Three-dimensional Structure of an Old-growth *Pseudotsuga-tsuga* Canopy and its Implications for Radiation Balance, Microclimate, and Gas Exchange

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ABSTRACT

We describe the three-dimensional structure of an old-growth Douglas-fir/western hemlock forest in the central Cascades of southern Washington, USA. We concentrate on the vertical distribution of foliage, crowns, external surface area, wood biomass, and several components of canopy volume. In addition, we estimate the spatial variation of some aspects of structure, including the topography of the outer surface, and of microclimate, including the within-canopy transmittance of photosynthetically active radiation (PAR). The crowns of large stems, especially of Douglas-fir, dominate the structure and many aspects of spatial variation. The mean vertical profile of canopy surfaces, estimated by five methods, generally showed a single maximum in the lower to middle third of the canopy, although the height of that maximum varied by method. The stand leaf area index was around 9 m^2 m^{-2}, but also varied according to method (from 6.3 to 12.3). Because of the deep narrow crowns and numerous gaps, the outer canopy surface is extremely complex, with a surface area more than 12 times that of the ground below. The large volume included below the outer canopy surface is very porous, with spaces of several qualitatively distinct environments. Our measurements are consistent with emerging concepts about the structure of old-growth forests, where a high degree of complexity is generated by diverse structural features. These structural characteristics have implications for various ecosystem functions. The height and large volume of the stand indicate a large storage component for microclimatic variables. The high biomass influences the dynamics of those variables, retarding rates of change. The complexity of the canopy outer surface influences radiation balance, particularly in reducing short-wave reflectance. The bottom-heaviness of the foliage profile indicates much radiation absorption and gas exchange activity in the lower canopy. The high porosity contributes to flat gradients of most microclimate variables. Most stand respiration occurs within the canopy and is distributed over a broad vertical range.

INTRODUCTION

Forest canopy structure is intimately related to important functional characteristics and processes of forests. Canopy vertical and horizontal structure controls of the absorption of photosynthetically active radiation (PAR) (for example, see Monsi and others 1973) and the production of forest ecosystems (Williams and others 1996) are examples of such relations. Structure influences canopy–atmosphere interactions such as turbulence, with important implications for deposition processes (Lovett and others 1982) and the exchange of water vapor, carbon dioxide (CO_2), and biogenic trace gases (Baldocchi and others 1988). Incorporating vertical structure into the scaling of physiological measurements of photosynthesis and transpiration can greatly improve estimates of ecosystem-level functions (for example, see Spies 1998). Moreover, structure is a forest characteristic that can be directly manipulated to enhance or restrict these ecosystem functions (for example, see Franklin and others 2002).

Numerous studies have been done of the functional (summarized by O'Neill and DeAngelis 1970) and horizontal (for example, see Kuiper 1988) structure of forests. However, there are few measurements of vertical structure and virtually none in all three dimensions of space. A crane access system at the Wind River Canopy Crane Research Facility (WRCCRF) is providing new insights into the complex structure and function of a forest canopy (Weiss 2000; Winner and others 2004). The Wind River forest is also one of the few old-growth stands that have been studied in detail for ecosystem-level exchange of important gases (Chen and others 2004; Paw U and others 2004; Winner and others 2004). At this site, the structural and functional aspects of an old, tall, and complex forest can potentially be integrated.

To reveal canopy involvement in ecosystem processes, our summary of aboveground structural features of the old-growth forest at the WRCCRF emphasizes vertical organization. We present information on the biomass, volume, and area distributions of trees and their crowns in this canopy. We present new, and sometimes conflicting, characterizations of forest structure that have been yielded by a variety of techniques and attempt to reconcile those differences. We estimate the vertical distribution of some important ecosystem processes. When possible, we connect structurally and functionally significant characteristics of the stand; otherwise, we suggest promising new measurements. Finally, we discuss how the vertical components of structure and function relate to developing concepts about old-growth forests.

METHODS

Study Site

The forest we describe is in a 4-ha plot, including the 2.3-ha circle accessible from the tower crane at the WRCCRF. This facility is in the T. T. Munger Research Natural Area of the Wind River Ranger District in the Gifford Pinchot National Forest in southern Washington, USA (45° 49'13.8'' N, 121° 57'6.9'' W). Relevant features of the forest community and associated biota are given in Shaw and others (2004). Although this stand is not the most massive or productive example of old-growth Douglas-fir/western hemlock (Smithwick and others 2002; Harmon and others 2004), it is similar to many in the central Cascades (Franklin and others 1981; DeBell and Franklin 1987; Franklin and DeBell 1988).

Stem Geometry and Biomass

The distribution of stems by species, diameter, and location is described in Shaw and others (2004). Live aboveground biomass was calculated from species-specific allometric regressions based on stem diameter at breast height (dbh) and height (Harmon and others 2004). The vertical distribution of sapwood was calculated, assuming it formed a hollow cylinder of constant thickness, by summing the sapwood mass for all trees by each meter of height. Dead wood biomass was estimated from the length and end diameters of snags (standing coarse woody material) and logs (downed coarse woody material). The height distribution of the snag biomass was estimated assuming that snags were cone frustrums in shape. Vertical variation in the respiration rate of sapwood, dead branches, and snags was estimated from the height distributions of each component, using tissue-specific respiration rates from Harmon and others (2004). The botanical authority is Hitchcock and Cronquist (1978).

Total Leaf Area

Estimates of the total leaf area of the stand were made in six ways and are summarized as the leaf area index (LAI), defined as either one-half the total leaf area per unit land surface or the projected

leaf area per unit land area. The first estimate involves the summation of leaf surface areas of individual trees, each estimated from allometric equations (following Van Pelt and North 1996). The second estimate derived from the gap-fraction inversion method (Martens and others 1993) using a program by Rich (1990) applied to upward-facing hemispherical images of the canopy taken at 33 understory locations within the crane circle (Weiss 2000). The third estimate used the Beer-Lambert law (for example, see Pierce and Running 1988; Smith 1992) using an understory mean transmittance measured by Parker and others (2002) and an extinction coefficient of 0.40 (Marshall and Waring 1986). The fourth estimate involved counting the number of leaf contacts in vertical transects throughout the canopy volume from the crane gondola (Thomas and Winner 2000b) and aggregating these with a rotated ellipsoid distribution of leaf angles (Thomas and Winner 2000a). A fifth estimate was based on remotely sensed estimates of equivalent water thickness (EWT), calibrated with data from various sources to yield LAI (Roberts and others 2004). Finally, Harmon and others (1998) estimated LAI by converting leaf litterfall mass to leaf area using specific leaf area, assuming an average leaf lifespan of 5 years.

Openness and Cover

The fraction of the sky viewed from the forest floor for each 10° annulus was estimated from understory hemispherical photographs (Weiss 2000). Zenithal openness was also estimated by Song (1998) using a canopy densiometer at every 5 m along 200-m transects on the forest floor. Parker and others (2002) measured the midday clear-sky understory transmittance of PAR along the same transects of Song (1998) with a horizontal resolution of about 0.02 m.

Canopy Vertical Structure

The vertical organization of the canopy was estimated five ways. The remote-sensing instrument SLICER (Scanning LIDAR Imager of Canopies by Echo Recovery) was flown over the site in November 1995. The LIDAR waveforms returned from this sensor were processed following the methods described in Lefsky and others (1999) and Harding and others (2001) to provide the vertical distribution of canopy surfaces. Parker (1997) derived another estimate of the relative canopy-height distribution by inverting the mean transmittance profile using the Beer-Lambert relation. Weiss (2000) obtained the vertical pattern of LAI using gap-fraction

inversion from hemispherical photographs taken from the crane gondola along the same vertical transects sampled by Parker (1997). Two additional methods modeled the three-dimensional shells of individual crowns using measurements of top height, crown depth, and radius of stems greater than 5 cm dbh ("crown shell" method). J. Chen (unpublished) calculated the fraction of stand area within and between crowns at several discrete heights for the stems within the crane circle. Based on measurements upslope and to the west of the crane circle, R. Van Pelt (unpublished) calculated the volumes of crowns within each height interval and adjusted these, by species, with allometrically estimated leaf areas, to yield leaf area density by height class.

Surface Topography

The shape of the outer canopy was measured in the summers of 1995 and 1996 using a laser rangefinder (LD90-3100 HS; Riegl Inc., Horn, Austria) oriented downward from the crane trolley basket at a fixed radius alongside the jib. The jib was slowly rotated through a full circle from a known starting angle while the rangefinder acquired distance measurements at 200 Hz. The trolley basket was then moved to a new radius, and the ranging was repeated through another rotation. The final data set is a series of 81 concentric observations in the 85-m radius of the jib. Cartesian coordinates for each range measurement were calculated from the radius and time of each observation and were adjusted for flexing of the jib under load. The original resolution of these data (1 m in radius and 0.04° in azimuth) was reduced in processing to 1 m overall. For each point, the depth of the canopy surface was subtracted from the depth to ground, yielding the local outer canopy height (LOCH). The cumulative distribution of LOCH, the hypsograph (Pike and Wilson 1971; Brockelman 1998), was calculated.

The LOCH values were interpolated to a 1-m square grid. The outer canopy surface area and volume were estimated with the trapezoidal rule (Press and others 1992). We calculated two measures of the surface irregularity: the standard deviation of LOCH ("rugosity," following Parker and Russ 2004) and the canopy surface area:ground surface area ratio ("rumple index," following Parker [*unpublished*]). The hypsograph does not specify the spatial scale of the openings and crowns that comprise the depth distribution. To estimate the dominant horizontal scales of height variation, semivariances of LOCH were calculated, grouped, and averaged for each meter of lag, and the trend of
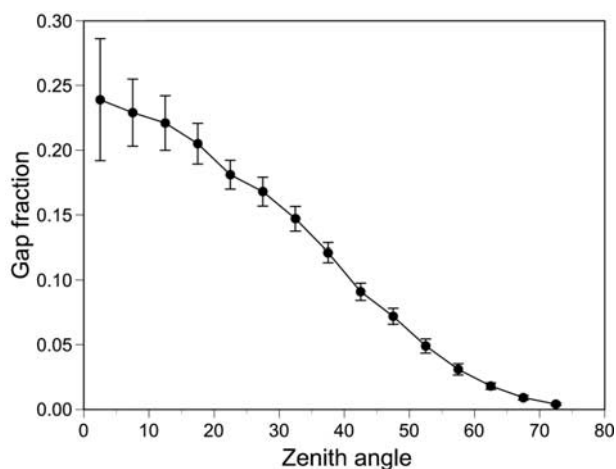
Figure 1. The change in understory gap fraction with zenith angle in the Wind River old-growth forest. The error bars are SDs.

these averages with lag was fitted with a spherical model (Isaaks and Srivastava 1989).

Microclimate

Nearly continuous observations of microclimate (temperature, humidity, PAR, and [CO_2]) have been made at several heights on the crane tower since 1998 (Newton and others 2000), to support simultaneous measurements of turbulent exchanges. The canopy albedo—the ratio of reflected: incident shortwave radiation (300–3000 nm)—was obtained from a pair of pyranometers located on the crane counterjib, 20 m above the canopy top (Mariscal and others 2004). Reflectance of PAR (400–700 nm) was measured by Parker (1997). Spatial variation was measured for PAR and broadband UVB transmittance in 16 profiles within the canopy (Parker 1997) and for PAR transmittance at 1 m in the understory (Parker and others 2002), both at midday under clear skies. The three-dimensional distribution of PAR transmittance in this canopy was also inferred from airborne waveform-recording LIDAR measurements (Parker and others 2001) and the dominant scale of horizontal variation was estimated, as described previously for structure.

RESULTS

Cover

The mean canopy openness seen from understory hemispherical images was highest (23% ± 22%) within 10° of the zenith but decreased almost linearly to zero at the horizons (Figure 1). The variability in openness decreased similarly: the horizon

is nearly always obscured, but the light environment directly overhead was quite variable. Song (1998) found a comparable (29.2% ± 22.5%) degree of zenithal openness and its variation using a densiometer. The midday transmittance of PAR at the same height averaged 0.081 (±0.204) along the same transects sampled by Song (Parker and others 2002).

Leaf Area Index and its Vertical Distribution

Aside from the low value from the gap fraction inversion method, most estimates of LAI clustered around 8.2–9.2 $m^2\ m^{-2}$ (Table 1). Estimates of the vertical distribution of surface area varied according to the method used. The profile of Weiss (2000) showed two maxima, at 5–10 and 30–35 m, but the other methods identified a single maximum of canopy surfaces vertically (Figure 2). There were differences in the height of the estimated maximum: from nearly at the ground in the airborne LIDAR (Lefsky) method to a height of nearly 24 m in the crown shell method of Chen. Mariscal and others (2004) calculated a similar height using the crown shell method and the same shell parameters.

The vertical organization of leaf area by species estimated by Van Pelt for an area near the crane circle indicated that the foliage of *Pseudotsuga menzeisii* was highest in this canopy, followed in decreasing height by *Tsuga heterophylla*, then *Abies amabilis*, and finally *Taxus brevifolia* (Figure 3a). There was also considerable overlap in the canopy positions of the species, especially for *T. heterophylla* and *A. amabilis*, two shade-tolerant species that should become more important as the stand continues to develop.

Vertical Organization of Top Heights and Biomass

The mean top height of the 100 tallest stems was 56.3 ± 3.1 m. Species differed in the vertical distribution of tops—most of the *P. menzeisii* were the tallest and *T. brevifolia* were the shortest (Figure 3b). *T. heterophylla* and *A. amabilis* were present at all but the highest levels, although the majority of their tops were in the lower half of the height distribution. This distribution may reflect the shade-tolerant nature of these species. The height distribution of *Thuja plicata* was uniform, unlike all other species. The distribution of top heights differed from that of leaf area or canopy surfaces (Figure 4), with live and dead tree heights having a distinct mode at the lowest heights. Stems in the lower canopy were more likely to be dead (10%–20%) than in the upper canopy (5%–10%). The mean top height for

Table 1.   Estimates of the one-sided Leaf Area Index (LAI) at the Wind River Canopy Crane Research Facility

Source	LAI (Year) (m² m⁻²)	Method
Van Pelt and North (1996)	12.3	Stem allometry
Harmon and others (1998)	9.2	Litterfall–foliage biomass conversion
Thomas and Winner (2000b)	9.3 ± 2.1 (1997)	Vertical line intercept
Thomas and Winner (2000b)	8.5 ± 2.2 (1998)	Vertical line intercept
Thomas and Winner (2000b)	8.2 ± 1.8 (1999)	Vertical line intercept
Roberts and others (2004)	8.4 (1998)	Remote sensing calibrated with LI-2000
Parker and others (2002)	6.3 (2000)	Beer-Lambert inversion
Weiss (2000)	3.7 ± 1.2 (1997)	Gap fraction inversion
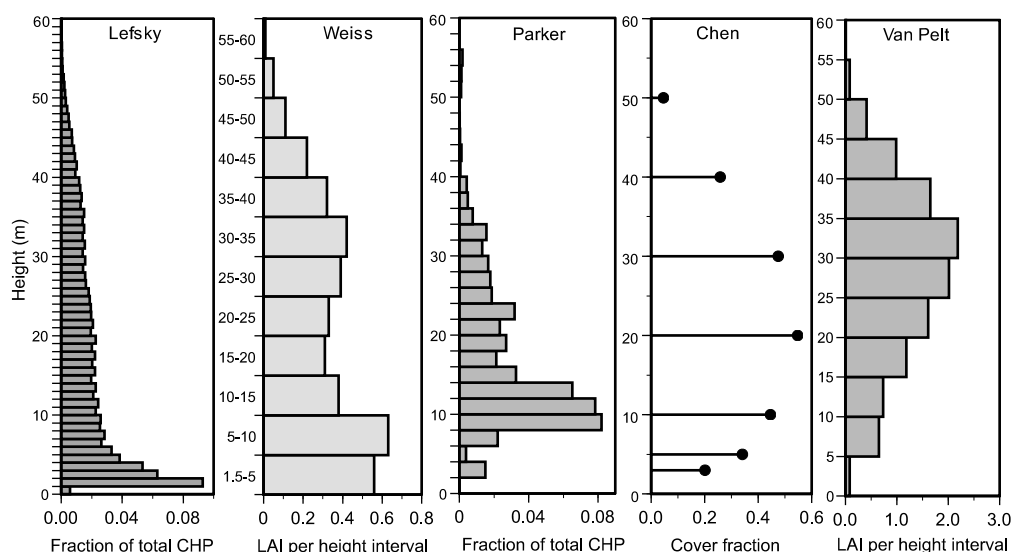
Figure 2. Vertical organization of the canopy in the Wind River old-growth forest from five different approaches. The panels are arranged from left to right in order of increasing height of the estimated canopy maximum.

P. menzeisii (about 52 m) (Figure 3b) was greater than its mean foliage height (Figure 3a), whereas for the other species, this pattern was reversed.

The vertical distribution of biomass in snags (standing coarse woody material) was similar to the vertical distribution of stem heights; both decreased asymptotically with height (Figure 5a). Nonetheless, there was appreciable dead biomass high within the canopy. Sapwood biomass had a different height distribution, with a linear decline up to 40 m and a rapid decline above that height (Figure 5b). *P. menzeisii* dominated both the sapwood and dead biomass components. The biomass in foliage and branches had a maximum at 8–10 m (Figure 5c).

Canopy Topography

The surface of the outer canopy within the crane circle had a complex three-dimensional structure

(Figure 6). The canopy surface was very open in the upper third; the upper crowns of trees were quite isolated from each other. The holes between the crowns can extend deeply into the lower third of the profile. Note that the downward-pointing rangefinder measured only the portion of the outer canopy viewable from above; undercut sections below the crowns were hidden. The estimated volume of forest included below the outer canopy surface in the crane circle was 625,383 m³, which implied a mean LOCH of 28.0 m in the 22,326 m² covered by the crane circle. The stand rugosity, the standard deviation of LOCH, was 16.2 m. The total surface area of the outer canopy was 277,042 m², yielding a rumple index of 12.4.

Canopy Hypsometry

The hypsograph of the outer canopy, the cumulative fraction of locations penetrating to a given
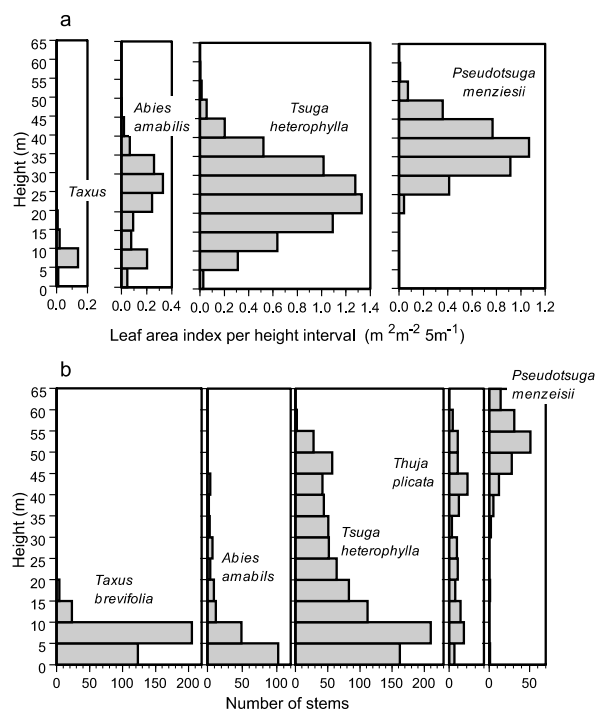
Figure 3. Vertical profile of **(a)** Leaf Area Index and **(b)** the top heights for the dominant tree species in the Wind River old-growth forest.

depth, illustrated that relatively little of the total surface area (less than 0.05) was found above 50 m (Figure 7). There was a nearly constant rate of area increase with height between 20 and 45 m and a more rapid increase in cumulative surface in the bottommost layers, from 4 to 20m.

Spatial Variation of Canopy Structure and Transmittance

The similarity of LOCH measurements changed with separation between measurement locations, as indicated by its semivariogram (Figure 8). The "nugget" semivariance, the minimum level of variation detectable with these measurements, was 6.3 m^2. The "range" (the distance within which measurements were spatially correlated) was 9.6 m. This distance was the mean separation between trees with dbh greater than about 65 cm, suggesting the dominant influence of larger trees in the variation in outer canopy topography.

Parker and others (2001) found that the semivariogram components of PAR transmittance varied with height in this stand. The range was about 15–20 m up to 40 m above ground, where it increased rapidly to 60 m at 43 m height; it then declined steadily above this height. The vertical pattern in both the nugget and sill semivariance followed the pattern of the variance, with broad peaks in the transition zone of the profile.

The canopy of the Wind River forest reflected little of incident solar radiation. Mean shortwave albedo, weighted by sun angle for the 1999 calendar year, was 7.3%. This was similar to the remote-sensing estimate of 7.9% $\pm$ 0.9% made by Roberts and others (2004) from an Airborne Visible/Infared Imaging-Spectrometer (AVIRIS) scene taken in July. Canopy reflectance was greatest (around 14%), although insolation was least, when the sun was near the horizon; it declined rapidly as solar elevation increased, deviating little from around 7% for angles over 30°.

DISCUSSION

Description of Canopy Structure

The Old-growth Stand at Wind River in Relation to Other Forests   The estimated aboveground biomass of the Wind River stand is among the highest reported in global comparisons (for example, the Woodlands data set in DeAngelis and others 1981), but it is in the low to middle portion of the range for old-growth forests in the Wind River Cascades (Smithwick and others 2002). It supports a very high biomass for its value of LAI (Figure 9), a common pattern in Pacific Northwest conifer forests (Frazer and others 2000).

Methodological Differences in Structural Measures Different methods can lead to divergent estimates of the same structural characteristic. In the case of the vertical distribution of surfaces (Figure 2), consideration of biases in each of the methods suggests that the actual surface area profile lies somewhere between those of Lefsky and those of Weiss and Parker. The shape of the profile obtained from waveform-recording LIDAR (Lefsky) is sensitive to the relative reflectivity of canopy and ground (Harding and others 2001). If the ground reflectivity were overestimated, the profile maximum would be higher in the canopy. The profiles of Weiss and Parker derive from measurements obtained mostly in spaces between crowns and may be biased to brighter conditions in the middle and lower canopy. Unbiased light profiles would result in a decline in the height of peak canopy surface area (Parker and others 2002). The crown shell method (Chen and Van Pelt) assumes that foliage characteristics (leaf area density, specific leaf area) are uniform within crowns and did not include trees with dbh less than 5 cm. The height of those surface area maxima would likely decline with a more realistic within-crown distribution of foliar characteristics and the inclusion of crowns of smaller stems.
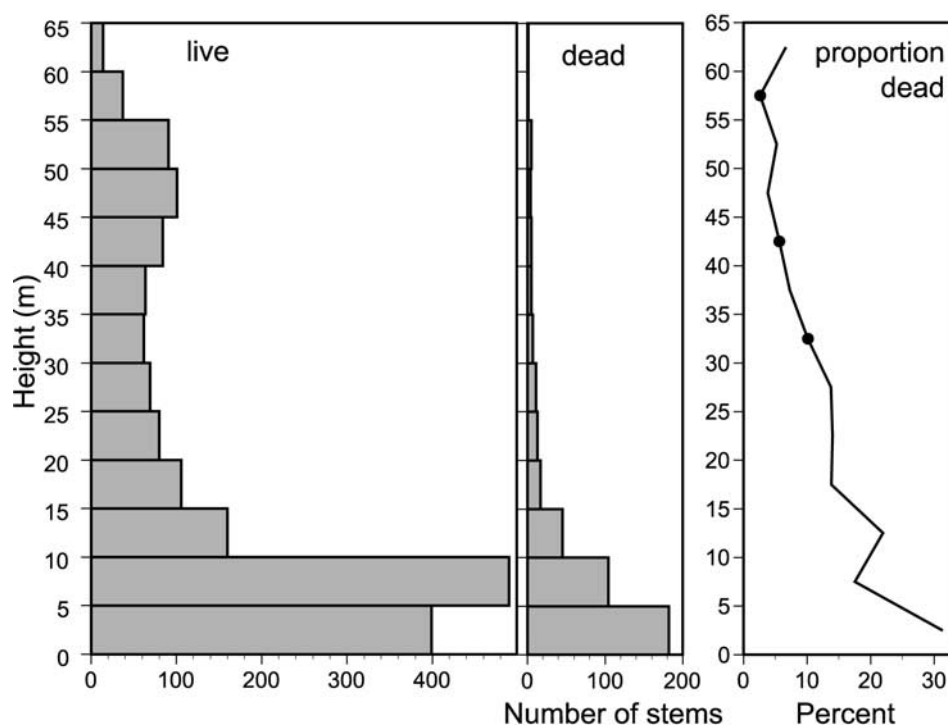
Figure 4. Vertical distribution of the top heights of live and dead trees and the proportion that are dead in the Wind River old-growth forest.
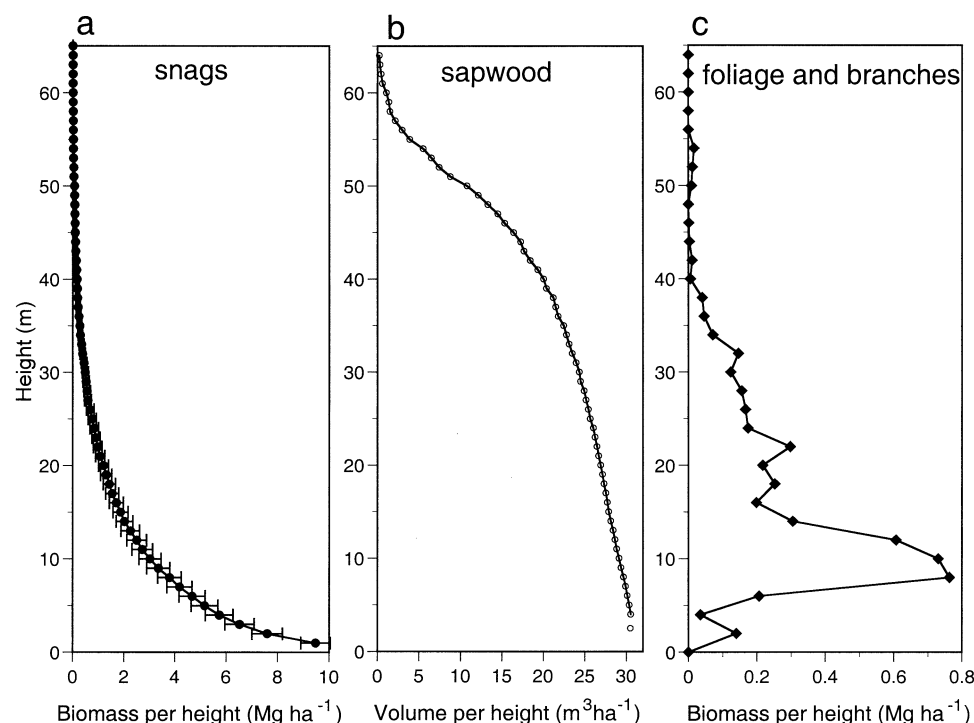

Figure 5. Vertical distribution of **(a)** snag biomass **(b)** sapwood volume in live trees, and **(c)** foliage and branch biomass in the Wind River old-growth forest. The error bars in panel a are SEs.

Methodological differences are also apparent in the range in LAI estimates (Table 1), although interannual variations, evident in the measurements of Thomas and Winner (2000b), have some effect. Each method differs in basic measurements, the geometric projection of canopy influences, and the

aggregation model, including the procedure to account for clumping. Parker and others (2002) found that the method of gap fraction inversion greatly underestimated stand LAI in this forest type, probably because it does not accommodate clumping at both foliage and whole crown scales (Weiss 2000).
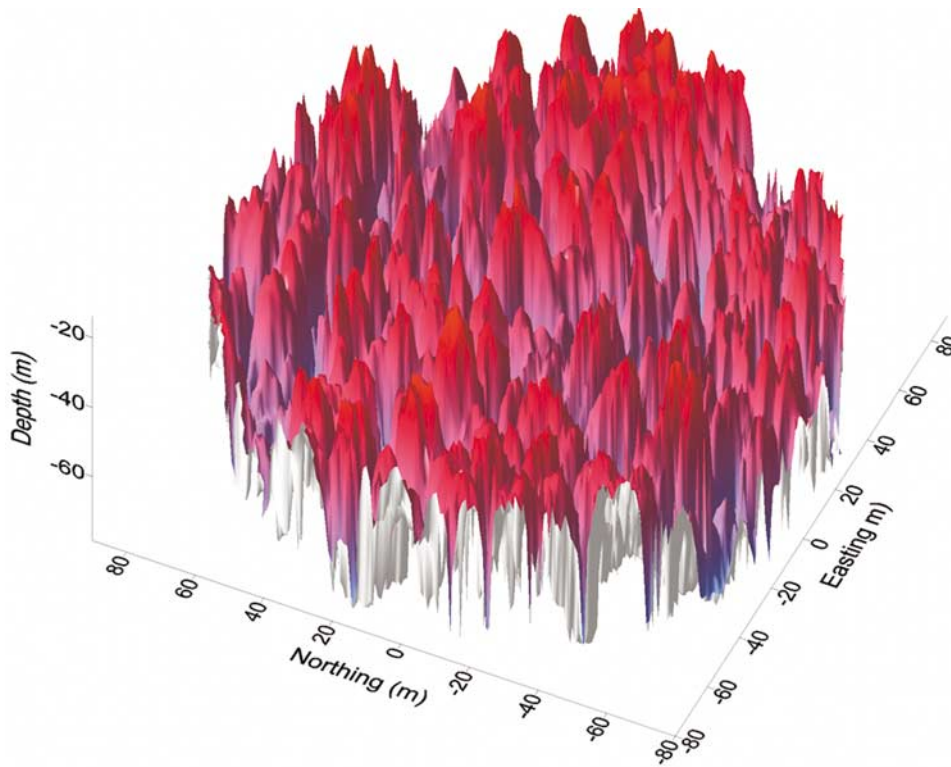
Figure 6. Topography of the outer surface of the Wind River old-growth canopy within the crane circle. The vertical axis gives depth below the crane jib. The horizontal resolution is 1 m.
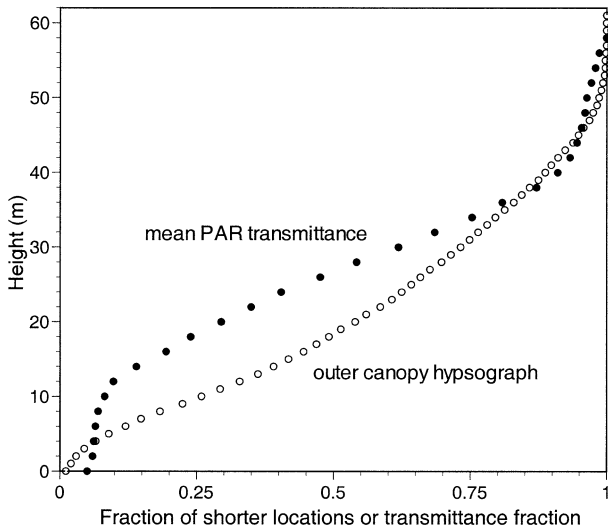

Figure 7. The cumulative fraction of the outer canopy surface area below a given height (the hypsograph, open circles) and the mean photosynthetically active radiation (PAR) transmittance profile (*filled circles*) of the Wind River old-growth forest.

Figure 8. Spatial variation of canopy structure of the Wind River old-growth forest expressed as a semivariogram of local outer canopy height. The curve is the fitted spherical model. The range was estimated to be 9.6 m; the nugget and sill semivariance were 6.3 and 288 m^2, respectively.

The approach of Thomas and Winner (2000b), from direct in-canopy measurements, seems least sensitive to assumptions.

Even a straightforward characteristic such as height can be variously estimated. The stand's tallest tree is 64.6 m, the mean PAR transmittance is
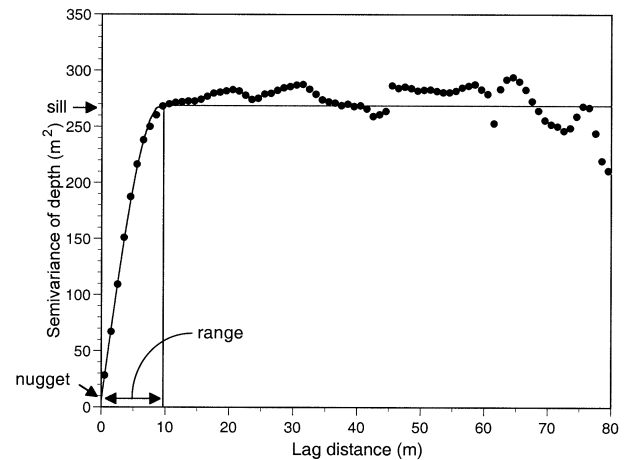
1.0 at 58 m, the mean height of the dominants is 56.3 m, and the average height of the outer canopy is 28 m. Much of this variation reflects a diversity of motivations: the site index of the stand serves a different purpose than does a knowledge of canopy topography. The effective height of the forest would be useful to know, but it will depend on the char-
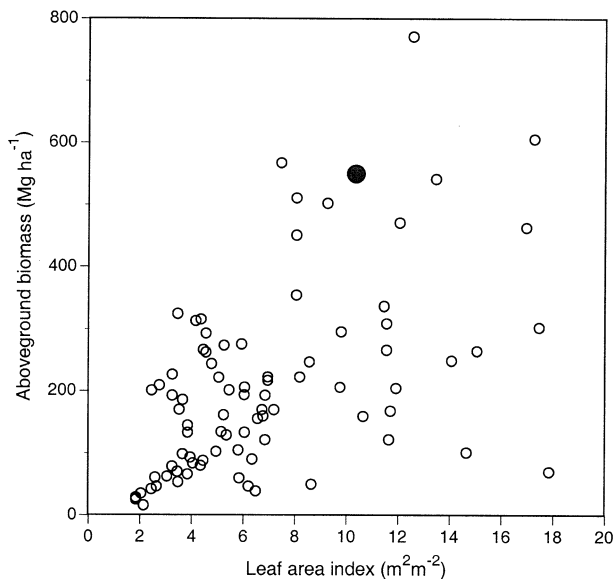
Figure 9. Aboveground biomass and leaf area index (LAI) in the Wind River old-growth forest (*solid circle*) in relation to other well-studied forests (*open circles*) from the Woodlands data set (DeAngelis and others 1981).

acteristic of interest; that is, the radiation-effective height could differ from a similar height for momentum. Also, vertical structures and functions are often compared among forests through normalizing by height (for example, see Kaimal and Finnigan 1994). Inappropriate or inconsistent definitions of height might compromise the utility of such comparisons.

Structural Characteristics of Pacific Northwest Old-growth Forests   The stand is dominated by relatively few large individuals of *P. menzeisii,* with numerous smaller *T. heterophylla,* and also many smaller stems of *Thuja plicata, Abies amabilis,* and *Taxus brevifolia* (Shaw and others 2004). Understory trees, such as *Acer circinatum,* are very numerous but rarely attain the 5-cm dbh limit for inclusion in the present analysis. About half of the total wood in the stand is in the long-lived pioneer *P. menzeisii,* but most of the foliage is carried by the shade-tolerant *T. heterophylla* (Figure 3a). The distribution of stem top heights mirrors the pattern of the diameter distribution: *P. menzeisii* is only found in the upper layers and largest diameter classes; the other species are found in smaller diameter and height classes and display foliage throughout lower canopy layers. Although it is 500 years old, the stand is dynamic. In the sense of Franklin and others (2002), this forest is in an early stage of old growth. In the absence of major disturbances, it will likely be dominated by *Tsuga* and *Abies* in the future. As the currently dom-

inant *P. menzeisii* trees die, the stand will decrease in maximum height and the zone of highest foliage density will shift to even lower levels of the vertical profile (become even more "bottom-heavy").

More than a quarter (25.5%) of aboveground biomass at Wind River is dead (214.4 Mg ha^{-1}) (Harmon and others 2004). Although most of the dead material is near the ground, 67.2 Mg ha^{-1} occurs above the forest floor in snags and dead branches. The height distributions of snags and live trees differ for several reasons. First, the mortality of shorter (usually younger) trees is greater than that of taller (often older) ones (DeBell and Franklin 1987). Next, snags fall apart differently than do live trees—snags of all species but *T. plicata* break several times as they fragment. If snags fell as intact stems, the height distribution of snags should be similar to that of live trees. Sequential loss of the tops of snags also leads to a decreased mean height relative to live trees.

The aboveground volume of wood (about 1677 m^3) is a small fraction (0.003 m^{3}m^{-3} on average) of the stand volume defined by the outer surface of the canopy (about 625,000 m^3). The mean leaf area density is 0.32 m^{2}m^{-3}, but this varies greatly in space. Foliage is a small component of the biomass volume, but it defines the shells of individual crowns (Van Pelt and North 1996). That is, the ecosystem bounded by the outer canopy surface has a low and variable biomass density. The fraction of the stand volume under the outer canopy that was empty ("porosity," after Dubrasich and others 1997) was estimated at 0.39 (G. G. Parker unpublished), which implies a leaf area density of 0.52 m^{2}m^{-3} in nonempty zones. Lefsky and others (1999), using waveform-recording LIDAR, distinguished several qualitatively different kinds of canopy volume in an age-series of Douglas-fir/western hemlock stands in the Cascades. In old-growth cases, they found that about 26% of the forest volume was in gaps open to the sky, 38% with surfaces that absorb two-thirds of incident radiation (collectively termed the "euphotic zone"), 23% absorbing the lowest third of light ("oligophotic"), and 13% in open volumes contained beneath a canopy shell. Moreover, each type of zone was distributed at all the heights in old-growth stands, in contrast with younger stands, where these zones were more vertically organized.

Although comparable observations of structure have not been reported in other stands, the canopy attributes we summarize here are consistent with the new understanding of old-growth structure. The enormous quantity of dead material, the variety of crown forms, and the abundance of broken or

suppressed stems and dead tops (Ishii and others 2000a, Ishii and others 2000b) are characteristic of old growth. The outer surface is extremely complex; both the rumple index and rugosity are greater than previously reported (Ford 1976; Parker and Russ 2004). Most views of the canopy vertical structure presented here indicate a single maximum, with a bottom-heavy distribution (Figure 2). That is, the majority of the material in this forest is contained in the middle and lower third of the height defined by the tallest trees. Until similar measurements are accumulated at other sites, the current observations can provide hypotheses on canopy aspects of old-growth structure.

Functional Implications of Canopy Structure

Short-wave Radiation Balance The Wind River old-growth canopy reflects little sunlight (Paw U and others 2004; Roberts and others 2004),—less than has been reported for any other conifer forest (Mukammal 1971; Stewart 1971; Tajchman 1972; Jarvis and others 1976), including boreal jack pine (Betts and Ball 1997; Ni and Woodcock 2000). The extreme complexity of the outer canopy surface (Figure 6), the bottom-heaviness of the canopy (Figure 2), and the proximity of much of the surface area to the ground (Figure 7) very likely contribute to the low albedo. The vertically elongated spaces between dominant trees permit deep penetration of incident radiation, but subsequent scattering and absorption within these spaces reduces whole-canopy reflectance (Dickenson 1983; Peterson and Nilson 1993). Albedo in older stands (over 200 years) in the Wind River region was significantly lower than in younger ones (Roberts and others 2004). Ogunjemiyo and others (*forthcoming*) found that these albedo variations were more closely related to canopy rugosity than to stand age. Albedo ranged from a maximum of 15% in stands with a smooth outer canopy (rugosity of 4 m) to a minimum of 5% where the canopy top was most complex (rugosity of 15 m). Stands with the most complex outer canopy could have as much as 10% more net radiation than stands with the most uniform surfaces. The fate of the available energy suggested by these albedo differences is unknown and should be investigated.

The energy associated with even small differences in albedo can be significant for heat exchange and microclimate. For example, Pielke and Avissar (1990) calculate that an albedo decrease of 1% is equivalent to an increase in air temperature of 0.67°C, on the order of the predicted near-term warming due to increased concentrations of radia-

tively active gases (Pielke and Avissar 1990). Also, albedo estimates made for entire scenes might misrepresent the radiation balance of particular landscape components (Ogunjemiyo and others *forthcoming*).

The shadowing caused by crowns and outer canopy openings makes a characteristic texture useful for identifying old-growth in remote-sensing images (Cohen and others 1990; Cohen and Spies 1992). The spatial scale of regeneration is also affected by such openings. Spies and others (1990) found that tree fall gaps in these forests can remain open for decades, in contrast to gaps in shorter stands at lower latitudes, which fill in relatively rapidly. The deep, narrow crowns of the conifers at Wind River and the low solar elevation angles in the Pacific Northwest displace the light made available from the gapping event away from the forest floor at the gap-making tree, a spatial disconnection between the site of the gap and the regeneration response (Canham and others 1990; Van Pelt and North 1996; Van Pelt and Franklin 2002).

Mean Microclimate Profiles, Turbulence, Coupling to External Environment The high surface rugosity and internal porosity of this stand may explain the uniformity in vertical profiles of temperature and relative humidity at the crane tower (Newton and others 2000). The in-canopy temperature and humidity generally track the variation of external conditions, suggesting close connection between interior and exterior conditions (low decoupling, in the sense of Jarvis and McNaughton (1986)). We expect this stand to have a very low canopy resistance and a relatively high rate of ventilation compared to less rugose and porous stands. The large volume of the canopy suggests that the storage component of water vapor and CO_2 budgets will be larger than in shorter stands. The large store of live and dead biomass might contribute to a substantial thermal lag, even high up in the canopy.

The PAR attenuation gradient in the old-growth stand at Wind River (0.04 m^{-1}) is more gradual than that in younger stands of this forest type ($0.06-0.12$ m^{-1}) (Parker and others 2002). The deep transition zone, where spatial variation and mean vertical change of PAR transmittance are highest (Parker 1997), implies a large volume for radiation absorption. The shape of the mean transmittance profile is similar in some respects to the stand hypsograph (Figure 7): both decline rapidly with height in the uppermost canopy, followed by a broad region of gradual decline in the middle heights. The transmittance profile is largely controlled by the heights of the first foliar surface encountered, because leaves of the dominant species

at Wind River absorb more than 80% of PAR (Roberts and others 2004). This is likely why transmittance profiles may be deduced from LIDAR waveforms (Parker and others 2001).

The difference between the transmittance and hypsographic profiles (Figure 7) might have several causes. First, the middle and lower portion of the light profile are probably biased to brighter areas (as was noted by Mariscal and others (2004)), owing to restrictions on gondola movements. Also, the shape of the hypsograph is affected by the scale of measurements—coarser-scale, more aggregated estimates of LOCH would result in a hypsograph with less curvature (M. A. Lefsky unpublished).

The shallow gradient in PAR transmittance suggests that upper-canopy competition for light is less intense than in younger stands with steep gradients. Species are widely distributed in height without aggregation in any specific layer (Figure 3). Many of the species at lower heights may receive relatively higher light levels than they would in younger stands (Parker and others 2002). The rumple index (12.4) is on the order of the stand LAI (Table 1), which suggests that much of the foliage in the stand is displayed at the extensive outer canopy, potentially exposed to direct light at some time of day. That is, we expect that the stand has a high solar equivalent leaf area (Cermak 1989) and sunlit leaf area (Campbell and Norman 1998). Although the rumple index is scale-dependent (it would be larger than 12.4 if based on a finer grid and smaller with measurements of coarser resolution), it nonetheless indicates an enormous surface area in the outer canopy.

Carbon Sinks and Sources   The sites of CO_2 sources and sinks are separated in the Wind River stand. Most CO_2 is assimilated where PAR transmittance declines rapidly, from 20 to 40 m (Figure 7), yet the majority of within-canopy respiration occurs 10–25 m above ground (Figure 10). Most of heterotrophic respiration is at the forest floor or below ground in this stand (82% of 5.77 Mg C ha^{-1} y^{-1}); only respiration from heart rot, snags, and grazers occurs above ground (from estimates in Harmon and others 2004). In contrast, autotrophic respiration occurs primarily above ground (66.3% of 13.09 Mg C ha^{-1} y^{-1}). Of the total stand respiration, more than half (51.5%) takes place within the canopy. Some components of this flux can be localized vertically on average (Figure 10). Of all snag respiration, half occurs within 7 m of the ground—lower than for foliage and small branches (14 m) and for sapwood (23 m). The heights of foliage-derived sources and sinks will vary locally
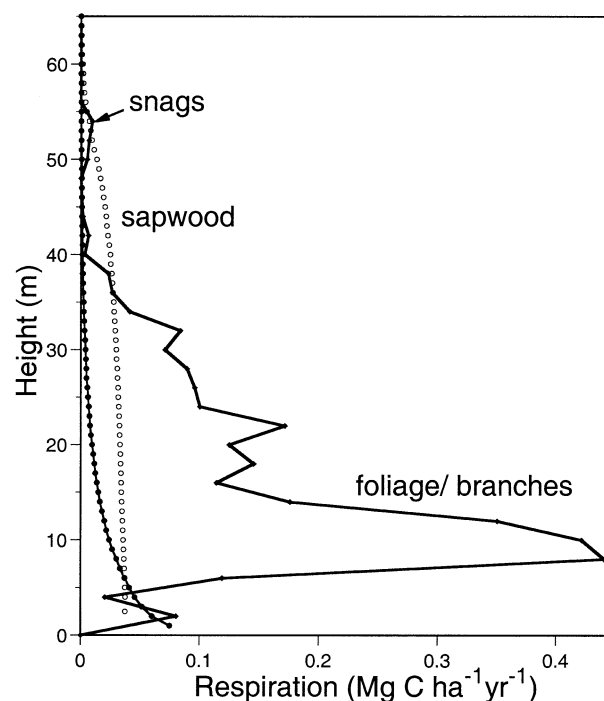

Figure 10. Estimated vertical variation in annual carbon dioxide flux from decomposition of snags, respiration of sapwood, and respiration of foliage and branches in the old-growth canopy at Wind River.

from the mean, as indicated by the outer-canopy rugosity.

In addition to being spatially separated, the two classes of respiration respond to different environment characteristics. Heterotrophic respiration is most closely linked to moisture and temperature of the soil, whereas autotrophic respiration is driven by air temperature (Harmon and others 2004). The differences in locations and controls have implications for net ecosystem exchange of carbon. For example, much of the heterotrophic respiratory flux may be tracked with chamber or eddy covariance measurements at the forest floor (Paw U and others 2004). However, the autotrophic portion must be estimated from various carbon pools, which at Wind River are largely in the canopy. Because net carbon exchange is often a small difference between large production and respiration fluxes (Harmon and others 2004), the influence of canopy structure on respiratory processes presents a significant challenge for the estimation of respiration and, ultimately, ecosystem carbon exchange.

Future Directions

The three-dimensional structure of an old-growth Douglas-fir/western hemlock forest is the result of a

development sequence with mechanisms that are now becoming better understood (Acker and others 2002; Franklin and others 2002; Janisch and Harmon 2002). Often the third dimension of canopy structural and functional characteristics is treated using average vertical profiles. However, the example of the complex Wind River canopy indicates that variability in the third dimension needs to be considered explicitly. Modeling approaches that can deal with such variation are available (Moorcroft and others 2001). Although few canopy processes have been studied volumetrically (for example, the PAR environment), it is clear that the variation is patterned and related to structure (Parker and others 2002). Additional spatially intensive studies of other variables (for example, microclimate attributes such as temperature, $[H_2O]$, $[CO_2]$, and momentum) and processes (turbulent eddy structure, ventilation, within-canopy storage, and net exchange of energy and material with the atmosphere) will certainly reveal additional associations with appropriate structures. Connections provided by such studies will lead to new theories of canopy physical and biotic environments and exchanges that take explicit account of their three-dimensional character. These in turn will provide a new basis for rational extrapolation of small-scale and high-resolution measurements, for the testing and verification of observation programs that are necessarily restricted to the ground, and for linking measurements in canopies to the products of remote sensors with high three-dimensional spatial resolution.

The large-scale structure of forest canopies has only recently been explored; understanding of its implications for microclimate, habitat, and atmospheric exchange is more recent still. The observations produced by new measurement and access systems are only now stimulating theories of structure–function interactions at the scale of whole canopies. We have attempted, in the current description of the old-growth forest at Wind River, to link some structural aspects with their functional consequences. Owing to the newness of the studies, these links are of variable strength. Some of the links (between the transmittance profile and outer-canopy hypsograph, for example) have a mechanistic basis. Others, such as the relation between albedo and canopy rugosity, are supported with remote sensing through comparisons with other stands. Still others (for example, microenvironmental decoupling with the free atmosphere) are conjectural. We expect that collaborative efforts such as those at the Wind River Canopy Crane Research Facility will harden these links and forge new ones

for understanding of forest ecosystems at large scales.

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