Crown structure of old-growth Douglas-fir in the western Cascade Range, Washington

Hiroaki Ishii and Megan E. Wilson

Abstract: Crown structure of old-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) is characterized by low live-branch density, numerous dead branches and epicormic branches, high branch-size variability, and large gaps in the crown. These features define structural complexity of the crown and create variable crown microenvironments. For the 60 m tall, 400-year-old Douglas-fir trees measured in this study, number of live branches decreased and dead branches increased from the upper to lower crown. Dead branches were found below the lowest live branch indicating that crown recession had occurred. Live-branch biomass culminated at 45 m and decreased markedly below 35 m. Numerous vertical gaps between branches occurred below 40 m. Epicormic branches accounted for 14.6–47.5% of the total number of live branches per tree and contributed to increased crown depth. Epicormic branches filled inner regions of the crown, and contributed to increased branch-size variability. A model of crown structure developed for young trees could be fit to the upper crown of the study trees but could not be applied to the middle to lower crown because of increased branch-size variability. Relative levels of photosynthetically active radiation in the crown decreased with decreasing height, but a local peak occurred around 35–40 m, coinciding with the height of marked decrease in live-branch biomass.

Résumé : La structure du houppier du douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) présent dans les forêts surannées est caractérisée par une faible densité des branches vivantes, de nombreuses branches mortes et branches adventives, une forte variabilité dans la taille des branches et de fortes trouées dans le houppier. Ces caractéristiques définissent la complexité structurale du houppier et y créent un micro-environnement variable. Pour les douglas de 60 m de hauteur et de 400 ans d'âge mesurés dans cette étude, le nombre de branches vivantes diminuait et le nombre de branches mortes augmentait de la partie supérieure à la partie inférieure du houppier. Des branches mortes ont été trouvées sous la dernière branche vivante, indiquant un élagage actif du houppier. La biomasse des branches vivantes culminait à 45 m et diminuait de façon marquée au-dessous de 35 m. De nombreuses trouées verticales entre les branches apparaissaient au-dessous de 40 m. Les branches adventives représentaient de 14,6 à 47,5% du nombre total de branches vivantes par arbre et contribuaient à augmenter la profondeur du houppier. Les branches adventives remplissaient la partie intérieure du houppier et contribuaient à augmenter la variabilité de la taille des branches. Un modèle de structure du houppier développé pour des jeunes arbres pouvait s'ajuster à la partie supérieure des arbres de l'étude mais ne pouvait être appliqué aux parties médiane et inférieure du fait de l'augmentation de la variabilité dans la taille des branches. Le rayonnement photosynthétiquement actif relatif dans le houppier diminuait avec la hauteur mais un pic local était présent vers 35–40 m, hauteur coïncidant avec la diminution marquée de la biomasse des branches vivantes.

[Traduit par la Rédaction]

Introduction

Old-growth Douglas-fir – western hemlock (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii* – *Tsuga heterophylla* (Raf.) Sarg.) forests of the Pacific Northwest of North America are characterized by multilayered canopies; a wide range of tree sizes; and the presence of canopy gaps, numerous snags, and abundant woody debris (Franklin et al. 1981; Spies and Franklin 1991). These elements of forest structure define "structural complexity" of old-growth forests and distinguish these forests from younger stands and plantations (Franklin and Spies 1991*a*). Structural features of old-growth forests also have important ecological functions that contribute to species diversity and ecosystem stability (Spies and Franklin 1988; Franklin and Spies 1991*b*; Hansen et al. 1991). In their review of the ecological characteristics of old-growth Douglas-fir – western hemlock forests of this region, Franklin et al. (1981) point out the importance of large, old trees of Douglas-fir in contributing to the structural complexity of these forests and describe the crown of these trees as "highly individualistic" and "irregular."

Studies on the structural characteristics of old-growth Douglas-fir – western hemlock forests have mainly focused on the ecosystem and stand scales for purposes of forest management (e.g., Franklin et al. 1981; Franklin and Spies

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H. Ishii[1,2] and M.E. Wilson.[3] College of Forest Resources, Box 352100, University of Washington, Seattle, WA 98195-2100, U.S.A.

[1]Corresponding author.
[2]Present address: Biosphere Dynamics Research Group, Institute of Low Temperature Science, Hokkaido University, Sapporo 060-0819, Japan (e-mail: hishii@pop.lowtem.hokudai.ac.jp).
[3]Present address: Cascadia Field Station, P.O. Box 352100, University of Washington, Seattle, WA 98195-2100, U.S.A.

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1991*a*; Spies and Franklin 1991). These studies demonstrated that many wildlife and plant species are dependent on the structural features of old-growth forests because of their specialized habitat requirements (Franklin 1992). For example, Schowalter (1989) found 61 species of arthropods in the canopy of an old-growth forest and only 16 in an adjacent young plantation stand in western Oregon. Spies and Franklin (1991) observed that understory species composition changed from dominance by salal (*Gaultheria shallon* Pursh) in young and mature stands of Douglas-fir to higher percentage of various herbaceous species in old-growth forests. Ecosystem- and stand-scale studies of the relationship between structure and function of old-growth forests have lead to new management practices that aim to enhance habitat diversity by incorporating structural features of old-growth forests, such as variable tree sizes, ages, and spacing; snags; and woody debris (McComb et al. 1993; Kohm and Franklin 1997; Smith et al. 1997). However, many of the structural features that directly affect habitat for small mammals, birds, arthropods, and epiphytes occur at smaller scales, such as the tree crown (Franklin et al. 1981; Maser et al. 1981; Carey 1989; McComb et al. 1993). For example, Ritchie (1988) showed that large-diameter branches serve as nest sites for marbled murrelets. Pike et al. (1977) and Clement and Shaw (1999) showed that structural features of old-growth Douglas-fir crowns are directly related to canopy epiphyte diversity. Just as structure and development of old-growth forests provide guidelines for management practices that aim to create old-growth habitat at the ecosystem and stand scales, studies of the structure and development of old tree crowns can provide guidelines for creating structural features and habitat at the tree-crown scale. Despite this, crown structure has only recently been considered in management practices for purposes of creating habitat (Berg et al. 1996).

Most studies on crown structure of Douglas-fir have focused on young and mature trees because crown structure 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). We are aware of only a handful of published studies focusing on crown structure of old Douglas-fir trees (Pike et al. 1977; Massman 1982; Clement and Shaw 1999; Ishii et al. 2000*a*). In addition to providing important ecological functions, the complex crown structure of old Douglas-fir trees influences the intensity and quality of light penetrating through the crown and creates a variable within-crown microenvironment (Denison 1973; McCune et al. 1997). Ishii et al. (2000*a*) found that repeated dieback and recovery processes during branch growth characterize crown structure in old Douglas-fir trees. The complex crown structure of old Douglas-fir trees develops as a result of the long-term interaction between tree growth and low-severity disturbances that cause damage, dieback, and death of branches and the main stem (Pike et al. 1977; Ishii et al. 2000*a*). Structural complexity at the tree-crown scale can be defined by the variability found in branch size, age, biomass, type (live or dead, original or epicormic), and spatial distribution within the crown. Dead branches that accumulate in the crown of old trees are likely to have ecological functions similar to woody debris and snags at the stand scale. Damage and dieback of the crown causes release of epicormic buds and the development of epicormic branches. Franklin et al. (1981) noted epicormic branches as a distinguishing structural feature of old Douglas-fir trees. Branch death also leads to formation of gaps in the crown and enhances variability of the crown microenvironment.

In this study, we characterize crown structure of old Douglas-fir trees through analysis of the spatial distribution of live and dead branches within the crown. We used nondestructive methods to distinguish epicormic branches and show how they contribute to enhancing crown structural complexity. We also measured the light environment within the crown to elucidate the effects of crown structure on the crown microenvironment. We discuss these results in relation to crown structure of young Douglas-fir, and to structural characteristics of old-growth forests at the stand scale, to infer the development and ecological functions of old Douglas-fir tree crowns.

Study site and methods

The study was conducted in a 450-year-old, old-growth Douglas-fir – western hemlock forest at the Wind River Canopy Crane Research Facility located in the Thornton T. Munger Research Natural Area, Gifford Pinchot National Forest in southwestern Washington State, U.S.A. (45°49′N, 121°57′W, altitude 355 m). The stand basal area is dominated by Douglas-fir and western hemlock. Western redcedar (*Thuja plicata* Donn ex D. Don), Pacific silver fir (*Abies amabilis*. Dougl. ex Forbes), and Pacific yew (*Taxus brevifolia* Nutt.) are also abundant. Other tree species in the stand include grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.), western white pine (*Pinus monticola* Dougl. ex D. Don), and Pacific dogwood (*Cornus nuttalii* Audubon). Franklin (1972) and Franklin and DeBell (1988) give a detailed description of the area.

Douglas-fir dominates in the upper canopy of the stand comprising nearly 70% of trees taller than 50 m in height (Ishii et al. 2000*b*). There are no Douglas-fir trees shorter than 30 m, and no regeneration of Douglas-fir is observed in the understory. Western hemlock dominates in the middle to lower canopy, representing more than 70% of trees ranging between 10 and 45 m in height. Western redcedar occurs in moderate numbers throughout all canopy levels, while Pacific silver fir and Pacific yew occur only in the middle to lower canopy below 40 and 20 m, respectively. See Ishii et al. (2000*b*) for a detailed description of the vertical structure and species composition of the forest canopy.

Crown structure

Six representative Douglas-fir trees were selected based on the size structure (diameter at breast height, tree height) of the Douglas-fir in the stand (Ishii et al. 2000*b*) for measurement of crown characteristics (Table 1). The Douglas-fir in the stand are believed to be a cohort that established after a stand-replacing major disturbance in the area about 500 years ago (Franklin and DeBell 1988). Breast-height age of the study trees were estimated from increment cores extracted at 1.4 m above ground. The cores were mounted, surfaced, and the number of rings on each core was counted. For cores that did not include the pith, the number of missing rings was estimated following methods described in Liu (1986). Breast-height age estimates of the study trees ranged from 395 to 415 years. These estimates agree with ages of stumps in nearby clearcuts (Franklin and DeBell 1988).

The six study trees were climbed using the single-rope technique (Lilly 1998; Clement and Shaw 1999), and all primary branches were numbered and distinguished as live (foliated) or dead (not foliated). Branch height above ground was measured to the nearest 0.05 m using a tape measure that was stretched verti-

Table 1. Structural characteristics of the six old-growth Douglas-fir trees studied.

Tree	Tree height (m)	DBH (cm)	Breast-height age (years)	Highest measured branch (m)
Tallest	61.6	135.3	415	59.35
Tall	61.0	126.9	410	59.35
Tall–medium	58.7	153.5	—[a]	57.65
Medium–short	53.8	104.3	405	51.75
Short	51.3	87.1	395	49.35
Shortest	50.8	93.9	405	48.75

[a]Breast-height age could not be accurately determined because of an incomplete core sample.

cally along the main stem of the tree. Branch diameter was measured immediately outside the branch collar using diameter tape or calipers to the nearest 0.1 cm. Branch length was measured to the nearest 0.1 m by extending a 1 in. wide (1 in. = 2.54 cm) engineer's tape from the main stem to the farthest foliated section of the branch. Measurements on branches in the upper 2–3 m of each tree were avoided because of safety concerns. Of the six sample trees, the tall–medium tree and short tree showed evidence of major damage to the main stem. The tall–medium tree had a flat top and was relatively short for its diameter compared with other trees, suggesting that the main stem may have been damaged and died back. The main stem of the short tree forked into two codominant stems at 37 m (about two-thirds of tree height). Branches on both stems were measured, and the taller stem was considered as the main stem.

Live branches of each tree were distinguished into original and epicormic branches (Fig. 1) nondestructively using the following criteria (Ishii 2000):

(1) Bark texture: Epicormic branches can be distinguished by the difference in bark texture relative to the main stem. Because of their younger age, the bark of epicormic branches is often smooth and light-gray colored, similar to the main stem of young *P. menziesii* trees. Original branches are as old as the part of the main stem they are attached to, and have rough, dark-brown bark that matches the bark of the main stem.

(2) Angle of insertion: Epicormic branches can be distinguished by their tangential angle of insertion to the main stem. Epicormic branches often grow out of the main stem at tangential angles because of their origin in the axils of branches. Original branches originate in the pith of the main stem and grow out at right angles.

(3) Associated dead or dying branch: Some epicormic branches have an associated older branch that is dead or dying. Several epicormic branches can sprout near the base of a dead or dying branch. The death of an older branch likely triggers release of several epicormic buds from near its base.

(4) Fan-shaped branch clusters: Some epicormic branches have a fan-shaped arrangement. Several epicormic branches can grow out from the same area of the main stem. These may thin out and leave behind three to four branches that are arranged in a fan-shaped cluster.

(5) Calluslike swell: Some epicormic branches grow out from a calluslike swell on the main stem. The growth of several epicormic branches from the same area of the main stem can result in a calluslike swell. The swell may persist after many of the epicormic branches thin out. In contrast, original branches have a smooth taper at the branch collar.

(6) Smaller relative diameter: Diameter of epicormic branches is often smaller relative to nearby original branches because of their younger age. Although suppressed original branches can also have small diameter, branch diameter can be used in conjunction with other characteristics above to distinguish epicormic branches.

The only way to know for certain if branches are epicormic is to destructively sample the main stem (Kozlowski 1971). However, extensive destructive sampling is often restricted in old-growth forest reserves, as was the case in this study. Although nondestructive methods have their limitations, these six criteria used in combination should provide a relatively accurate method for distinguishing epicormic branches. In most cases, epicormic branches were easily distinguishable as they were clearly morphologically different from original branches (Fig. 1).

The crown of each study tree was divided into 5-m height intervals above ground. For all trees, the topmost height interval was less than 5 m (see highest measured branch in Table 1). The total number of live and dead branches were summed for each height interval. In addition, the percentage of dead branches relative to the total number of live and dead branches was calculated for each height interval.

We used (branch diameter)^2 × branch length as an index of branch biomass for the live branches. This measure is analogous to (tree diameter)^2 × (tree height) which has been shown to be correlated with tree biomass (Fujimori et al. 1976). Estimates of live-branch biomass were summed for each 5-m height interval, and the percentage of total biomass in each height interval was calculated relative to the total for the whole tree.

Gaps in the crown were quantified by subtracting the height of each live branch from the height of the branch above it (branch height difference). Frequency distributions of the branch height differences for the six study trees were used to characterize vertical spacing of live branches and to define vertical gaps in the crown.

Various models have been proposed for describing the crown structure of coniferous trees. Crown profile models predict crown width or crown radius at a given height (e.g., Nepal et al. 1996; Biging and Gill 1997; Hann 1999), while other models predict maximum and (or) average branch size at a given height in the crown (e.g., Colin and Houllier 1992; Maguire et al. 1999). Many of these models include assumptions of structural characteristics for young and mature trees. For example, the model proposed by Maguire et al. (1991) assumes monotonic increase in branch size with decreasing height and may only apply to crown structure before canopy closure. Some models assume functional relationships among crown dimensions and branch size (Maguire et al. 1999). However, crown structure of old Douglas-fir trees is highly variable, and functional relationships observed in young and mature trees may not be applicable. For this reason, we chose to use a relatively simple and flexible model of crown structure proposed by Nepal et al. (1996) and applied previously to old Douglas-fir trees by Ishii et al. (2000*a*):

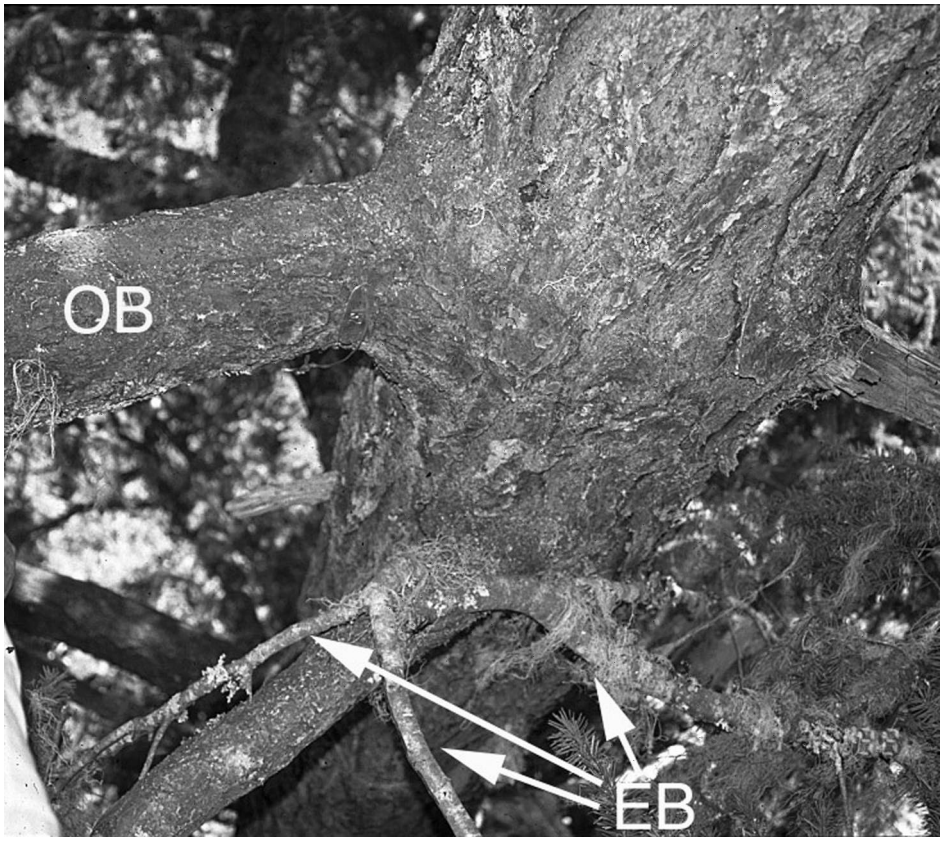
$$[1] \qquad Z = a\mathrm{RBD}^b(1 - \mathrm{RBD})^c$$

This equation defines branch size (Z) as an allometric function of relative branch depth (RBD), where

$$[2] \qquad \mathrm{RBD} = \frac{\text{tree height} - \text{branch height}}{\text{tree height} - \text{lowest live branch height}}$$

where a is a coefficient and b and c are scaling exponents. Because branch age increases with decreasing height in the crown, crown structure of the upper crown of old Douglas-fir trees may be similar to that of young and mature trees, while crown structure of the middle to lower crown may be more variable. This transition may be evident in the relationship between branch size and branch height. We used piecewise regression to determine the height where crown structure of old Douglas-fir trees could no longer be described using eq. 1:

Fig. 1. Epicormic branches (EB) of old-growth Douglas-fir were distinguished from original branches (OB) using a combination of morphological characteristics: smooth bark texture, tangential 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.



$$[3]\qquad \begin{cases} Z = a\mathrm{RBD}^b(1-\mathrm{RBD})^c, & \mathrm{RBD} < h \\ Z = ah^b(1-h)^c, & \mathrm{RBD} \geq h \end{cases}$$

Equation 3 was fit separately to the relationship between relative branch depth and branch diameter and to the relationship between relative branch depth and branch length of original branches of each tree. Parameters *a*, *b*, *c*, and *h* were estimated iteratively using the nonlinear least squares function in SYSTAT version 5.2.1 (SYSTAT, Inc., Evanston, Ill.). Initial values for *a*, *b*, and *c* were set to estimates derived when eq. 1 was fit to all original branches using nonlinear least squares regression. The initial value for *h* was set to the midpoint between the top of the tree and the lowest original branch. Equation 1 has a limitation in that branch size at the bottom of the live crown is constrained to zero. This did not hamper fitting of eq. 1 to the original branches, as the lowest live branch for five of the six trees was an epicormic branch, i.e., the bottom of the live crown was much lower than the lowest original branch. For the tall–medium tree, the lowest live branch was an original branch, and this branch was excluded from the analysis.

Light environment

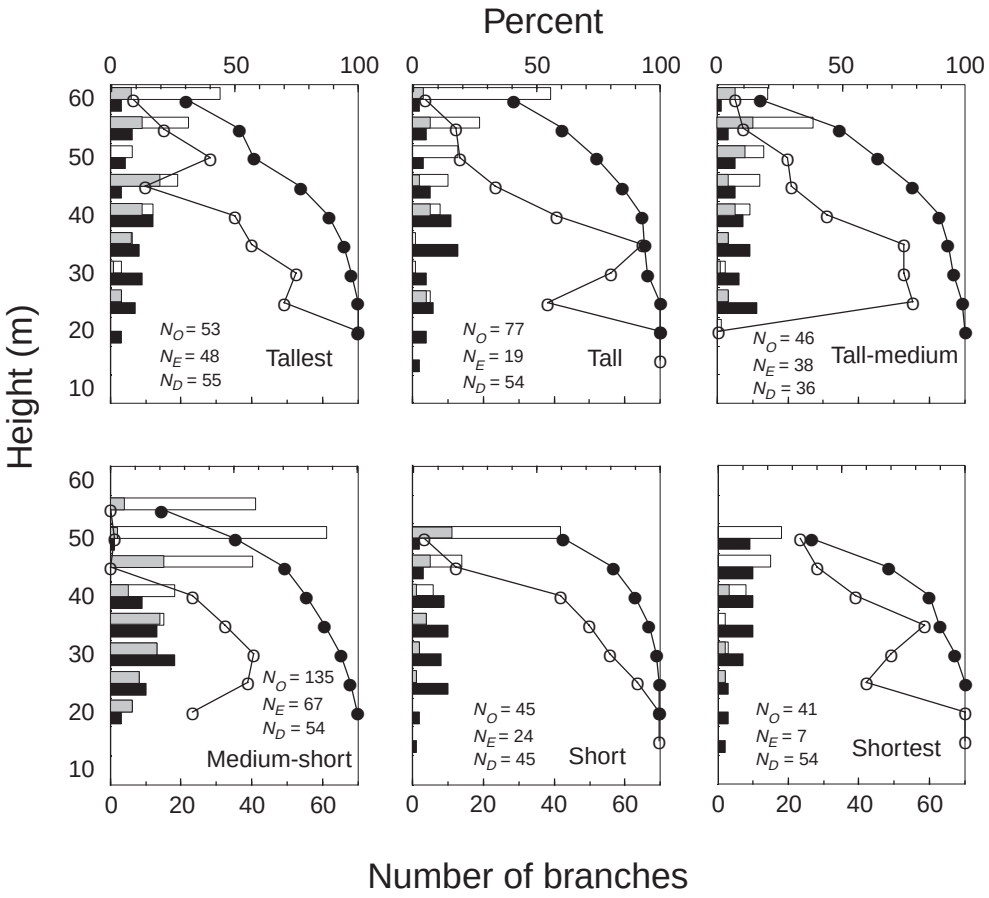
Vertical changes in light environment within the crown was measured at 5-m height intervals using the Sunfleck PAR ceptometer (Decagon Devices Inc., Pullman, Wash.), which uses several quantum sensors along a 1 m long bar to calculate average photon flux density of photosynthetically active radiation (PAR) over a given area. Measurements were taken over a 45° area around the main stem centered around the four cardinal directions near the mid-height of each 5-m height interval. Measurements within the crown and in a nearby field were taken simultaneously on an overcast day to obtain relative PAR.

Results

Crown structure

The greatest number of live branches was found in the top two 5-m height intervals for all study trees (Fig. 2). Forty-nine (tall–medium tree) to 81% (short tree) of the total number of live branches in each tree was found in the top two height intervals. Live branch number generally decreased with decreasing height, and the fewest number of live branches was found in the lowest or second lowest height interval, at 20–30 m, for all trees. The height interval with the greatest number of dead branches differed among trees, ranging from 40 m for the tallest tree to 25 m for the tall–medium tree and short tree. The percentage of dead branches in each height interval generally increased with decreasing height. In all trees except the tall–medium tree, dead branches were found below the lowest live branch, indicating that the live crown had receded. While the total number of live branches ranged from 48 (shortest tree) to 202 (medium–short tree), the total number of dead branches remained relatively constant across trees ranging from 45 (short tree) to 55 (tallest tree). Epicormic branches were found throughout all height intervals of the study trees, and accounted for 14.6 (shortest tree) to 47.5% (tallest tree) of the total number of live branches in each tree. Epicormic branches accounted for a large propor-

Fig. 2. Vertical distribution of original branches (open bars), epicormic branches (shaded bars), and dead branches (solid bars) for the six old-growth Douglas-fir trees. Circles with lines show cumulative percentage of live branches (solid circles) and the percentage of dead branches (open circles) for each height interval. The total number of original branches (N_O), epicormic branches (N_E), and dead branches (N_D) are also shown for each tree.



tion of live branches in the lower crown of each tree. Of the live branches below 35 m, 57 (tall tree, shortest tree) to 100% (short tree) were epicormic branches. For the medium–short tree and short tree, all live branches in the lowest 15 m of the live crown were epicormic. These results suggested that epicormic branches contributed to increasing crown depth and maintaining foliage in the lower crown of the study trees.

Vertical distribution of live-branch biomass estimates was unimodal, and the greatest biomass was found at 45 m for all trees (Fig. 3). This corresponded to the fourth height interval from the top for the tallest tree, tall tree, and tall–medium tree, the third height interval for the medium–short tree, and the second height interval for the short tree and the shortest tree. Forty-six (shortest tree) to 81% (tallest tree) of the total estimated live-branch biomass of each tree was found above 45 m. Estimated biomass declined sharply at 35 m for all trees. The degree of decline was less marked for the shortest tree than for the other trees. Compared with their contribution to live-branch number, epicormic branches contributed relatively little biomass; 6.5 (medium–short tree) to 25.3% (tallest tree) of the total live-branch biomass for each tree.

Frequency distributions of branch height differences for each tree were strongly positively skewed, and most branch height differences were less than 0.2 m (Fig. 4). This indicated that most branches were vertically clustered. Frequency distributions were continuous from 0 up to 1.2–1.6 m, but all trees showed a gap in the frequency distribution around 2 m. Therefore, we defined vertical gaps in the crown as branch height differences greater than 2 m. The number of vertical gaps greater than 2 m varied from tree to tree (Fig. 5, arrows). The medium–short tree had one gap of 2.8 m at 18.8 m in height, while the tall tree had five gaps ranging in size from 2.0 to 4.2 m at heights from 20.6 to 38.4 m. All gaps occurred below 40 m with the exception of one gap at 46 m for the tallest tree.

Branch diameter and branch length of original branches generally increased with decreasing height (Figs. 5 and 6). Variability in branch diameter and branch length of original branches was relatively small in the upper crown but increased with decreasing height. At a given height in the crown, epicormic branches were generally smaller in diameter and shorter in length than original branches and contributed to increased variability of branch size, especially in areas of the crown where large original branches were found. For example, for the tallest tree, the largest original branches occurred between 35 and 45 m and ranged in size from 17.1 to 26.4 cm in diameter and 4.1 to 9.4 m in length, while epicormic branches at the same height ranged in size from

Fig. 3. Vertical distribution (bars) and cumulative percentage (solid circles) of estimated live-branch biomass for the six old-growth Douglas-fir trees. Open and shaded bars show original branches and epicormic branches, respectively. The percentage of total live-branch biomass represented by epicormic branches (EB) is also shown for each tree.

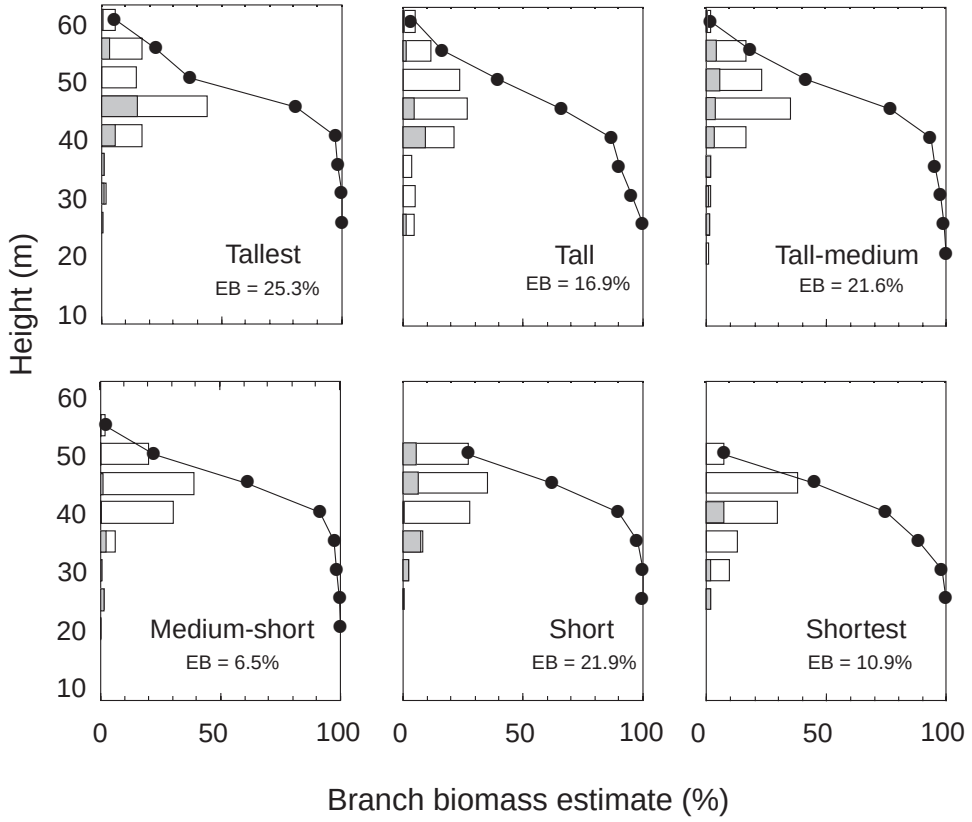
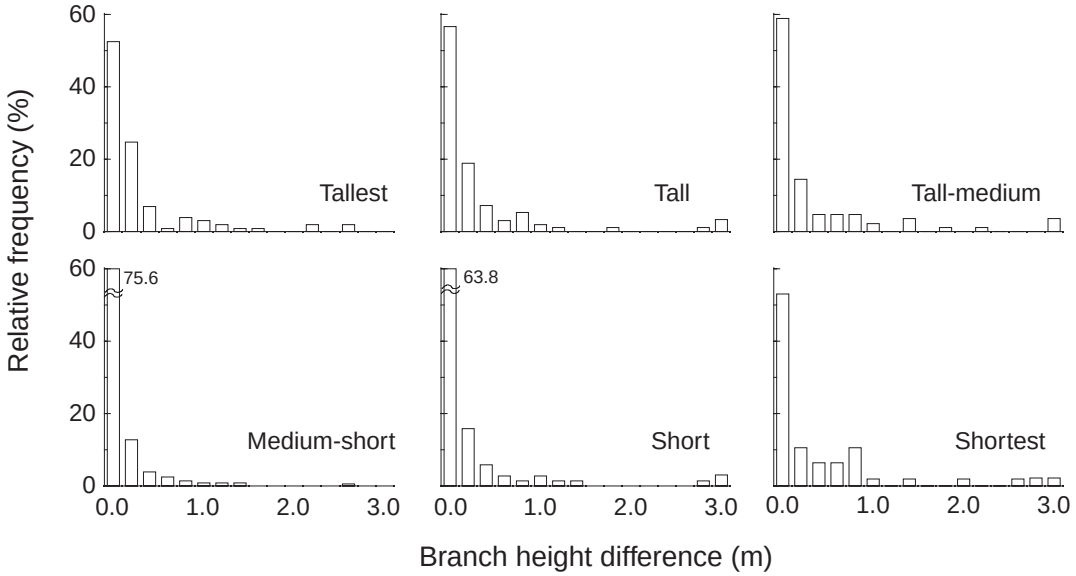


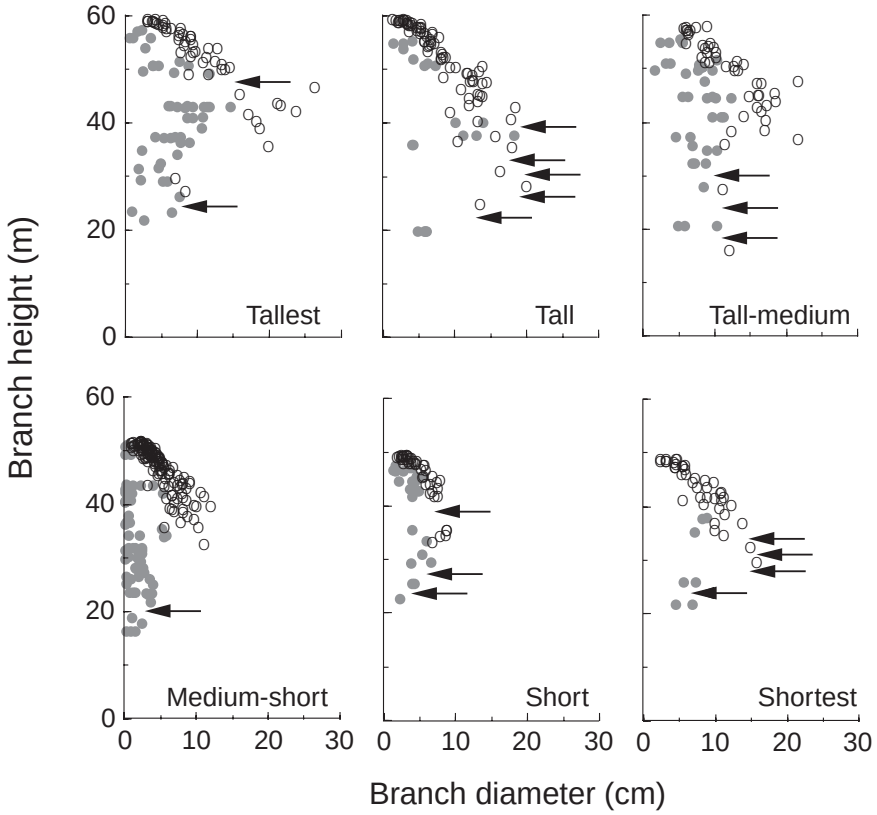
Fig. 4. Relative frequency distribution of branch height differences (vertical distance between live branches) for the six old-growth Douglas-fir trees.



2.8 to 15.1 cm and form 2.2 to 7.7 m. Epicormic branches filled the inner regions of the crown inside the "outer crown" formed by original branches (Fig. 6). The vertical extent of the region of the crown filled by epicormic branches varied from tree to tree.

Nonlinear least squares fits of eq. 3 to the original branches of each tree showed that, for five of the six study trees, the allometric relationship between branch height and branch size represented by eq. 1 could not be applied to all original branches (Fig. 6). Values for h ranged from 0.252 to 0.792

Fig. 5. Vertical distribution of branch diameters of original branches (open circles) and epicormic branches (shaded circles) for the the six old-growth Douglas-fir trees. Arrows show gaps in the crown with branch height differences greater than 2 m.



for branch diameter and 0.349 to 0.642 for branch length (Table 2). Equation 1 could only be fit to all original branches of the shortest tree for branch diameter. However, in all other cases, eq. 1 could only be fit to original branches in the upper one fourth to two thirds of the live crown.

Light environment

Both relative PAR and variability of relative PAR in the four cardinal directions generally decreased with decreasing height in all trees (Fig. 7). A local peak in relative PAR was observed at 40 and 35 m for all trees except the shortest tree. For example, for the tallest tree, relative PAR decreased from 54.4 to 17.4% from 60 to 45 m, then increased to 30.1% at 35 m, and decreased again to 15.6% at 25 m. The height of the local peak in relative PAR corresponded to the height where a sharp decline in live-branch biomass was observed (Fig. 3).

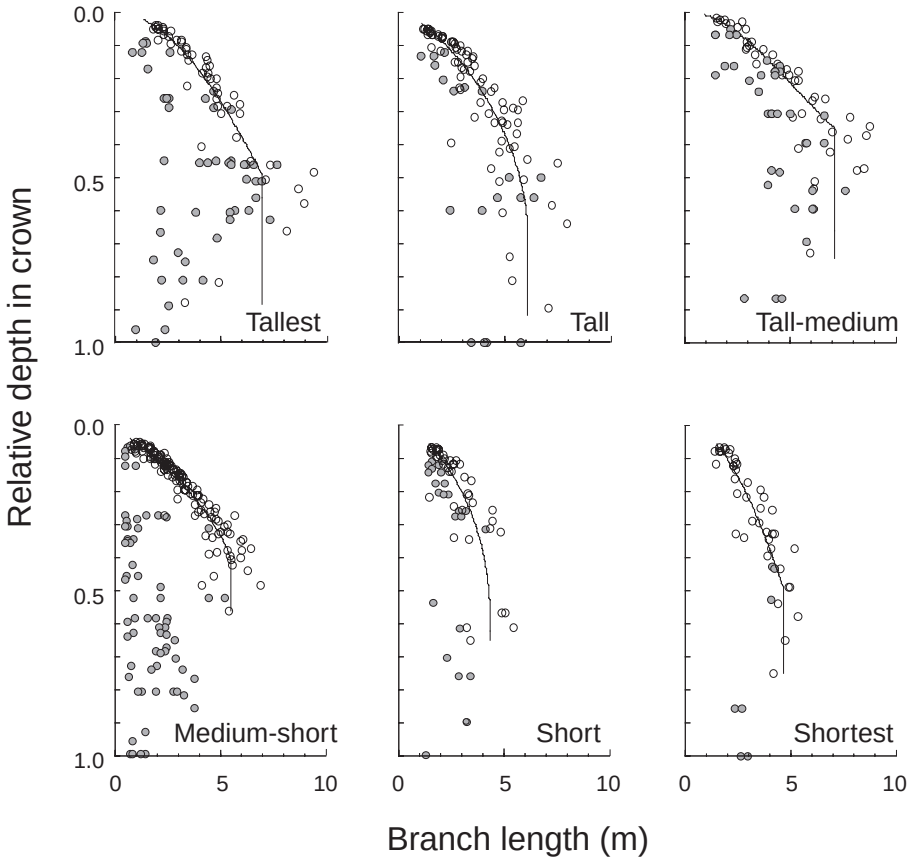
Discussion

Our results provide a quantitative analysis of structural complexity of old-growth Douglas-fir – western hemlock forests at the tree-crown scale and advances previous qualitative observations of the structural characteristics of old Douglas-fir tree crowns. The crown structure of old Douglas-fir trees are characterized by low live-branch density compared with younger trees, numerous dead branches and epicormic branches, large gaps in the crown, and highly variable branch sizes. The structural complexity of old Douglas-fir crowns results in variable within-crown light environment. As discussed below, these structural features likely develop as a result of the combined effects of growth, damage, dieback, and death of original branches and the production of epicormic branches.

Crown structure

As much as 81% of the total number of live branches of the six study trees occurred in the top 10 m. Live-branch numbers in the top 10 m of the study trees translates to branch densities (mean live branch number per vertical metre of main stem) ranging from 3.8 (shortest tree) to 15 (medium–short tree) for the top two height intervals. Live-branch densities for 10- to 20-year-old Douglas-fir range from 8 to 21 branches per vertical metre of main stem (Maguire et al. 1994; St. Clair 1994; Kershaw and Maguire 1995). This indicates that the top 5–10 m of the old-growth Douglas-fir trees in this study have live-branch numbers comparable with that of young trees. However, live-branch numbers decreased with decreasing height and were much lower in the lower crown. Young trees have several branches that occur in whorls at the same height on the main stem, as well as numerous internodal branches (Jensen and Long 1983; Maguire et al. 1994). Internodal branches tend to be shorter in length than whorl branches (Maguire et al. 1994) and are likely to be suppressed and more short lived. Kershaw et al. (1990) found that branch longevity ranged from 4 to 72 years for Douglas-fir trees up to 130 years old. Although it is more difficult to distinguish whorl branches and internodal branches in old trees, percentage of live original branches that had the same height measurement (branch height

Fig. 6. Vertical distribution of branch lengths of original branches (open circles) and epicormic branches (shaded circles). Lines show nonlinear least-squares fits of eq. 3 to the original branches. Vertical axis shown in relative branch depth (RBD).



difference = 0 m) were, in order of tree height, 26, 17, 13, 54, 48, and 25% for the six study trees. These may represent remnant whorl branches. These numbers indicate that, although many branches are vertically clustered (branch height difference <0.2 m), 46–87% of original branches of old Douglas-fir trees occur singly, suggesting that several whorl branches have died. Both number and percentage of dead branches increased from upper to lower crown, also suggesting that considerable branch death had occurred. Maguire (1994) estimated that rates of branch mortality ranged from 1.2 to 6.2 branches/year per tree for 30- to 50-year-old Douglas-fir trees. This suggests that many dead branches would accumulate in the crown of old trees. However, the total number of dead branches was relatively constant across the six study trees, suggesting that branch mortality and shedding of dead branches reaches equilibrium in the crown of old Douglas-fir trees. Grier and Logan (1977) estimate that the amount of dead branches in the canopy of old-growth Douglas-fir forests ranges from 3240 to 5320 kg/ha. In addition, branch death occurs as the live crown recedes after crown closure (Maguire and Hann 1990; Maguire 1994). Five of the six study trees showed evidence of past crown recession with dead branches extending lower down the crown than live branches.

In all six study trees, maximum estimated live-branch biomass occurred at 45 m. It is not clear why this height is constant across the six study trees. The Douglas-fir trees in this stand have reached maximum tree height and crown expansion has stopped (Ishii 2000; Ishii and Ford 2001). At this stage of crown development, it may be possible that overall stand conditions, such as the vertical distribution of light in the forest canopy, influence the vertical distribution of biomass more than the growth pattern of individual trees. Maximum biomass was found in the upper half of the live crown for all six study trees. Massman (1982) found that maximum needle surface area occurs in the upper half of the live crown of old-growth Douglas-fir trees in Oregon. At the stand scale, Easter and Spies (1994) showed that maximum leaf area index of Douglas-fir moves upward in the canopy with increasing stand age from 92 to 525 years. In contrast, Maguire and Bennet (1996) and Jensen and Long (1983) observed that maximum foliage mass and foliage area occurs in the lower half of the live crown in young trees (10–39 years old). For the six study trees, the pattern of biomass distribution above 35 m was similar to that of young Douglas-fir trees. However, all six study trees showed a sharp decline in branch biomass at 35 m, and live-branch biomass extended in small amounts further down the crown for another 10–15 m. Top-heavy distribution of live-branch biomass and the sparsely distributed small branches extending to the lower crown may be a crown structural feature that characterizes old Douglas-fir trees.

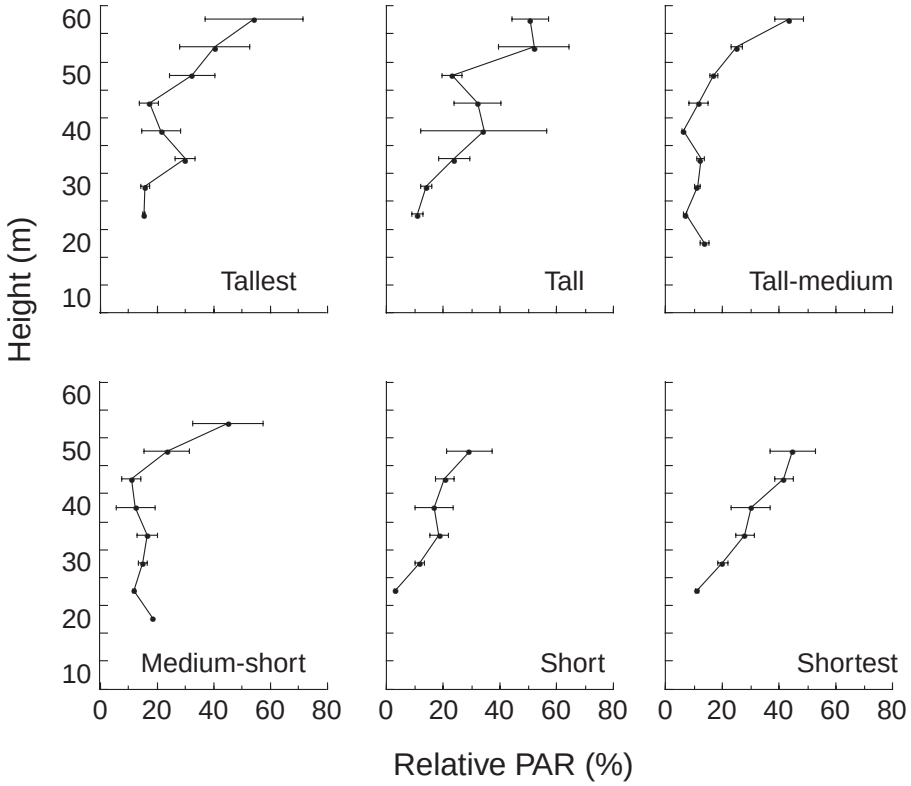
Many branches of the six study trees were vertically clustered within 0.2 m of each other, especially in areas with high live-branch numbers. Based on the relative frequency distribution of branch height differences, we were able to de-

Table 2. Parameter estimates of the piecewise regression of crown form for the six old-growth Douglas-fir trees.

Tree	Lowest RBD[a]	Branch diameter					Branch length				
		a	*b*	*c*	h^b	r^2	*a*	*b*	*c*	h^b	r^2
Tallest	0.883	16.873	0.474	–1.058	0.380 (46.4)	0.736	9.626	0.512	–0.069	0.490 (42.2)	0.770
Tall	0.900	39.785	0.914	0.503	0.645 (34.9)	0.879	11.982	0.707	0.351	0.642 (35.3)	0.817
Tall–medium	0.729[c]	3.681	–0.138	–4.489	0.252 (47.9)	0.787	8.651	0.457	–0.655	0.349 (43.8)	0.871
Medium–short	0.568	33.715	0.998	0.819	0.376 (39.7)	0.783	23.947	1.062	0.989	0.403 (38.7)	0.907
Short	0.656	32.788	0.926	1.120	0.452 (38.7)	0.884	9.523	0.651	0.506	0.563 (35.7)	0.702
Shortest	0.751	19.223	0.623	0.053	0.792 (28.5)	0.837	6.617	0.528	–0.031	0.496 (36.9)	0.830

[a]RBD, relative branch depth.
[b]Values in parentheses are absolute heights (m).
[c]Lowest original branch at RBD = 1.0 was excluded from the analysis.

Fig. 7. Mean relative PAR in each 5-m height interval for the six study trees. Error bars are 1 SD of the variation in the four cardinal directions.



fine vertical gaps in the crown as branch height differences greater than 2 m. Several such gaps were found in the lower crown of the six study trees below 40 m. Their irregular distribution suggests that gaps in the crown may be formed by stochastic small-scale disturbances causing branch death. The crown of young Douglas-fir is characterized by continuous vertical distribution of live branches (Maguire et al. 1994). In contrast, Denison (1973) observed gaps up to 23 m between branches of old Douglas-fir and suggested that such gaps contribute to increasing variability of the crown microenvironment. Just as gaps in the canopy enhance variability of the understory microenvironment at the stand scale, gaps in the crown should contribute to creating variable microenvironment within old Douglas-fir crowns.

Death of original branches and formation of gaps in the crown may stimulate release of epicormic buds from the main stem of old Douglas-fir trees. Production of epicormic branches often occurs in response to exogenous stimuli, such as damage and defoliation or increased light, water, and nutrients (Zimmermann and Brown 1971). Pike et al. (1977) and Ishii et al. (2000*a*) observed extensive damage and dieback of branches in old Douglas-fir trees that may cause production of epicormic branches. In four of the six study trees, more than one third of the total number of live branches were epicormic. Epicormic branches occurred throughout the crown and accounted for most of the branches in the lower crown of the study trees. At a given height, epicormic branches tend to be smaller in size than the original branches and contribute to increasing branch-size variability, especially in areas of the crown where large original branches are found. Epicormic branches filled the inner regions of the crown inside the outer crown formed by original branches. The vertical extent of the region of the crown filled by epicormic branches varied from tree to tree, sug-

gesting that the growth and disturbance history of the crown varies among individual trees. These results indicate that epicormic branches contribute to maintaining the number of live branches within the crown and to increasing crown depth of old Douglas-fir trees.

The allometric relationship between branch height and branch size represented by eq. 1 could be applied to all original branches for only the branch diameters of the shortest tree. For five of six trees, eq. 1 could only be fit to original branches in the upper one-fourth to two-thirds of the live crown. This demonstrated that crown structure defined by original branches was similar to that of young and mature trees for the upper crown of the study trees, while increasing variability in branch sizes with decreasing height made it more difficult to model crown structure of the middle to lower crown. Original branches in the upper crown are relatively young and likely to have structural characteristics similar to young and mature trees. In contrast, original branches in the middle to lower crown are older and likely to have suffered damage or dieback and subsequent recovery over their long life-span, resulting in more variable branch sizes (Ishii et al. 2000*a*). Age estimates of branches destructively sampled from three of the six trees for a different study (Ishii and Ford 2001), showed that original branches sampled from the upper crown (above 45 m) had 79–105 annual rings at the branch base, while those sampled from the middle crown (around 35 m) had 126–162 annual rings. The annual ring counts may not translate directly to branch age, as branches of Douglas-fir are known to have missing rings (Reukema 1959; Kershaw et al. 1990). Nevertheless, they suggest that original branches in the middle crown of old Douglas-fir trees may be more than 50 years older than those in the upper crown.

Light environment

Stand-scale light environment of old-growth forests are more open and more spatially variable compared with younger stands (Easter and Spies 1994; Parker 1997; Frazer et al. 2000). Variability in the light environment has been attributed to the structural complexity of old-growth forests. We found a similar relationship at the tree-crown scale between crown structure and within-crown light environment for old Douglas-fir trees. Relative PAR decreased from the treetop down to 50–40 m for all trees. This corresponds to the upper crown, where crown structure is similar to that of young trees. Studies on within-crown light environment of young coniferous trees have found monotonic decrease in relative light intensity with decreasing height (e.g., Hashimoto 1983; Kurachi et al. 1986). In addition, models of stand-level photosynthesis assume monotonic decline in light intensity with decreasing height (Russell et al. 1989; Oker-Blom et al. 1991). However, for the old Douglas-fir trees in this study, a local peak in relative PAR was observed at 35 and 40 m. Below 40 m, live branch numbers decreased, and several gaps occurred in the crown. Estimated live-branch biomass decreased markedly at 35 m for all trees, and more than 50% of live branches below 35 m were small epicormic branches. This allows more diffuse light to penetrate into the crown, resulting in increased PAR. The local peak in relative PAR in the lower crown may be a unique characteristic of the variable within-crown light environment of old Douglas-fir trees.

Conclusion

We found several structural features that characterize old Douglas-fir crowns and distinguish them from young and mature trees. Branch death results in low live-branch density in the middle to lower crown, accumulation of dead branches, formation of gaps in the crown, and crown recession. Production of epicormic branches results in extension of crown depth, filling of the inner regions of the crown, and increased branch-size variability. The upper crowns of old Douglas-fir trees have crown structure similar to that of young and mature trees. However, the lower crown is characterized by low branch density, numerous dead branches and epicormic branches, and low live-branch biomass, which results in increased penetration of diffuse light. These structural features are the result of the combined effects of the growth and death of original branches and production of epicormic branches and characterize crown structure of old-growth Douglas-fir.

Variation in branch size and their spatial distribution contributes to diversity of habitats in much the same way that variation in tree size and distribution do at the stand scale. Just as large old trees are important structural features of old-growth forests, large, old original branches have important ecological functions. In their comparative study of managed and old-growth boreal forests in northern Sweden, Esseen et al. (1996) found that epiphytic lichen biomass was strongly related to amount and persistence of available substrate, i.e., size and age of branches. They conclude that epiphytic lichen biomass and diversity in managed forests are limited by small young branches that provide only a small amount of substrate and short time for colonization and growth. Abundance of dead branches characterizes old Douglas-fir crowns as do snags at the stand-scale. At the stand-scale, density of large-diameter standing dead trees are an indicator of vertebrate and invertebrate animal diversity (Franklin et al. 1981; Franklin and Spies 1991*a*). Similarly, at the tree-crown scale, density and distribution of dead branches within the crown are likely to be related to diversity of small mammal, bird, and arthropod populations that utilize these branches for habitat. Dead branches also provide nutrient-rich substrate for epiphyte establishment (Denison 1973; Pike et al. 1977). Large, unevenly distributed gaps characterize old-growth Douglas-fir – western hemlock forests at the stand scale (Spies et al. 1990) and contribute to enhancing variability of the light environment (Frazer et al. 2000). Similarly, large gaps between branches characterize old Douglas-fir crowns and contribute to increased variability of the within-crown light environment. Old-growth forests are characterized by continuous regeneration and recruitment of trees resulting in variable tree sizes and a multilayered canopy. We showed that production of epicormic branches has similar functions at the tree-crown scale.

Aspects of structural complexity at the tree-crown scale presented in this study adds a new dimension to the definition of structural complexity of old-growth Douglas-fir – western hemlock forests. This basic information can be used

as a guideline for silvicultural prescriptions that take into account crown-scale structural features for purposes of creating habitat. For example, pruning of whole branches and parts of branches in various parts of the crown may simulate small-scale disturbances and produce old-growth crown characteristics by creating gaps in the crown, stimulating release of epicormic branches, and increasing variability in branch size. Basic knowledge of the structure and function of old-growth forests from the tree crown to the stand and ecosystem scales is essential for management of old-growth forest structure at multiple scales.

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