Development of Canopy Structure in *Pseudotsuga menziesii* Forests in the Southern Washington Cascades

Robert Van Pelt and Nalini M. Nadkarni

ABSTRACT. We quantified stand-level structural diversity in eight stands of temperate coniferous forests that ranged in age from 50 to 950 years in the southern Washington Cascade Range. Stands were chosen based on the dominance, or former dominance in the case of the oldest stands, of *Pseudotsuga menziesii*. In addition, to avoid confusing patterns of structural development, only stands that had a single disturbance of origin were used. Within each stand, randomly located transects were laid out that were proportional in size to the dominant tree height. Tree heights and diameters ranged up to 90 m and 309 cm, respectively. A total of 5,737 trees among the 32 transects were mapped and measured for height, diameter, crown height, and four crown radii. The structure of the canopy in the younger stands is a simple, fairly even monolayer. This contrasts with the older stands, which have a very complex, highly diffuse canopy with extreme variability in both horizontal and vertical dimensions. The stands with the highest structural complexity were between 500 and 650 years old and retained from 17 to 76 *Pseudotsuga* stems/ha. Our oldest site had only one living *Pseudotsuga*/ha. Mean diameter of just the *Pseudotsuga* trees was less than 55 cm for stands less than 200 years and over 180 cm for the most complex old-growth stands. One measure of stand structural diversity, the standard deviation of dbh, ranged from less than 25 (stands less than 200 years) to values greater than 50 (most complex old-growth sites). A similar relationship exists when using the standard deviation of height. Large snags and logs important for wildlife were present only in the old-growth stands and were abundant in the most structurally diverse stands. FOR. SCI. 50(3):326–341.

Key Words: Stand development, crowns, canopies, Pacific Northwest, Douglas-fir.

FOREST STRUCTURE concerns the three-dimensional spatial arrangement of forest elements. Structural diversity is a measure of the horizontal and vertical variability of the structural elements within a forest (Staudhammer and LeMay 2001), which influences biodiversity and ecosystem function (Whittaker 1972, Aber et al. 1982, Kimmins 1997, Spies 1998).

The tremendous height and structural complexity of the old-growth *Pseudotsuga menziesii* (hereafter, *PSME*) forests of the Pacific Northwest have attracted the attention of

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ecologists for over two decades (Waring and Franklin 1979, Franklin et al. 1981, Parker 1996). The diverse structural elements they support and the large amounts of biomass and necromass they accumulate affect critical functional attributes of the region, including carbon storage (Maser et al. 1988, Harmon et al. 1990, Smithwick et al. 2002), modification of microclimate (Chen et al. 1999), and maintenance of wildlife habitat (USDA Forest Service 1991, Bull et al. 1997, Lindemayer and Franklin 2002). Their cathedral-like qualities of form and light have also inspired a sense of wonder, as manifested in the art and poetry of the region (Stewart 1984, WCWC 1989).

When low-to-mid elevation forests in the Pacific Northwest reach an age of about 200 years, they are considered to be old-growth (Franklin et al. 1981, Franklin and Spies 1991). These complex forest formations contain high biological diversity (Sillett 1995, McCune et al. 2000, Carey et al. 1999, Sillett et al. 2000, Winchester and Ring 1999). A greater understanding of how these forests develop their complex structure and how this structure affects forest functioning is key to learning how to conserve biological diversity in managed landscapes.

Over the last decade, discussions of forest structural diversity have influenced the political climate of forestry in the Pacific Northwest. When wildlife biologists documented the old-growth association of the Northern Spotted Owl (Forsman 1980), policy on federal lands changed dramatically. Although these changes were first based on the preservation of individual species (Thomas et al. 1990), they ultimately focused on the structural elements of forested ecosystems (FEMAT 1993). Key among the structural elements are large diameter snags (Thomas et al. 1979, Spies et al. 1988), logs (Maser et al. 1988), and large green trees with a diversity of mid- and subcanopy trees (Franklin et al. 1981, USDA Forest Service 1991).

In this article, we synthesize a detailed quantitative analysis of forest structure that occurs at the stand level in a variety of *PSME*-dominated forests of different ages in the Pacific Northwest. This is part of a larger-scale study to create database tools for canopy ecologists (Nadkarni and Cushing 2001). Our approach was to take ground-based measurements of the forest structural elements and then model the crowns in three-dimensional (3-D) space. Stand measurements were compared in terms of canopy variability and canopy development in both horizontal and vertical contexts.

Although the design of this project shares some characteristics of classic chronosequence research (e.g., Trofymow et al. 1997), it differs from that approach to successional research in that stands were selected to encompass the full range of structural conditions present in individual *PSME* trees rather than focusing on finding identical sites with different-aged forests. This includes variations in factors such as site productivity, elevation, and microclimate, which are reflected in different plant associations and the physical structure of the forests (Daubenmire 1952, Franklin 1966, Dyrness et al. 1974). In addition, initial density and early growth rates of current old-growth forests may have been different than today's young and mature forests, even on similar sites (Tappeiner et al. 1997), although see Winter et al. (2002).

Study Sites

Many natural *PSME* forests originated after one or more fire events and have grown and matured with no further major disturbance events (McArdle et al. 1961, Henderson et al. 1989, Agee 1991). Many other *PSME* forests, particularly those on the drier or southern end of the Pacific Northwest, develop complex structures from moderate disturbances that create multi-age cohort stands (Morrison and Swanson 1990, Acker et al. 1998, Sillett and Goslin 1999). In this study, we used only stands that had one apparent origin event followed by natural, within-stand mortality events (e.g., competition, decay, windthrow). Eight forest stands were selected, all located in the southern portion of the Washington Cascades. Study sites were limited to Experimental Forests, Research Natural Areas (RNAs), or Mt. Rainier National Park (Figure 1).

Four of the stands were within the Wind River Experimental Forest (WREF), including the old-growth stand at the Wind River Canopy Crane Research Facility (WRCCRF, Shaw et al. 2004). Three of these were the sites of earlier research on canopy gaps and were chosen for their extensive, undisturbed conditions (Spies et al. 1990, Van Pelt et al. 1992, Gray and Spies 1996, Van Pelt and Franklin 1999). Three other sites were located at Mt. Rainier National Park and were selected from the extensive permanent sample plot (PSP) network database held at Oregon State University (Franklin and Van Pelt 1990, Acker et al. 2001).

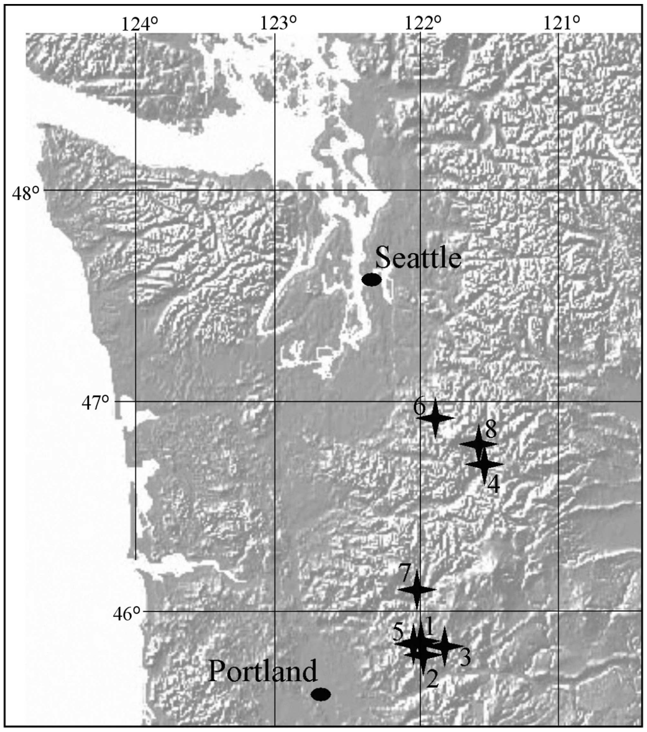

Figure 1. Study site locations. Numbers refer to sites as described in the text.

These are permanent, mapped research plots, most of which were established in the 1970s. The remaining site at Cedar Flats RNA was chosen to represent one of the most structurally complex forests within the Cascadian forest biome. Information on site history from natural and human disturbances was taken from previous studies (Topik et al. 1986, Franklin et al. 1988, Van Pelt 1995, Acker et al. 2001) and from ecologists familiar with the sites (Table 1, Figure 2).

Site 1: Wind River Experimental Forest—Plantation (PL)

This site represents the youngest stand, which is a naturally regenerated *PSME* stand that developed following clearcut logging in 1952.

Site 2: Wind River Experimental Forest—Martha Creek (MC)

This site resulted from the Yacoult burn, a 100,000-ha fire that occurred during the fall of 1902. The combination of the surviving individual trees, an abundant seed year, and probably seed surviving on killed trees allowed rapid establishment of a new *PSME* stand.

Site 3: Wind River Experimental Forest—Panther Creek (PC)

Much of the area on the east side of the Wind River Valley burned during a fire or series of fires around 1845. The tree canopy is nearly pure *PSME* with shade-tolerant species (*sensu*. Minore 1979) such as *Tsuga heterophylla* (*TSHE*) and *Thuja plicata* (*THPL*) present in places. The understory consists of a dense layer of shrubs and small trees.

Site 4: Mt. Rainier National Park—Ohanapecosh (OH)

The southeast corner of Mt. Rainier National Park, in the vicinity of the Ohanapecosh Campground, contains examples of ca. 280-year-old *PSME*/*TSHE* forest that has been considered old-growth forest (Franklin et al. 1981).

Site 5: Wind River Experimental Forest—Trout Creek (TC)

The old-growth forests at Wind River are dominated by *PSME* and *TSHE*. Based on ring-counts of stumps in nearby clearcuts, there is no evidence of major fire episodes at the site for at least 350 years, although some trees were more than 500 years old when cut in the 1970s (Franklin and Waring 1980). The study site is characterized by gently sloping terrain on the lower slopes of Trout Creek Hill.

Site 6: Mt. Rainier National Park—Carbon River (CR)

The forests along the Carbon River are among the few remaining examples of low-elevation alluvial old-growth *PSME*/*TSHE* forest. The oldest trees are *PSME* that are in the 500-year range, and the stand is dominated by *TSHE* and *THPL*. The understory is characterized by dense growth of mosses, ferns, and shrubs.

Site 7: Cedar Flats Research Natural Area—Cedar Flats (CF)

Cedar Flats RNA was protected for its representation of Cascadian *THPL* swamps. The non-wetland parts of the area are dominated by *PSME*/*TSHE* forest. These stands are 600–650 years old and are among the largest and tallest known forests in the Pacific Northwest. The immense crowns support abundant epiphyte communities.

Site 8: Mt. Rainier National Park—Chinook (CH)

This site represents the oldest stand of trees. The current forest originated approximately 950 years ago. The structure of the canopy is simpler than the *PSME*-dominated stands of the old-growth at Wind River, Carbon River, and Cedar Flats. Very large *TSHE* and *THPL* are present at the site, but only a few *PSME* remain—regenerating shade-tolerant species are in great abundance.

Field Procedures

Sample areas at each site were located in large, relatively flat blocks of forest with care to ensure plot boundaries were well away from clearcut edges. Each study site was mapped with aerial photographs and/or Forest Service and Park Service inventory geographical information system (GIS) layers. Stand polygons were generated using a GIS, and stand boundaries were chosen from the GIS-generated polygons.

At each site, four transects were selected as the sample units, or replicates, and were located inside of the stand polygons with random starting points and directions.

Table 1. Summary of site characteristics. The Carbon River stand is on an alluvial flat, and the Cedar Flats stand is on swampy ground, thus reducing a need for summer precipitation at both sites. Precipitation data does not include condensation from fog, which can add 10–30% at all of these sites.

Site		Elevation (m)	Age	Slope (% aspect)	Plant association*	Precipitation (cm) Ann.	July–Sep.	Snowfall	Temp (°C) (annual Ave.)
PL	Plantation	624	50	0–15% SE	*TSHE/BENE*	253	12	233	0–17.5 (8.0)
MC	Martha Creek	582	100	5–20% S	*TSHE/BENE/GASH*	253	12	233	0.6–17.8 (8.5)
PC	Panther Creek	732	157	0–15% W	*TSHE/BENE/GASH*	264	13	254	0–17.5 (7.8)
OH	Ohanepecosh	622	~280	0–10% SW	*TSHE/ACTR*	197	14	385	2.2–14.2 (7.9)
TC	Trout Creek	613	~500	0–10% S	*TSHE/VAAL/GASH*	253	12	233	0–17.5 (8.0)
CR	Carbon River	607	~500	0%	*TSHE/POMU/OXOR*	346	18	137	3.1–11.8 (7.5)
CF	Cedar Flats	411	~650	0%	*TSHE/TITR*	317	20	77	5.0–14.4 (9.7)
CH	Chinook	841	~950	0%	*ABAM/VAAL*	210	17	462	–0.6 –13.8 (6.6)

* Based on Topik et al. 1986 and Franklin et al. 1988. *TSHE*, *Tsuga heterophylla*; *BENE*, Berberis nervosa; *GASH*, *Gaultheria shallon*; *ACTR*, *Achlys triphylla*; *VAAL*, *Vaccinium alaskaense*; *POMU*, *Polystichum munitum*; *OXOR*, *Oxalis oregana*; *TITR*, *Tiarella trifoliata.*

Transects were located on the ground using global positioning satellites (GPS) and surveyed in with rebar at the endpoints. The mean height of canopy dominants was determined from previous research or our reconnaissance work and was used to determine transect size. Transect dimensions were designed to be large enough to capture the needed variability but small enough not to oversample. The final dimensions were 3.0 × 0.3 times the mean dominant tree height following ideas introduced by Kuiper (1988) and Van Pelt (1995). For example, a stand in which the mean dominant tree height was 50 m tall would be sampled by four transects, each of which was 150 m × 15 m.

Within each transect, all trees (including dead stems) greater than 5 cm dbh (1.37 m above the ground) were measured for location (x, y coordinates), species, dbh, height, crown height, and four cardinal crown radii. Many of the standing dead stems had decayed or snapped at a point below 1.37 m, so dbh was estimated. Their decay classes were assessed with a subjective scale (1–9) used in Pacific Northwest forests (Maser and Trappe 1984) as standard protocol by the Permanent Sample Plot project (Hawk et al. 1978, Acker et al. 2001). Mapping of stems was accomplished by setting up a transect line using 100-m tapes, compass, and rebar. The x coordinate of each tree was the distance along the tape at which the tree occurred. A laser rangefinder (Impulse 200LR, Laser Technologies, Inc.) provided the y coordinate (distance from the tape). Anomalies of tree form were noted (e.g., broken top, spike top, or wounds).

The transects were also used for subsampling small trees, shrubs, and logs. In a subtransect 10% as wide as the main transect, trees not yet measured but greater than 50 cm in height were mapped and measured for species, basal diameter, height, crown height, and average crown diameter. All other woody plants (including shrubs) taller than 50 cm in height were also sampled in this subtransect. These were measured for species, height, and basal diameter. The exception to this sampling protocol was *Acer circinatum* (*ACCI*) stems, which, due to their arching, curved growth form, were not considered trees even though their size can exceed 5 cm dbh. For individuals over 5 cm dbh, dbh was recorded rather than a basal diameter, but only for stems within the subtransect.

Downed logs were sampled using a line intercept down

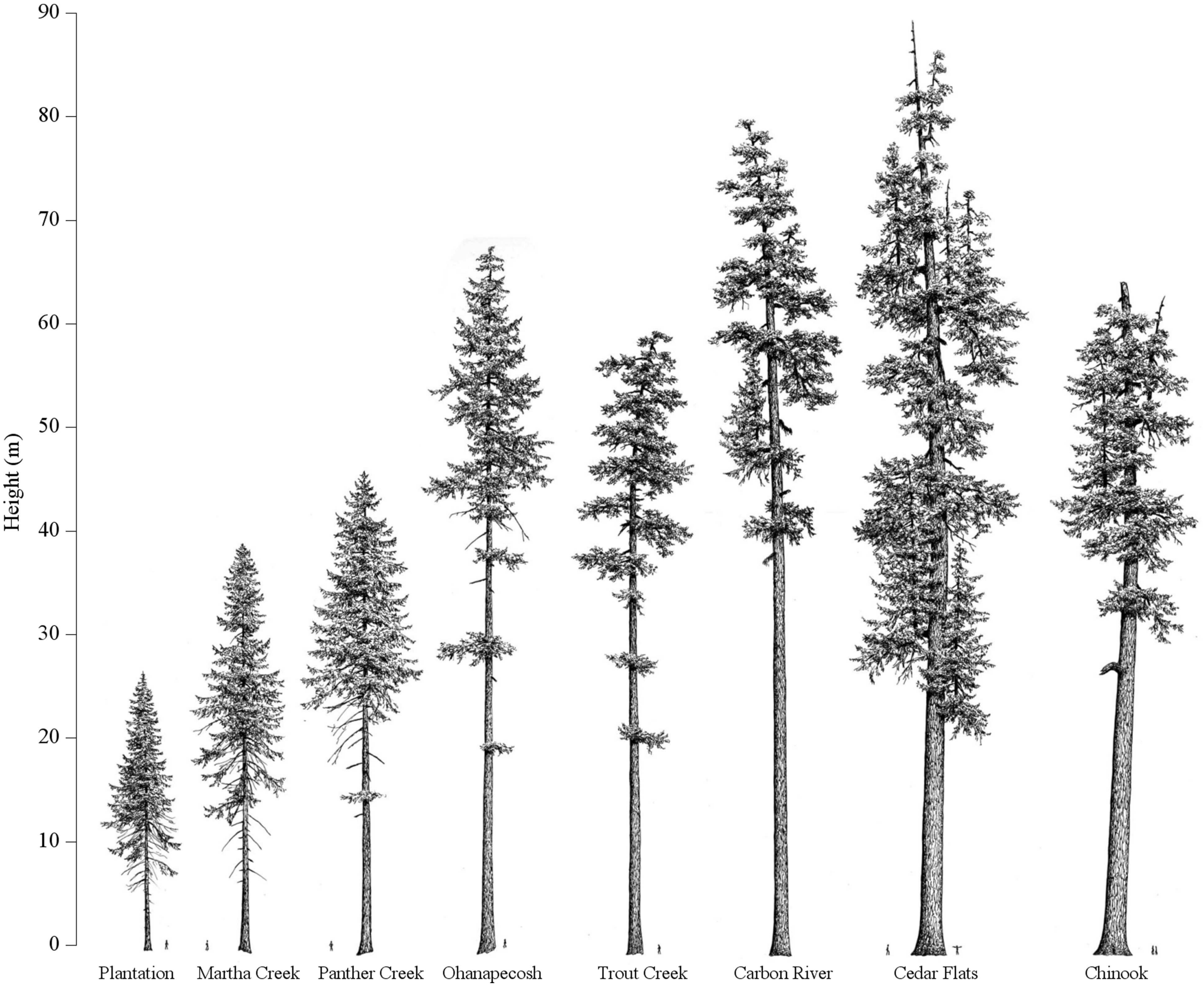

Figure 2. Detailed drawings to scale of a dominant tree from each of the eight sites. This will at least give a visual comparison of the size and structural changes discussed in the text.

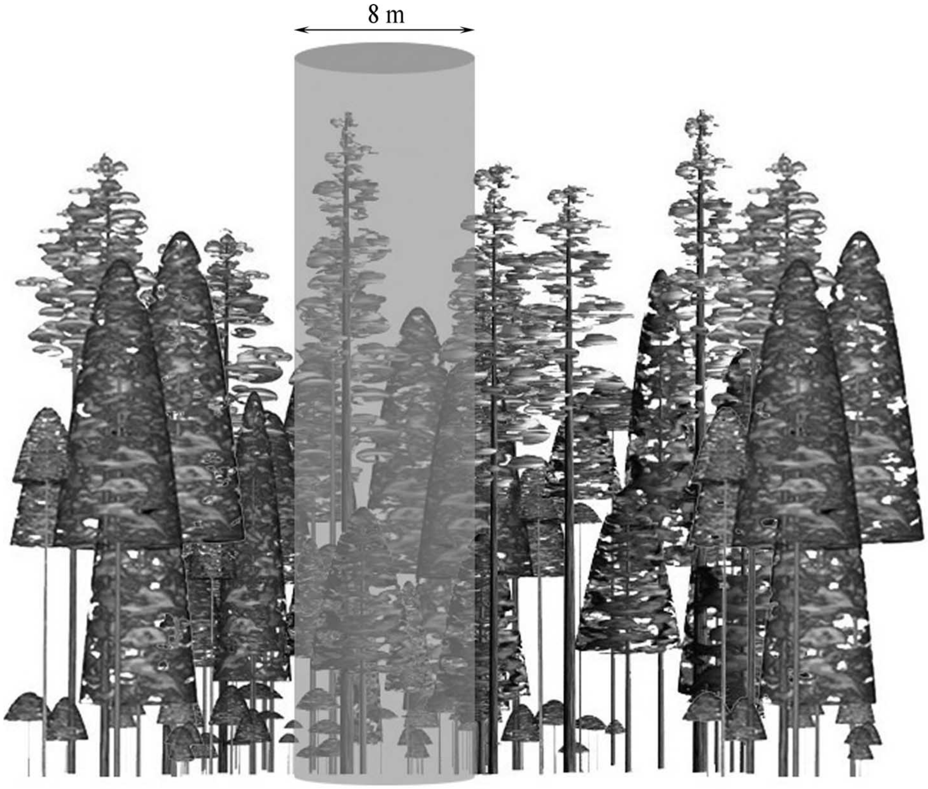

Figure 3. Illustration of the 8-m diameter cylinder used to sample crown volume for use in the semivariance analysis.

the middle of the transect. For each log, the two points where each side of the tape was intersected by the log were recorded, and the log diameter was also measured at that point. The species and decay class (five classes, Maser and Trappe 1984) were also recorded.

In each stand, a subset of trees for each species was chosen for stem volume measurements using a survey laser (Criterion 400, Laser Technologies, Inc.) to develop regression equations to predict volume from height and dbh. A total of 217 trees from among six species were used from the eight sites.

Analysis

Crown Models

Crown models were used to estimate crown locations based on mapped and measured parameters and then shaped as simple conics (Van Pelt and North 1996, Van Pelt and Franklin 2000). The models allow for the precise location of crown parameters in 3-D space. The crown dimensions of all trees were summed to generate 3-D solid volumes of the amount of occupied space. These were then "sliced" at 5-m intervals and summed by species for each 5-m layer. Although this approach is not appropriate for trees as individuals, these models work well at the stand scale (Van Pelt and North 1999). The crown radii data for each tree were then imported into a GIS, and maps of canopy projections were used to estimate the amount and sizes of gaps within each site.

Semivariance Analysis

Semivariance analysis is an aspect of geostatistics that was developed in the mining industry to help solve 3-D statistical problems (Matherton 1963, Cressie 1988). This has been applied in ecological research (Robertson 1987, Legendre and Fortin 1989). For example, Cohen et al. (1990) used semivariance analysis to examine scale and variability in remotely sensed data of Pacific Northwest forests. Van Pelt and Franklin (2000) used it to analyze the scale and pattern of variability of crown occupancy of six old-growth conifer forests.

The semivariogram profile of a measured variable can be modeled in comparison to an experimental curve called the theoretical semivariogram. Outputs from this comparison of the theoretical model to the experimental semivariogram function are the "sill," "range," and "nugget." Sill refers to the point at which the theoretical curve levels off, which is equal to the variance, or square of the standard deviation (σ^2). Range is the distance where the spatial dependence of a measured variable is maximized and beyond which the data are no longer autocorrelated. With transect data, the range is the dominant scale of pattern in distance units, beyond which the semivariance becomes approximately equal to the population variance of the measured variable (Knighton and Wagnet 1987). Nugget represents the random variance within the measured data not affected by a change in location. We prepared semivariograms for each site using the modeled crown volumes along the transect length.

Table 2. Summary of canopy volume distribution and stand dimensions. Listed are the total volume of canopy occupied by each species at each site, total basal area by species, stem wood volume, and the tallest individual at each site by species.

Research site	Species	Canopy volume (m^3 ha^{-1})	Basal area (m^2 ha^{-1})	Stem volume (m^3 ha^{-1})	Height (m)
Plantation	*Cornus nuttallii*	691	0.2	1	7
	Tsuga heterophylla	7,693	2.7	23	18
	Pseudotsuga menziesii	48,280	33.1	378	25
	Totals	56,664	36.0	402	
Martha Creek	*C. nuttallii*	154	0.1	1	12
	T. heterophylla	126	0.1	2	21
	P. menziesii	59,789	78.3	1,305	49
	Totals	60,068	78.6	1,308	
Panther Creek	*C. nuttallii*	1,408	0.4	2	11
	T. heterophylla	4,901	0.4	18	40
	P. meziesii	72,408	74.7	1,363	52
	Totals	78,717	76.3	1,383	
Ohanapecosh	*Thuja plicata*	3,941	1.5	25	53
	T. heterophylla	68,221	20.8	393	61
	P. menziesii	57,627	75.3	1,782	73
	Totals	130,605	99.1	2,200	
Trout Creek	*Taxus brevifolia*	1,755	1.3	9	15
	Abies amabilis	10,563	5.4	87	47
	T. heterophylla	111,387	24.4	413	55
	P. meziesii	66,570	64.1	1,261	62
	Totals	191,089	96.1	1,770	
Carbon River	*T. plicata*	22,583	27.2	386	73
	T. heterophylla	102,774	36.0	778	76
	P. menziesii	45,106	45.0	825	82
	Totals	172,795	109.5	1,989	
Cedar Flats	*T. plicata*	34,447	49.5	650	70
	T. heterophylla	65,228	19.1	308	61
	P. menziesii	85,418	74.6	1,575	90
	Totals	189,089	144.1	2,550	
Chinook	*A. amabilis*	52,900	42.0	692	56
	T. plicata	1,840	4.7	55	47
	T. heterophylla	42,753	23.0	334	59
	P. meziesii	3,470	4.7	47	61
	Totals	100,985	74.8	1,128	

To transform the canopy volume into a consistent, continuous form for using semivariance analysis, an imaginary cylinder was created at each sample point along the transect. This provides a "moving window" that measures canopy volume throughout the transect. All parts of tree crowns that fell within the cylinder were summed, and that value became the value for that spot on the transect. Due to the small size of the youngest stand, an 8-m diameter cylinder was the largest size possible (Figure 3). This was repeated every 2 m on all transects. We treated the values for a given transect similar to a time series, where distance along the transect was used instead of time. We then analyzed these series with a semivariance function to determine the variance and the dominant scale of the pattern within the series.

Principal Component Analysis

Principal component analysis (PCA) is a mathematical technique that transforms a number of potentially correlated variables into a smaller number of uncorrelated variables called principal components. The first principal component accounts for as much of the variability in the data as possible, and each succeeding component accounts for as much of the remaining variability as possible (Kendall 1975, Jolliffe 1986). The basic goal in PCA is to reduce the dimensionality of multivariate data. Principal component analysis was performed on a cross products matrix of Pearson correlation coefficients (i.e., centered and standardized by the standard deviation, McCune and Mefford 1999) among 13 stand-level structure variables (mean crown volume, standard deviation of crown volume, crown volume ratio, semivariance sill, semivariance lag, *PSME* density, *PSME* quadratic mean diameter, *PSME* basal area, *TSHE* basal area, total basal area, standard deviation of dbh, maximum height, and total stem density). The goal of this analysis was to elucidate dominant gradients of structure among the eight sites.

Results

Stand Characteristics

A total of 5,737 trees were mapped and measured on the 32 transects at the eight sites. Tree height and dbh ranged up to 90.3 m and 309 cm, respectively. The most obvious general stand-level trend was that height and canopy volume increased with increasing age of the stands, with two exceptions (Table 2). The TC stand (500 years old) had the

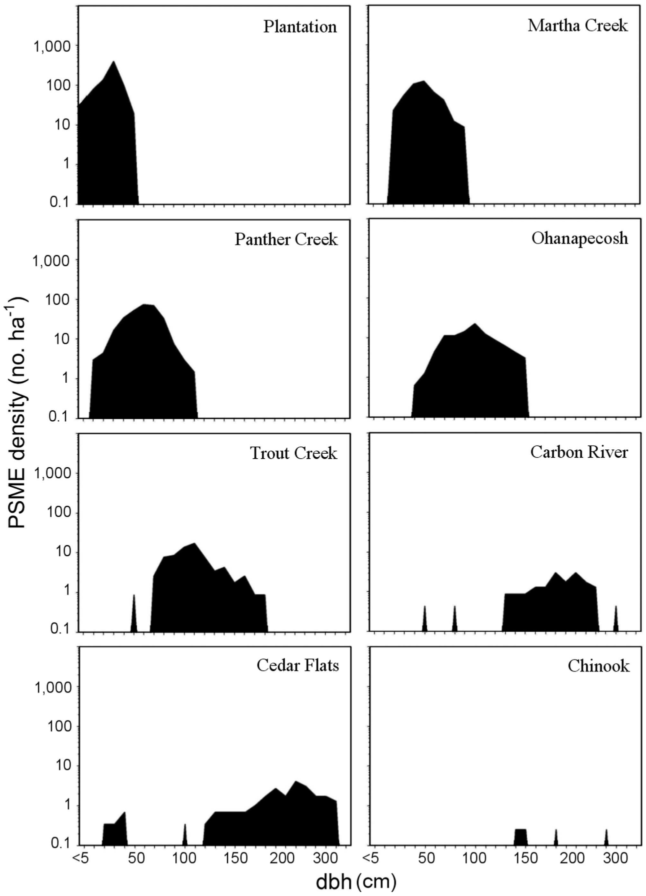

Figure 4. Diameter distribution for *PSME* among the eight sites. Note the vertical scale is logarithmic and the horizontal scale is not linear.

highest total canopy volume, which was largely due to the dominance of *TSHE* at this site. The site had an abundant *PSME* canopy, but the trees were relatively short and small for their age, reflecting a lower site productivity for this species at this site. At all of the sites, the canopy volume for *PSME* did not vary much. The youngest stand had a smaller *PSME* canopy volume, which is to be expected of this rapidly growing site. The lower stem density at the CR (500 years old) produced a smaller canopy volume at that site, both for *PSME* and the site as a whole. The *PSME* canopy volume at the CH site (950 years old) was greatly reduced, because most of its *PSME* population had long since died. CH, while having a higher proportion of *ABAM* than the other sites, was reduced in crown volume, basal area, and stem volume compared to the other old-growth sites.

Although the basal area and stem volume were highest at CF, the values for *PSME* stem volume were similar for several of the sites. The stem volume contributed by the relatively few huge *PSME* trees at CF was comparable to many of the sites, even the mature sites of MC and PC, which were composed of a much greater number of smaller trees. The difference in total volume was largely due to the contributions from the shade-tolerant species present in significant amounts in all of the older sites (Table 2).

The pattern of greater diameter of the *PSME* trees with increasing stand age was accompanied by decreasing density (Figure 4, Table 3). The presence of a few small *PSME* trees at both CR and CF is contrary to popular knowledge about regeneration strategies of this species. In both cases, large gaps caused by tip-ups of small groups of large trees provided an opening for this otherwise shade-intolerant tree. In addition, the preferred mineral soil seedbed of *PSME* was provided by the large root-wads of the fallen trees. However, this phenomenon (0.8 trees/ha at CR and 1.3 trees/ha at CF) was rare. The apparently small dbh *PSME* at TC represents suppressed but very old trees growing on poor microsites. The greater relative size and abundance of the shade-tolerant components (*TSHE*, *THPL*, *ABAM*, *TABR*) in the older sites was also evident. Indeed, when the shade-tolerant components were combined, the five sites >250 years old became quite similar (Figure 5, Table 2).

In this study, the standard deviation of dbh increased with stand age, with two exceptions (Table 3). The oldest site (CH) had a relatively low stand value due to the high density of small- to medium-sized shade-tolerant trees, causing it to rank similarly with the mature forest PC (150 years old). In addition, OH (280 years old) had a higher value than the older TC stand (500 years old). The 500-year-old *PSME* trees at TC are for the most part shorter and thinner than at OH. The basal area for the sites as a whole also increased in a similar manner with the same notable exceptions (Table 3).

Because complete inventories of heights are not often

Table 3. Stand characteristics for each site. The first column in each of the six categories listed are shown for all trees, followed by that for *PSME* alone. Stem count and basal area are per hectare values and include all trees >5 cm dbh. Mean diameter and the standard deviation of diameter are in centimeters, mean height and standard deviation of height are in meters, basal area is in m^2.

	Stem count		Mean dbh		σ dbh		Mean height		σ height		Basal area	
Site	Stand	*PSME*	Stand	*PSME*	Stand	*PSME*	Stand	*PSME*	Stand	*PSME*	Stand	*PSME*
PL	1,207	750	17.3	22.2	9.3	8.4	14.1	18.3	7.3	5.8	36.0	33.1
MC	469	455	42.5	43.5	17.4	15.0	33.6	34.5	8.8	7.4	78.6	78.3
PC	435	309	40.6	53.2	23.4	16.1	29.2	38.5	15.8	7.7	76.3	74.7
OH	327	105	48.7	92.6	37.4	22.8	30.6	57.9	22.4	7.8	99.1	75.3
TC	525	76	33.5	104.3	34.9	23.1	18.8	48.6	17.1	5.8	96.1	64.1
CR	285	17	44.1	184.0	52.7	42.6	25.5	68.8	21.5	10.8	109.5	45.0
CF	226	23	60.5	206.1	66.7	46.6	27.8	71.1	21.8	15.8	144.1	74.6
CH	974	1	20.4	190.5	24.4	52.1	26.5	51.2	14.2	7.8	78.3	4.7

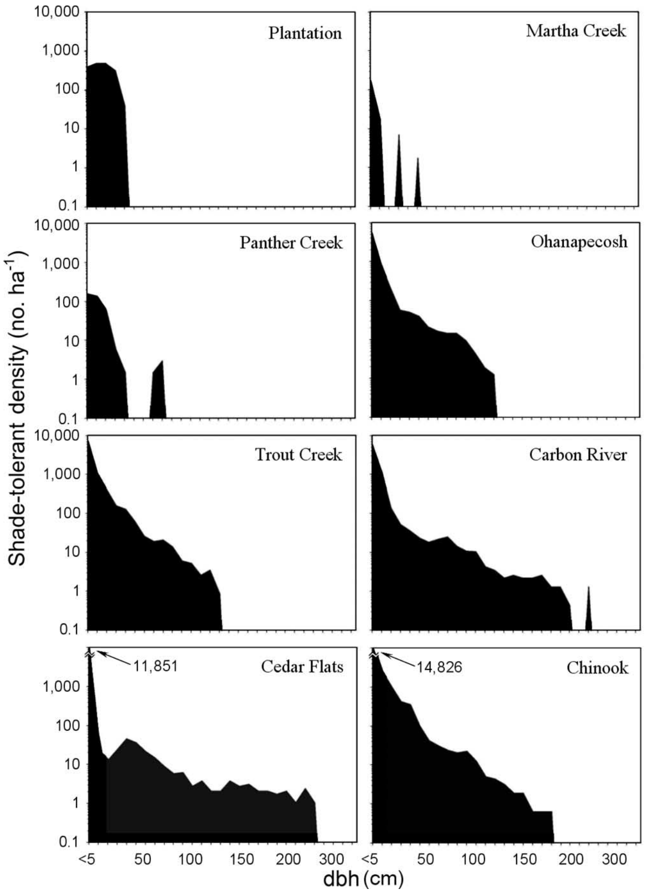

Figure 5. Diameter distribution for the shade-tolerant trees among the eight sites. The plantation has an unusually high number of shade-tolerant trees due to its proximity to an old-growth forest and thus an abundant seed source.

collected, metrics based on height are seldom used; however, in this case we had over 5,700 height measurements. The mean height of *PSME* or the standard deviation of height for the stand as a whole can also be used as a measures of structural complexity. These metrics behaves similarly to that of dbh, although are less dramatic (Table 3). The notable exception is the OH site, which scored the highest on the standard deviation of height. This "young" old-growth site has abundant shade-tolerant representation, but these are mostly in the smaller size classes. In addition, the main canopy of *PSME* still retains over 100 trees/ha, most of which exceed 55 m tall. This factor combined with the "missing" middle story of shade-tolerants results in the high standard deviation.

The abundance of snags that are most important for wildlife (decay class 4–6) is highest in the old-growth sites (Table 4). None of the large (over 1 m diameter) highly decayed snags appear until the old-growth stage (>250 years). Although the CR site has slightly more large, high-quality snags than CF, it also has the lowest density of live *PSME* among the old-growth sites, excepting only CH.

The amount and decay state of logs varied widely among sites. The percentage of the stand covered by logs varied from 4 to 27% (Table 5). The high value of percent cover by logs at the MC site was due to very high densities of *PSME* (455/ha at age 100, Table 3) that is actively undergoing competitive thinning, together with old logs that were legacies from the pre-1902 forest (Table 5). The mean MC log diameter and standard deviation of diameter are biased upward by this legacy from the preceding old-growth forest.

Vertical Distribution of Canopy Structural Elements

Using the crown models from all of the measured trees, a site-by-site comparison of composite crowns portrayed the vertical distribution of crowns among the eight sites (Figure 6). The PL site had the tightest range and sharpest peak of canopy distribution, which is typical of young *PSME* stands (Maguire and Bennett 1996). The shade-tolerant component dominated the mid- to lower-canopy positions in the old-growth sites. The development of the shade-tolerant component in the older stands causes the bulk of the canopy volume to be in the lower half of the vertical space, leaving the *PSME* canopy emergent above this. The dominant pattern of *PSME* development can be seen if it is separated from the other species (Figure 7). The six sites depicted showed that the total volume of tree crowns did not change much on maturity, but that this volume became stretched over a greater vertical space within the forest with increasing age. These data and the standard deviations for the vertical distribution of *PSME* crowns were summarized in

Table 4. Snag characteristics. Included are statistics for the population of snags from the current cohort most useful for wildlife (decay classes 4–6). Note that the standard deviation for both diameter and height increases more rapidly than do the means. Both Carbon River and Cedar Flats have snags in excess of 80 m tall. The snags/ha columns on the far right list the total number of snags/per hectare larger than the given diameter class (cm). Note that only stands >250 years have high-quality snags greater than 1 m in diameter.

	Snags/ha		dbh (cm)		Height (m)		Volume (m^3 ha^{-1})		Snags/ha		
Site	*PSME*	Total	Mean	σ	Mean	σ	*PSME*	Total	>50	>100	>150
PL	46	46	10.2	4.2	7.6	3.0	0.1	0.1	0	0	0
MC	197	197	18.5	10.6	10.2	7.4	24.7	26.5	6	0	0
PC	27	27	25.5	11.4	13.9	9.6	16.1	16.1	4	0	0
OH	31	33	72.5	30.3	16.0	13.5	418.7	529.4	28	8	0
TC	27	35	72.7	42.1	16.5	15.3	175.8	175.9	28	10	2
CR	25	66	83.9	66.7	21.3	16.2	438.5	526.9	18	13	6
CF	9	20	88.9	67.5	21.5	21.6	507.8	541.3	12	10	5
CH	2	27	74.7	37.7	14.2	9.2	82.2	191.4	23	4	1

Table 5. Log characteristics for each site. Highly decayed logs were often unidentifiable to species. These appear in the "All" columns.The average diameter size for all trees and *PSME* alone is higher for the Plantation site than for either of the next two sites due to the legacy of logs from the previous old-growth forest. Note the large mean diameter for *PSME* in the old-growth stands.

		Diameter (all trees)		Diameter (*PSME* only)		Volume (m^3 ha^{-1})	
Site	Land covered (%)	Mean	σ	Mean	σ	All	*PSME*
PL	7.8	37.1	21.8	35.0	24.6	296	152
MC	15.7	21.8	21.8	26.4	24.1	531	473
PC	3.8	25.4	15.1	26.3	15.0	106	105
OH	17.9	35.4	21.6	49.1	26.0	665	209
TC	9.4	36.8	28.5	53.3	41.8	400	186
CR	27.0	46.5	32.0	74.3	50.9	1,171	416
CF	16.7	53.9	37.2	86.2	36.8	886	527
CH	12.0	35.5	24.7	98.4	22.2	486	100

Table 6. While the peak generally rose to values in the mid 40s, the standard deviation of that peaks rose dramatically to values in the low- to mid-teens. Again, the TC site had lower values due to the shorter stature of the forest.

Horizontal Distribution of Canopy Structural Elements

Based on modeled measurements, the volume of space occupied by the canopy and its height was calculated along the length of each transect. These data had many characteristics of a time series, only with distance replacing time. Canopy gaps were depicted as dips in the series, while the high points of the series were larger trees or dense clusters of trees (Figure 8, Table 7). The semivariance sill value was proportional to stand age until the CH site was reached. Because the mean canopy value and the variation of these series data will both naturally increase with the increasing size of the canopy, a way to standardize the variation in the canopy volume distribution among the sites was to examine the ratio of the standard deviation of canopy volume with the means (Table 7). This ratio clearly indicated that the variability increased faster than the means, indicating increased structural complexity. The values generally increased from youngest through old-growth forests. The CH site maintained a high ranking with this measure of canopy structure, probably due to its large open areas near dense aggregates of tree crowns.

Canopy gaps were defined as holes greater than 10 m^2 present in all but the understory canopy layer. The size of canopy gaps was positively related to stand age (Table 8). The gaps in the youngest three stands reflected the presence of holes in the main canopy, whereas the remaining sites reflected *TSHE* filling in many of those gaps from below. The oldest three sites had open canopies, although the lower figure for the CR site, which had a very open upper canopy, reflected a large proportion of subcanopy *TSHE* (Table 8). The development of gaps as stands age offset any increases in canopy volume. The gaps were not only slightly larger as stands age, but total gap area was also highest in the oldest stands. The youngest three sites had similar gap percentages (Table 8), which were based exclusively on *PSME* mortality associated with competitive thinning or irregular initial canopy closure spacing.

Principal Components Analysis

PCA eliminated multicollinearity among the 13 structural variables and extracted three significant components (eigenvalues 8.90, 2.15, 1.17), accounting for 68.5, 16.5, and 9.0% of the total variation in the original 13 variables, respectively (Table 9a). The stand variables associated with structural complexity were all correlated with the first principal component (PC1). About half of the remaining variability was accommodated by PC2, which was strongly correlated with *PSME* basal area. Most of the residual variability (PC3) was correlated with the semivariance lag.

The relativized stand scores along PC1 clearly provided a ranking of overall structural complexity (Table 9b). In this analysis, the CH site dropped to the level of OH, a "young" old-growth site. Stand age was positively correlated with overall structural complexity (PC1) (Table 9c). When the CH site was removed from this analysis, the *r* value for this correlation increased to 0.969. Thus, structural complexity increased linearly with stand age until *PSME* disappeared from the stand.

Discussion

For all of the measurements of canopy structural diversity presented in this article, there was a positive relationship with increasing stand age—except for the oldest site, which had lost most of its *PSME*. The growth and development of large *PSME*, and their subsequent death, must then account for the majority of this variability. Overall, stand-level structural heterogeneity increases over time (Ishii et al. 2004). Horizontally, stands move from relatively evenly spaced canopies with small gaps to increasing aggregations of crowns resulting in sections of dense canopy and larger gaps. Stands begin with a simple, tight, vertical *PSME* crown distribution. The vertical distribution of crowns becomes increasingly diffuse via height growth, differentiation, crown expansion, and the addition of a shade-tolerant component. Thus, in a volume of space gradually increasing in height as stands age, progressively larger tree crowns occupy that space. However, canopy gaps are simultaneously increasing in size and extent (also see Song

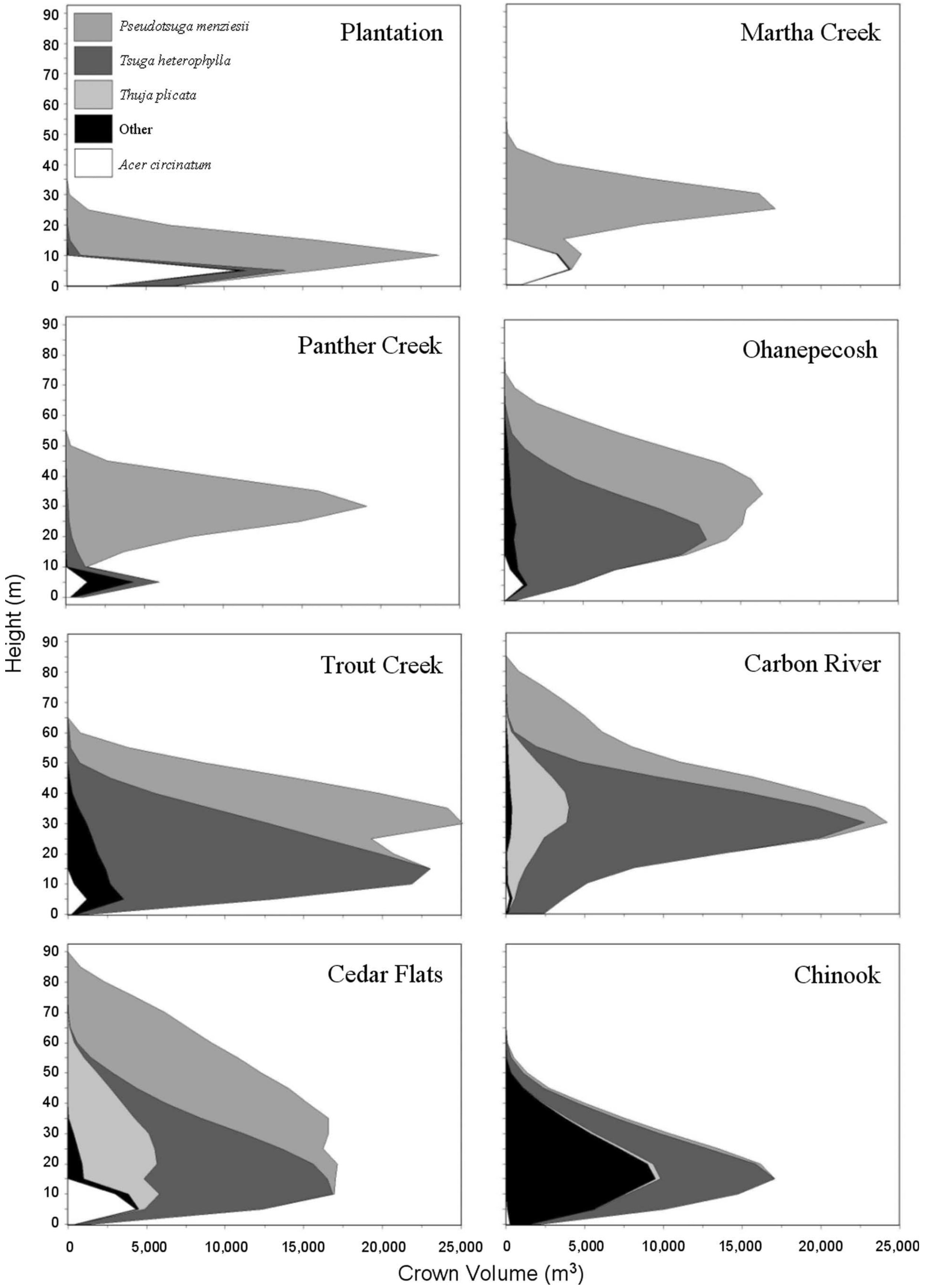

Figure 6. Crown volumes by species for the eight sites. The "Other" category refers to mostly *Cornus nuttallii* in the first three sites, and mostly *Abies amabilis* and *Taxus brevifolia* in the last five sites.

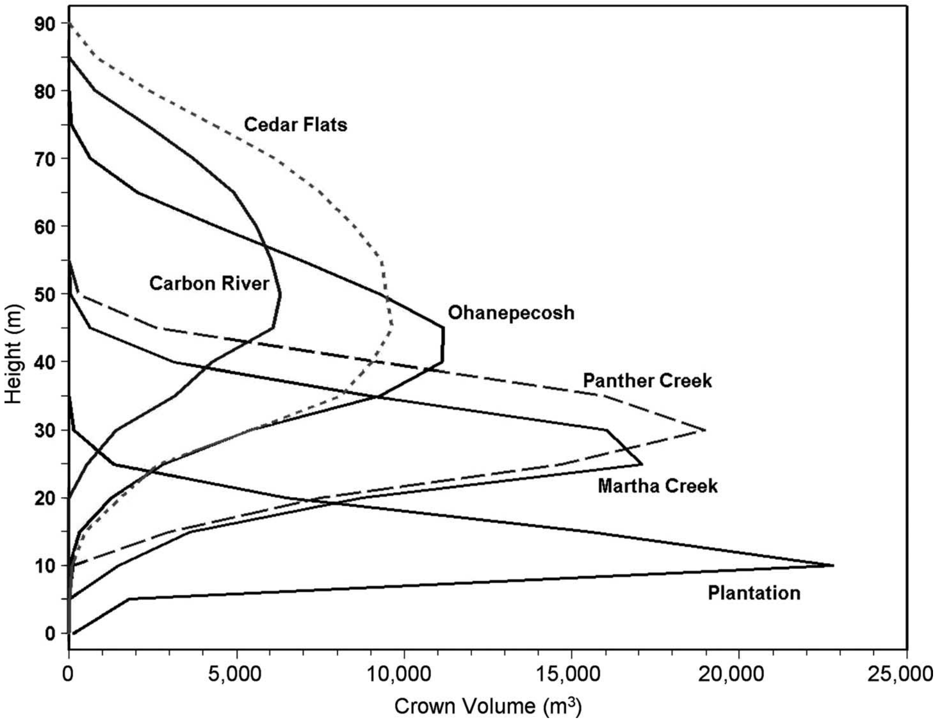

Figure 7. Canopy volume for *PSME* alone, extracted from Figure 6 for six of the sites. Note the lifting of the *PSME* crowns followed by a deepening of the crowns as one proceeds through the sequence.

Table 6. Vertical distribution of *PSME* crowns. Peak refers to the height where the maximum volume in *PSME* crown volume occurs for that site. The standard deviation of that vertical distribution is also given. CH is shown, but the standard deviation was not possible for too few data.

Site	Peak (m)	σ (m)
PL	11.2	4.43
MC	26.7	7.06
PC	30.3	7.31
OH	42.2	10.96
TC	37.1	8.27
CR	50.7	12.55
CF	46.6	15.35
CH	39.8	NA

et al. 2004). These two counteracting phenomena combine to transform the canopy from the relatively even, homogeneous structure of a young or mature forest into the extremely variable, heterogeneous structure of an old-growth forest. When the larger and taller *PSME* are no longer a dominant part of the canopy (as the CH site in this study), much of the horizontal variability remains, although the vertical variability is much simplified.

Many of the live, large trees at these *PSME*-dominated old-growth sites have some of the qualities of snags (e.g., cavities, rot pockets) that make them potential habitats for many of the wildlife species that use large snags (Thomas et al. 1979, USDA Forest Service 1991, Bull et al. 1997). Disease pockets, small-scale wind events, and insect attacks can all affect the state of a forest's dead wood component at a given point in time (Bull et al. 1997). The PL value is almost entirely due to older logs left after logging in 1952. The high values at both OH and CR are in part due to aggressive infestations of *Phaeolus schwinitzii*, a root rot that weakens lower stems and upper root collars of *PSME* and is the most common single cause of death in old-growth *PSME* (Bible 2001, Franklin et al. 2002).

Large *PSME*, both living trees and standing snags, in older forests represent the bulk of old-growth habitats in these forests, including the majority of substrates for epiphytic lichens (Pike et al. 1977, Sillett 1995, McCune et al. 2000) as well as prime nesting and denning sites for wildlife (Carey and Johnson 1995, Franklin et al. 2002). The fact that *PSME* is the largest structural element in these forests and also a pioneer species is somewhat unusual. This situation contrasts with some tall stature forests, where the largest tree species can perpetuate themselves in the stand without need of stand-replacing disturbances. For example, *Sequoia sempervirens* and *Sequoiadendron giganteum* maintain their presence in the forests that they dominate via shade-tolerance and small to moderate fire-based regeneration, respectively (Sawyer et al. 2000, Caprio and Swetnam 1995, Agee 1993), and *Liriodendron tulipifera* in the Smoky Mountains of eastern North America creates its own self-replacing gaps by virtue of large crowns that punch correspondingly large holes in the canopy after treefalls (Runkle 1985). *Eucalyptus regnans* forests of Victoria and Tasmania are perhaps most similar to *PSME* forests; their dominant trees are also pioneers rarely capable of regeneration within the forest without stand-replacing fires (Ashton 2000).

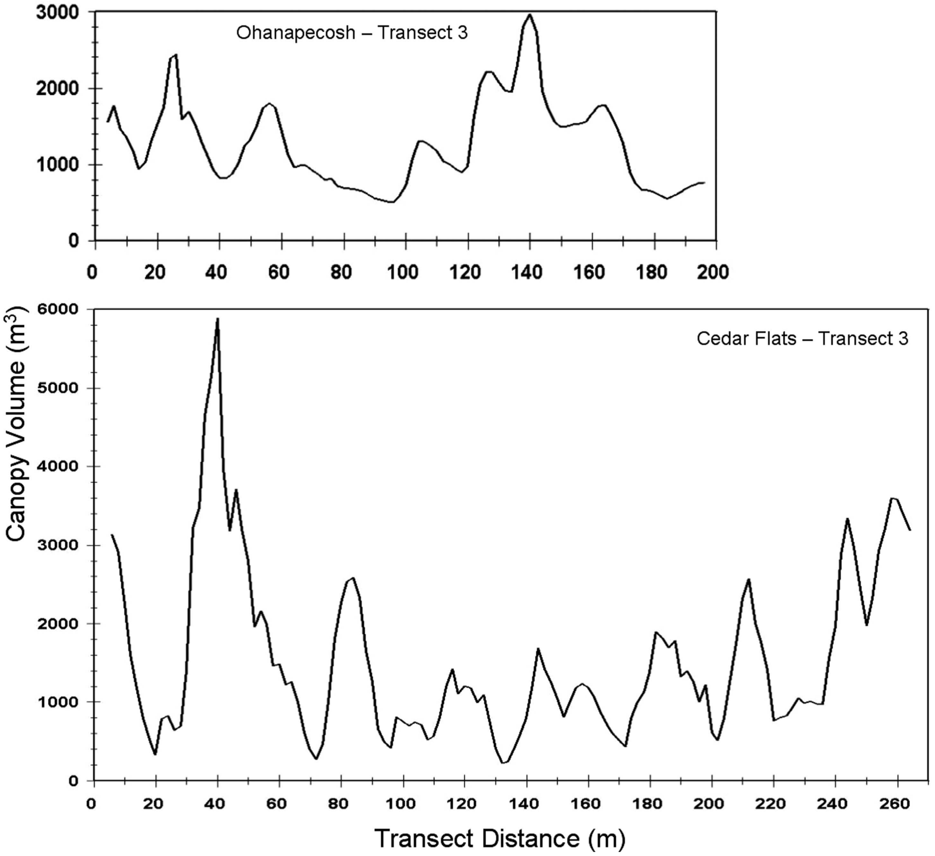

Figure 8. An example of the canopy density series curves used in the semivariance analysis. Only two of the transect curves are shown.

Table 7. Horizontal variability. The sill and range are outputs from the semivariance analysis. The mean canopy is the mean of all of the 8-m diameter cylinders for each site. The square root of the sill is equivalent to the standard deviation of all of the 8-m diameter cylinder measurements. The ratio column is the ratio of the square root of the sill over the mean canopy measure.

Site	Sill τ	Range (m)	Mean canopy (m^3)	$\sqrt{\text{Sill}} = \sigma$ (m^3)	Ratio
PL	7,929	28.0	271	89	0.329
MC	28,130	9.3	381	168	0.440
PC	36,460	11.9	439	191	0.435
OH	260,400	38.4	1,034	510	0.494
TC	505,200	8.8	1,181	711	0.602
CR	732,000	75.0	1,429	856	0.599
CF	1,060,000	18.0	1,552	1,030	0.663
CH	212,900	26.8	704	461	0.655

The presence of regenerating *PSME* in established old-growth stands (CR and CF) is unusual, but not rare. In this study, these were situations where tip-up mounds had provided elevated mineral soil in blowdown patches large enough to allow abundant light into the understory. In other forests where this phenomenon has been observed, it invariably is on very productive sites, rather than sites of moderate productivity. In the rainforest valleys of the western Olympic Peninsula, regenerating *PSME* are occasionally found on south-facing bluff scarps that allow much greater light even in fairly closed-canopy situations. The influence of wind and decay on these moist sites also maintains a fairly open canopy throughout the life of the forest (McKee

Table 8. Gap statistics. Gap (%) refers to how much of each forest stand is gap, based on canopy projections. Gap size refers to the sizes of actual gaps, both mean size and the standard deviation, in square meters.

		Gap size (m^2)	
Site	Gap (%)	Mean	σ
PL	18.6	11.6	1.6
MC	22.6	21.0	3.6
PC	19.2	31.2	7.0
OH	9.1	13.9	3.1
TC	13.7	27.4	8.8
CR	13.1	58.7	24.4
CF	26.5	116.1	47.7
CH	31.2	63.3	21.9

Table 9. Results from PCA. (a) Thirteen structural measures from each of the eight stands were compared. The first axis captures 68.5% of the variability and clearly is related to structural complexity. σ represents the standard deviation; qmd is the quadratic mean diameter. (b) Relativized stand scores from (a). (c) A second matrix contained the eight stands as well as two environmental variables. When the Chinook site is removed from the analysis, the *r* value for age becomes 0.969. Bold indicates significance.

	PC1	PC2	PC3
a) Mean crown volume	**0.97**	0.06	0.1
σ crown volume	**0.96**	0.06	–0.14
Crown volume ratio	**0.81**	–0.15	–0.56
Semivariance sill	**0.93**	0.07	–0.04
Semivariance lag	0.38	–0.47	**0.79**
PSME density	**–0.9**	0.13	0.1
PSME qmd	**0.89**	–0.39	–0.14
PSME basal area	0.1	**0.98**	0.13
TSHE basal area	**0.81**	–0.4	0.24
Total basal area	**0.94**	0.34	–0.04
σ dbh	**0.96**	0.18	0.11
Max height	**0.93**	–0.11	–0.02
Total density	–0.65	–0.66	–0.29
b) Plantation	0	0.372	0.45
Martha Creek	0.216	1	0.344
Panther Creek	0.258	0.964	0.409
Chinook	0.55	0	0
Ohanepecosh	0.568	0.819	0.705
Trout Creek	0.644	0.768	0.107
Carbon River	0.869	0.393	1
Cedar Flats	1	0.921	0.06
c) Age	**0.731**	–0.501	–0.41
Elevation	–0.406	–0.573	–0.062

et al. 1979). In experimental openings in old-growth forests, *PSME* regeneration did not occur until the openings were 30–35 m in diameter (Gray and Spies 1996).

Our results should not be viewed from the perspective of chronosequence research. Our aim was to select stands that display the full range and structural development of *PSME*. Naturally, because time is one of the major factors influencing this, the stands are for the most part arrayed along a time line. Even though we selected stands that have had no major disturbances since stand creation, there were differences in site quality and initial conditions. As has been shown by others, mature *PSME* forests vary greatly as to the amount and timing of the formation of the shade-tolerant component, especially *TSHE* (Kuiper 1994, Franklin et al. 2002). For example, our stands MC and PC both originated after very large, hot fires. The seed availability for the shade-tolerant species was thus very low, with the result that they currently contain fewer of these species then many similar forests of the same age (Keeton 2000).

Historically, humans in the Pacific Northwest region have reduced the area of old-growth forests and replaced it with plantations of the same dominant species (i.e., *PSME*). These second-growth forests exhibit much simpler structural attributes, as has been shown here and elsewhere (Spies and Franklin 1991, Dubrasich et al. 1997). They are efficient at producing wood for lumber and pulp, but forest ecologists, wildlife managers, and artists often discount their value as diverse habitat – each tree is nearly the same shape and size as every other tree. Despite these contrasting forest conditions, many studies have documented that, given time, these structurally impoverished monocultures will evolve into old-growth forests (Spies and Franklin 1991, Kuiper 1994, Franklin et al. 2002, Winter et al. 2002).

What is not clear, however, is how the structural changes induced by individual trees growing older and larger can elicit many other, subtler changes in other aspects of forest structure at the stand level, which may in turn affect aspects of whole-forest function. The quantitative study of replicated stands in forests of different ages that examine the details of within-tree dynamics has never been attempted.

One example of a within-tree process by which stand structure develops is the development of epicormic branching. Epicormic branches occur abundantly on primary branches of *PSME* (Ishii and Ford 2001), but they can also develop on the main stem at the locations of dead or former branches (Bryan and Lanner 1981, Ishii and Wilson 2001). Many of these stem-based epicormic branches occur below the main crown and often produce distinct, fan-like branch formations in areas of the bole that are otherwise free of branches (Van Pelt and North 1999, Ishii 2000). Naturally occurring stands are often dense and poorly differentiated with respect to height. As self-shading develops, lower branches die, the crown recedes and 'lifts' relative to the total height of the stand. Later, as trees grow taller and more light penetrates the canopy, epicormic branches develop in the lower crown (Kramer and Kozlowski 1979). This "crown lowering" continues, creating characteristic deep crowns of *PSME* in old-growth forests (Van Pelt and North 1999, Ishii and Wilson 2001). Many other processes of stand structural development, however, remain unknown.

Since 1999, we have been investigating the processes by which young forests undergo the striking changes we see in structural diversity and functional characteristics. As a subset of a larger-scale study to create database tools for canopy ecologists, the goal of this larger study was to produce a detailed quantitative analysis of the structural development that occurs at the stand level, tree level, and branch level in a range of *PSME* forests. In addition, a suite of functional measurements have been carried out concurrently to elucidate the controls that structural attributes have on forest function. Our approach was to take ground-based measurements of the forest structural elements and then model the crowns in 3-D space, then go into those same trees and carry out a more detailed analysis. Currently, we are examining this same collection of eight sites in much more detailed, branch-based analyses.

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