolepis* Liebm.), California black oak (*Q. kelloggii* Newb.), and Oregon white oak (*Q. - garryana* Dougl. ex Hook.).

Bingham and Sawyer (1991) developed ecological definitions of young (40-100 yr), mature (101-200 yr) and – old-growth (>200 yr) Douglas-fir/hardwood forests. These definitions depict average conditions for the live tree, dead wood, and understory components of each forest age-class. As other authors have done (Spies and Franklin, 1991), we used stepwise discriminant analysis to identify the distinctive structural properties of each forest age-class. The most powerful discriminators among the forest age-classes were overstory components associated with the basal areas of the dominant size classes of Douglas-fir and hardwood trees. While we described basal area and density distributions of live trees, we did not include the condition of canopy trees in our study. Many of these conditions, such as the percentage of trees with broken or dead-topped crowns, leaning boles, fungal or mistletoe infestations, fall scars, fire scars, and bole or root cavities have been found to be important when describing the character of old-growth forests (Franklin *et al*., 1981; Spies and Franklin, 1988; Spies and Franklin, 1991).

In this study, we characterized the canopy structure of young, mature, and old-growth Douglas-fir/hardwood forests, emphasizing the crown, bole, disease, disturbance, and cavity conditions of canopy trees. We had three goals. First, we wanted to describe the general canopy structure of young, mature, and old-growth Douglas-fir/ hardwood forests. We then looked more specifically at the crown, bole, disease, disturbance, and cavity conditions of canopy trees. Our goal here was to determine if the percentages of canopy trees with certain conditions differed significantly among young, mature, and old-growth Douglas-fir/hardwood forests. We also wanted to determine which tree condition variables provide the greatest discrimination among forest age-classes. Our third goal was to contribute data which could be used to strengthen existing definitions of Douglas-fir/hardwood forests. We emphasized old-growth by developing a summary table for the canopy characteristics of old growth Douglas-fir/hardwood forests. The results from this study should be useful for expanding the existing definitions of young, mature, and old-growth Douglas-fir/ hardwood forests.

Methods

Study Location and Environment

The study was conducted at elevations below 1200 m in the coastal mountains of northern California and the

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[2] USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, Arcata, CA 95521
[3] Humboldt State University, Department of Biological Sciences, Arcata, CA 95521

Klamath Mountains of northwestern California and southwestern Oregon (Figure 1). The terrain of both regions is rugged, characterized by abrupt changes in aspect, slope, and soil properties. Most soils supporting Douglas-fir/hardwood forests originated from sedimentary or granitic rocks. Wet winters and dry summers are typical of the region. Annual precipitation is variable. Yearly averages range from 650 to >2000 mm with the interior mountains receiving small to moderate amounts of their precipitation as winter snow. Temperatures are variable as well. Typical monthly averages are below 8°C in the winter, but can exceed 20°C in the summer.

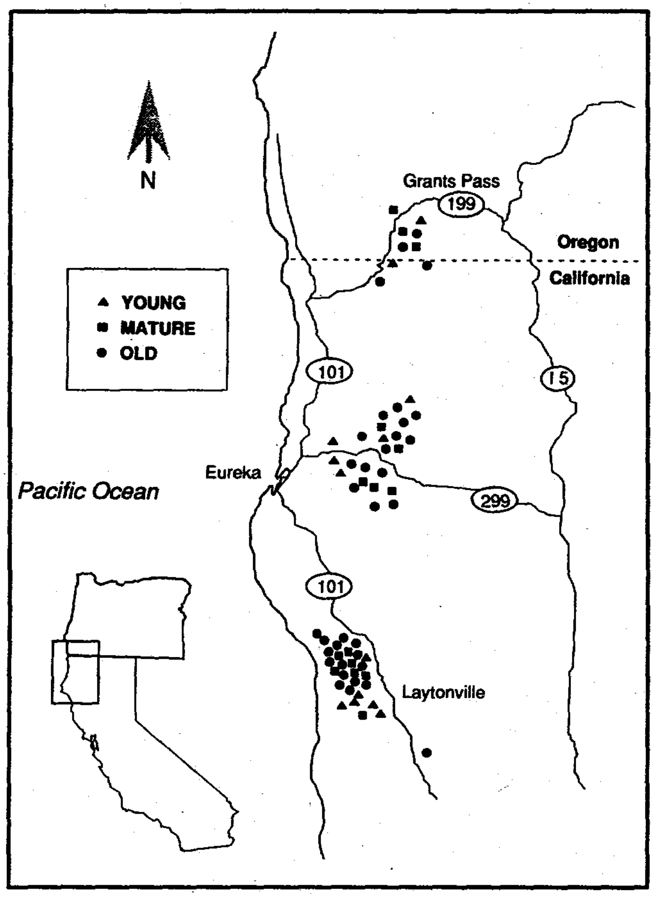

Figure 1. *Location of stands in northwestern California and southwestern Oregon.*

Fire has played an important role in the origin and development of Douglas-fir/hardwood forests (Agee, 1991; Atzet *et al.,* 1988). Fires ignited by lightning are common in the region. Prior to settlement, these fires burned unchecked. At a catastrophic scale, these fires were responsible for maintaining am in early stages of stand development. However, studies of fire return intervals in Douglas-fir/hardwood forests (Anonymous, 1983; Wills, 1991) suggest that the majority of fires were not stand replacing fires. Often, stands burned repeatedly at intervals ranging from 10 to 150 years. These repeated fires of low to moderate intensities have been ecologically important to the development of the old-growth structure we see today in the Douglas-fir forests of southwestern Oregon and northwestern California (Agee,1991).

Study sites

The 62 stands used for this study were the same as those used to develop ecological definitions of young, mature, and old-growth Douglas-fir/hardwood forests (Bingham and Sawyer, 991). The stands were randomly selected from a pool of candidate stands proposed by local ecologists. Stand elevations ranged from about 360 m to 1150 m. Stand sizes ranged from 5 ha to more than 100 ha. Thirty-three stands were on public lands managed by the Forest Service or by the Bureau of Land Management. Seven stands were on private lands managed for timber production. The remaining 22 stands were located on the Northern California Coast Range Preserve. This 3200 ha old-growth forest preserve is owned cooperatively by the California Nature Conservancy and the Bureau of Land Management.

In stands <20 ha, data were collected in three 0.1 ha plots per stand. Larger stands were sampled using five 0.1 ha plots. Species, diameter at breast height (dbh), and height-class were recorded for all am ≥5 cm dbh. A canopy status (Burns, 1983) was assigned to each tree based on its position in the tree canopy. 1n stands with two-tiered canopy structures, the assignment was made based on the tree's status in either the hardwood or conifer tier. Codes indicating the condition of the crown (*e.g.*, . dead-topped, broken-topped, sparse) and of the bole (*e.g.*, sweeping, leaning, multiple) of each tree were recorded. Indications of disease and disturbance (*e.g.,* fungal conks, mistletoe, resinosis, scars from lightning, aft fall, or fire), and the type and location of cavities (*e.g.*, excavated, mid-bole, root) were also recorded. Multiple codes could be recorded for each group of tree conditions. For example, a tree could have more than one crown condition, more than one bole condition, and more than one kind of cavity. Thirty-five codes were used for characterizing the condition of trees. Aspect, slope, and other site data were collected for each plot as well.

Tree ages in young and mature stands were collected by increment coring a minimum of three dominant or codominant canopy Douglas-fir am from at least three plots. Tree ages in old-growth stands were determined from ring counts on stumps along adjacent roads or clearcuts, or from increment cores, or by a combination of methods. Mean stand ages ranged from 40 to 560 yrs and were used to place each stand into one of three forest age-classes. There were 14 young (40-100 yr) stands that originated after logging, 15 mature (101-200 yr) stands, seven of which had originated after logging, and 33 old-growth (>200 yr) stands.

Data analyses

All analyses were restricted to data from trees that had either codominant, dominant, or emergent canopy status. Descriptive statistics were used to characterize the density, diameter, and height class distributions of canopy trees. None of these statistics were included in subsequent stepwise discriminant analyses or one-way analysis of variances.

The 35 tree condition variables were divided into five categories: crown condition, bole condition, disease condition, disturbance condition, and cavity condition. Each category was further divided by species group (canopy conifers or canopy hardwoods) resulting in 70 variables in 10 sets. The percentages of canopy conifer and hardwood trees exhibiting each crown, bole, disease, disturbance, and cavity condition were calculated by stand. Distributions of the variables were tested for normality using the Shapiro-Wilk statistic (SAS,1988). Those that failed the test were transformed with an arcsine transformation and retested

Twenty-five variables from nine sets (Table 1) passed the tests for normality and were used in a series of nine independent stepwise discriminant analyses (SAS,1988) following the same general methods used in Bingham and Sawyer (1991) and Spies and Franklin (1991). One reason for performing the separate analyses was to determine the major differences among the forest age-classes in each of the tree condition categories for conifers and hardwoods independently. The ratio of variables to samples within each age-class was another reason for conducting independent discriminant analyses. The ratio was too high to perform a single stepwise analysis on all variables. Such an analysis would run a high risk of retaining unstable variables with poor discriminatory power (SAS,1988). By analyzing separate variable sets, the ratio of variables to samples was kept low, and the likelihood of including variables with poor discriminatory power was reduced. The stepwise analyses reduced each category of variables to subsets of one or more variables with significant discriminatory power. A partial F test with a significance level of $p<0.10$ was used to select and retain variables.

The subsets of variables retained by the nine independent analyses were combined for a final stepwise analysis. The purpose of this last analysis was to identify the strongest discriminators among those selected from each of the nine tree condition categories.

Some variable may exhibit little or no discriminatory power but still show significant differences among groups. Such variables are still valuable for descriptive purposes. Therefore, variables that were included but not retained by the stepwise procedures were analyzed for significant differences among forest age-classes using one-way analysis of variance (SAS,1988).

Forty-five variables failed the tests for normality and. were therefore not included in the stepwise discriminant analyses. These variables were analyzed for inter-age class differences using Kruskal-Wallis nonpatametric analyses (SAS,1988).

Table 1. *Nine tree condition categories and variable sets included in the stepwise discriminant analyses. All variables are percentages of canopy trees with each condition. Variables analyzed after arcsine transformations are indicated by a star "*".*

	Crown condition of canopy conifers
	Conifers with broken-topped crowns
*	Conifers with multiple tops
*	Conifers with half crowns
*	Conifers with an upturned leader
	Crown condition of canopy hardwoods
*	Hardwoods with half crowns
*	Hardwoods with sparsely foliated crowns
	Bole condition of canopy conifers
	Conifers with leaning boles
*	Conifers with sweeping boles
*	Conifers with forked or multiple boles below breast height
	Bole condition of canopy hardwoods
	Hardwoods with leaning boles
*	Hardwoods with arching boles
	Hardwoods with forked or multiple boles below breast height
	Disease condition of canopy conifers
	Conifers with swollen knots
*	Conifers with conks on lower bole
*	Conifers with resinosis (oozing sap)
	Disturbance condition of canopy conifers
*	Conifers with fall scars
*	Conifers with fire-blamed bark
	Disturbance condition of canopy hardwoods
*	Hardwoods with fall scars
*	Hardwoods with fire scars
*	Hardwoods with scars of unknown origin
	Cavity condition of canopy conifers
*	Conifers with basal cavities
*	Conifers with root cavities
	Cavity condition of canopy hardwoods
	Hardwoods with mid-bole cavities
*	Hardwoods with basal cavities
*	Conifers with root cavities

Results

Canopy Structure

High densities of small to medium sized conifers and hardwoods dominated the canopy of young stands (Table 2). Hardwood densities were generally much higher than conifer densities, but the mean diameters (dbh) of hardwoods and conifers were very similar (Table 2). In most young stands, distinct conifer and hardwood canopy tiers were poorly developed with few trees greater than 40 m tall (Figure 2). The highest densities of conifers were in height classes 16 to 32 m. Hardwoods were most abundant in height classes 12 to 24 m.

Table 2. *Means[1] and 95% confidence limits of the means (in parentheses) for tree densities and diameters of canopy conifers and hardwoods in young, mature and old-growth stands.*

	Forest Age-Class		
	Young n = 14	Mature n = 15	Old-growth n = 33
Density (stems/ha)			
Conifers	203.2	14.9	58.5
	(131.7 - 274.7)	(88.1 – 141.9)	(49.8 - 67.2)
Hardwoods	324.5	131.3	102.5
	(180.9 - 468.1)	(71.2 - 191.4)	(75.5 – 129.5)
Diameter (dbh-cm)			
Conifers	35.8	66.7	96.2
	(30.2 - 41.4)	(58.0 - 75.4)	(90.4 - 102.0)
Hardwoods	29.7	30.1	38.7
	(23.7 - 35.7)	(26.4 - 33.8)	(35.0 – 47.4)

[1] All values calculated from trees with either codominant, dominant, or emergent canopy status

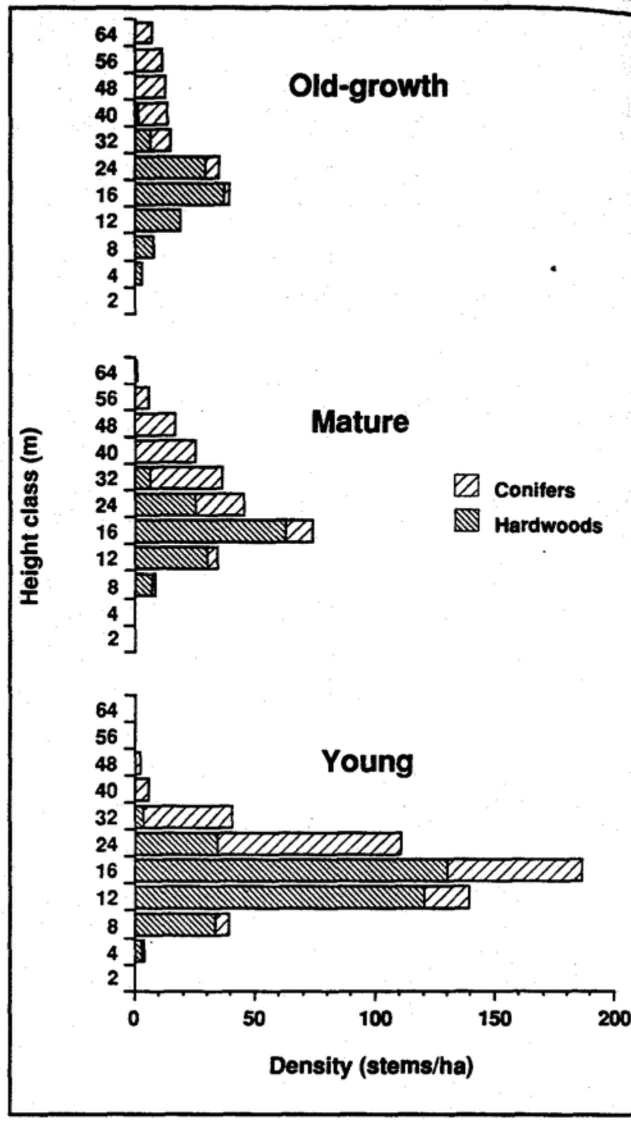

Figure 2. *Canopy profiles of hardwood and conifer height classes and tree densities in young, mature, and old-growth forests. Profiles include only trees with codominant, dominant, or emergent canopy status. Tree densities decrease and a two-tiered canopy develops with age. From young to old-growth the maximum height of the hardwood layer remains relatively stable, while the maximum height of the conifer layer increases, forming a distinct canopy tier above the hardwoods.*

The density of canopy trees in mature forests averaged about one-half that of young stands (Table 2). The mean density of hardwoods in mature forests was only slightly higher than the density of conifers. The mean dbh of hardwoods was comparable to that of young stands, while the mean dbh of conifers was nearly twice that of young stands (Table 2). In mature stands, defined conifer and hardwood canopy tiers were often evident, but the canopy rarely exceeded 56 m tall (Figure 2). The mean densities of conifers were highest in height classes 24 to 48 m and hardwood densities were highest in height classes 12 to 24 m.

Old-growth forests had the lowest density of canopy trees, averaging about one-third that of young stands (Table 2). The hardwood density in old-growth was nearly twice as high as the density of conifers. The mean dbh of hardwoods was slightly higher than the hardwood dbh' in young stands (Table 2). However, the conifer dbh was nearly three times that of young stands. Distinct conifer and hardwood canopy tiers were well developed in old-growth with most conifers exceeding 40 m in height, but few hardwoods exceeding 32 in tall (Figure 2). Conifer densities were highest in height classes 40 to 56 m with trees often exceeding 64 m tall. As in young and mature stands, hardwood densities were highest in height classes 12 to 24 m.

Stepwise Discriminant Analyses

Crown condition. The analysis of the variable set for conifer crown conditions (Table 1) retained the percentage of conifers with broken-topped crowns (Table 3). The percentage of canopy conifers with broken tops was highest in old-growth, averaging two to four times higher than that of mature and young stands.

Only one of the two hardwood crown conditions analyzed; the percentage of hardwoods with sparse crowns (open with dead or dying branches), had significant discriminatory power (Table 3). Mature stands averaged the highest percentage of these trees in the canopy, and old-growth averaged the lowest.

Bole condition. No variables were retained by the stepwise discriminant analyses of the conifer or hardwood bole condition variable sets (Table 1).

Table 3. *Means[1], 95% confidence limits of the means (in parentheses), and F values for canopy tree condition variables that were selected by the stepwise discriminant analyses (all variables significant at p<0.05).*

	Forest Age-Class			
	Young n = 14	Mature n = 15	Old-growth n = 33	F
Crown condition of conifers				
Broken-supped crowns	1.1	1.8	4.5	4.7
	(0 – 2.3)	(0.6 - 3.0)	(2.9 - 6.3)	
Crown condition of hardwoods				
Sparse crowns	2.1	4.6	0.8	4.7
	(0 - 4.6)	(0.5 - 9.7)	(0 - 1.6)	
Disease condition of conifers				
Conks an lower bale	2.6	8.1	18.6	11.1
	(0.5-4.7)	(2.4- 13.8)	(13.5 - 23.7)	
Resinosis	4.1	7.4	9.6	3.1
	(0.2 - 8.1)	(4.2 - 10.6)	(6.6 - 12.6)	
Disturbance condition of conifers				
Fire-blackened beds	2.4	12.9	68.0	78.4
	(0 - 5.2)	(1.2 - 24.6)	(60.2 - 75.8)	
Disturbance condition of hardwoods				
Fire scats	9.4	17.9	22.9	3.2
	(0.6 - 18.2)	(6.9 - 28.9)	(16.0 - 29.8)	
Cavity condition of conifers				
Basal cavities	0.7	1.6	11.4	22.5
	(0 – 2.0)	(0.1 - 3.1)	(7.8 - 15.0)	
Root cavities	2.3	1.8	8.9	4.0
	(0.7 - 3.9)	(0.4 - 3.2)	(5.6 - 12.3)	
Cavity condition of hardwoods				
Basal cavities	17.6	25.5	38.2	4.3
	(1.5 - 27.6)	(13.8 - 37.2)	(29.6 - 46.8)	
Combined tree conditions				
Fire-blackened bark	2.4	12.9	68.0	78.4
	(0 - 5.2)	(1.2 - 24.6)	(60.2 - 75.8)	

[1]Means an percentages of canopy trees with each condition

Disease condition. The analysis of the variable set for conifer disease conditions (Table 1) retained two variables. The percentage of conifers with fungal conks on the lower half of the bole, and the percentage of conifers with resinosis were significant discriminators (Table 3). Both conditions were highest in old-growth.

Indications of disease on hardwoods was uncommon in all forest age-classes. The distributions of hardwood variables were not normal and transformations were unsuccessful. Therefore, no variable set was analyzed.

Disturbance condition. One variable, the percentage of trees with fire-blackened bark, was retained by the analysis of conifer disturbance conditions (Table 1). The differ ence among age-classes was extremely high (Table 3). Fire-blackened bark was observed on an average of 68% of the canopy trees in old-growth; compared to 13% and 2% in mature and young stands, respectively.

The analysis of the hardwood variable set retained only the percentage of trees with fire scars (Table 3). In old-growth stands, the percentage of canopy hardwoods with fire scars was more than twice that observed in young stands. Fire scars on hardwoods in young stands occurred primarily on residual trees left over from the previous stand. In all age-classes fire scars were often associated with cavities.

Cavity condition. Two cavity conditions of conifers, the percentage of canopy trees with basal cavities, and the percentage of trees with root cavities were included in the stepwise analysis (Table 1). Both conditions provided significant discrimination among the age-classes (Table 3). The percentage of conifers with either basal or root cavities was 2 to 10 times higher in old-growth than in mature and young stands.

The percentage of canopy hardwoods with cavities near the base of the bole was the only cavity condition that provided significant discriminatory power (Table 3). Old-growth had the highest percentage of hardwoods with basal cavities with a mean of 38%. In all age-classes, root, basal, and mid-bole cavities were more common in hardwoods than in conifers.

Combined tree conditions. The nine independent stepwise discriminant analyses retained nine variables from seven of the tree condition variable sets. These variables were combined for a tenth and final stepwise analysis. The analysis of the combined variable set retained one variable, the percentage of canopy conifers with fire-blackened bark (Table 3). The same variable was retained by the stepwise analysis of the variable set for conifer disturbance conditions. The other eight variables included in the final analysis contributed no additional significant discrimination. To test the stability of the fire-blackened bark variable, several stepwise analyses were run on subsets of the samples and in different combina tions of variables. Each analysis retained only the percent age of conifers with fine-blackened bark.

Spearman rank correlation analysis (SAS,1988) of all nontransformed variables showed positive correlations between a large number of tree conditions and fire-blackened bark. Nineteen tree conditions were signifi cantly correlated ($p < 0.05$) with the percentage of canopy conifers with fire-blackened bark. Most of the correlations were only weak to moderate ($r = 0.3$ - 0-6) and included the percentages of canopy conifers with cavity conditions (root, mid-bole), with crown conditions (broken-topped, dead-topped), and with disease conditions (conks, swollen knots, burls, and resinosis). The highest correlation ($r = 0.7$, $p <.001$) was with the percentage of conifers with basal cavities. There were also significant correlations between the percentage of hardwoods with fire scars and several hardwood variables. The strongest correlations were with the percentage of hardwoods with basal cavities ($r = 0.7$, $p < 0.001$) and the percentage of hardwoods with mid-bole cavities ($r = 0.6$, $p <0.001$).

One-Way Analysis of Variance

Although they had no significant discriminatory power; the 16 variables not retained by the stepwise discriminant analyses of the tree condition variable sets were examined again using one-way ANOVA. The percentage of canopy conifers with fall scars, caused by falling branches or trees, was the only variable that differed significantly ($p < 0.05$) among the forest age-classes (Table 4). One other variable, the percentage of conifers with swollen knots, was marginally significant ($p < 0.1$). Both tree conditions were highest in old-growth.

Kruskal-Wallis Analyses

The Kruskal-Wallis tests of the 45 variables not included in the stepwise analyses identified nine additional tree conditions that were significantly different ($p < 0.05$) among young, mature, and old-growth forests (Table 4). Seven variables had their highest values in old-growth. The greatest difference between old-growth and the younger classes was in the percentage of canopy conifers with fire scars. The percentage of conifers with dead tops, the percentage of conifers(with fungal conks on the upper bole or in the crown area, the percentage of hardwoods with fire-blackened bark, and the percentage of conifers with excavated cavities were all notably higher in old-growth as well. The percentage of canopy hardwoods with pistol-shaped bases and the percentage of hardwoods with swollen bases were highest in young stands. How ever, both variables averaged less than 1 % in all forest age-classes.

Table 4: *Means[1], 95% confidence limits of the means (in parentheses), F values (from oneway ANOVA) or Chi-square values (from Kruskal-Wallis test) for tree condition variables that showed significant[2] differences among forest age-classes.*

	Forest Age-Class				
	Young n = 14	Mature n = 15	Old-growth n = 33	F	Chi-sq.
Conifers with dead-topped crowns	0.1 (0 - 0.3)	0.5 (0 - 1.2)	4.2 (1.8 - 6.7)		9.6***
Hardwoods with pistol-shaped boles	0.4 (0 - 0.8)	0.1 (0 - 0.4)	<0.1 (0 - 0)		14.0****
Hardwoods with swollen base	0.9 (0 - 2.2)	<0.1 (0 - 0)	0.1 (0 - 0.2)		6.9**
Conifers with burls	0.2 (0 - 0.7)	0.5 (0 - 1.1)	3.2 (1.5 - 4.9)		8.1**
Conifers with conks on upper bole or crown	0.3 (0 - 0.7)	2.2 (0.3 - 4.1)	8.3 (5.3 - 11.4)		14.4****
Conifers with swollen knots	3.2 (1.0 - 5.3)	2.1 (0.8 - 3.4)	5.4 (3.2 - 7.6)	2.6*	
Conifers with fire sears	<0.1 (0 - 0)	1.0 (0 - 2.3)	10.1 (6.2 - 14.0)		25.8****
Conifers with fall scars	1.3 (0 - 2.5)	1.1 (0 - 2.3)	5.2 (2.7 - 7.8)	4.2**	
Hardwoods with fire-blackened back	1.2 (0 - 2.4)	1.8 (0- 3.9)	8.4 (2.1 - 14.7)		6.2**
Conifers with excavated cavities	0.2 (0 - 0.5)	0.3 (0 - 1.0)	4.6 (1.4 - 7.9)		9.4***
Conifers with mid-bole cavities	0.2 (0 - 0.5)	<0.1 (0 - 0)	1.5 (0.5 -2.5)		5.9**

[1] Means are percentages of canopy trees with each condition
[2] Significance levels (p): *=<0.1, **=<0.05, ***=<0.01, ****=<0.001

Discussion

Canopy Structure

From about 40 to 100 years of age, the canopy of young Douglas-fir/hardwood stands is a dense mixture of two or more tree species. Hardwoods outnumber conifers, although conifers grow in moderate to high densities. The diameters and heights of the canopy conifers are very similar to those of the hardwoods. The average stand dbh for either group of trees rarely exceeds 40 cm and the majority of the trees are less than 32 m tall. Conifer densities are higher than hardwood densities in taller height classes, but few trees exceed 40 m. The character istic canopy structure is less than 40 m tall, vertically and horizontally homogeneous, and lacking separate conifer and hardwood tiers.

During the second century of development, natural dynamics reduce the density of canopy trees, usually by 50% or more. Hardwoods undergo the greatest mortality. The greatest decrease in hardwood numbers occurs in trees less than 24 m tall. Conifers decrease in numbers in the small to medium size classes as well, but the density of trees greater than 40 m tall increases considerably. Still, the density of trees greater than 56 m is low and variable. The average dbh of canopy conifers increases to twice that of canopy hardwoods, but rarely exceeds 90 cm in mature stands. Conifer heights continue to surpass those of hardwoods and as stands approach 200 years a two-tiered canopy structure is usually apparent. Tree damage and mortality from climatic stress, competition, insects, disease, and stand disturbances, such as fires, storms, and other physical forces increase the spatial diversity of the canopy.

By the time stands are into their third century of development, they have the two-tiered canopy structure characteristic of old-growth Douglas-fir/hardwood forests. During this stage natural thinning decreases the density of canopy trees by another 30% to 40%. Canopy conifers undergo a greater decrease in density than hardwoods. However, the average dbh for both groups of trees increases. Most dramatic is the increase in conifer diameters. The majority of old-growth stands have an average dbh exceeding 90 cm for canopy conifers while the average hardwood dbh usually remains below 40 cm. As in mature stands, hardwoods less than 32 m tall clearly dominate the smaller canopy height classes. The density of conifers greater than 48 m tall increases and a well developed conifer tier, sometimes exceeding 64 m in height, dominates over the hardwood tier. These large conifers are often spaced irregularly, sometimes appearing to be in groups. The spacing of smaller conifers and hardwoods can be just as irregular, often forming pure or mixed patches. Openings in the canopy tiers are an integral part of its structure. Small openings can form from individual tree fragmentation or mortality. Larger openings form from group or patch mortality caused by a variety of biological or physical forces (Spies and Franklin, 1989). These openings are important to hardwood and conifer regeneration (Hoover, 1988) and to maintaining the highly diverse old-growth canopy structure.

Tree Condition

Few conditions showing significant differences among the age-classes had their highest percentages in either young or mature stands. Young stands had the highest percentages of hardwoods with boles that were either pistol-shaped or swollen at the base. Hardwoods common to Douglas-fir/hardwood forests are capable of profuse sprouting under a wide variety of conditions, but especially after disturbance from logging or fire (Burns and Honkala, 1990). Often, the rootcrowns or bases of mature trees that have sprouted repeatedly are enlarged or swollen. Some species develop rootcrowns with diameters in excess of 2 or even 4 m (Burns and Honkala,1990). All of the young stands we studied originated from logging methods practiced more than 40 years ago. The higher percentages of hardwoods with pistol-shaped and swollen bases were probably associated with tree damage, and sprouting of trees, stumps, or rootcrowns that remained after logging.

Mature stands had the highest percentage of canopy hardwoods with sparse crowns. The mature stage of stand development is characterized by a dense conifer layer over-topping the hardwoods. Tanoak is considered tolerant of shade. However, madrone, chinquapin, and oaks (*Quercus* spp.) common to Douglas-fir/hardwood forests are all classified as intermediate to shade-intolerant (Burns and Honkala, 1990). The over-topping by conifers suppresses canopy hardwoods with intermediate to low shade-tolerance, increasing the percentage of hardwoods with stressed crowns. Conifer densities are lower in old-growth resulting in reduced competition and a greater percentage of canopy hardwoods with healthy crowns.

As Douglas-fir/hardwood stands age, the percentages of canopy trees with broken-topped crowns, dead-topped crowns, resinosis, fungal conks; fire-blackened bark, root cavities, and basal cavities increases. Several of these tree conditions can provide weak to moderate discrimination among young, mature, and old-growth Douglas-fir/hardwood forests. The condition with the greatest discriminatory power was the percentage of canopy conifers with fire-blackened bark. Other indications of past fire disturbance, such as the percentage of conifers and hardwoods with fire scars showed significant differences among the age-classes and were highest in old-growth as well. Fire disturbance on canopy trees was observed in 100% of the old-growth stands we studied. While such disturbance conditions have limited value for characterizing forest stands, they may provide some insight into the development of other tree conditions. Correlation coefficients indicated that a large number of tree conditions may be linked to past fine disturbance. Dead or damaged crowns can result from fine induced stress. Fungal conks and resinosis are often found on tree boles with fire scars or blackened bark. Cavities form directly from burned out areas in tree bases and rootcrowns. Small cavities or fire scars may be enlarged through excavation by vertebrates. In addition, knots and scars caused by fires are likely sites of fungal and insect infection in conifers and hardwoods (Burns and Honkala, 1990). These infected areas can turn into cavities through decay. Decayed and exposed wood burns readily, and repeated foes often enlarge existing scars or cavities.

Fire has been a critical force in the development of old-growth Douglas-fir forest throughout its range (Agee, 1991). In the Klamath region and adjacent coast ranges, the chance that one or more fires will occur during two plus centuries of stand development is high. Studies (Agee,1991; Wills, 1991; Atzet *et al*., 1988; Anonymous, 1983) show that fire frequencies in these forests range from 10 to 150 years. These fires can pass through stands without killing high percentages of canopy trees, but many trees are left damaged, scarred, and stressed.

Conclusions

The canopy structure and tree condition of old-growth Douglas-fir/hardwood forests are the result of more than two centuries of development influenced by disturbances, including fire. As a forest ages the density of canopy conifers decreases, while their diameters and heights increase. The bigger trees command more area. Senes cent trees and trees suppressed by shade are likely candidates for removal from a stand by natural thinning. Canopy hardwood densities change as well, but their diameters and heights remain relatively constant. The conifers form a tier that often towers more than 30 m above the hardwood tier. Mortality, tree fall, and fragmentation in both tiers from biological and physical forces add to the structural diversity of the canopy. The likelihood of one or more non-stand replacing fires influencing and modifying stand development is high. Fires bum through these forests damaging or killing individuals or groups of trees. Openings created by fires and other disturbances provide opportunities for regeneration of future canopy recruits. Conifers become established; and remaining hardwood boles or root crowns sprout The surviving structure includes large canopy conifers and hardwoods with damaged crowns, chaired bark, and new scars and cavities, likely sites of future attack by fungi or other damaging agents. Decay and subsequent fires enlarge existing scars and cavities, especially in hardwoods which are more susceptible to damage from fire. This dynamic process continues for hundreds of years, maintaining the high diversity in structure and tree conditions characteristic of the old-growth Douglas-fir/hardwood forest canopy (Table 5).

Table 5. *Average canopy structure and tree condition of old-growth Douglas-fir/hardwood forests. Values are means and 95% confidence limits of the means (in parentheses).*

Canopy: Upper tier dominated by Douglas-fir over a lower tier of hardwoods. Total canopy cover of 71 (68 - 74) %[1]

	Conifers[2]	Hardwoods[2]
Diameter (dbh-am)	96 (90 - 102)	39 (35 - 42)
Density of canopy trees (stems/ha)	59 (50 - 67)	102 (75 - 130)
Density of trees >90 cm dbh (stems/ha)	27 (24 - 31)	1 (0 - 2)
Percent of canopy trees with:		
Broken-topped crowns	4.5 (2.7 - 6.3)	0.6 (0 – 1.2)
Dead-topped crowns	4.2 (1.8 - 6.7)	0.7 (0 - 1.7)
Half crowns	5.3 (3.1 - 7.5)	9.3 (5.5 - 13.1)
Sparse crowns	1.3 (0.1 - 2.5)	0.8 (0-1.6)
Upturned leaders	2.9 (1.3 - 4.5)	0.6 (0.1 - 1.1)
Leaning holes	30.5 (25.0 - 36.0)	61.4 (52.9 - 69.9)
Forked or multiple bole below breast height	6.3 (3.9 - 8.6)	32.3 (24.2 - 40.4)
Conks on lower bole	18.6 (13.5 - 23.7)	0.2 (0 - 0.4)
Conks on upper bole or crown	8.3 (5.3 - 11.4)	<0.1 (0 - 0)
Resinosis	9.6 (6.6 - 12.6)	0.3 (0 - 0.6)
Fire scars	10.1 (6.2 -14.0)	22.9 (16.0 - 29.8)
Fire blackened-bark	68.0 (60.2 - 75.8)	8.4 (2.1 - 14.7)
Fall scars	5.2 (2.7 -7.8)	9.7 (3.0 - 16.5)
Excavated cavities	4.7 (1.4 - 7.9)	0.5 (0 - 1.2)
Mid-bole cavities	1.5 (0.5 - 2.5)	17.0 (9.8 - 24.1)
Basal cavities	11.4 (1.8 - 15.0)	38.2 (29.6 - 46.8)
Root cavities	8.9 (5.6 - 12.3)	12.4 (7.5 - 17.2)

[1]From Bingham and Sawyer, 1991.
[2]All values calculated from trees with codominant, dominant, or emergent canopy status (intermediate and suppressed trees not included).

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Technical Coordinators

Richard R. Harris
Extension Forestry Specialist
Cooperative Extension
University of California

Don C. Erman
Director
Wildland Resources Center
University of California

Editor

Hannah M. Kerner
Cooperative Extension
University of California

WILDLAND RESOURCES CENTER
DIVISION OF AGRICULTURE AND NATRAL RESOURCES
UNIVERSITY OF CALIFORNIA
145 Mulford Hall, Berkeley, California 94720
(510) 642-0263

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Retrieval terms: biological diversity, Klamath Province, Northwestern California, biodiversity, ecology, ecosystem

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