

Canopy Structure in a 650-Year Douglas-Fir Chronosequence in Western Washington: Distribution of Canopy Elements and Open Space

Roman J. Dial, Nalini M. Nadkarni, and Charles D. Jewell III

Abstract: Using within-canopy, side-viewing light detection and ranging (LiDAR), we measured canopy structure in a Douglas-fir (*Pseudotsuga menziesii*) chronosequence. We present foliage profiles, canopy composition, and a new metric quantifying the vertical distribution of open space, supporting and extending results from other structural studies. Foliage distribution shifted from vertically uniform in the youngest stand (50 years), to a canopy surface peak in mature forests (100–160 years old), to a near-ground maximum in old-growth (650 years). Leaf area index in old-growth and mature forests was similar but was smaller in young forest. Canopy composition changed with age: relatively more dead elements in young, boles in mature, and diversity in old-growth canopies. Older forest had greater mean and variance in open space than younger forests. Open space was vertically uniform in young, unimodal in mature, and greatest in the upper canopy in old-growth forests. Our results provide an integrated description of canopy structure over more than half a millennium, highlighting solid structure and its complement, open space. The unique element we present—open space—provides novel insights into the assessment of forest structure. This study provides a means to compare forests across ages, from immature to old-growth, with an additional canopy variable available for developing relationships between canopy structure and function. FOR. SCI. 57(4):309–319.

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UNTIL RECENTLY, a forest's canopy was defined as its uppermost region, usually visualized as the top surfaces of emergent and dominant trees (Parker 1995). Canopy structure was considered a static, solid entity, often portrayed through profile diagrams as graphical “snapshots” of a forest at a particular place and time (Richards 1983). In the last 30 years, however, the conceptual view of a forest's canopy and structure has expanded in three ways. First, the scope of the canopy has been extended to include all aboveground parts of a forest ecosystem. Whitmore (1975) called the canopy “the total plant community above the ground,” Parker (1995) called it “the combination of all leaves, twigs, and small branches in a stand of vegetation; the aggregate of all the crowns”, and Moffett (2000) called it “the above-substrate plant organs within a living community.” Second, the structure of forest canopies is now considered from a dynamic, rather than static, standpoint, as researchers place their study sites in a temporal perspective (Janisch and Harmon 2002, Van Pelt and Nadkarni 2004, Pypker et al. 2005, Bond et al. 2007, Van Pelt and Sillett 2008). Third, the open air or “free-space” situated among the solid canopy components of leaves, branches, and boles has been recognized as a measurable and critical forest ecosystem component (Emmons and Gentry 1983, Lieberman et al. 1989, Connell et al. 1997, Lefsky et al. 1999, Dial et al. 2004a). Moffett (2000)

referred to space as a means of putting the “canopy into canopy biology.”

In all forests, the solid canopy elements (e.g., foliage, limbs, boles, detritus, and soil), together with open space, form the structure through which physical processes operate and arboreal organisms live, reproduce, disperse, die, and regenerate. The interactions between solid structures and the open space around them affect physical functions such as light transmittance (Terborgh 1985, Caldwell et al. 1986), wind attenuation (Raupach et al. 1996), and the moderation of temperature and relative humidity (Freiberg 1997). The air spaces surrounding solid canopy structures affect patterns and amounts of nutrient deposition in throughfall and dryfall and create a medium through which gases, pesticides, pollutants, and aerosols flow (Nadkarni and Sumera 2004, Staelens et al. 2006). Open space is also important for biotic characteristics of the forest: the display, movement, and foraging of organisms, including recruitment through active dispersal of vertebrates (Emmons and Gentry 1983, Dial 2003) and more passive transport of aerial plankton such as spores (Aylor 1999), pollen (Di-Giovanni et al. 1996), seeds (Okubo and Levin 1989), and invertebrates (Lindo and Winchester 2008). Thus, a current definition of the forest canopy should include not only the aggregate of the crowns in the forest (Parker 1995) but also

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the open space surrounding canopy elements (Moffett 2000, Dial et al. 2004a).

The earliest methods used to measure canopy structure were the ground-based ocular estimates of MacArthur and Horn (1969), whose techniques to calculate leaf area index (LAI) and canopy profile diagrams were later modified for airborne light detection and ranging (LiDAR) data by Lefsky et al. (1999). Within-crown techniques have also been developed to describe forest structure based on the spatial distribution of canopy elements (e.g., Ishii and Ford 2001, Van Pelt et al. 2004, Sillett and Van Pelt 2007). Data from individual trees in sample plots are often used to portray stand-level structural diversity and scaled upward to estimate whole-forest measures of wood and foliage volumes and crown distributions (Van Pelt and Nadkarni 2004). Song et al. (2004) used geographic information systems (GIS) with canopy modeling and statistical tools to describe the three-dimensional structure of an old-growth Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco) forest. Song et al. (2004) treated open space as two-dimensional canopy gaps, the ground area directly underneath an opening from the canopy surface to ground, which is the classic definition of a gap (Runkle 1982). However, the classic canopy gap is an extreme of a distribution of empty space in a canopy (Lieberman et al. 1989, Connell et al. 1997). To more fully characterize the distribution of empty space vertically across a forest canopy, Dial et al. (2004a) used within-canopy movement rope-based techniques (Dial et al. 2004b) and side-viewing LiDAR to measure, quantify, and visualize canopy open space.

In this study, we describe the vertical distribution of open space and canopy elements across a chronosequence of Douglas-fir forests from 50 to 650 years old. Douglas-fir-dominated stands that are considered “old-growth” (>175–250 years old) (Franklin et al. 1981, Franklin and Van Pelt 2004) have long been of special interest (Franklin and Dyrness 1973, Franklin et al. 1981), because they provide unique habitats for wildlife (Forest Ecosystem Management Assessment Team 1993), including endangered species such as the marbled murrelet (*Brachyramphus marmoratus*) and the northern spotted owl (*Strix occidentalis caurina*). The role of old-growth in atmospheric carbon balance is less certain. Because of measurement uncertainties and temporal variation in photosynthesis vis-à-vis respiration, old-growth Douglas-fir forests may function as carbon sinks or sources or maintain equilibrium (Field and Kaduk 2004, Harmon et al. 2004). More detailed studies of old-growth canopy structure, like this one, could better inform us as to their carbon balance.

Although important ecologically and economically, only

very small areas of old-growth Douglas-fir forests remain, with most original old-growth replaced by young or late-successional forests after logging. Ground-based characterization of old-growth forests typically include tall snags, large fallen logs, and standing live trees with complex and diverse crowns (Franklin et al. 1981). Those ground-based measures of old-growth forests show large variances (Spies and Franklin 1991). Old-growth canopies similarly show high spatial variability in canopy structure and structural diversity (Ishii and Wilson 2001, Van Pelt et al. 2004, Van Pelt and Sillett 2008). The temporal scale needed to establish old-growth has limited our understanding of how a Douglas-fir forest changes its canopy structure and function through time. Examining the structure of forests across a chronosequence can yield valuable insights into how they develop and in turn influence ecological function.

Our overall goal is to develop a conceptual model of stand canopy development that includes empty space, a model complementary to one developed for individual crown development in Douglas-fir (Van Pelt and Sillett 2008). A stand model offers a critical first step in understanding the relationship between canopy structure and function. In this study, we compared both open space and solid structure of five sites spanning 650 years in forest age (Van Pelt and Nadkarni 2004, Van Pelt and Sillett 2008). These sites represent immature (~50 years old), mature (100–200 years old), and old-growth (>250 years old) age classes of Douglas-fir dominated forests located in the southern Cascade Mountains of Washington State.

Methods

Study Sites

We collected data from five of the eight permanent research sites of Van Pelt and Nadkarni (2004). Theirs is a long-term study of forest stand development that established a chronosequence spanning 900 years in southcentral Washington State in Gifford Pinchot National Forest and Mount Rainier National Park (Van Pelt and Nadkarni 2004, Van Pelt et al. 2004, and Van Pelt and Sillett 2008). Our study sites represent a 650-year subset of the full chronosequence using the five sites that are located within the Gifford Pinchot National Forest, each a different age, from 55 to 650 years old (general stand data in Table 1, detailed site descriptions in Table 1 of Van Pelt and Nadkarni 2004, and detailed crown structure data in Table 3 of Van Pelt and Sillett 2008).

Table 1. Names and characteristics of the five study sites

Site name	Age (yr)	Elevation (m asl)	Aspect	Slope (%)	Tallest tree (m)	No. vertical transects
Plantation (PC)	Immature (50)	620	SE	0–15	25	4
Martha Creek (MC)	Mature (~100)	580	S	5–20	49	30
Panther Creek (PC)	Mature (~160)	730	W	0–15	52	6
Trout Creek (TC)	Old-growth (~350)	610	S	0–10	62	8
Cedar Flats (CF)	Old-growth (~650)	410	level	0	90	23

Data are from Van Pelt and Nadkarni (2004).

Douglas-fir (*Pseudotsuga menziesii*) dominated all sites, but each site varied by age, height, and diversity. Four of our five sites were located within 15 km of each other at the Wind River Experimental Forest (described by Shaw et al. 2004), with a fifth site, Cedar Flats Research Natural Area, located 35 km northwest of Wind River Experimental Forest. All sites had preexisting permanent transects and ready access to the tops of large trees from the work of previous canopy researchers (Van Pelt and Nadkarni 2004, Van Pelt et al. 2004, Van Pelt and Sillett 2008). These tall trees formed the end points of horizontal traverse lines that supported vertical sampling transects.

Data Collection

We gained access to the tallest trees in each site using modified mountain-climbing (Perry 1978) and arborist techniques (Dial and Tobin 1994). We then established horizontal traverses with two 9-mm static polyester or nylon climbing ropes that connected trees at the highest points determined safe as structural anchors (approximately 15- to 30-cm stem diameter). Each horizontal traverse provided an anchor for vertical sampling transects, similar to the sampling array described in Dial et al. (2006) (Figure 1). The vertical sampling transects consisted of 9-mm static climbing ropes positioned at randomly selected locations in three of the five study sites and at systematic locations at Cedar Flats (CF) and Martha Creek (MC). These transect lines allowed us to sample nearly the entire height of the canopy via rope ascenders. Some of the uppermost portions 1–5 m from the canopy surface were unavailable because of slack in the traverse line necessary to minimize forces placed on anchor trees (Dial et al. 2004b).

The number of vertical transects varied by site (Table 1). Sample points were systematically located at 1-m intervals

from the ground to the top of each transect, located at the traverse line, except that CF sample points were located at 2-m intervals. At each sample point, an observer measured distance-to-nearest canopy element for $n = 18$ sample distances ($n = 12$ for CF), located at 20° azimuth (30° azimuth for CF) intervals, similar to methods illustrated in Figure 1 of Dial et al. (2004a).

We recorded the distance (in meters) to the nearest canopy element using a digital laser rangefinder (Impulse 200 LR model; LTI, Englewood, CO) at each sample azimuth (in degrees using a flux compass, MapStar module; LTI), and the identity (species when possible and type of structure) of the canopy element. We used a personal digital assistant (PDA) computer (iPaq model; Hewlett Packard, Palo Alto, CA) to directly download the data from the instruments (Cushing et al. 2003, Dial et al. 2004a, 2006).

Data Analysis

Canopy Element and Empty Space

Canopy elements were classified as live dominant (i.e., live Douglas-fir), nondominant (other trees), dead, nonvine maple shrub, and vine maple (*Acer circinatum*, Pursh). Elements were further categorized as foliage, limbs, and boles. We estimated free space as the open space in each forest canopy using the measured distances between the observer and the canopy elements surrounding the observer. Because this is a measure of distance and not volume, we refer to the spatial measurements as free distance, d (in meters).

Element Density

We also used free distance measurements to calculate the density of elements in the forest. We assume that, on average, an observer, located at random along a line segment

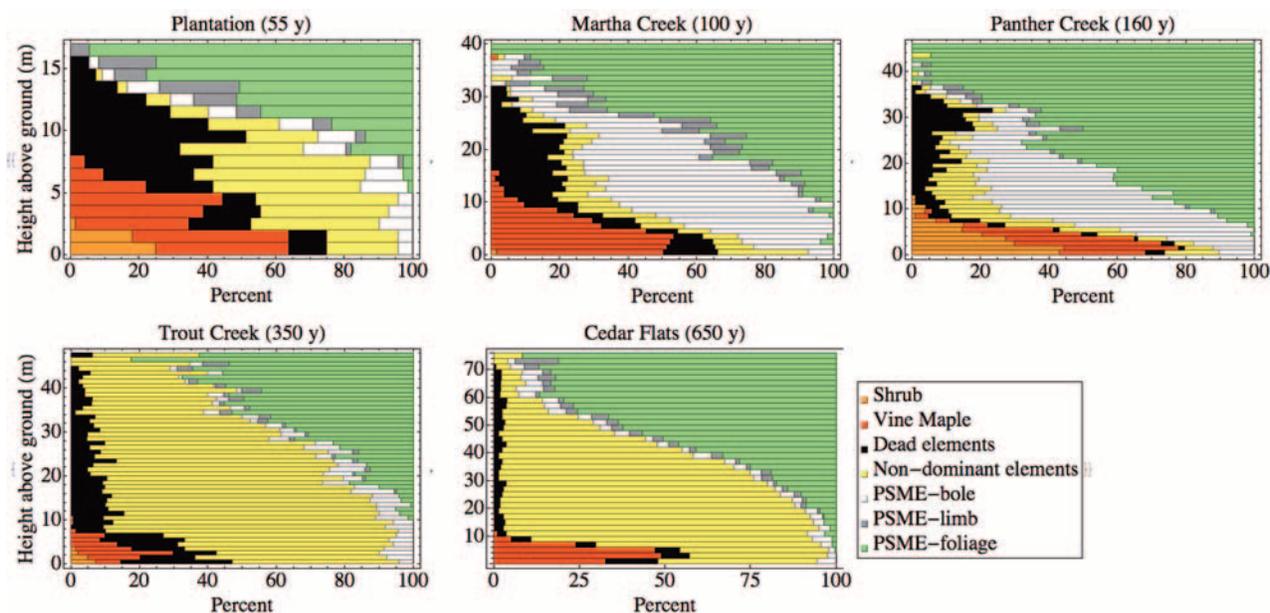


Figure 1. Canopy composition as relative abundance of canopy elements in five forest stands of various ages. The vertical axis is height interval aboveground, and the horizontal axis is percent composition in that height interval. The vertical axis differs in scale among panels to highlight the relative canopy composition across each stand's canopy. PSME, live Douglas-fir elements; Non-dominant elements, live, non-Douglas-fir tree elements; Shrub, nonvine maple shrubs.

connecting two canopy elements, will be located midway between them. This assumption is equivalent to an observer's location being uniformly distributed between one element (at distance 0) and another (at distance x), with the expected position at $x/2$, giving an expected mean free distance $d = x/2$. Thus, the expected distance between two canopy elements is $x = 2 \times d$. At each sample point (z, y) , with height z along transect y , we replicated free distance measures to canopy elements as n observations. These free distance measures represented distances between intersections of a line (the laser's beam) with canopy elements, and we used them to estimate total element density and foliage density at each point (z, y) . To calculate mean element density δ (elements/m) at (z, y) , we first aggregated all free distance measures at the sample point (z, y) [where each free distance is symbolized as $d_i(z, y) = x_i(z, y)/2$] as the arithmetic mean, then multiplied by 2, and inverted, because if n = total elements is observed, then

$$\begin{aligned} \bar{\delta}(z, y) &= \frac{\sum \text{intersections of a line with elements}}{\sum \text{distances between elements}} \text{ at point } (z, y) \\ &= \frac{n}{\sum_{i=1}^n x_i(z, y)} = \frac{n}{\sum_{i=1}^n 2d_i(z, y)} = \frac{n}{2 \sum_{i=1}^n d_i(z, y)} \\ &= \frac{1}{2} \times \frac{n}{\sum_{i=1}^n d_i(z, y)} = \frac{1}{2\bar{d}(z, y)}. \end{aligned} \quad (1)$$

Foliage Profiles and LAI

We calculated foliage density at height z , along transect y , calling it LAI(z, y) and measuring it in leaves/m, and used that derived measure to estimate mean element density (Dial et al. 2006). In particular, we used the form of equation 1 but included only free distance measures to foliage and not stems (boles and limbs) or dead canopy elements. This approach meant that we replaced $\bar{\delta}(z, y)$ with LAI(z, y), n with number of foliage observations only, and $d_i(z, y)$ with measures to foliage only. Foliage density at height z , averaged over all transects, we defined as LAI(z) and plotted as foliage profiles for each stand. To investigate the homogeneity of canopy structure, we applied the Kolmogorov-Smirnov one-sample test (with $\bar{\delta}$ adjustment; Sokal and Rohlf 1995) as a goodness-of-fit test to a vertically uniform distribution of foliage. We used a tabled value (Rohlf and Sokal 1995) to find the critical maximum difference, D , in cumulative foliage density between observed and expected. The null hypothesis was that each canopy profile represented a uniform foliage profile, where foliage density, LAI(z), was uniform in z . We used the number of height samples as n in the test, and we used n intervals to determine the distribution of foliage that was uniformly distributed across the canopy. $P < 0.05$ indicated that we reject the null hypothesis of foliage that was uniformly distributed across the vertical profile. Multiplying LAI(z, y) by sample interval length, Δz , and summing over all heights gave an estimate of number of leaf layers along transect y , a value conceptually identical to LAI for that transect. We used the

mean across all transects in a stand as the LAI estimate for that stand.

Results

Canopy Composition

The vertical distribution of canopy elements varied with stand age (Figure 1), except for vine maple, which remained mostly below 10 m aboveground level (agl) across all sites. Across all ages at mid-canopy (halfway between the ground and canopy surface) *Pseudotsuga* foliage remained roughly half of all observed canopy elements (Figure 1). In the youngest forest (Plantation [PL]), we documented a greater proportion of dead elements throughout the canopy than at other ages, reaching up to 50% of all canopy elements at ~10 m agl. Mature forest sites had element distribution profiles with distinctive mid-canopy bole zones, lacking in other stands, which reached a peak of more than 50% of all elements as boles at ~10 m agl for each mature site, just above the vine maple zone. Mature forests also lacked diversity in nondominant canopy elements. Old-growth forests showed distinctive differences in the vertical distribution of canopy elements mid-canopy, where nondominant elements made up a substantial proportion of both the mid-canopy (from approximately 10 m agl to 10 m below the canopy surface) and upper canopy elements (Trout Creek [TC]). In contrast with other stands, dead elements in old-growth were relatively most abundant low in the canopy.

Non-Douglas-fir elements (foliage, limbs, and boles) were uncommon in young or mature forests above 5 m. In contrast, nondominant elements from at least four species of tree, including western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), western redcedar (*Thuja plicata*, Donn ex D. Don.), pacific yew (*Taxus brevifolia* Peattie), and silver fir (*Abies amabilis* Douglas ex Forbes), extended the full depth of the canopy in old-growth. The presence of these species in old-growth reflects the fact that the forest canopy there is more diverse than that in younger forests. The upper canopy in all forests was mostly Douglas-fir limbs and foliage.

From the youngest to oldest forest canopy we noted three expected general patterns that illustrate a well-known successional progression of replacement of light-demanding Douglas-fir with more shade-tolerant species: the species diversity of the canopy surface increased, whereas immediately below the canopy surface *Pseudotsuga* limbs and foliage decreased in relative abundance; nondominant trees replaced *Pseudotsuga* boles and dead elements; and at the lowest canopy levels the relative abundance of shrubs decreased and that of non-*Pseudotsuga* trees increased.

Canopy Empty Space

Overall canopy empty space, as measured by free distance, increased in both its magnitude and its variability with forest age (Figure 2). Mean \pm SD of free distance (\bar{d} , averaged over all heights and transects) for the oldest stand (CF-650, 32.0 ± 58.5 m, $n = 9,677$ distances) were about 6 and 12 times, respectively, that of the youngest stand (PL, 5.3 ± 4.6 m, $n = 1,117$ distances), and approximately 3

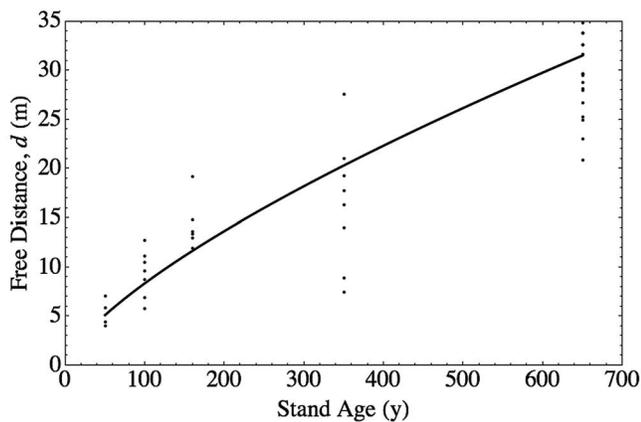


Figure 2. Relationship between mean open space (measured as free distance) and stand age. Each datum is the arithmetic mean of all free distances measured by an observer within a stand's canopy along a single vertical transect. The curve, fit using the nonlinear fit algorithm in Mathematica version 7.0 (Wolfram Research Inc. 2009), is free distance = $0.32 \times \text{age}^{0.71}$ (adjusted $R^2 = 0.95$).

times that of the mature stand (MC, 11.6 ± 18.1 m, $n = 16,164$ distances; Panther Creek [PC]-160, 14.2 ± 14.6 m, $n = 4,143$ distances). Mean free distance (averaged over vertical transects) increased with forest age as a power function (exponent = 0.71), both significantly so and with a reasonably good fit (Figure 2).

Vertical profiles of empty space varied with forest age (Figure 3). All five sites were similarly structured in open space near the ground (<5 m agl), with mean free distance generally <5 m. The youngest forest (PL) was the most vertically uniform, with a range in mean free distance by height of approximately 3 m (2.4–5.5 m) throughout its canopy. Both mature forests exhibited a mid-canopy “bulge” in free distance, with mean free distances of 10–20 m at heights of 10–25 m agl, which then narrowed to mean free distances <5 m near the canopy surface. The bulge effect was more pronounced in PC with a larger, mid-canopy peak in free distance from 10 to 25 m agl. The two old-growth sites also shared a unique pattern. In contrast with younger forests, mean free distances increased with height from near ground level upward through the canopy, a pattern more pronounced in the older forest (CF).

Overall, the pattern of open space showed a shift in vertical distribution across the chronosequence. Open space near ground level remained relatively uniform across the forest ages. However, a closed and narrow-spaced canopy surface above a bulging mid-canopy with large open spaces characterized mature forests, which contrasted with the open upper canopy above a filled mid-canopy in old-growth.

Foliage Density

Canopy profiles of LAI(z) varied with stand age (Figure 4) as did their departure from vertically uniform foliage as measured with a one-sample Kolmogorov-Smirnov test with δ adjustment (Sokal and Rohlf 1995). Foliage was vertically uniform in the youngest stand (PL: Kolmogorov-Smirnov, $D_0 = 0.055$, $n = 17$, $P > 0.25$), heavily concen-

trated in the upper canopy in the mature stands (MC: Kolmogorov-Smirnov, $D_0 = 0.358$, $n = 46$, $P < 0.01$; PC: $D_{0.5} = 0.358$, $n = 46$, $P < 0.01$), uniform in early old-growth (TC: Kolmogorov-Smirnov, $D_1 = 0.055$, $n = 48$, $P > 0.25$), and more concentrated lower in the canopy in the oldest-growth (CF: Kolmogorov-Smirnov, $D_1 = 0.201$, $n = 38$, $P < 0.01$). Foliage density near ground level in mature and old-growth was similar at 0.1–0.2 leaves/m. Among stands, the foliage density was highest in mature forests with more than 0.5 leaves/m in the upper canopy. When averaged, LAI in mature forests (8.72) was slightly higher than that in old-growth (8.58), both of which were more than twice that in the young forest (3.27). However, not every sample transect passed above the canopy surface in the youngest site, but it is unlikely that missing those would double or triple the LAI estimate there overall.

Discussion

Our results relate to five facets of canopy and whole forest ecology. First, the congruence of composition and structure can be related to the idea of canopy strata (Richards 1983, Parker and Brown 2000). Second, canopy structure as visualized and quantified here supports and extends results from other structural studies, including those using single-tree approaches (Van Pelt and Nadkarni 2004, Van Pelt et al. 2004, Sillett and Van Pelt 2007) through stand level (Franklin and Van Pelt 2004) and those using whole-forest approaches (Lefsky et al. 1999, Parker et al. 2004b). Third, a vertical profile of open space provides another metric to compare forests across ages, extending the classic two-dimensional view beyond simple gap fraction or percent sky. Fourth, this study provides additional canopy variables for developing relationships between canopy structure and function, which can be classified into structure and habitat relationships and structure and physical processes. Finally, we can place these data in the context of conceptual models of forest canopy development (Nadkarni and Sumera 2004, Van Pelt and Sillett 2008).

Canopy Strata

The distribution of air space bears on the phenomenon of forest stratification. Richards (1983) used the idea of forest strata to describe the vertical patterning seen in tropical forests. However, Parker and Brown (2000) argued that the concept of forest canopy stratification is not useful in forest science. Our study across this 650-year chronosequence supports the idea of repeatable patterns of congruence between structure and composition, patterns that are usefully viewed as canopy zones (e.g., understory, bole, inner crown, and canopy surface).

This language and these concepts are useful to describe changes in forest structure over time. In particular, we found a near-ground zone (1–7 m agl) dominated by vine maple and characterized by small open spaces to be nearly ubiquitous across the chronosequence. In another study of six forests that spanned 90° of latitude and 130° of longitude using sampling methods similar to those used in this study,

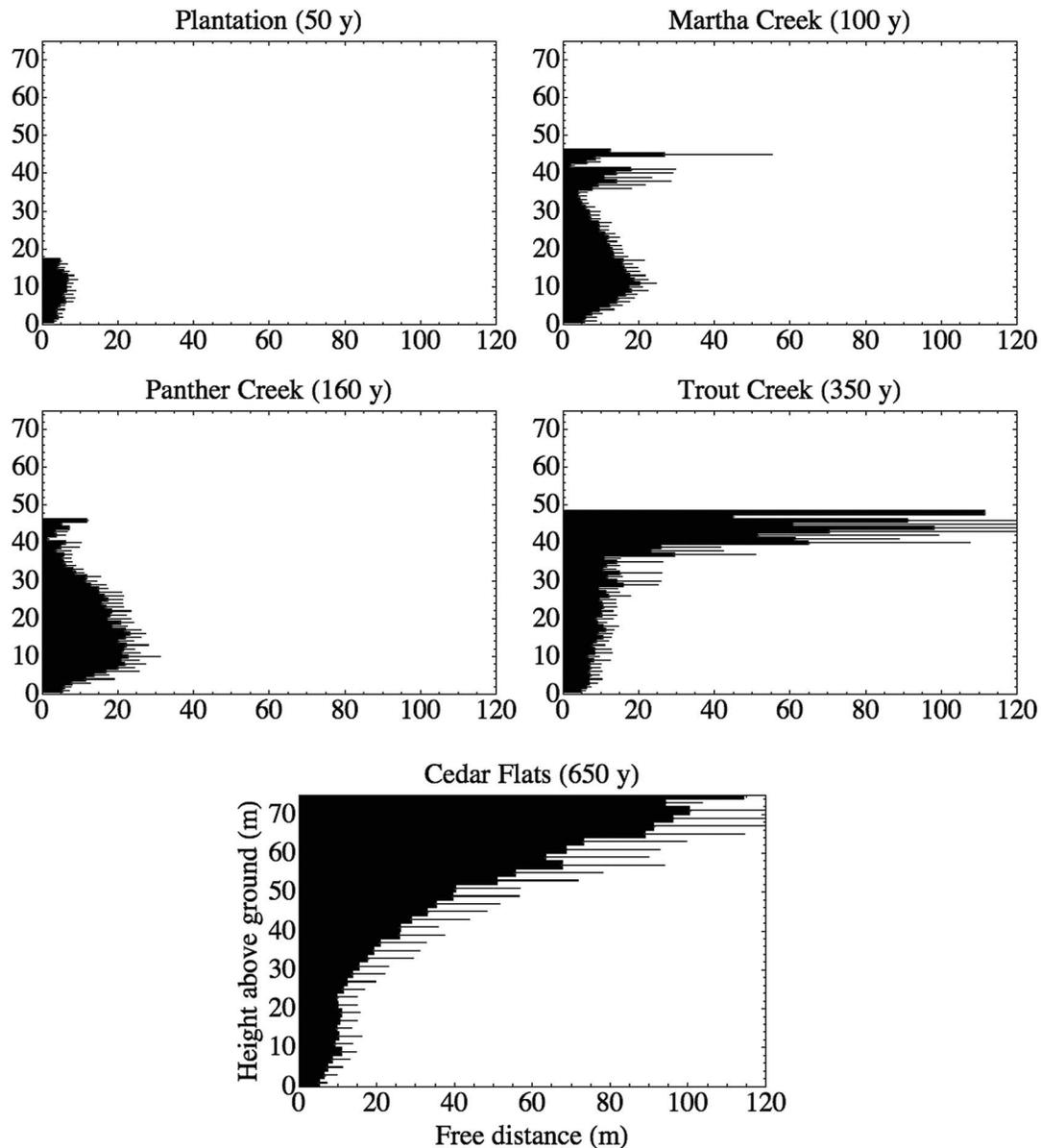


Figure 3. Canopy profiles of the distribution of open space, measured as free distance, across a chronosequence. Thick black bars indicate mean values averaged across transects. Thin bars extend 1 SD beyond the mean value to indicate variability.

Dial et al. (2004a) consistently detected a near-ground (below 5–10 m agl) zone of vegetation unrelated taxonomically to the dominant trees in each forest but with high foliage density and small open spaces. Our study showed that the near-ground zone of small open spaces increased in height across the chronosequence, supporting a well-known pattern that individual understory plant growth reacts to a changing light environment. Likewise, the canopy surface can be viewed as a ubiquitous interface between atmosphere and forest that is characterized by its unique composition of dominant foliage and limbs. As documented by Ishii et al. (2004), the canopy surface increases in both openness and its spatial variability from young forest to old-growth. We also documented a bole zone as a characteristic of mature forests, a zone identified by Dial et al. (2004a).

As an example of the usefulness of a canopy zonation language, we discuss a case study comparison by Van Pelt

et al. (2004), who compared a 350-year-old Australian *Eucalyptus regnans* stand (Wallaby Creek, Victoria, Australia) to our 650-year-old CF site. Both forests are similar in height and other stand attributes. The canopy profiles of open space and composition for Wallaby Creek from Dial et al. (2004a) showed that the forest's open-space structure and element composition had the characteristic zonation shown here as a mature forest with an understory, a bole zone, and a relatively small open space below the canopy surface. Thus, the substantial differences Van Pelt et al. found between the two forests, Australian and Cascadian, are differences more likely due to where the stand is in its successional development. Likewise, the two Alaskan forests and the Costa Rican tropical lowland forest in Dial et al. (2004a) may probably be better described as mature forest, rather than old-growth, because the two Alaskan stands have bole zones, and all three have a narrow-spaced canopy

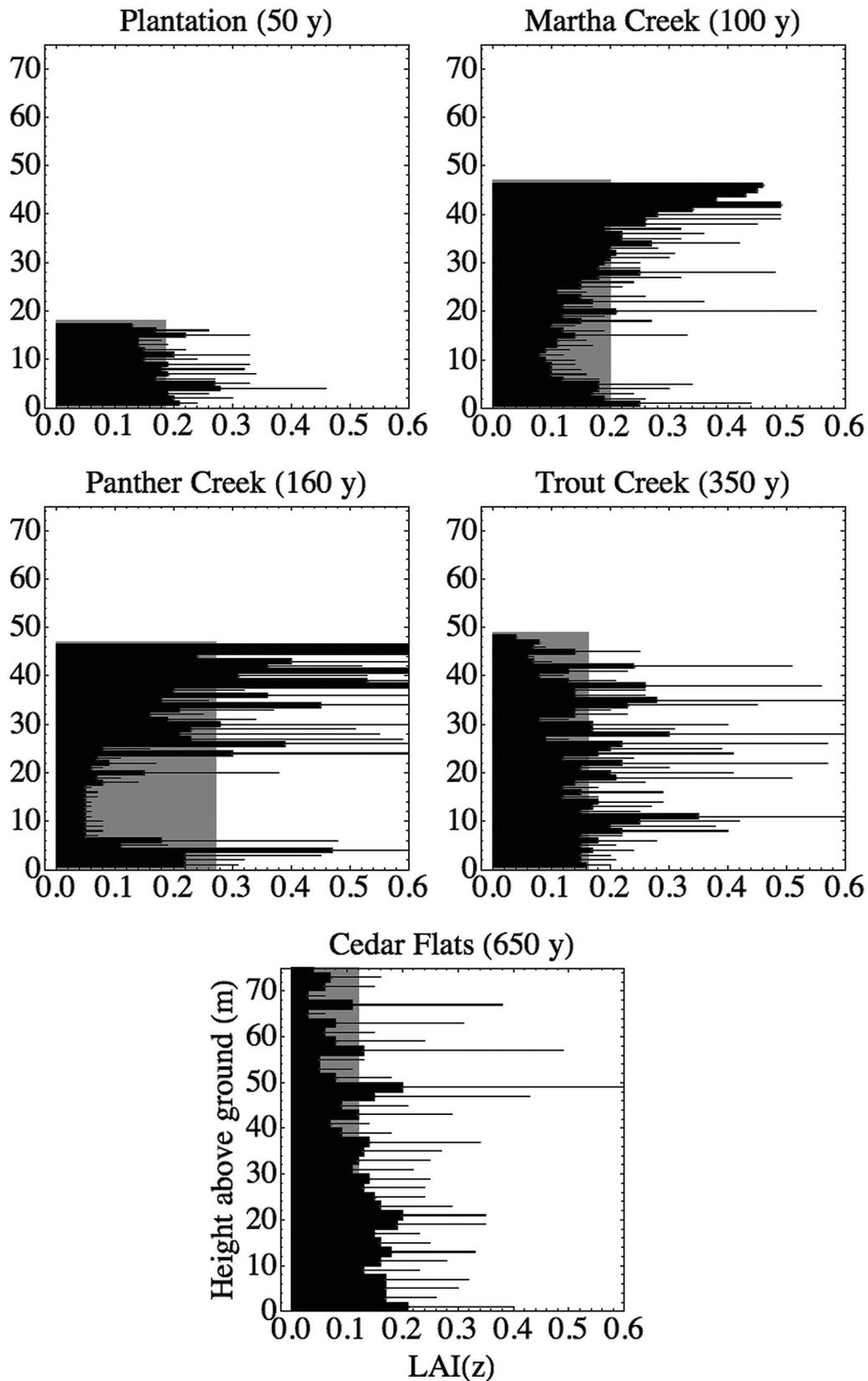


Figure 4. Canopy profile of leaf density, $LAI(z)$, measured as leaves/m at height z , across a chronosequence and compared with uniform distributions of foliage. Thick black bars indicate mean values averaged across transects. Thin bars extend 1 SD beyond the mean value to indicate variability. The gray area represents a uniform vertical distribution of foliage. Summing $LAI(z)$ for each transect and then averaging over all transects gave the following: Plantation $LAI = 3.27$ ($n = 4$ transects); Martha Creek $LAI = 8.12$ ($n = 23$ transects); Panther Creek $LAI = 9.33$ ($n = 6$); Trout Creek $LAI = 7.81$ ($n = 8$); and Cedar Flats $LAI = 9.35$ ($n = 23$ transects).

surface. More profiles from these and other forests will help to delineate canopy zonation, a concept we feel is both useful and natural.

Canopy Structure

Canopy structure is traditionally described using foliage profiles that show the vertical distribution of leaves and other canopy elements in the canopy. These are often vertically integrated to give a total stand value for LAI, an estimate that has been useful in landscape and global gas exchange models that scale up from leaf surface area. A variety of methods have been used to estimate LAI, most of which apply an indirect approach. Parker et al. (2004b) compared vertical structure in foliage distribution at the Wind River Canopy Crane (WR), an old-growth Douglas-fir site, using five methods (e.g., crane-based light measures and aircraft-based LiDAR). They concluded that the direct, within-canopy leaf contact measurements of Thomas and Winner (2000) were least sensitive to assumptions. Their estimates for the WR site were probably underestimates, because the crane is limited to canopy sampling in places where the gondola will physically fit: that is, points with less foliage. In mature Douglas-fir forests in British Columbia, Coops et al. (2007) found that ground-based optical methods were biased for understory and low canopy foliage, whereas aircraft-based LiDAR was biased for upper canopy layers. In this study, we report somewhat higher LAI in mature and old-growth stands but substantially lower LAI in young forest (Table 2). The Thomas and Winner (2000) estimates using crane-based vertical line intercept methods are within our old-growth range. Another estimate for LAI at CF using “foliar units” (Van Pelt et al. 2004) is 23% higher than ours; the estimate using the foliar unit methodology applied at WR (Parker et al. 2004b) is 41% higher than Thomas and Winner’s estimate. The foliar unit method (Parker et al. 2004b, Van Pelt et al. 2004) showed maximum foliage biomass at approximately 30 m agl at WR and 20 m agl at CF, similar to where we found maximum foliage density at CF. Airborne LiDAR (Lefsky et al. 1999) identified maximal foliage density at low heights in old-growth (~20 m agl in 61-m tall forest) and higher density in mature stands (~35 m agl in 51-m tall forest), observations consistent with ours.

Uniformity of Canopy Density

Cumulative LAI is the independent variable in the application of the Beer-Lambert law to light transmission through forest canopies (e.g., Parker 1995). Commercial instruments using light transmittance (e.g., the Li-Cor LAI-2000 plant canopy analyzer) base estimates of stand LAI on the Beer-Lambert law. A key assumption of application of the Beer-Lambert law is that leaves, like solute in a solution, are uniformly distributed vertically across the canopy. The observation that three of the five canopies we sampled were not uniform in foliage (Figure 4) suggests that commercial instruments using light transmittance to estimate LAI may produce inaccurate results. Foliage profiles constructed using within-canopy measures will be substantially more accurate and fine-scaled than those using ground-based light transmittance methods. Within-canopy estimates of foliage density will also aid in understanding physical processes that may reflect variability in foliage as well as relate canopy organisms to their foliage use.

Applying a tree-centered approach at a vertical resolution of 5 m, Van Pelt and Nadkarni (2004) reported on the same five sites described here. That study perceived forest canopies as collections of geometric solids; the approach here treats canopy objects as small, more diffuse elements such as foliage, boles, and limbs. Nevertheless, the foliage profiles should show some similarities and do so in several respects. Both approaches documented that MC and PC have bimodal distributions in the vertical distribution of foliage. However, compared with the solid-canopy view, we found the following: the youngest site was essentially uniform in its foliage density profile; mature forests supported peak foliage ~10 m higher in the canopy than Van Pelt and Nadkarni depicted; and old-growth forests had foliage profiles that decreased in density upward from ground level. The last two observations agree with Franklin and Van Pelt (2004) and Parker (1997). Our observations of old-growth foliage profiles more closely match those reported using LiDAR for old-growth Douglas-fir sites (Lefsky et al. 1999, Parker et al. 2004b). We suggest that the differences between the canopy profiles presented here and in Van Pelt and Nadkarni (2004) are primarily methodological. The methods used here accentuate the openness of forest canopies, whereas geometric model approaches emphasize the solid nature of especially large trees. Likewise, in Parker et

Table 2. Comparisons of LAI estimates by method and forest stand age

Site	Age	LAI	Method	Reference
Cascades, WA	Immature	3.3	In-canopy side-view LiDAR	This study
Cascades, OR	Immature	6.7	Airborne LiDAR	Lefsky et al. (1999)
BC, Canada	Immature	8.7	Ground-based Beer-Lambert	Frazer et al. (2000)
Cascades, OR	Mature	7.9	Airborne LiDAR	Lefsky et al. (1999)
Cascades, WA	Mature	8.7	In-canopy side-view LiDAR	This study
BC, Canada	Old-growth	8.5	Ground-based Beer-Lambert	Frazer et al. (2000)
Cascades, WA	Old-growth	8.6	In-canopy side-view LiDAR	This study
Cascades, WA	Old-growth	8.8	In-canopy leaf contact	Thomas and Winner (2000)
Cascades, OR	Old-Growth	9.1	Airborne LiDAR	Lefsky et al. (1999)
Cascades, WA	Old-growth	11.5	In-canopy foliar units	Van Pelt et al. (2004)
Cascades, WA	Old-growth	12.3	In-canopy foliar units	Parker et al. (2004b)

al.'s (2004b) comparison of techniques estimating foliage profiles at the WR site, methods identified as Beer-Lambert inversion, crown shell modeling, and solid models produced profiles less like the ones observed here; methods identified as LiDAR and gap-fraction inversion showed the near-ground peak of foliage in old-growth that we observed.

The method we describe here is best described as a within-canopy, side-viewing LiDAR. Originally, the processing of the airborne LiDAR data for forest canopies followed the theory developed by MacArthur and Horn (1969). Here, we averaged sample distances from a point, doubled, and then inverted to estimate mean element density, as we sample at 1- to 2-m vertical intervals and measure horizontal distances to nearby objects from within the canopy, rather than from below or above. Thus, our technique is more finely scaled than other LiDAR studies.

Vertical Profiles of Open Space

Connell et al. (1997) characterized canopy open space as more than simple surface-to-ground gaps. Canopy profiles of empty space from around the Pacific showed that forests of different species composition and climate can still share similar structure when viewed as open space (Dial et al. 2004a), a result extended by this study. Open space may offer a better metric that avoids the specific adaptations of individual species when structure is measured. Furthermore, we expect that wind movement, gas exchange, and throughfall within forest canopies will also be best understood in the distribution of open space. We suggest that the relative positioning of solid structures within canopy open space determines canopy functions and that understanding canopy functions requires location and quantification of both solids and space.

Here, we suggest that in Gifford Pinchot National Forest of the Southern Cascades, Douglas-fir forests change quantitatively in the abundance of open space and qualitatively in the distribution of that space over time. We expect other immature Douglas-fir canopies to also be vertically uniform in both open space and solid structure. The two mature forest canopies measured here showed a strongly unimodal vertical distribution of open space at mid-canopy, whereas the two old-growth forests were very open at the top and closed in open space as the ground was approached. The open space profiles of Figure 3 would predict that more throughfall and light penetrate into the mid-canopy of the old-growth stands than into that of the mature or young forest stands. The profiles also suggest that air movement above and below the canopy surface in mature forests might be decoupled, whereas in old-growth atmospheric movement of air may be quantitatively attenuated by the canopy.

We expect that these characteristics strongly affect the arrival of light, moisture, and other resources into the canopy and so affect the distribution and abundance of arboreal organisms living there. For instance, the high diversity of lichens and other epiphytes at mid-canopy levels of old-growth may be the result of substantial open space above them, allowing for both more resources (light, moisture, and nutrients) and higher recruitment. Likewise, birds may find that the combination of large open space among denser

foliage in mid-canopy old-growth enhances ease of movement and foraging. Future canopy studies that incorporate space, solids, and organisms may prove fruitful in understanding structure and function relationships.

Conclusions

This study has shown the internal structure and composition of a Douglas-fir forest chronosequence. The sample size we have is small and although our results support and extend well-known principles of ecological succession in forests, it is worthwhile to note that values will vary greatly by site, initial stand densities, and major environmental events such as the normal heterogeneous effects of moisture distribution, insect and disease attacks, and storm events. The results also suggest that multiple use management of forests may fruitfully consider the vertical distribution of space within stands. It may be possible to accelerate the vertical spatial structure of a forest by selectively cutting limbs and foliage inside the canopy to increase light and rainfall penetration both to foliage within the canopy and to ground level, possibly accelerating habitat use by old-growth species. Because we find repeatable patterns of congruence between the physical structure and space of forest canopies and their composition, the idea of "canopy zones" is a useful concept that can aid in management for wildlife and habitat, because these classifications can characterize the position and location of biological activities in the canopy, much as subtidal and intertidal zones do in marine biology. We also note that use of upward oriented LiDAR (e.g., Parker et al. 2004a) would provide a quicker and less expensive means of identifying and quantifying the spatial extent of these zones, as the methods described in this article are more labor-intensive and time-consuming than the technique of Parker et al.; however, the degree of correspondence needs to be established between below canopy, above canopy, and within-canopy measurement techniques.

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