Three-Dimensional Canopy Structure of an Old-Growth Douglas-Fir Forest

Bo Song, Jiquan Chen, and Janet Silbernagel

ABSTRACT. In this study, the structurally heterogeneous canopy of a 12-ha plot in an old-growth Douglas-fir forest was analyzed using three-dimensional (3-D) canopy modeling, geographic information system (GIS), and spatial statistics. Using this approach, we were able to depict how species composition and spatial distribution affect the 3-D structure of canopies. We were also able to slice the canopy and calculate the canopy coverage at various heights, and therefore were able to calculate the cumulative canopy volume at individual crown bases. Information generated by GIS allowed us to calculate how much area canopies or canopy openings occupy. Total canopy volume (243,641 m^3/ha) was dominated by western hemlocks (67.1%) and Douglas-firs (23.7%) in this plot. Western hemlocks and Douglas-firs also dominated the canopy coverage, with 65.7% and 25.5% average coverage, respectively. Average total canopy coverage was 84.3% with variations between 78.7% and 89.9% among the 12 1-ha subplots, implying that 15.7% of the stand consisted of canopy openings. Coverage of the canopy projection changed greatly from the lower to the upper canopy layers, with the maximum at about 20 m high. We also examined spatial relationships among groups of trees at different heights and at various scales using bivariate Ripley's K analysis. We found that different species of the understory layer showed different spatial relationships relative to the overstory canopy layer. Likewise the same species in the understory layer showed different spatial relationships when the overstory species differed. This approach provided a useful tool for characterizing 3-D forest canopies, and the results will be very helpful for examining leaf distribution, understory light environment, understory vegetation, and microclimate. FOR. SCI. 50(3):376–386.

Key Words: Canopy opening, vertical structure, GIS, Ripley's K analysis.

REALISTIC REPRESENTATION OF CANOPY STRUCTURE in three-dimensional (3-D) space is a necessary initial step in studying canopy-related ecological processes. Parker (1995) defined canopy as "the combination of all leaves, twigs, and small branches in a stand of vegetation; it is the aggregate of all the crowns." As an interface between forests and the atmosphere, canopies receive and release energy and materials (e.g., carbon dioxide and water) through photosynthesis, respiration, and evapotranspiration, and thereby create a microclimatic regime within the canopy (Chen et al. 1993, 1999) that drives understory processes (Song 1998, Van Pelt and Franklin 1999, 2000, Quinby 2000). Forest canopies also determine ecosystem processes and functions such as microhabitats for

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plants and wildlife (Dial 2004), properties of the forest floor (e.g., sun flecks, throughfall), and even belowground processes such as energy flux, regeneration, decomposition, and respiration (Runkle 1991, Naumburg and DeWald 1999, Nadkarni and Sumera 2004). The spatial and temporal properties of these biophysical processes are directly related to horizontal and vertical arrangement of forest canopies and their changes at multiple temporal scales (Parker and Tibbs 2004).

In some environments, foliage arrangement in 3-D space may be much more important than the total amount of foliage (Van Pelt 1995, Ishii et al. 2004). A tall, multi-layered forest may have a much greater volume for foliage to occupy, hence a more open canopy. Thus, understanding of how crowns occupy the 3-D space has been the subject of numerous studies (Van Pelt 1995, Song et al. 1997, Chen and Bradshaw 1999, North et al. 2004). One traditional approach to quantify the canopy structure is the leaf area index (LAI; Gholz 1982, Franklin and Waring 1980). However, these LAI values can be misleading in reflecting the potential light levels in the understory (Brown and Parker 1994). For example, an even-aged mono-layered forest may have the same LAI value as a multi-layered forest, but the understory light conditions under these two forest canopies can be very different from each other. The traditional use of two-dimensional (2-D) canopy projection analysis is of little use because forest stand biomass is unevenly distributed vertically. Hubbell and Foster (1986) measured the vertical distribution of foliage and the spatial distribution of stems, but they didn't integrate the canopy structure with 2-D spatial pattern of trees. Effective methods are now available for analyzing the complex 3-D structures of canopies. These methods include point pattern analysis (Chen and Bradshaw 1999), 3-D canopy modeling (Silbernagel and Moeur 2001, Song et al. 1997, Song 1998, Van Pelt and Franklin 2000), remote sensing (Harding et al. 2001, Lefsky et al. 2002), and application of geographic information systems (GIS; Song et al. 1997).

Description of crown architecture is the first step in modeling forest canopies. Terborgh and Petren (1991) treated crowns as cylinders, and Van Pelt and North (1996) treated crowns as several geometric shapes, such as cylinders, cones, and paraboloids. Song et al. (1997) extended this approach by using a set of equations to simulate crown shapes. Our study objectives were to: (1) present a new approach of slicing forest canopies using a stem-mapped database of an old-growth Douglas-fir forest in southern Washington, (2) understand how species composition and spatial distribution of trees affect the characteristics of canopies in 3-D space, and (3) discuss potential applications of the methods and results in relevant forestry research.

Methods

In this study, forest canopies were simulated by modeling individual crowns, which were then placed onto the spatial locations of corresponding trees. This process required knowledge of tree locations, heights, crown lengths, and crown shapes. GIS ArcView (V3.2, Environmental Systems Research Institute, Redlands, CA) was used to analyze the canopy structure both horizontally and vertically. To quantify how stem distribution may affect canopy structure, bivariate Ripley's K analysis was used to examine their spatial randomness. Details of how 3-D canopy modeling, GIS, and spatial statistics were used for analyzing 3-D canopy structure are described below.

Study Site

Our study site was located at the Wind River Canopy Crane Research Facility (WRCCRF) in the T.T. Munger Research Natural Area of the Wind River Experimental Forest, 45°48′ N, 121°58′ W, on the Gifford Pinchot National Forest in southern Washington. This 450-year-old forest stand is dominated by Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*), with the dominant trees averaging 55 to 65 m (maximum 67 m) tall. Other tree species include western redcedar (*Thuja plicata*), western white pine (*Pinus monticola*), Pacific silver fir (*Abies amabilis*), grand fir (*A. grandis*), and noble fir (*A. procera*). Understory trees include Pacific yews (*Taxus brevifolia*). The site is in the Wind River valley at 355 m above sea level, within the southern Washington Cascade Range (Shaw et al., in press). The forest represents the end-point of age, biomass, and structural complexity gradients in coniferous biomes of the western Cascades (Franklin et al. 2002).

Field Data Collection and Analysis

A 12-ha (400 × 300 m) plot was established at the study site between 1994 and 1998 (Figure 1). Trees with diameters at breast height (dbh) greater than 5 cm were measured and identified to species. Their coordinates (x, y) and elevation (z) were measured using a computerized total surveying station (WILD TC600 Total Station, Leica Geosystems AG, Heerbrugg, St. Gallen, Switzerland). Crown dimension detail was collected from a canopy crane that had a 75-m vertical reach and an 85-m radius. The crown radii of different species were measured at various vertical heights from the crown's top to its base, at up to four cardinal directions (sometimes the gondola of the crane could not access all four directions). Because only 26 trees were measured using the canopy crane, the maximum crown radii of the additional 194 trees were measured from the ground using a meter tape and a compass. The Laser Impulse Rangefinder (Laser Technology Inc., Centennial, CO) was used to measure the crown base heights. Regression models developed from field measurements of dbh and the maximum crown radii were used to estimate the maximum crown radii of all live trees (>5 cm in dbh) within this 12-ha plot. To get the heights of all live trees (>5 cm in dbh), regression models of dbh and height relationships were developed by species from field measurements. One set of tree height data was measured from the ground (225 trees) using the Criterion Laser (Laser Technology Inc.), and another set of height data was measured from the crane (307 trees). All data that were collected using different methods were calibrated before they were combined.

Canopy structure was modeled based on a stem map and

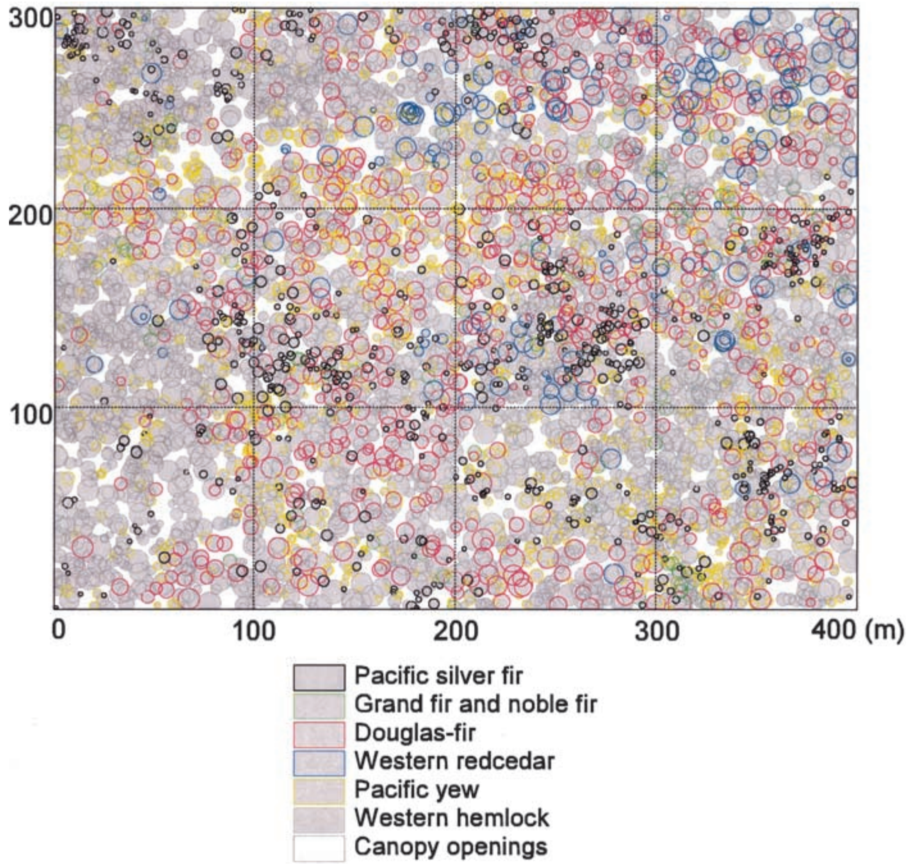

Figure 1. Crown projection of a stem-mapped 12-ha (400 × 300 m) old-growth Douglas-fir forest in the Wind River Canopy Crane Research Facility in southern Washington. Different colors and sizes of the circles represent different species and crown sizes. Blank spaces are canopy openings.

a crown geometry model and then tested using independent field data (Song et al. 1997, Song 1998). The vertical shapes of crowns are very important in characterizing crown shells. After comparing various crown models (Van Pelt and North 1996, Baldwin and Peterson 1997, Biging and Samantha 1997, Dubrasich et al. 1997, Song et al. 1997, Silbernagel and Moeur 2001), a flexible and relatively simple model, the generalized Poisson density function, was used to characterize various vertical crown shapes. This model is flexible for different shapes and, more importantly, each parameter provides an explicit interpretation for the crown vertical profile. Although the crown model was designed to simulate asymmetric crown shapes, field investigation showed that the differences among crown radii along four cardinal directions were smaller than the errors of the field measurement, thus these differences were ignored.

GIS ArcView was used to explore the 3-D canopy structure and to analyze the variation across horizontal space. The outputs of the model include the total projection of canopies of all trees in the plot and canopy cross-section (slicing) at six heights (5, 10, 20, 30, 40, and 50 m) for all species collectively, as well as each of the six individual species: Douglas-fir, western hemlock, western redcedar, Pacific silver fir, Pacific yew, and other firs (grand fir and noble fir, which were grouped because of their low density). Locations were classified into two categories, canopies and canopy openings, using ArcView.

Using a unique crown geometry model for each species, each individual crown volume was calculated cumulatively by slicing the crown at 1-m intervals from the crown base to the top of the canopies. While this method assumed that tree crowns were solid foliage, it kept the 3-D spatial arrangement of the crowns intact (Song et al. 1997, Song 1998, Van Pelt and Franklin 2000). The 12-ha study area was overlaid with a grid map so that individual 1-ha subplots could be analyzed (the grid size = 100 × 100 m, or 1 ha, and n = 12). We calculated statistics (e.g., mean, standard deviation) of the canopies such as crown projections at a given height, crown volume of the stand, and cross-section of a species using a replicated measure of $n = 12$.

Several comparisons were made using either the live stems of the same species at different heights or stems of different species at different heights to see how the overstory canopy of large trees would affect the understory layer of small trees. Based on a preliminary comparison of the canopies (Song 1998), we chose trees with heights ≤5 m as the understory layer group and trees taller than 45 m as the overstory layer group to further explore whether distinct features existed for these two layers. Within the 12-ha plot, the understory canopy was mainly Pacific silver firs, Pacific

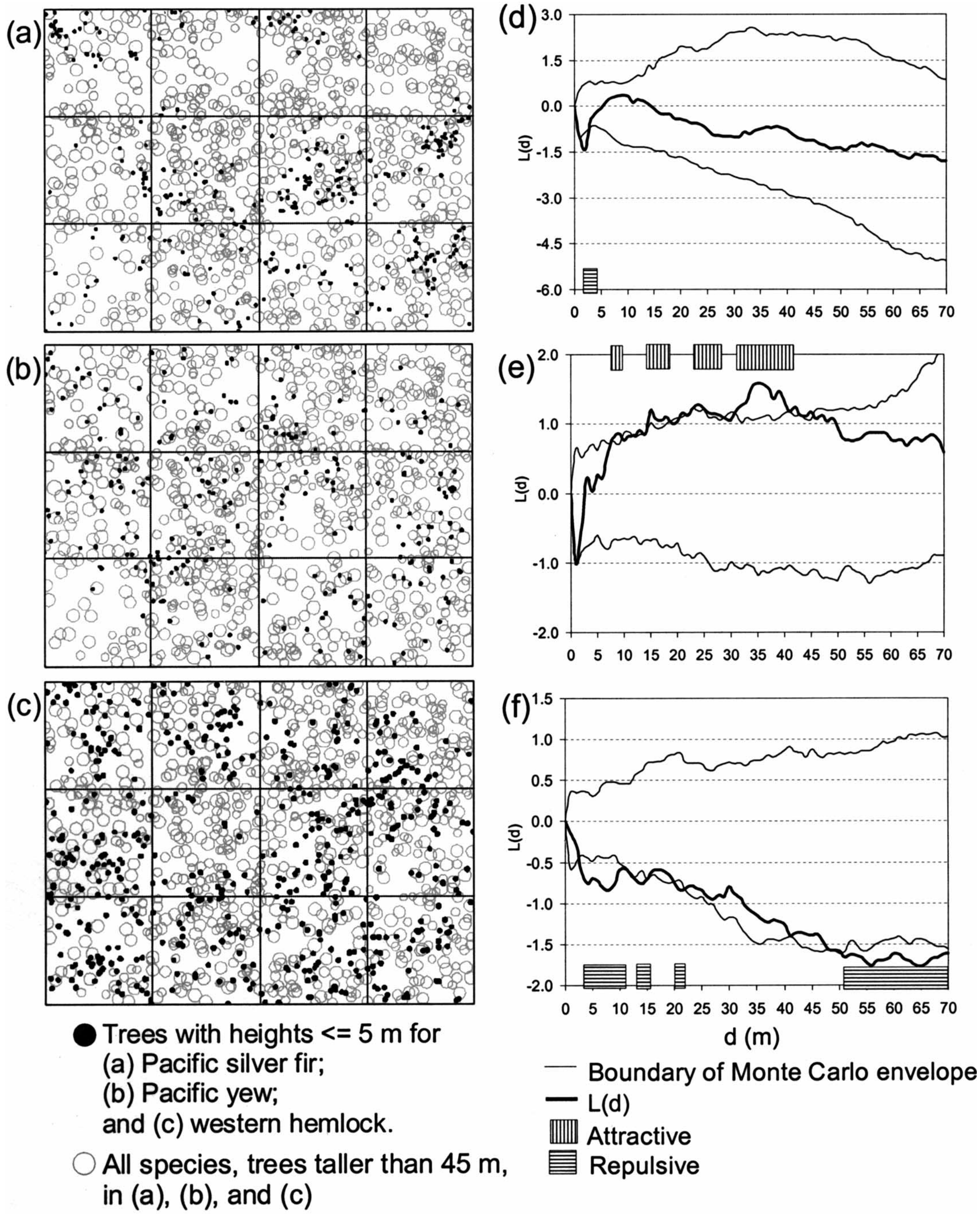

Figure 2. Canopy projections of understory Pacific silver firs (a), Pacific yews (b), and western hemlocks (c) compared to the overstory canopy layer of all species. Size of circles represents crown sizes. Panels d, e, and f show bivariate Ripley's K analyses of the spatial relationships of understory Pacific silver firs, Pacific yews, and western hemlocks to the overstory canopy layer, respectively. When the thick solid line is above the Monte Carlo envelope (two thin lines), understory trees have attractive responses to the overstory canopy layer, but when the thick solid line is below the envelope, understory trees have repulsive responses to the overstory canopy layer.

yews, and western hemlocks, while the overstory canopy was mainly western hemlocks and Douglas-firs (Chen et al. 2004).

Our initial analysis indicated that small Pacific silver firs, Pacific yews, and western hemlocks (shorter than 5 m) showed different spatial relationships to the distribution of large trees (taller than 45 m). Because the spatial distribution of large western hemlocks and Douglas-firs was different, their spatial relationships to small western hemlocks were also different. To facilitate our effort in quantifying how stem distribution may affect canopy structure, bivariate Ripley's K analysis was used to examine their spatial randomness (Ripley 1977, Diggle 1983, Moeur 1993, Van Pelt 1995). Bivariate Ripley's K is widely used for analyzing the

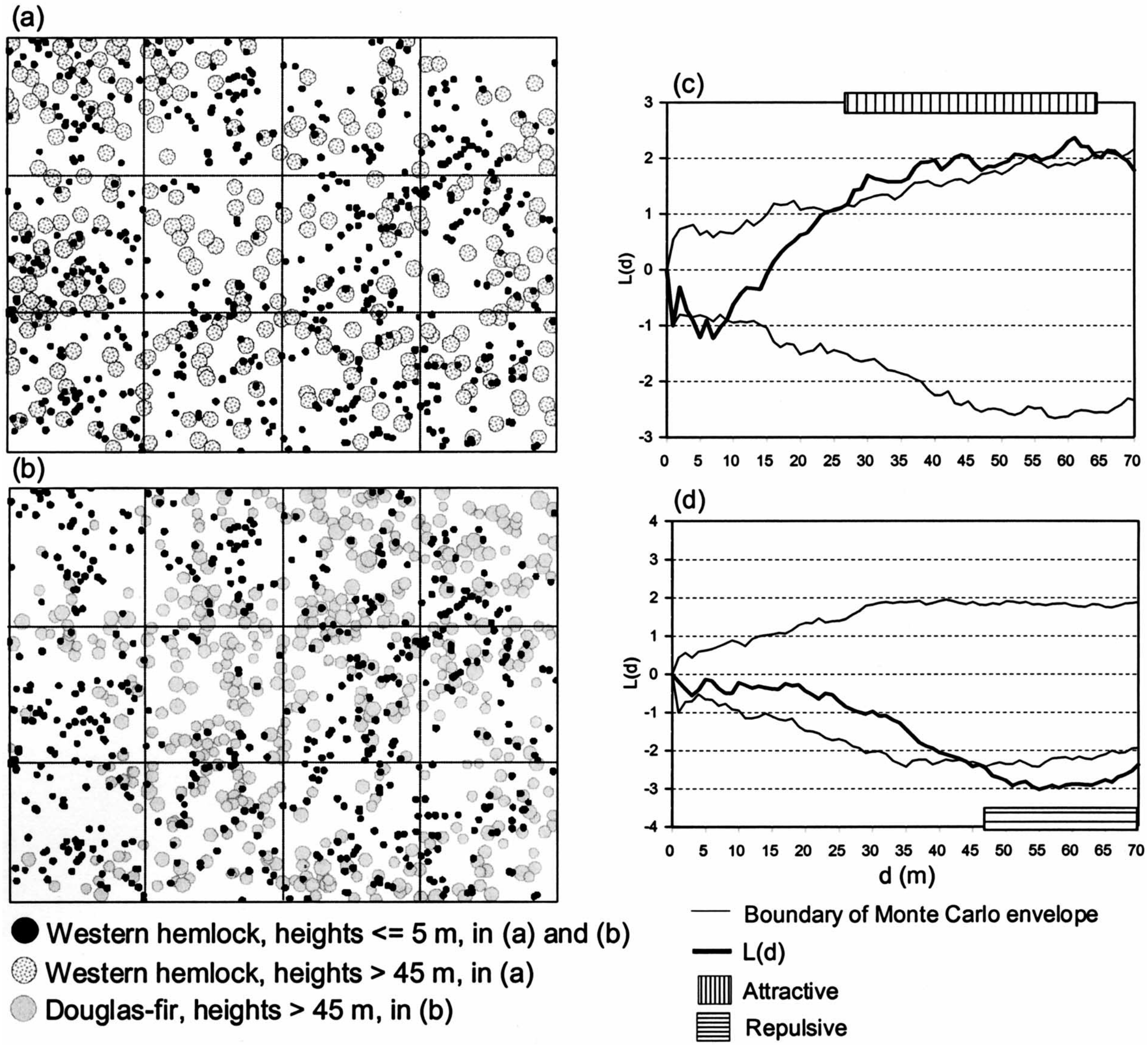

Figure 3. Canopy projections of understory western hemlocks compared to the overstory layer of western hemlocks (a) and Douglas-firs (b). Panels c and d show bivariate Ripley's K analyses of spatial relationships of understory western hemlocks to the overstory layer of western hemlocks and Douglas-firs, respectively. The interpretation of the figure follows that of Figure 2.

spatial relationship of one data set to another data set. Software developed by Moeur (1993) was used for bivariate Ripley's K analyses. One hundred Monte Carlo runs were performed to generate a 90% ($2\alpha = 0.05$) Monte Carlo envelope (two thin lines in Figure 2, d–f, and in Figure 3, c and d), so that observed and hypothesized distributions could be compared at this significance level. The spatial relationship between two different data sets in a plot were then determined by $L(d)$, $K(d)$'s square root transformation (Diggle 1983), an index that is used to identify the spatial relationship (thick and bold lines in Figure 2, d–f, and in Figure 3, c and d). The null hypothesis was that the spatial pattern of one data set is independent of another data set ($L(d) = 0$). Larger than expected (positive) $L(d)$ indicates an attraction between two data sets. Conversely, smaller than expected (negative) $L(d)$ indicates a repulsion between two data sets.

Results

Western hemlocks and Douglas-firs dominated the canopy, with 65.7% and 25.5% average ($n = 12$) coverage, respectively (Table 1). Average total canopy coverage was 84.3% with variations between 78.7% and 89.9% among the 12 1-ha subplots (Table 1), implying that 15.7% of the stand consisted of canopy openings. Total canopy volume (243,641 m^3/ha) was also dominated by western hemlocks (67.1%) and Douglas-firs (23.7%, Table 1). Forest composition measured by canopy characteristics (cover or volume) was different from that based on stems (i.e., density). For example, Pacific yews accounted for 22.1% of the total stems in the plot but contributed only 12.6% and 2.0% of overall canopy cover and volume, respectively.

There appeared to be distinct canopy patchiness among tree species and a complex structure across the 12-ha plot

Table 1. Canopy coverage and volume of six species in a 12-ha plot of old-growth Douglas-fir forest.

	Species						
	ABAM	ABGP	PSME	TABR	THPL	TSHE	Total
Density							
No. of trees/ha	49.9	4.1	31.1	96.4	14.1	241.9	473.5
Percent (%)	11.0	0.9	7.1	22.1	3.2	55.3	100.0
Canopy coverage (%)							
Minimum	0.3	0.3	11.0	7.9	0.0	58.0	78.7
Mean	4.7	2.6	25.5	12.6	6.6	65.7	84.3
Maximum	10.4	5.0	39.5	16.6	24.4	76.9	89.8
Standard deviation	2.7	1.3	8.8	2.8	7.4	5.6	3.2
Canopy volume (m^3/ha)							
Minimum	109	466	21,489	3,030	2,118	124,743	204,059
Mean	1,423	3,116	57,691	4,865	15,586	163,559	243,641
Maximum	3,635	6,870	97,888	8,033	56,734	204,559	279,336
Standard deviation	997	1,806	21,924	1,394	16,923	27,133	23,096

ABAM, *Abies amabilis* (Pacific silver fir); ABGP, *Abies grandis* and *A. procera* (grand fir and noble fir); PSME, *Pseudotsuga menziesii* (Douglas-fir); TABR, *Taxus brevifolia* (Pacific yew); THPL, *Thuja plicata* (western redcedar); and TSHE, *Tsuga heterophylla* (western hemlock).

(Figure 1). Canopy projections showed irregular shapes of canopy openings, with some being linear and highly connected across the stand. Western hemlocks, Douglas-firs, and western redcedars had larger crowns than other species. Crown sizes vary in a wider range for western hemlocks. Across the stand, there existed clustered patches of Pacific silver firs with small crowns, whereas dispersed Pacific yews also had small crowns but no obvious clumping.

There were also clear vertical changes in canopy patchiness, including species composition and spatial distribution of canopy patches (Figure 4, a–f). At intermediate canopy layers (10–30 m heights), species richness and coverage were higher (Figure 4, b–d). At 50 m aboveground, the canopy was mostly dominated by Douglas-firs (Figure 4f). Above 30 m height, Pacific yews were absent and very few Pacific silver firs were present (Figure 5, a and d). In contrast, there were almost no Douglas-fir crowns below 20 m (Figure 5c). Among the six species, Pacific silver fir had the lowest canopy cover (maximum canopy cover only reached 1.5%; Figure 5a, Table 1), whereas western hemlocks had the highest cover (maximum canopy cover greater than 50%; Figure 5f, Table 1). Western hemlocks dominated the canopy below 35 m height and reached their maximum canopy coverage at about 20 m height (Figure 5f). The main canopy cover of Pacific yews was from 5 to 10 m in height, with the maximum canopy coverage at about 5 m height, and they disappeared above 20 m height (Figure 5d). The crowns of Douglas-firs first appeared at 10 m high, dominated above 35 m height, and reached maximum coverage at about 40 m high (Figure 5c). Although there were few western redcedars (only 6% of all live trees), their coverage was not small and was distributed across almost all canopy layers (5–40 m high) and reached the maximum at about 10 m height (Figure 5e). Western redcedars had a highly variable distribution among the 12 subplots at different heights (Figure 5e). Coverage of total canopy projection and openness also changed greatly from the lower to the upper canopy layers, with the maximum canopy coverage at about 20 m high (Figure 6).

Discussion

In this study, we characterized the 3-D canopy structure by modeling crown size and shape, and then placing the simulated crowns onto the spatial locations of corresponding trees. Because crowns were put onto the field measured stem map, 2-D structure of an assemblage of crowns and the 2-D association of stems were associated. Applications of quantitative methods provided a useful means to simulate canopy structure, while GIS provided spatially explicit maps and related information for further analysis. We analyzed the canopy of a 12-ha old-growth Douglas-fir forest by slicing the canopies at various vertical levels for reconstruction of their features in a 3-D space. Our analysis was also performed in the context of species composition and spatial relationships among trees of different groups. Spatial point pattern analysis (e.g., Ripley's K) allowed us to determine the heterogeneity of the canopy structure at different scales as any crown is attached with a specific stem, and to understand how species composition and spatial distribution affect the formation of the 3-D canopies. 3-D canopy modeling with explicit spatial information allowed us to slice the canopy at any height, and to calculate the canopy cross-section at any height, thus allowing the estimation of the cumulative canopy volume of either individual crowns or the entire stand. Also, the application of GIS for canopy mapping provided a new perspective of forest canopy structure for effective analysis of the canopy structure in both horizontal and vertical dimensions. In addition, it provided spatially explicit maps and spatial relational databases. Information generated by GIS allowed us to quantify the exact coverage for both canopy and canopy openings.

A forest is composed of multiple trees of different species. Classical structural analysis and description has placed much focus on the boles (e.g., dbh and diameter distribution, basal area, and height), likely because of timber production needs (Chen and Bradshaw 1999). Recently, emphasis on canopies in forestry research has increased due to their critical roles in regulating ecosystem processes and

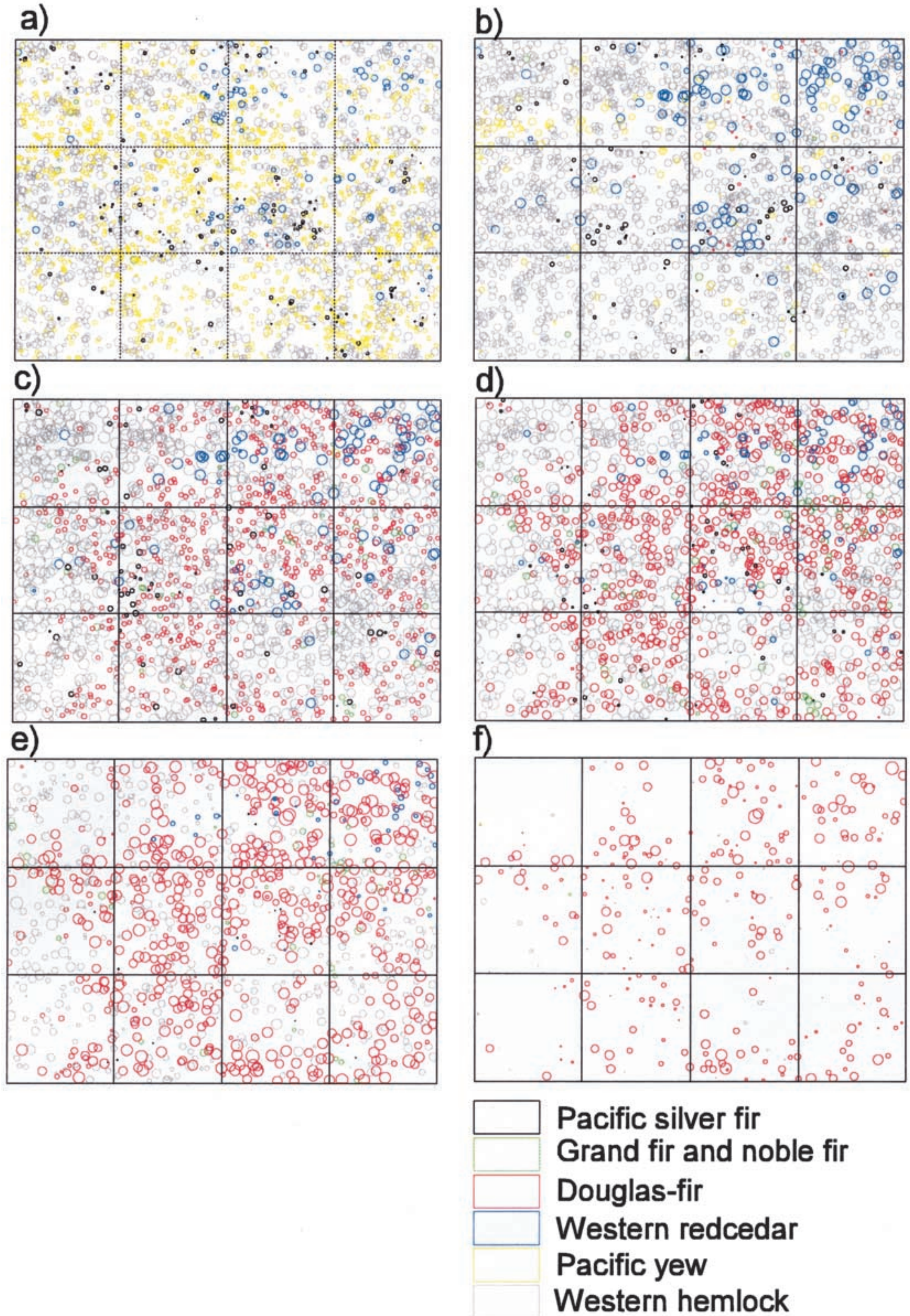

Figure 4. Sliced canopy covers at 5, 10, 20, 30, 40, and 50 m heights. Circle sizes represent the sliced crown sizes at these heights.

overall function. While stand characteristics based on stem data will remain necessary measurements, results generated in this study clearly indicate that forest structure based on canopy characteristics might differ from those based on stems. For example, the old-growth Douglas-fir forest in this study was shown to be dominated by western hemlocks, Pacific yews, and Pacific silver firs when stem data was used (Table 1, Chen et al. 2004), yet Douglas-fir was significantly more important than Pacific yews and Pacific silver firs when canopy cover or volume were used as a basis for comparison (Table 1).

Runkle (1982) defined canopy gaps as the land surface

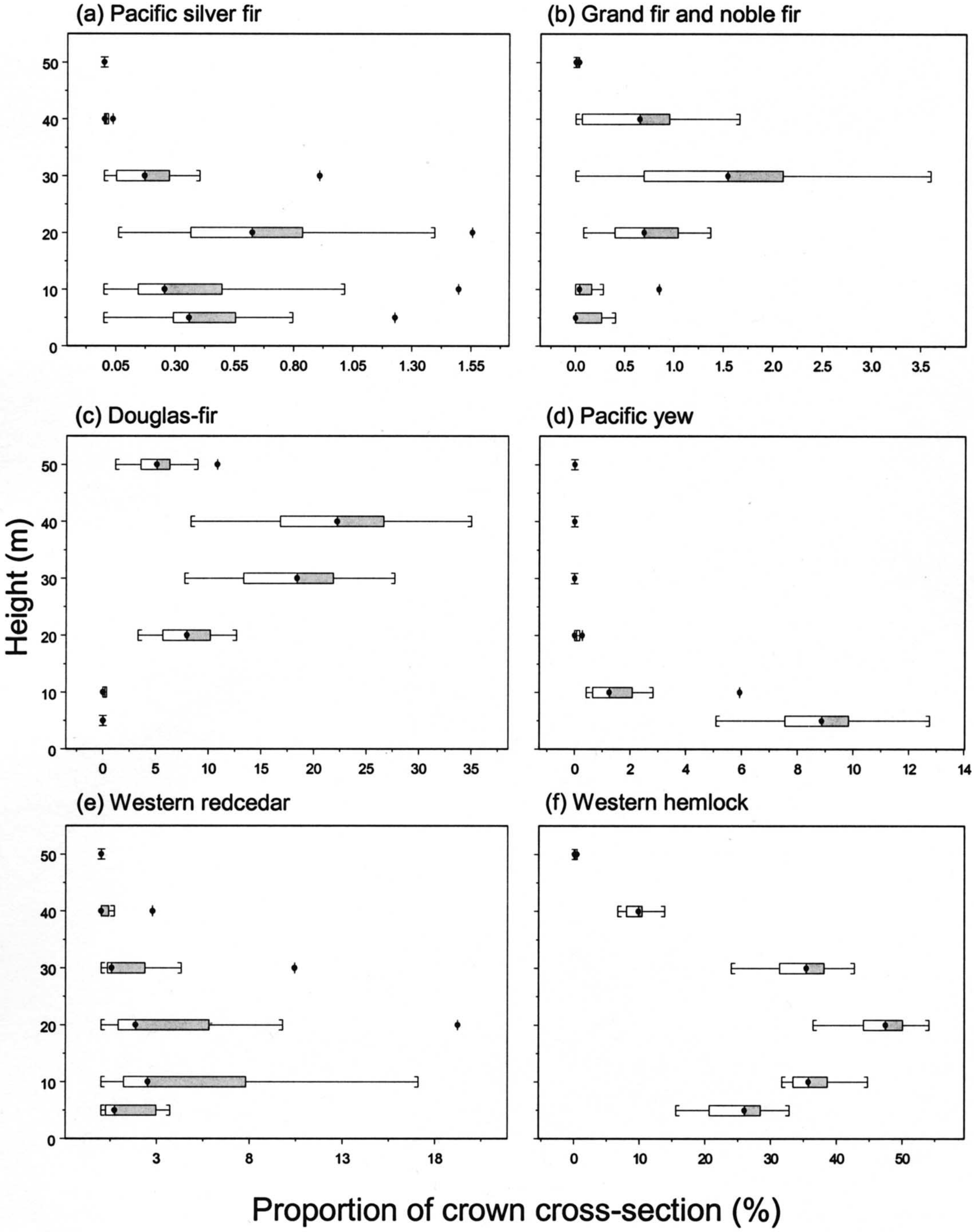

Figure 5. Boxplots showing the vertical distribution of canopy coverage (%) of different species at heights of 5, 10, 20, 30, 40, and 50 m (a–f, respectively). The whisker tail on the left shows the minimum; the left side of the bar, with blank and gray parts, shows the lower quartile; the dot between blank and gray parts of the bar shows the median; the right side of the bar shows the upper quartile; the whisker tail on the right shows the maximum; and the dots outside whisker tails show the outliers. Longer bars and longer tails represent higher variability of canopy coverage per hectare.

directly under a canopy opening, and a minimum of 25 m^2 in size is generally used in the literature (e.g., Runkle 1990, Spies et al. 1990). In addition, canopy gaps are usually treated as being relatively round or elliptically shaped and isolated across the stand. The results of this study suggested that when looking at larger scales (more than one gap), canopy gaps in this old-growth Douglas-fir forest were highly connected and characterized by shapes more complex than ellipses. The median gap size in this old-growth Douglas-fir forest was 85 m^2 (about the area of a circle of 5.2 m radius; Spies et al. 1990). Van Pelt (1995) also concluded that gaps, created mainly by large trees falling, were not big because of the generally narrow crowns of these large trees. The results of this study were consistent with their findings at fine scales, but when looking at the canopy projection of this 12-ha plot at large scales, larger

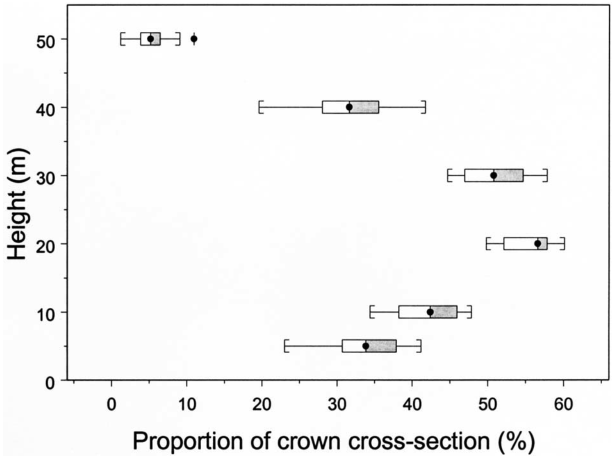

Figure 6. Boxplots showing the vertical distribution of the coverage (%) of total canopy projection at heights of 5, 10, 20, 30, 40, and 50 m. The interpretation of the figure follows that of Figure 5.

irregularly shaped and highly connected canopy openings were very common. These openings were larger than the crowns of at least two large trees (314 m^2, with two large trees whose radii were about 7 m).

The techniques used in this study provided a useful tool for characterizing 3-D forest canopies, and the results will be very helpful for examining leaf distribution, understory light environment, understory vegetation, and microclimate. For example, understanding foliage distributions in 3-D space is critical for many physiological processes such as photosynthesis. Although we assumed that tree crowns were solid foliage and ignored the gaps between branches, which resulted in estimations of canopy volume larger than the field-collected data, this approach still provided us insights into canopy volume estimation and 3-D canopy dimension. In the future, such estimates can be improved by studying canopy structure in more detail at the crown branch level.

The modeling approach used in this study has general applicability in characterizing 3-D canopies of various forests. An innovation in this study was the use of a flexible and relatively simple model to simulate crown shapes. The parameters in the crown model have explicit interpretations related to crown measurement. To simplify the model, the principle of self-similarity among different tree sizes of the same species for crown shapes was applied. The modeled canopies are more accurate in this study because the models were parameterized from a set of detailed crown dimensional data, collected from a canopy crane and from the ground, along with a field measured stem map of all trees. When simulating a canopy of a 12-ha plot, it is difficult to accurately estimate the errors. However, our results were consistent with studies done by others, e.g., the median gap size in this old-growth Douglas-fir forest is 85 m^2 (about the area of a circle of 5.2-m radius, Spies et al. 1990). The modeling output was compared to field measured canopy openings along two 400-m transects, and the consistency of the patterns (wavelet comparison, Song 1998) between field data and the simulation results demonstrated that this modeling approach was reliable.

Crown projections for all live trees of various heights provided additional insight regarding spatial characteristics of the forest, including the spatial relationships and interactions between individuals and species. Two-dimensional crown overlapping is reasonable because different crowns use different vertical spaces, crowns overlaps when one looks down the canopy from the sky (Figure 1). At a constant height, tree crowns in three-dimensional canopies seldom overlap with each other to avoid mechanical abrasion (Spies et al. 1990). The field observations in this study also support this conjecture. However, crown projections showed that there were some overlaps particularly in the lower canopies (Figure 4). This may be attributed to a failure to consider tree leaning in the model. In reality, quite a few trees (especially Pacific yews) grew together, yet leaned away from each other and their crowns did not overlap. In this model, crowns were treated as solids. Therefore, the volume of the canopy may be overestimated, because real crowns are filled with plenty of open space (Pike et al. 1977, Jensen and Long 1982, Van Pelt 1995).

Slicing the canopy at various heights is a technique to gain additional insights into the spatial structure of the forest, such as the spatial relationships and interactions between and within species at specific heights. This would be useful in exploring wildlife habitat value. Birds, for example, use different layers and positions within the canopies for feeding, nesting, breeding, and other activities. With detailed canopy structure, one can simulate the virtual movements of individuals or populations for a better understanding of their behaviors and dynamics. Similarly, this information would be useful for addressing many issues concerned with species diversity and abundance of canopy dwelling organisms (e.g., lichens, bryophytes, and invertebrates).

Vertical canopies of the old-growth Douglas-fir forest varied greatly across the horizontal space (Figure 4). In some locations, the canopy was characterized as dense understory layers with low coverage of the overstory layer. In other locations across the stand, there was high canopy cover of intermediate layers yet low cover of both lower canopy layers and overstory layers. This detectable canopy patchiness (Figures 1 and 4) was clearly the result of a combination of stem point patterns of different species (Figures 4 and 5) and height structure, which resulted in a complex mosaic or canopy patchiness across the stand (Figure 1). While further comprehensive studies are necessary to understand the formation and dynamics of canopy patchiness, it is clear that many functions of the forest are associated with these patterns. Chen et al. (2004) reported that spatial distribution of the aboveground biomass is directly related to the composition and structure of canopies. Others (Van Pelt 1995, Song 1998, Mariscal et al., in press) also found that understory vegetation and solar radiation could be predicted with high confidence levels. Using crown models such as the one we described, our results also indicate that the delineation of both canopy and canopy openings should be expanded to three dimensions, especially in old-growth forests where extremely tall crowns create a cylindrical canopy opening in space (Van Pelt 1995).

The 3-D canopy structure provided in this study requires spatial information about stem distribution, dbh-height relationship, and crown geometry. This information is not available for many sites—an obvious shortfall for the application of our methods in structural analysis. However, whenever such information is available, the resulting structural analysis would be tremendously valuable for both theoretical research and management. For example, with canopy patchiness at the vertical level, one could precisely trace light or throughfall (Marisical et al. in press, Nadkarni and Sumera 2004) in predicting other related properties such as photosynthetic rate and soil moisture dynamics. Finally, it is also well-known that many species are active only within a range of vertical canopies, suggesting that spatial characteristics of the canopies within this range (Figure 4) should be the primary focus of study. For management practices, our approach allows one to simulate various harvest methods (Swanson and Franklin 1992) while providing new canopy synthesis (Figures 4–6) within a GIS platform.

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