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Age-related development of crown structure in coastal Douglas-fir trees

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Abstract

We compared crown structure among 20-, 40-, and 450-year-old Douglas-fir (*Pseudotsuga menziesii* Mirb. (Franco) var. *menziesii*) trees, and present a conceptual model of crown development. The model is based on the idea that the tree crown can be considered a vertical chronosequence of cohorts of branches that increase in age from upper- to lower-crown. Mean branch volume increased from upper- to lower-crown following the exponential or general logistic growth curve. Maximum branch volume occurred in the lower-crown for 20- and 40-year-old trees, while it occurred in the middle-crown for 450-year-old trees. For the 20- and 40-year-old trees, branch death did not occur in the upper-most part of the crown, and branch density decreased exponentially for the lower one-half and two-thirds of the crown, respectively. For the 450-year-old trees, branch death occurred and branch density decreased exponentially for the full extent of the crown. Epicormic branches increased branch density in the lower-crown, and moderated the rate of decrease in branch density. For the 20- and 40-year-old trees, branch diameter distributions changed from an abundance of small-diameter branches in the upper-crown, to positively skewed bimodal distributions in the middle-crown, and unimodal distributions comprised of surviving large-diameter branches in the lower-crown. For the 450-year-old trees, branch diameter distributions in the upper-crown were unimodal consisting mostly of original branches. In the middle- to lower-crown, branch diameter distributions were bimodal comprised of small-diameter epicormic branches and large-diameter original branches. For the 20- and 40-year-old trees, the relationship between mean branch volume and branch density showed two distinct phases. In the upper-crown where branch death was not observed, and mean branch volume increased with decreasing height while branch density remained relatively constant. In the middle- to lower-crown where branch death occurred, mean branch volume increased while branch density decreased exponentially with decreasing height. For the 450-year-old trees, branch death occurred, and mean branch volume increased while branch density decreased exponentially with decreasing height for the full extent of the crown. The relationship between mean branch volume and branch density after the onset of branch death defined the *branch self-pruning line/curve*. This relationship reflected sequential changes in the population structure of cohorts of branches growing under increasingly shady conditions as the crown grows taller and new cohorts develop above old ones. As a result of the combined effects of branch growth and death, vertical distribution of branch volume shifted toward the upper-crown with increasing tree age.

Keywords: Branch growth; Branch self-pruning; Epicormic branches; Crown development; *Pseudotsuga menziesii*; Tree aging

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1. Introduction

Structural characteristics of old-growth forests have important ecological functions that contribute to species diversity and ecosystem stability (Spies and Franklin, 1988; Franklin and Spies, 1991b; Hansen et al., 1991). In the Pacific Northwest Coast of USA, structural attributes of old-growth forests, such as variability in tree size structure and abundance of large-diameter standing dead trees, have been proposed as an indicator of vertebrate and invertebrate animal diversity (Franklin et al., 1981; Schowalter, 1989; Franklin and Spies, 1991a; Carey and Johnson, 1995). Large, old trees of coastal Douglas-fir (*Pseudotsuga menziesii* Mirb. (Franco) var. *menziesii*) are important structural components of old-growth forests in this region. Franklin et al. (1981) describe the crown of old Douglas-fir trees as ‘‘highly individualistic’’ and ‘‘irregular’’, and emphasize the importance of crown structure in creating stand structural characteristics unique to old-growth forests of this region. The complex crown structure of old Douglas-fir trees provides habitat for birds, small mammals, canopy arthropods, and epiphytes (Pike et al., 1977; Schowalter, 1989; Hansen et al., 1994; Carey and Johnson, 1995). While the development of stand structure from young to old-growth forests has been investigated in detail (Spies and Franklin, 1991; Arsenault and Bradfield, 1994; Acker et al., 1998; Franklin et al., 2001), the processes and mechanisms through which crown structure of old trees develops is relatively poorly understood.

Crown structure of young and mature Douglas-fir trees have been studied in detail because it is directly related to tree growth and yield (e.g., Jensen and Long, 1983; Maguire and Hann, 1987; Webb and Ungs, 1993; Maguire et al., 1994; Maguire and Bennett, 1996). Many such studies aim to develop static models that derive crown structure from easily measured tree characteristics such as diameter at breast height (DBH), tree height and stand density. Predictive relationships that determine crown structure of young and mature trees break down as trees age and reach maximum size because the crown of old trees experiences extensive damage followed by reiteration and re-growth (Ishii et al., 2000). The complex crown structure of old trees is difficult to characterize quantitatively. Characterization of the crown structure of old trees is, therefore, often qualitative: flat or broken tops; cylindrical profile; large, old branches; numerous epicormic branches (e.g., Denison, 1973; Franklin et al., 1981). Only a few studies have quantitatively assessed crown structure of old Douglas-fir trees in detail (Pike et al., 1977; Massman, 1981; Ishii et al., 2000; Ishii and Wilson, 2001). To our knowledge, no attempt has been made to integrate studies of the crown structure of young and mature Douglas-fir trees with that of old trees to infer age-related changes in crown structure from young to old trees.

Bond (2000) defines old age in trees as the developmental stage after maximum tree height is reached. Branch growth continues even after height growth and expansion of projected crown area have stopped, resulting in a cylindrical crown profile in old trees, compared to the more conical profile of young and mature trees (Ishii et al., 2000). Branch death occurs from self-pruning and damage over the long life-span of the tree, and dead branches accumulate in the crown (Ishii and Wilson, 2001). In a recent review of the structural development of Pacific Northwest coniferous forests, Franklin et al. (2001) suggest that the live-crown of Douglas-fir trees recedes upward following canopy closure, but as the forest canopy becomes more open in old-growth forests (Spies and Franklin, 1991), crown depth is extended by the production of epicormic branches in the lower crown. Ishii and Wilson (2001) showed that epicormic branches contribute to increasing branch number and extending crown depth in old Douglas-fir trees. These studies suggest that branch growth, branch death, and production of epicormic branches are important processes in crown development from young and mature trees to old trees of Douglas-fir.

In this paper, we compare crown structure of 20-, 40-, and 450-year-old trees of coastal Douglas-fir using stand-level structural development from young to old-growth stands as a conceptual analog for crown development. Because branches increase in age from upper- to lower-crown, the tree crown can be considered as a vertical chronosequence of cohorts of branches in various stages of development. The crown of young trees consists of cohorts of branches in early stages of development, while that of old trees consists of branches in later stages of development. In this analogy, branch growth corresponds to tree growth, branch death to tree death, and production of epicormic branches to tree recruitment. We investigate patterns of branch growth, branch death and production of epicormic branches within the crown, and relationships among these processes to develop an integrative conceptual model of crown development from young to old trees of coastal Douglas-fir.

2. Study site and methods

The study was conducted in 20-, 40- and 450-year-old stands of naturally established coastal Douglas-fir in the Wind River Ranger District, Gifford Pinchot National Forest in southwestern Washington State, USA (45°N, 121°W; altitude 350 m). In this region, Douglas-fir establishes as a cohort following large-scale disturbance, and dominates in early stages of forest succession (Franklin and Hemstrom, 1981). The 20- and 40-year-old stands originated after clear-cut harvesting, and are dominated by Douglas-fir. Stand height is approximately 15 and 30 m, stand density is 2125 and 1420 trees/ha, and stand basal area is 20.5 and 64.8 m^2/ha, respectively. The 450-year-old stand originated after stand-replacing fire, and is dominated by Douglas-fir and western hemlock (Franklin, 1972; Franklin and DeBell, 1988). Stand height is approximately 60 m, stand density is 435 trees/ha, and stand basal area is 82.1 m^2/ha. The three stands are located within 10 km of each other, have similar site conditions, and represent typical young and old stages of development for naturally established Douglas-fir stands in this region.

2.1. Field measurements

Five to six trees in each stand were chosen for measurement of crown structure (Table 1). The sample trees were chosen on the basis of DBH and tree height

Table 1
Structural attributes and parameter estimates for the sample trees of Douglas-fir[a]

Stand age	Tree	Tree height (m)	DBH (cm)	Crown ratio	Mean branch volume parameters				Branch density parameters			
					a or *p*	*b* or *q*	*r*	R^2	ρ_0	*k*	R^2	H_{rel} [m][b]
20												
	1	16.3	22.1	0.86	15.12	16.78	0.409	0.855	1001.53	0.596	0.970	0.5 [9.1]
	2	15.2	24.9	0.86	15.27	59.14	0.783	0.817	178.12	0.325	0.937	0.5 [8.3]
	3	14.9	20.8	0.82	0.383	0.342		0.845	469.43	0.468	0.986	0.5 [8.3]
	4	14.4	15.2	0.62	4.16	13.98	0.404	0.752	1412.18	0.543	0.985	0.4 [8.7]
	5	13.9	21.3	0.94	10.29	123.88	1.198	0.943	245.67	0.463	0.730	0.7 [9.2]
40												
	1	36.3	46.7	0.39	82.81	71.13	0.534	0.968	107.35	0.316	0.783	0.6 [30.8]
	2	34.7	43.6	0.50	48.92	82.16	0.698	0.963	180.11	0.470	0.962	0.8 [30.8]
	3	32.0	49.9	0.42	2.52	0.336		0.884	240.34	0.470	0.962	0.8 [28.7]
	4	31.5	30.3	0.40	17.25	41.31	0.516	0.750	49.21	0.288	0.740	0.8 [28.0]
	5	30.0	30.0	0.52	0.744	0.366		0.882	42.45	0.353	0.743	1.0 [28.9]
450												
	1	61.6	135.3	0.63	3245.54	2271.55	2.243	0.986	5.31 (8.88)	0.341 (0.243)	0.729 (0.869)	1.0 [59.4]
	2	61.0	126.9	0.66	1838.33	39.17	0.914	0.773	9.61 (8.49)	0.421 (0.325)	0.872 (0.690)	1.0 [59.4]
	3	58.7	153.5	0.73	1912.26	9510.58	4.232	0.969	4.36 (8.52)	0.323 (0.362)	0.898 (0.796)	1.0 [57.7]
	4	53.8	104.3	0.70	848.28	22.79	0.701	0.949	50.31 (17.54)	0.788 (0.270)	0.948 (0.892)	1.0 [51.8]
	5	51.3	87.1	0.54	232.12	11.66	1.144	0.577	7.54 (7.94)	0.414 (0.300)	0.589 (0.621)	1.0 [49.4]
	6	50.8	93.9	0.55	1233.24	16.00	0.556	0.902	7.87 (5.35)	0.404 (0.265)	0.943 (0.735)	1.0 [48.8]

[a] Within each stand, trees are in order of decreasing tree height. Crown ratio: (tree height − lowest live branch height)/tree height. Parameter estimates for branch volume of the 450-year-old trees are for original branches only. Estimates for branch density including epicormic branches are shown in ( ).

[b] The relative height below which Eq. (10) showed the best fit. Figures in [ ] show absolute height (m) equivalent to the relative height-class.

to cover the range of tree sizes observed in each stand. In the 20- and 40-year-old stands, the five sample trees in each stand were accessed from scaffolding towers. Persons taking the measurements climbed the trees while anchored to the tower by a harness and rope. For the 450-year-old stand, the six sample trees were accessed by the single-rope technique (Moffett and Lowman, 1995) using a rope that was anchored to the main stem of the sample tree. The top 1–2 m of the sample trees could not be reached due to safety concerns, and was not measured. For all live (foliated) primary branches on the sample trees, branch height above ground was measured using a tape measure that was stretched vertically along the main stem of the tree. Branch diameter was measured immediately outside the branch collar using calipers for small branches and diameter tape for large branches. For the 20- and 40-year-old stands, branch length was measured for six branches on each sample tree. The crown of each tree was divided into three sections of equal depth: upper-, middle- and lower-crown. Two branches were chosen at random from each section on the northeast or southwest side of the tree. Diameter and length measurements for these branches were then pooled for each stand to obtain the following significant linear relationship between branch diameter (d, cm) and length (l, m):

$$l = 0.741d + 0.47 \quad (F = 98.34,\ P < 0.01,\ R^2 = 0.830), \tag{1}$$

$$l = 0.849d + 0.22 \quad (F = 137.85,\ P < 0.01,\ R^2 = 0.810) \tag{2}$$

for the 20- and 40-year-old stands, respectively. These relationships were used to estimate branch length from measured branch diameter for all branches of the sample trees. Because such a predictable relationship between branch diameter and length does not hold for old trees (Ishii et al., 2000), branch lengths were individually measured for all branches of the sample trees of the 450-year-old stand by extending a 1 in. wide engineer's tape from the main stem to the farthest foliated section of the branch. For the 450-year-old trees, branches were also distinguished as being original (originated from the terminal bud of the main stem) or epicormic (originated from epicormic buds). Epicormic branches were distinguished non-destructively using several morphological characteristics: young bark, tangent angle of insertion to the main stem, multiple branches originating from a small area of the main stem, and smaller diameter relative to nearby original branches. See Ishii and Wilson (2001) for a detailed description of the distinguishing morphological characteristics of epicormic branches.

2.2. Measures of crown structure

The height above ground of each branch was translated into relative height (H_{rel}) in the measured live crown:

$$H_{rel} = \frac{\text{branch height} - \text{lowest live branch height}}{\text{measured live crown depth}}, \tag{3}$$

where

$$\text{measured live crown depth} = \text{highest measured live branch} - \text{lowest live branch}. \tag{4}$$

The measured live crown of each tree was then divided into 10 height-classes of equal depth based on the relative height of each branch. Branch diameter squared multiplied by branch length was used as an indicator of individual branch volume (v):

$$v = d^2 l. \tag{5}$$

This volume measure is analogous to $(\text{tree diameter})^2 \times$ tree height, which has been shown to be correlated with tree biomass, and is expressed in terms of cm^2 m sensu Fujimori et al. (1976). This unit was used so that branches of varying sizes from the three stands could be expressed in reasonable digits. Using this measure, mean branch volume (V) was calculated for each height-class. Branch density (ρ_B: mean number of branches per vertical meter of main stem) for each height-class was calculated as:

$$\rho_B = \frac{\text{number of branches in height-class}}{\text{depth of height-class}}. \tag{6}$$

2.3. Analysis of crown development

The processes of branch growth, death and recruitment was analyzed using stand development as a conceptual analog. Long and Smith (1984) recognize five stages of development of even-aged stands.

A. Initially, the stand is composed of small trees growing without competitive interaction.
B. Growth rates decline with the onset of competition, coinciding more or less with canopy closure.
C. Stand biomass and foliage area reach their maximum (full site occupancy). A size hierarchy develops among trees as a result of intraspecific competition.
D. Competition-induced mortality begins with the death of smaller, suppressed trees.
E. Individual tree sizes culminate, and large trees are unable to fill gaps created by mortality. Tree recruitment occurs in these gaps.

Because branches increase in age from upper- to lower-crown, the vertical change in mean branch size, branch density and branch size distribution within the tree crown can be considered as a chronosequence of cohorts of branches in various stages of development. In this analogy, branch growth corresponds to tree growth, branch death to tree death, and production of epicormic branches to tree recruitment.

Increase in tree size with increasing age initially follows the exponential growth curve during periods of increasing growth rate (stage A of Long and Smith (1984), see also Hozumi (1973)). Eventually tree size reaches maximum (stage B), and tree growth is well represented by the general logistic growth curve (Hozumi, 1973; Niklas, 1994). Applying these models of tree growth, increase in mean branch volume (V, cm^2 m) from upper- to lower-crown was fitted by the exponential growth curve:

$$V = a\exp(bH_{\text{rel}}), \tag{7}$$

or the general logistic growth curve:

$$V = \frac{p}{1 + q\exp(-rH_{\text{rel}})}. \tag{8}$$

Parameters a, b, p, q and r were estimated using non-linear least-squares regression. Parameter p in Eq. (8) is the regression estimate of the maximum attainable branch volume. For the 450-year-old trees, the model of branch growth was applied to only the original branches which sequentially increase in age from upper- to lower-crown. Epicormic branches which vary in age depending on when they were released were excluded from the analysis.

The decrease rate in tree density caused by competition-induced mortality (stage D of Long and Smith, 1984) is relatively constant and can be represented by the negative exponential model (Hozumi, 1973; Silvertown, 1987):

$$\rho = \rho_0 \exp(-ct), \tag{9}$$

where ρ is the tree density, ρ_0 the initial tree density, t the time, and c a constant. Applying this model, vertical change in branch density from upper- to lower-crown was modeled as a negative exponential process:

$$\rho_{\text{B}} = \rho_0 \exp(-kH_{\text{rel}}), \tag{10}$$

where ρ_{B} is the branch density, and ρ_0 and k the parameters estimated using non-linear least-squares regression. In young trees, branch death does not occur in the upper-crown where branches receive sufficient light. In such cases, Eq. (10) may only be applicable to lower parts of the crown. The range of height-classes with the best fit of Eq. (10) was assessed by the highest r^2-value obtained.

During stand development, competition-induced mortality occurs as a result of asymmetric competition where large trees have disproportionately greater growth rates than small trees, and eventually outcompete the small trees. The resulting pattern of growth and death of individual trees leads to changes in tree size distribution during stand development (Ford, 1975; Mohler et al., 1978; Hara, 1988). Initially, there is little variation in size among individual trees (stages 1–2 of Long and Smith, 1984). However, as the stand develops, small differences in size are augmented, because of differences among trees in their growth rate. With further stand development, a size-hierarchy develops and the size distribution becomes increasingly positively skewed and then bimodal (stage C). In later stages of stand development, small, suppressed trees begin to die, and the stand is comprised mainly of the surviving large trees (stage D). To infer the pattern of branch growth and death from upper- to lower-crown and with increasing tree age, we investigated the vertical change in branch diameter distributions of the sample trees.

The development of even-aged stands is characterized by the relationship between mean tree mass (W)

and stand density (ρ):

$$W = A\rho^B, \quad (11)$$

where A is a coefficient, and B the scaling exponent. The development of crown structure from upper- to lower-crown and with increasing tree age was inferred from the relationship between mean branch volume (V) and branch density (ρ_B) of the sample trees.

Finally, the vertical distribution of branch volume was investigated for each sample tree by calculating total branch volume for each height-class. This was used to infer age-related changes in the vertical distribution of crown biomass with increasing tree age resulting from the combined effects of branch growth, branch death, and production of epicormic branches.

3. Results

In all three stands, mean branch volume generally increased from upper- to lower-crown (Fig. 1). For the 20-year-old trees, vertical change in mean branch volume for four of the five sample trees was best fitted by the general logistic growth curve, while for Tree 3, the exponential growth curve yielded the best fit (Table 1, mean branch volume parameters). The shortest 20-year-old sample tree, Tree 5, had one small residual branch in the lowest height-class which was excluded from the regression analysis. For the 40-year-old trees, vertical change in mean branch volume for three of the five sample trees was best fitted by the general logistic growth curve, while the exponential growth curve yielded the best fit for Trees 3 and 5. For the 450-year-old trees, vertical change in mean branch volume was best fitted by the general logistic growth curve for all six sample trees. Trees 1 and 3 each had two small residual original branches in the lowest height-classes which were excluded from the regression analysis. Regression estimates of p, the maximum attainable branch volume, ranged from 4.16 to 15.27 cm^2 m for the 20-year-old trees, 17.25–82.81 cm^2 m for the 40-year-old trees, and 232.12–3245.54 cm^2 m for the 450-year-old trees. For the 20- and 40-year-old trees, maximum branch volume occurred in the lower-crown below $H_{rel} = 0.3$, while for the 450-year-old trees maximum branch volume occurred in the middle-crown between 0.3 and 0.7. In addition, Trees 4 and 5 of the 450-year-old stand had no original branches below $H_{rel} = 0.3$.

Branch density generally decreased from upper- to lower-crown in all sample trees (Fig. 2). Branch density for the 20- and 40-year-old trees ranged from 0.82 to 57.02 and 0.68 to 64.10 branches/m, respectively. Branch density of original branches of the 450-year-old trees were considerably lower: 0.24–18.60 branches/m. When epicormic branches were included, branch density of 450-year-old trees increased to 0.24–20.31 branches/m. For the 20-year-old trees, Eq. (10) was best fitted to the lower one-half to two-thirds of the crown below $H_{rel} = 0.4-0.7$ (Table 1, branch density parameters). These relative heights corresponded to 8.3–9.2 m above ground, and this

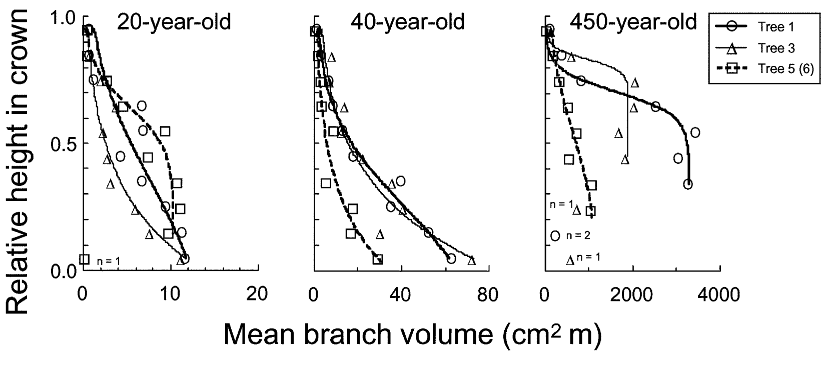

Fig. 1. Vertical change in mean branch volume for the tallest, medium and shortest sample trees of 20-, 40- and 450-year-old Douglas-fir. Lines show non-linear least-squares regression fits of Eq. (7) or (8), depending on which model best fit the data. Data for the 450-year-old trees are for original branches only. Residual small branches in the lower crown ($n = 1$ or 2) were excluded from the regression analysis. Note the varied horizontal axis ranges.

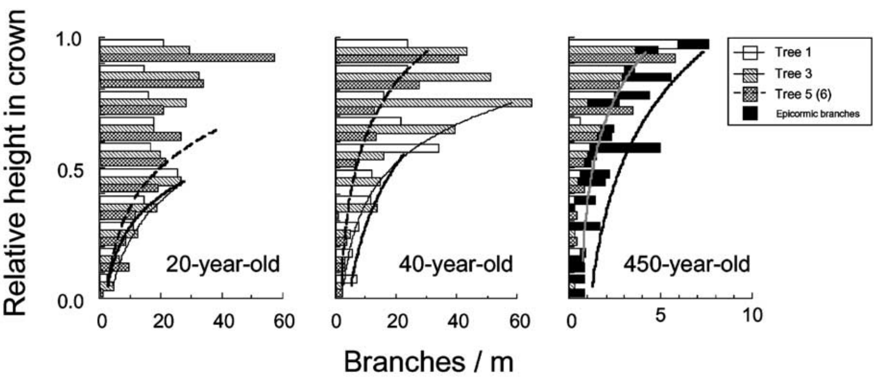

Fig. 2. Vertical change in branch density for the tallest, medium and shortest sample trees of 20-, 40- and 450-year-old Douglas-fir. Lines show non-linear least-squares regression fits of Eq. (10) to the range of height-classes that yielded the best fit as assessed by the greatest r^2-value obtained. For the 450-year-old trees, original and epicormic branches were distinguished. As an example, the comparison of the regression lines fitted to only the original branches (light line) and to all branches (dark line) are shown for the tallest tree (Tree 1). Note the varied horizontal axis ranges.

absolute height was relatively constant across the sample trees. For the 40-year-old trees, Eq. (10) was best fitted to the lower two-thirds to the full extent of the crown below $H_{rel} = 0.6-1.0$. These relative heights corresponded to 28.0–30.8 m above ground, and this absolute height was relatively constant across the sample trees. For the 450-year-old trees, Eq. (10) was best fitted to the full extent of the crown for all six sample trees. Regression estimates of k, the mean rate of decrease in branch density, were similar across stands ranging from 0.325 to 0.596 for the 20-year-old trees, 0.288 to 0.470 for the 40-year-old trees, and 0.341 to 0.788 for original branches of the 450-year-old trees. Epicormic branches occurred throughout the crown of the 450-year-old trees, and were most numerous below $H_{rel} = 0.5$. When epicormic branches were included in the regression analysis, estimates of k decreased for five of the six sample trees. This indicated that epicormic branches contribute to moderating the rate of decrease in branch density from upper- to lower-crown as shown by the two regression lines in Fig. 2 for Tree 1.

Frequency distributions of branch diameter showed transitions from an abundance of small-diameter branches in the upper-crown, to positively skewed bimodal distributions in the middle-crown, and unimodal distributions comprised of only a few large-diameter branches in the lower-crown (Fig. 3). For the 20-year-old trees, branch diameter distributions between $H_{rel} = 0.8$ and 1.0 showed an abundance of small-diameter branches. Between $H_{rel} = 0.2$ and 0.8, the range of branch diameters increased to include large-diameter branches and became bimodal. Between $H_{rel} = 0.0$ and 0.2, branch size distributions were unimodal, and mainly comprised of a few large-diameter branches with modes ranging from 1.5 to 2.5 cm. A similar pattern of vertical change in branch diameter distributions was observed for the 40-year-old trees. For the 450-year-old trees, branch diameter distributions between $H_{rel} = 0.8$ and 1.0 were unimodal and mostly comprised of original branches with modes ranging from 2.0 to 8.0 cm. Between $H_{rel} = 0.4$ and 0.8, the range of the branch diameter distributions increased to include large-diameter branches and became bimodal. Epicormic branches comprised the small-diameter classes (<14 cm for Trees 1, 2, and 3 and <7 cm for Trees 4, 5, and 6), while original branches comprised the large-diameter classes ($\geq$14 and $\geq$7 cm). The lower crown, between $H_{rel} = 0.0$ and 0.4, was comprised of small-diameter epicormic branches (2–12 cm in diameter), and few residual original branches (6–24 cm).

For the 20- and 40-year-old trees, the relationship between mean branch volume and branch density showed two distinct phases (Fig. 4). In the upper-crown, above the relative height where exponential decrease in branch density was observed, mean branch volume increased with decreasing height in the crown while branch density remained relatively constant (Fig. 4, filled symbols). Below this height,

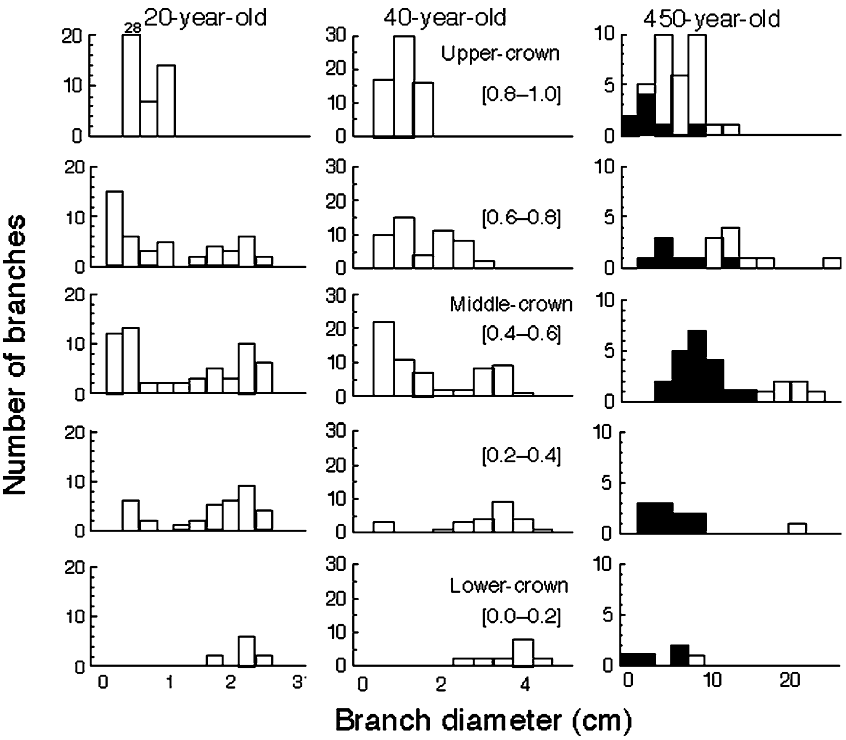

Fig. 3. Vertical change in branch diameter distribution for the tallest sample trees of 20-, 40- and 450-year-old Douglas-fir. For the 450-year-old tree, filled bars indicate epicormic branches. Figures in [ ] indicate range of relative heights (H_{rel}). Other sample trees showed similar trends. Note the varied horizontal and vertical axes ranges.

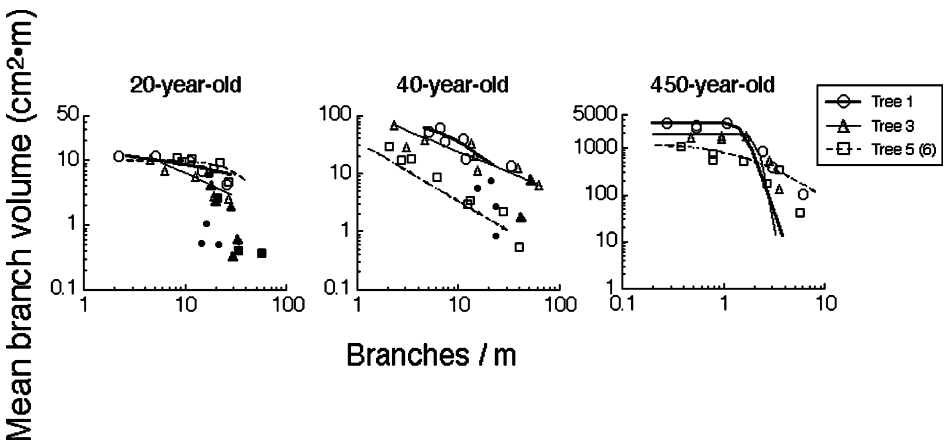

Fig. 4. The relationship between mean branch volume and branch density for the tallest, medium and shortest sample trees of 20-, 40- and 450-year-old Douglas-fir. Symbols and lines are as in Fig. 1. Filled symbols indicate relative height-classes above the height where exponential decrease in branch density was observed, i.e. Eq. (10) was not fitted to these height-classes. Lines show the general relationship between mean branch volume and branch density derived by combining the regression estimates for each variable. Note the varied horizontal and vertical axes ranges.

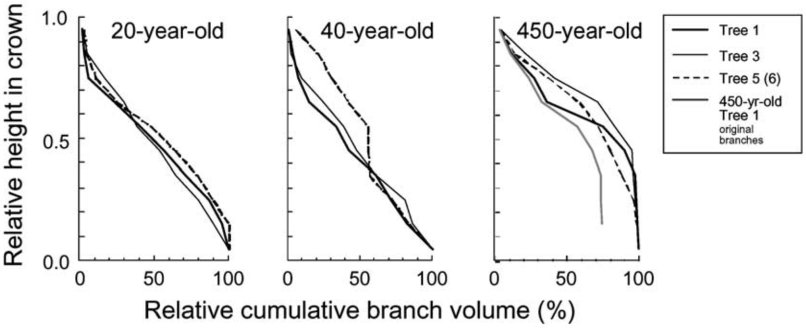

Fig. 5. Vertical distribution of branch volume for the tallest, medium and shortest sample trees of 20-, 40- and 450-year-old Douglas-fir shown in terms of relative cumulative distributions of total branch volume for each height-class. As an example, the comparison of the vertical distribution of branch volume for all branches (thick dark line) and only the original branches (thick light line) is shown for the tallest 450-year-old tree.

mean branch volume increased while branch density decreased exponentially (Fig. 4, open symbols). The first phase was not observed for the 450-year-old trees because branch density decreased exponentially for the full extent of the crown. The pattern of change in the relationship between mean branch volume and branch density was estimated by combining the regression estimates for each measure shown in Table 1. For trees that were best fitted by the exponential growth curve, the relationship between mean branch volume and branch density was represented by a linear relationship with a negative slope, e.g., Tree 3 of the 20-year-old stand and Trees 3 and 5 of the 40-year-old stand. For trees that were best fitted by the logistic growth curve, the relationship between mean branch volume and branch density was represented by a convex curve, e.g., Trees 1 and 5 of the 20-year-old stand, Tree 1 of the 40-year-old stand and all sample trees of the 450-year-old stand.

Vertical distribution of branch volume shifted toward the upper-crown from 20- and 40-year-old trees to 450-year-old trees (Fig. 5). For the 20- and 40-year-old trees, about 50% of the total branch volume occurred in the upper half of the crown above $H_{\mathrm{rel}} = 0.5$. For the 450-year-old trees, this value increased to 80–90%. For the 450-year-old trees, original branches accounted for most of the branch volume in the upper half of the crown, while epicormic branches contributed 13.0–57.5% of the total branch volume in the lower half of the crown. This is illustrated by the example in Fig. 5 for Tree 1 where original branches comprise about 65% of the total branch volume above $H_{\mathrm{rel}} = 0.5$ (thick light line). This number increases to about 85% when epicormic branches are included (thick dark line).

4. Discussion

The vertical change in mean branch volume from upper- to lower-crown was well represented by the exponential or general logistic growth curves. For most trees, the general logistic growth curve showed the best fit. In the upper-most part of the crown, branches are growing in full sun, and the positive feedback between branch growth and foliage production results in exponential growth (Ford, 1992). In the middle- to lower-crown, branch growth slows as light availability decreases with decreasing height, and eventually mean branch volume culminates. These changes in branch growth pattern result in the logistic growth curve observed for most sample trees. The few small residual branches in the lower-crown of some sample trees suggest that branch growth is suppressed below the crown height where maximum branch volume is attained. Ford (1982) found that branch growth rates were highest for the top six whorls in the crown of polestage Sitka spruce (*Picea sitchensis* (Bong.) Carr.), and that branch growth slowed below the height where needle death balanced new needle production within branches. The inflection point of the general logistic growth curve likely corresponds to the height where branch growth rate begins to decline in Douglas-fir. In young coniferous trees, maximum branch size is attained in the lower-crown, and branch size decreases slightly below this height (Colin and Houllier, 1992; Mškinen and Colin, 1998; Maguire et al., 1999). In this study, maximum branch volume was attained in the lower-crown for the 20- and 40-year-old trees, while it occurred in the middle-crown for the 450-year-old trees. Franklin et al. (1981) observed that old Douglas-fir trees have deep, sparsely branched crowns compared with young and mature trees. The lower-crown of old Douglas-fir trees is comprised mostly of epicormic branches, and original branches are confined to the upper one-half to two-thirds of the crown (Ishii and Wilson, 2001). As a result, the largest original branches are found in the middle-crown of old Douglas-fir trees, and maximum branch volume occurs at higher relative positions in the crown than for young and mature trees.

The relative height below which branch density decreased exponentially increased with increasing tree age. This suggested that branch death occurs at higher relative heights in the crown for old stands than for young stands. Exponential decrease in branch density occurred in the lower one-half to two-thirds of the crown for 20-year-old trees, while it occurred in the lower two-thirds to the full extent of the crown for the 40-year-old trees. These relative heights corresponded to areas where dead branches were observed in the crown. For the 450-year-old trees, branch density decreased exponentially for the full extent of the crown. Ishii and Wilson (2001) found that dead branches occurred in the entire crown of the 450-year-old trees, and were most abundant in the middle- to lower-crown where the number of original branches decreased significantly. In terms of absolute height above ground, branch density decreased exponentially below 8.3–9.2 m above ground for the 20-year-old trees, while for the 40-year-old trees this occurred below 28.0–30.8 m. The constancy of this height within each stand suggests that stand-level canopy structure and light conditions have strong influence on the height below which branch death occurs. The height below which branch density decreased exponentially for the 20- and 40-year-old stands roughly corresponds to the height where crown closure is attained, i.e. where neighboring crowns overlap.

Kellomäki and Väisänen (1988) and Mškinen and Colin (1999) found that branch death did not occur in the upper-most part of the crown of 5 to 76-year-old plantation trees of Scots pine (*Pinus Sylvestris* L.) in Finland. They also found that after the onset of branch death, live branch number decreased linearly with decreasing height. Kellomäki and Väisänen (1998) propose that the maximum number of branches that can be sustained over a given crown projection area is determined by stand-level conditions such as light, nutrient availability and tree density. Chiba (2001) found that live branch number decreased exponentially and dead branch number increased exponentially with decreasing height in the crown of young hinoki cypress (*Chamaecyparis obtusa* Sieb. et Zucc.) in Japan. The differences among tree species in the pattern of decrease in live branch number with decreasing height in the crown may reflect differences in relative shade-tolerance. The amount of light decreases less rapidly from upper- to lower-crown for shade-intolerant species such as Scots pine that have relatively sparse crowns and form open stands. In contrast, less shade-intolerant hinoki cypress and Douglas-fir have denser crowns and form dense stands. These differences in crown structure and stand density may account for the steep exponential decline in live branch number with decreasing height observed in hinoki cypress and Douglas-fir compared with Scots pine. Similarly, because Douglas-fir stands become more open as they reach the old-growth stage (Spies and Franklin, 1991), old trees may be able to support more branches in the lower-crown. Franklin et al. (2001) suggest that this change in stand light condition stimulates production of epicormic branches in the lower-crown of old Douglas-fir trees. In this study, we found that epicormic branches were most abundant in the middle- to lower-crown of the 450-year-old Douglas-fir trees. In addition, epicormic branches moderated the rate of decrease in branch density (k) by increasing branch density in the middle- to lower-crown.

The vertical change in branch diameter distributions is the result of the combined effects of increase in branch size (branch growth) and decrease in number of branches (branch death) from upper- to lower-crown. The upper-crown of the 20- and 40-year-old trees consisted of small-diameter branches with little variation in branch size. The mean and range of branch sizes increased from upper- to middle-crown indicating that some branches increased in size with decreasing height, while others grew little and remained in the small-diameter classes. The bimodal distribution in the middle-crown reflected development of a size hierarchy, and indicated that large branches have disproportionately greater growth rate than smaller branches. The lower-crown consisted of only large-diameter branches, indicating that small-diameter branches died and only large-diameter branches survived. The progression of branch diameter distributions from upper- to lower-crown is similar to that observed during stand development (Ford, 1975; Mohler et al., 1978; Hara, 1988). In the case of crown development, branches that grow to be large and those that are suppressed may be predetermined morphologically. Whorl shoots on the main stem tend to be larger in size than internodal shoots when first produced, and whorl branches tend to be larger in size than inter-whorl branches (Jensen and Long, 1983; Maguire et al., 1994). Although we did not distinguish whorl branches and inter-whorl branches in this study, observations suggested that the hierarchy in branch size structure resulted from differences in growth rate of the two branch types, and that the surviving large branches in the lower-crown of the 20- and 40-year-old trees were mostly whorl branches. For the 450-year-old trees, the upper-crown consisted mostly of original branches. Epicormic branches occurred throughout the crown and were smaller in diameter than the original branches. In the middle- to lower-crown, branch diameter distributions were bimodal comprised of small-diameter epicormic branches and large-diameter original branches. Ishii and Wilson (2001) showed that vertical gaps greater than 2 m commonly occur in the crown of old Douglas-fir trees. Death of large original branches and formation of vertical gaps in the crown likely stimulates production of epicormic branches leading to branch recruitment.

Comparison among stands of the relationship between mean branch volume and branch density elucidated the pattern of crown development with increasing tree age. For the upper-crown of the 20- and 40-year-old trees, above the relative height where exponential decrease in branch density was observed, mean branch volume increased with decreasing height, while branch density remained relatively constant except for small variations probably due to annual fluctuations in branch production. For the middle- to lower-crown, mean branch volume increased while branch density decreased exponentially with decreasing height. This change occurred along a straight line for trees that showed exponential branch growth, and along a convex curve for trees that showed logistic branch growth. For the 450-year-old stand, mean branch volume increased while branch density decreased exponentially with decreasing height following a convex curve for the full extent of the crown. We define this relationship between mean branch volume and branch density after the onset of branch death as the branch self-pruning line/curve. During stand development, the relationship between mean tree size and tree density follows the self-thinning line after the onset of competition-induced mortality. Several researchers have found that the slope of the self-thinning line equals $-\frac{3}{2}$ on a log–log plot for even-aged stands undergoing self-thinning (Yoda et al., 1963; White and Harper, 1970; Long and Smith, 1984; Westoby, 1984). We found that, for branch self-pruning, the slope of the linear relationship between mean branch volume and branch density was less steep than $-\frac{3}{2}$, or that it decreased with decreasing height in the crown, as illustrated by the convex-curve relationship. The slope of the self-thinning line is known to become less steep under stressful conditions such as limited light and nutrient availability (Westoby and Howell, 1982; Morris and Myerscough, 1991; Londsdale and Watkinson, 1982). Westoby and Howell (1982) found that the slope of the self-thinning line became less steep when populations of *Trifolium subterraneum* L. were transferred from full day-light to shade conditions. Londsdale and Watkinson (1982) found that populations of *Lolium perenne* L. thinned along a slope of -1 when planted under deep shade, and moderate levels of shading decreased the intercept of the self-thinning line. The changes from upper- to lower-crown in the relationship between mean branch volume and branch density after the onset of branch death can be interpreted as sequential changes in the population structure of cohorts of branches growing under increasingly shady conditions as the crown grows taller and new cohorts develop above old ones. The relationship between mean branch volume and branch density after the onset of branch death, i.e. the shape of the branch self-pruning line/curve, may be the result of a sequential decline in the slope and/or intercept due to increasing shade from upper- to lower-crown.

The vertical distribution of branch volume shifted toward the upper-crown with increasing tree age.

Young coniferous trees have conical crown form where maximum branch size occurs near the lower-crown (Colin and Houllier, 1992; Maguire et al., 1999). In old trees, branch growth continues even after height growth has stopped, and the crown becomes more cylindrical as large branches occur in the upper-crown (Ishii et al., 2000). As a result, branch biomass shifts upward from young and mature trees to old trees. Maguire and Bennett (1996) and Jensen and Long (1983) found that maximum foliage mass and foliage area occurs in the lower half of the live crown in young Douglas-fir trees (10–39 years old). In contrast, Massman found that maximum foliage area in old Douglas-fir trees occurs in the upper half of the live crown. These results suggest that distribution of branch biomass becomes increasingly "top-heavy" in old Douglas-fir trees as original branches increase in size and lower-crown branches are self-pruned. For the 450-year-old trees, epicormic branches contributed to increasing total branch volume in the lower half of the crown. Epicormic branches are produced mainly in the lower-crown of old Douglas-fir trees as the canopy becomes more open in old-growth stands (Spies and Franklin, 1991; Franklin et al., 2001). As a result, epicormic branches work to redistribute branch biomass more evenly within the crown of old Douglas-fir trees.

5. Conclusion

Comparison of crown form among young and old trees using the stand development analog provided an integrative approach to understanding how crown structure develops with tree age in coastal Douglas-fir trees (Fig. 6). The complex crown structure of old trees develops as a result of branch growth, branch death and production of epicormic branches following stages similar to that of stand development. Just as large residual trees and recruitment of trees enhance

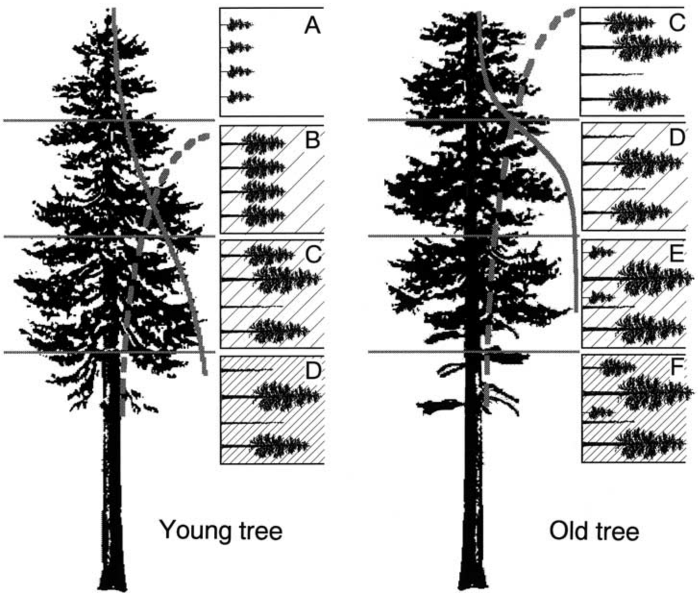

Fig. 6. The conceptual model of crown development based on the stand-development analog. Mean branch size increases from upper- to lower-crown following the general logistic growth curve (solid line), while branch density decreases exponentially (broken line). The resulting pattern of vertical change in mean branch size and branch density is similar to that observed during stand development with the additional effect of increased shading from upper- to lower-crown. Letters A–E correspond to the stages of stand development as proposed by Long and Smith (1984), plus one further stage of development following tree recruitment (F). Young trees consist of cohorts of branches in early stages of development: branch growth is exponential and branch death does not occur in the upper-crown (A–B), maximum branch size is attained and branch density decreases exponentially due to branch death in the lower-crown (C–D). Old trees consist of cohorts of branches in later stages of development: dead branches occur throughout the crown (C–F), maximum branch size is attained in the middle-crown (D–E), and branch recruitment occurs by production of epicormic branches (E–F).

structural complexity of old-growth stands (Swanson and Franklin, 1992; McComb et al., 1993; Arsenault and Bradfield, 1994; Tappeiner et al., 1997; Zenner, 2000), large original branches and production of epicormic branches enhance structural complexity of the crown of old Douglas-fir trees. Acker et al. (1998) propose that the transition from young to old-growth forest structure occurs between 80 and 100 years for coastal Douglas-fir stands. Franklin et al. (1981) suggest that the characteristic crown structure of old Douglas-fir trees develops between 100 and 200 years. A comparative study of crown structure including trees in this important developmental stage is currently underway that should elucidate how crown structure of Douglas-fir changes during the transition from mature to old-growth stands. Studies of crown development provide a 'canopy perspective' of the development of stand structure with increasing stand age, and have important implications for conservation and management of the structural attributes of old-growth forests.

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