Old-Growth Forest Canopy Structure and Its Relationship to Throughfall Interception

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ABSTRACT. Structural elements of the forest canopy such as foliage, branches, and epiphytes intercept, retain, and regulate inputs of matter and energy to the forest floor in spatially variable ways. Most studies of forest structure-function have analyzed relationships between canopy structure and the spatial distribution of inputs at the forest stand level. Few studies have focused on within-canopy spatial scales or identified the functional roles of particular structural components. Our objective was to quantitatively assess the amount of canopy structural material to a critical functional attribute: canopy interception of rainfall. We investigated forest canopy structure with a novel technique, "vertical canopy cylinder transects," that uses access from a construction crane in an old-growth coniferous forest in Washington State. We characterized the diversity and composition of forest structural elements (tree foliage and branches by species, epiphytes by functional group) and found the majority of the foliage and epiphytes concentrated in the upper- to mid-canopy, with some vertical stratification of the epiphyte functional groups. We also quantified one aspect of forest function, the volume and variability of throughfall interception. We documented a strong relationship between the amount of structural elements and rainfall interception ($R^2 = 0.79$). This approach of quantifying three-dimensional canopy structure at particular locations had higher predictive ability for throughfall volume than previous approaches that were not able to gain direct access to canopy components. FOR. SCI. 50(3):290–298.

Key Words: Canopy crane, forest ecology, hydrology, throughfall, Wind River.

THE COMPOSITION AND SPATIAL VARIABILITY of forest structure has been a major focus of forest ecological study, especially as it relates to functional attributes (Parker 1995). It is important to quantify these relationships because canopy structural elements—foliage, branches, and epiphytes—function to intercept, retain, modify, and conduct inputs of matter and energy to the forest floor. Most forest structure-function studies have analyzed relationships between canopy structure and the spatial distribution of inputs at the stand level (e.g., Sehmel 1980). Little research has focused on within-canopy (i.e., branch-level) spatial scales. The specific functional roles of particular structural components are also poorly known. In this article, we describe the three-dimensional (3-D) distribution

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of tree and epiphytic canopy elements in a complex old-growth temperate coniferous forest using data collected from a canopy crane. We relate the amount of cover of each canopy component to the amount of throughfall intercepted on the forest floor.

Past research has indicated that the spatial configuration of forest components at the stand level leads to spatial variation in matter and energy inputs to the forest floor. Relationships have been documented between elements of canopy structure and functional characteristics such as the quantity and spatial distribution of solar radiation (De Wit 1965, Endler 1993), litterfall (Welbourn et al. 1981), wind (Brünig 1970), atmospheric nutrients (Lovett 1981, Lindberg et al. 1986), fog drip (Sigmon et al. 1989), and pollutants (Mooney et al. 1987).

Forest canopy structure-function studies at the within-stand level have been limited by the difficulties associated with gaining access to and measuring complex 3-D canopies (Moffett and Lowman 1995). Traditional ground-based structural measurement techniques (e.g., Bouten et al. 1992) and use of remote sensing imagery (Nelson et al. 1984) have lacked sufficient detail for accurate predictions. Within-canopy methods (e.g., single rope techniques) result in detailed but small or biased data sets (e.g., Nadkarni 1985, Sillett 1994). With the recent application of construction cranes to gain access to the 3-D volume of tall complex forests, however, it is now possible to quantify the vertical component of canopy structure in unprecedented ways that are nondestructive, repeatable, and that reveal both the amount and location of particular canopy structural components at the species or functional group level (Parker et al. 1992). In particular, this tool can potentially help identify how forest canopies affect the amounts and spatial distribution of atmospheric inputs to the forest floor. This is especially important because human activities such as harvesting, thinning, and pruning canopy components can radically alter the distribution and abundance of structural elements with only poorly known consequences to forest function.

Our study was focused on the effects of within-stand and within-tree (hereafter, localized) canopy structural elements by using a novel technique to quantitatively relate canopy structure to patterns of throughfall. We established "vertical canopy cylinder transects" using a construction crane that had been installed to study an old-growth forest in western Washington. Our research goals were to: (1) quantify canopy structure above and around discrete points on the forest floor; (2) determine spatial relationships in throughfall volume and variability at sample points directly below the sampled cylinders; and (3) analyze relationships between canopy structure and throughfall volume and variability within the forest.

Materials and Methods

Site Description

The study site is at the Wind River Canopy Crane Research Facility (WRCCRF) in the T.T. Munger Research Natural Area of the Gifford Pinchot National Forest (45°49′13.76″ N, 121°57′06.88″ W). The facility is a coop-

erative scientific venture among the University of Washington, the United States Forest Service Pacific Northwest Research Station, and the Gifford Pinchot National Forest. The site is on the lower slopes of Trout Creek Hill, an inactive quaternary shield volcano. The elevation is 370 m, and the topography is gentle with a mean slope of 5%. The climate is characterized by relatively dry warm summers and cool wet winters. Annual precipitation is ca. 2,500 mm with less than 10% occurring between June and Aug. Much of the winter precipitation occurs as snow (ca. 2,300 mm annually). The mean yearly temperature is 8.7° C with a mean Jan. temperature of 0.0° C and July temperature of 17.5° C (Kemp and Schuller 1982).

The forest is approximately 450 years old and is classified as a late successional state of western hemlock-Douglas-fir forest. The canopy is composed of *Pseudotsuga menziesii* (Mirb) Franco (Douglas-fir), *Tsuga heterophylla* (western hemlock), *Thuja plicata* (western red cedar), *Abies amabilis* (Pacific silver fir), *Abies grandis* (grand fir), *Abies procera* (noble fir), and *Pinus monticola* (western white pine). Understory trees include *Taxus brevifolia* (western yew) and *Cornus nuttallii* (Pacific dogwood). Shrubs that reach heights of over 2 m include *Acer circinatum* (vine maple), and *Corylus cornuta* var. *californica* (California hazelnut) (Kemp and Schuller 1982).

At the center of the study site, a construction crane (85-m tall Liebherr 550HC tower construction crane with a 90-m boom) was installed in 1994 (Shaw et al. 1993, Morell 1994). The hanging gondola can move horizontally on the jib and vertically on a descending cable, providing access to the crowns of 1,078 trees that are located within the 2.3-ha "crane circle" below the rotating jib.

Plot Installation and Stand Measurements

Trees in the crane circle were measured by staff scientists at the WRCCRF in 1994. A 4-ha (200 m × 200 m) square plot was divided into 64 subplots (25 × 25 m). All live and dead trees greater than 2 m tall and 5 cm dbh were measured. The tree base (x,y,z) spatial coordinates, dbh, height, and species were recorded for each tree (D. Shaw, WRCCRF, June 30, 1994). We established a set of "sample locations" at the corner points of all of the subplots within reach of the crane's gondola with the exception of six points that were in the road or stream ($n = 32$ sample points, Figure 1).

We assessed the quantity of canopy structural elements (foliage, branches, epiphytes) with a modified version of the cylinder probe technique (Wilson 1965, MacArthur and Horn 1969, Sumida 1995, Figure 2). The crane's gondola was positioned directly over each sample point, and a weighted measuring tape was lowered through the canopy to touch the sample point. An assistant on the ground checked the accuracy of the transect location. The tape was secured to a branch above the gondola and to the ground sampling point in a manner that retained the vertical orientation of the tape. For each sample point, we established an imaginary cylinder with the tape as its centerline. The gondola was then lowered through the canopy, parallel to
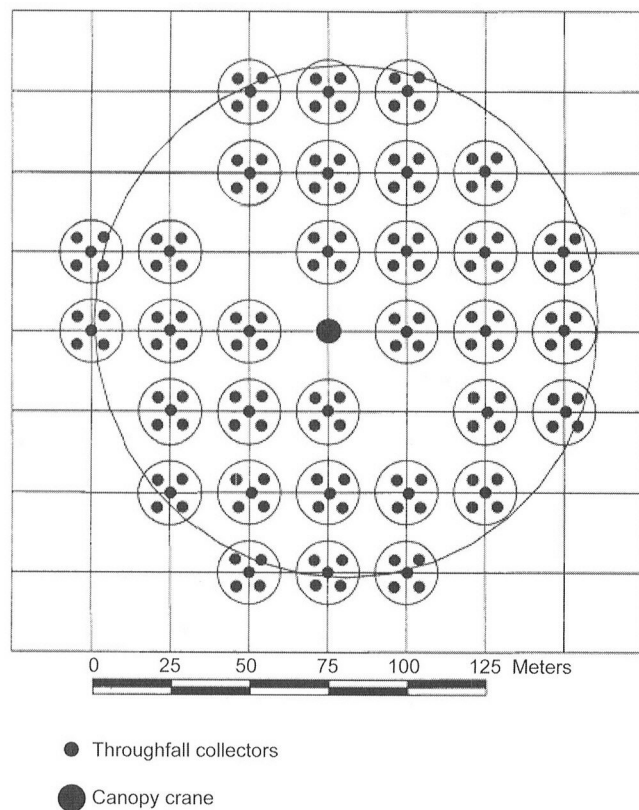
Figure 1. Schematic of the sampling locations for the primary forest. The large ring within the large square indicates "crane circle," the sampling area accessible to the gondola of canopy crane. The 32 small circles represent the sampling locations for collecting throughfall. Each of the small black dots represents a single throughfall collector. The amount of throughfall collected in the five collectors for each sampling interval was averaged to generate a mean throughfall volume for each sample location.

the transect. From the canopy top to a level 15 m above the forest floor, all material within a cylinder the radius of 1 m was measured. From 15 m to 1.5 m above the forest floor, all material within a cylinder the radius of 0.5 m was measured. These two radii were selected to roughly approximate a stacked volume that was judged to be the volume of canopy affecting throughfall, based on our observations of falling rain at the WRCCRF. The distance was checked with a meter stick attached to a telescoping pole that extended from the gondola.

Within each cylinder, the upper and lower heights of all structural components (branches, foliage, and epiphytes) that intercepted the cylinder were measured to the nearest decimeter. Canopy material was classified as either tree structural component or as epiphyte. Structural components were subdivided into foliage (which implicitly includes branches) and live or dead branches that were greater than 3 cm in diameter and void of foliage. The tree components were further divided by species, and epiphytes were divided into functional groups following McCune (1993). The quantity of material was estimated on a scale of 1–5 (1 = the lowest density observed; 5 = the highest density). The amount of each structural component in each cylinder was

calculated by multiplying cylinder depth for each sample segment by its quantity rating. The total amount of each component in each cylinder was calculated by multiplying the length of the transect it occupied (in decimeters) by the area of the circle. We then summed up all of these volumes to get a "canopy cylinder quantity rating" (dimensionless) for each structural component and for the total amount of material directly above a given sampling point on the ground (Figure 2).

Throughfall Measurements

We measured throughfall and estimated its variability for each of the 32 sample points. Individual throughfall collectors consisted of plastic funnels (210 mm orifice diameter) that were secured to 2 l plastic bottles with rubber tubing, with a maximum capacity of 53 mm of rainfall. Collectors were supported 1.5 m above the forest floor in a metal basket welded to rebar. At each sample location, an array of collectors was placed with one in the centerpoint and four at the corners of a 0.75 × 0.75 m square. These encompassed the small-scale spatial variability of throughfall at a given point ($n = 160$ collectors). The throughfall for the five collectors were measured individually to determine the within-location versus among-location variability.

Sampling was conducted from 12 June and 13 Nov. 1997. Seven collections were made, which included 14 separate rain events. Collection periods varied between 1 and 10 days (mean = 5.3 days). Throughfall patterns are reported to be highly variable during rain events of weak or strong intensity, but are less variable during rain events of intermediate intensity (10–40 mm day^{-1}) (Jackson 1975, Loustau et al. 1992), so we limited our data to rain events of intermediate intensity. For all collections used in the analyses, the mean incident rainfall was 23 (SD = 12.6) mm per collection period.

Throughfall for each collector was the amount of precipitation caught in each collector. Relative throughfall was calculated as a percentage of the measured throughfall relative to precipitation that was measured with five collectors in a large clearing adjacent to the study site over the same period. Variability of rainfall collected in the open was only ca. 4–10% of variability under the canopy for each rainfall event. Mean normalized throughfall was calculated by dividing the relative throughfall collected in each of the 32 collection locations by the mean of relative throughfall for all sample locations for that collection period.

The amount of variability contributed by individual collectors within a given sampling location relative to the amount of variability of a given sampling location relative to the study site was examined with a one-way analysis of variance (ANOVA) for each collection period. For this analysis, the five individual funnels at each sampling location were treated as replicates for each of the 32 sample locations. An ANOVA was performed separately for each of the seven collection events. We used simple linear regression analysis to relate the mean normalized throughfall values from the sample location to the canopy structural measurements directly above the sample locations.
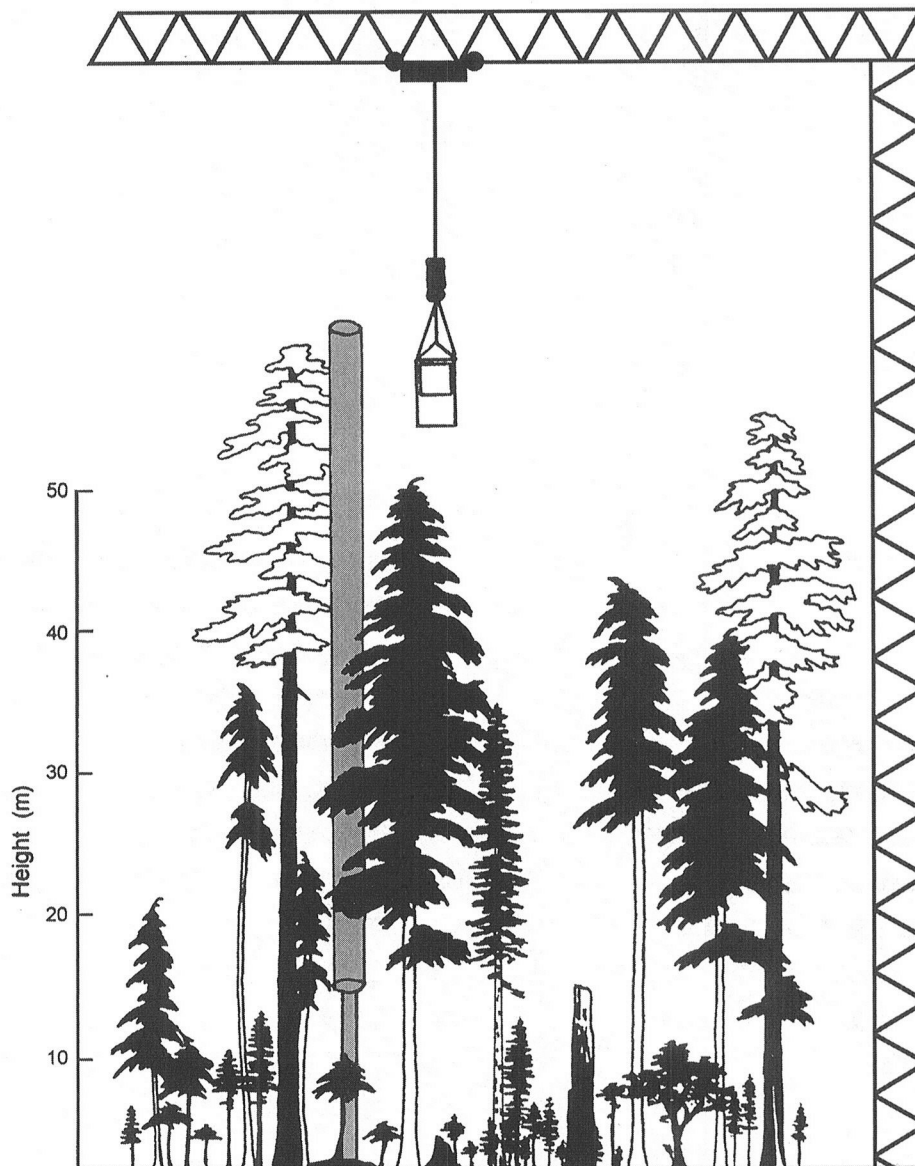
Figure 2. Schematic of a "canopy cylinder transect" depicting the crane's gondola, sample trees, and the outline of a vertical canopy cylinder transect.

Results

Forest Structure and Composition

The forest is composed of an uneven-aged canopy and is dominated (by stem count) by the shade-tolerant *T. heterophylla*. Forest sample plots have a mean stem density of 446 trees ha^{-1}. The tree height distribution for the primary forest shows a peak for trees less then 10 m tall (mostly suppressed shade-tolerant species) and a relatively even distribution of trees between 10 and 55 m tall with diameters between 10 and 180 cm (Table 1).

Canopy Structure and Composition

Total projected forest floor area and total volume of all canopy cylinders was 364 m^2 and 6123 m^3, respectively. This is equivalent of 1.8% and 0.4% of the total projection area and forest volume, respectively. Cylinder heights ranged between 1.5 m (in an open location) and 35.6 m (for a cylinder immediately adjacent to a dominant *P. menziesii*), with a mean (SD) cylinder depth of 12.6 (8.4) m.

The distribution of tree foliage varied with tree height (Figure 3A). Over 70% of tree foliage was located in the middle two-thirds of the canopy (between 10 and 50 m), with only very small amounts in the topmost and lowest sections. Foliage was also distinctly stratified by species, with *P. menziesii* dominating in the upper canopy and *T. heterophylla* and *T. brevifolia* in the lower canopy, and *T. plicata* occurring at intermediate heights (Figure 3B).

Overall, 64% of the measured cylinder units were occupied by epiphytes. Epiphyte distribution closely paralleled that of foliage, with greatest amounts in the upper- to mid-canopy (Figure 4A). The proportion of epiphyte composition by functional groups were: alectorioids, 45%; "other" lichens, 37%; cyanolichens, 10%; and bryophytes,

Table 1. Stand-level composition and structural characteristics of trees in the study site. Analyses were based on an inventory of a 4-ha study plot. The diameter at breast height (dbh, cm) and tree height (m) are for live stems only.

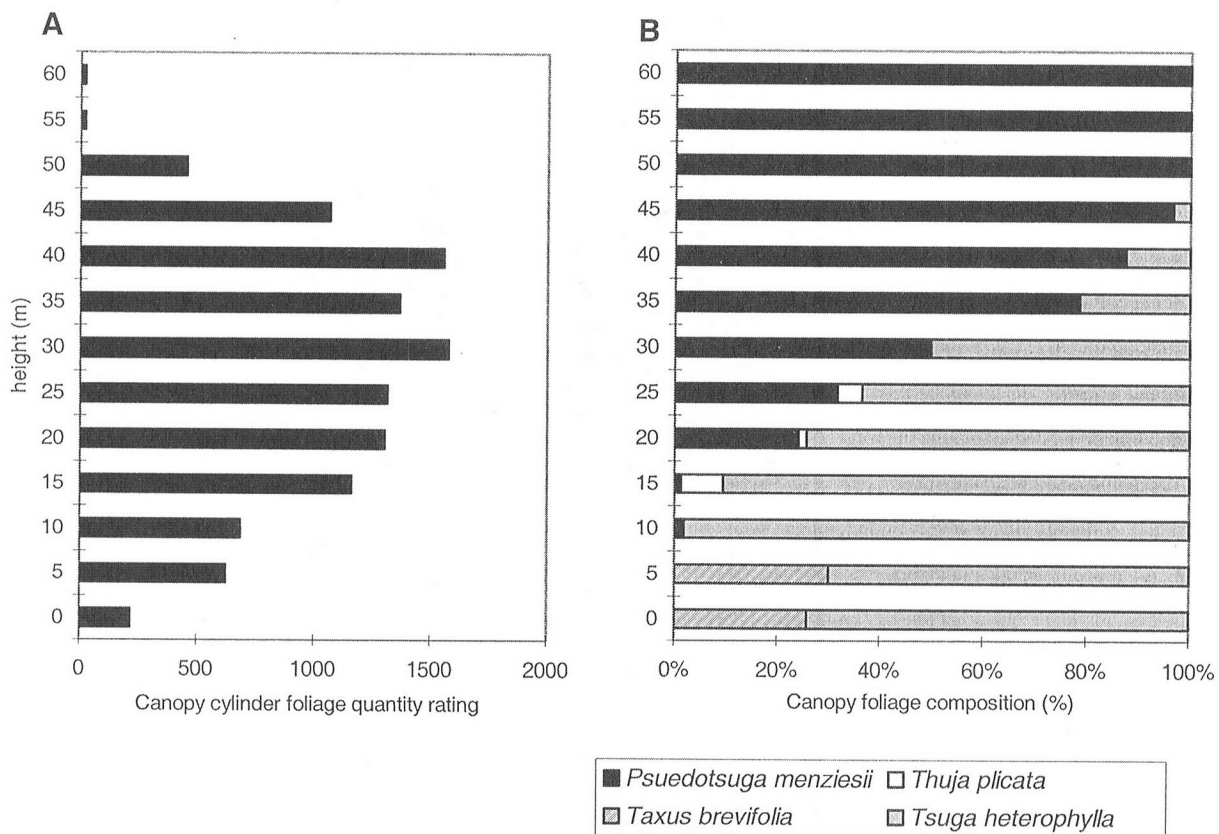| Species | No. of stems | | dbh (SD) | Tree height (SD) |
	Live	Dead		
Abies amabilis	48	7	9.2 (6.7)	8.0 (6.1)
A. grandis	5	5	50.9 (18.9)	38.8 (13.1)
A. procera	1	0	—	—
Cornus nutallii	2	0	5.5 (0.6)	5.7 (1.9)
Pinus moticola	0	4	—	—
Pseudotsuga menziesii	38	52	114.3 (21.9)	53.8 (5.7)
Taxus brevifolia	90	7	15.5 (12.0)	7.0 (3.1)
Thuja plicata	30	3	55.4 (48.6)	26.4 (17.3)
Tsuga heterophylla	230	14	30.2 (26.5)	21.9 (15.4)
Total	349	92	36.4 (37.7)	20.5 (18.2)

Figure 3. Vertical distribution of foliage in the study area, measured with cylinder transects. (A) Total quantity of foliage by canopy height. Canopy cylinder quantities (x-axis) were calculated by multiplying cylinder segments by relative quantity ratings and then summing over the total canopy height. (B) Percent canopy foliage composition by tree species.

8%. Epiphytes displayed striking stratification, with alectorioids occupying the topmost branches, "other" and alectorioid lichens in the upper canopy, cyanolichens in the mid- to lower canopy, and bryophytes restricted to the lowest levels of the forest (Figure 4B).

There appeared to be a disproportionate amount of epiphytes in the mid-upper canopy relative to the distribution of foliage (Figure 3A and 4A). The proportion of the substrate occupied by epiphytes was a constantly high level for the top half of the canopy. It then declined steadily to ca. 20% of substrate until a level of 10 m above the forest floor where it increased to ca. 70% cover (Figure 5). The increase

for the 0–10 m height zone was related to an increase in bryophyte cover, which dominates this zone.

Throughfall Volume, Variability, and Relationships to Canopy Structure

The amount of throughfall reaching our sample points varied considerably, depending on both location and collection period. The mean volume for an individual location for a single rainfall event varied between 10.7 and 46.8 mm (mean = 23.7 mm; SD = 12.6).

The variability of throughfall volume within sampling locations (five funnels per location) was very low relative to
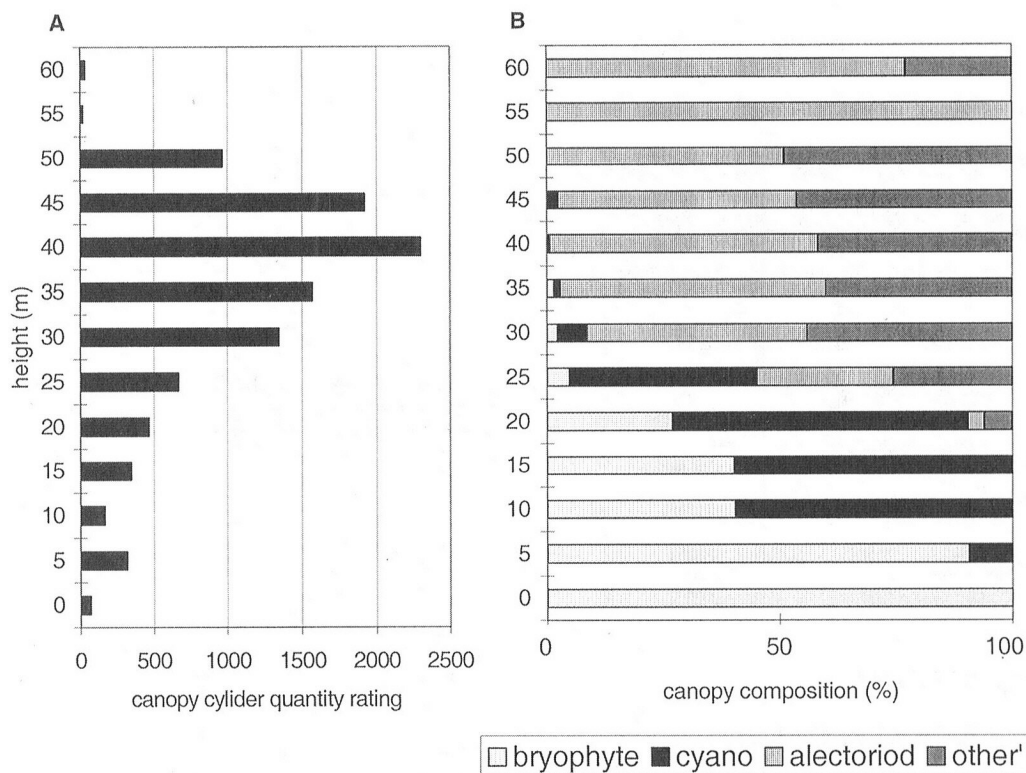
Figure 4. Vertical distribution of epiphytic functional groups for the primary forest measured with canopy cylinder transects. (A) Total epiphyte abundance by canopy height. Canopy cylinder quantities (x-axis) were calculated by multiplying cylinder segments by relative quantity ratings and then summing over the total canopy height. (B) Percent epiphytic composition by functional group.

variability among sampling locations (32 locations within the site) for each of the seven collection intervals (one-way ANOVA, $P < 0.0001$) (Figure 6). This means that there is a very strong "signature" for collectors at a given point (i.e., collectors that have high volumes consistently get high volumes across different rainfall events). This indicates that there is a strong influence of local canopy structure on throughfall volume. The mean volume and variability of intercepted throughfall varied with the collection period (Figure 7).

We found a highly significant relationship ($P < 0.001$) between mean throughfall volume at a given sample location and the cylinder depth of all tree structural components (Figure 8). Because epiphytes and foliage are always associated with branches, and because nearly all branches in the primary forest were associated with epiphytes, these component types were nonindependent, and we were not able to distinguish the relative impact of foliage versus epiphytes on throughfall interception and retention.

Discussion

One major function of forest canopies is the processing of precipitation as it flows through the forest (e.g., Jackson 1975, Doley 1981, Herwitz 1985). Process-oriented forest hydrology models that explain and predict the interception and subsequent evaporation of rainfall have been a primary focus of canopy hydrology research since the pioneering work of Rutter et al. (1971). Model variations have since

been developed to incorporate greater realism and practicality: single-layer physical or theoretical models (Rutter et al. 1975, Massman 1980 and 1983), multi-layer canopy models (Sellers and Lockwood 1981), stochastic models (Calder 1986 and 1996), and analytical or practical models (Gash 1979, Mulder 1985). Inherent in all of these models is the simplifying assumption that the physical factors that control forest hydrologic dynamics are spatially homogenous, which is fundamentally a weakness of applying physically based models to heterogeneous environments (Beven 1989). Understanding the complex relationships between throughfall heterogeneity and canopy structure is essential for making predictions about forest hydrology and for implementing certain forest management goals.

We quantified forest structural elements within the canopy with direct measurements using the canopy crane. Our results corroborate those obtained from ground-based methods. Based on the vertical light radiation budget, Parker (1997) identified three light layers within this forest: "dim zone" (0–12 m), "transition zone" (10–40 m), and "bright zone" (>40 m). The vertical distribution of foliage as calculated from the cylinder transect data closely parallels these light zones (Figure 3A). The shade-intolerant *P. menziesii* dominates the bright zone, the shade-tolerant *T. heterophylla* attains dominance within the transition zone, and the dim zone is shared by *T. heterophylla* and the understory *T. brevifolia* (Figure 3B).

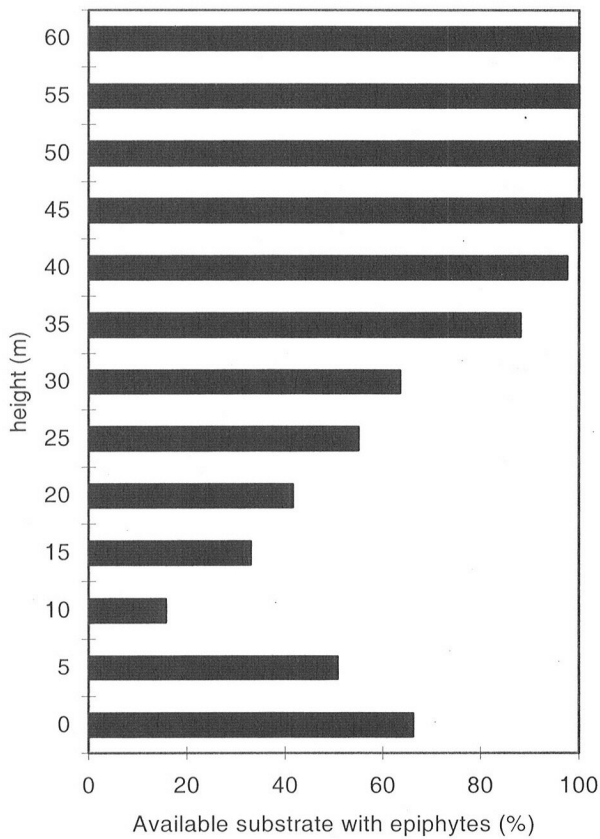We found a highly significant relationship ($P < 0.001$)

Figure 5. The distribution of the percent of stem substrate that is occupied by epiphytes in the vertical profile of the canopy in our study site. This was derived by calculating the proportion of our vertical canopy cylinder quadrants that contained epiphytes as a proportion of the quadrants that contained branches.
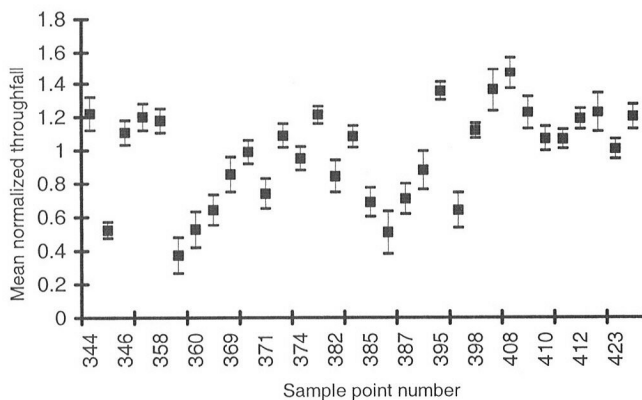

Figure 6. Variability of normalized throughfall volume for each sample location for each rainfall event. Each point represents the mean of the five collectors for each sampling location on the forest floor. Note that the variability for different rainfall events is large relative to the variability for a single sample location.
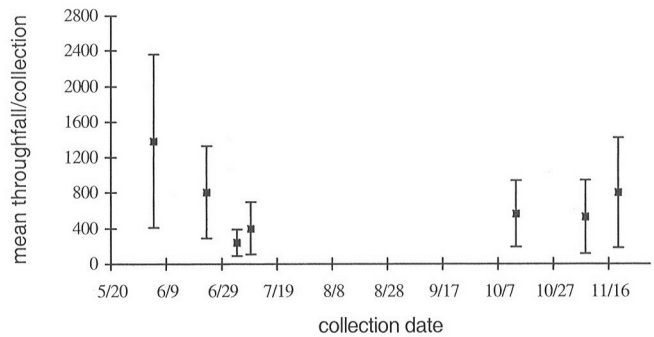
Figure 7. Mean throughfall (mm) for all sampling locations for each sample collection. Each point represents the mean of the five collectors for each sampling point averaged overall of the seven collection periods for that sampling point. Error bars are ±1 SD.
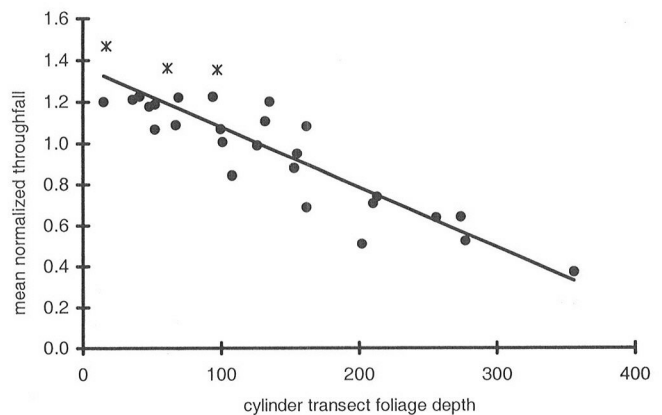
Figure 8. Relationship between mean normalized throughfall per sample point for all sample locations and the estimated amount of foliage (dm^3) in canopy cylinders measured directly above each sampling location ($n = 32$ locations); $R^2 = 0.79$.

tinguish the relative impact of foliage versus epiphytes on throughfall interception and retention. Manipulations in the field or laboratory will be needed to differentiate the relative contributions of canopy components on forest canopy function.

Our results on the distribution and stratification of epiphyte functional groups are also consistent with other epiphyte distribution research carried out at this site, which used the crane for access. McCune and his colleagues documented similar patterns on the distribution of lichen functional groups, but did not report on the distribution of the substrate, as he was restricted to visual estimates of the lichens (McCune et al. 1997). Studies of epiphytic lichen distribution on *T. heterophylla* stems (Lyons et al. 2000) and *P. menziesii* (Clement and Shaw 1999) near our study site documented a similar vertical stratification within different strata of the forest and heights of individual trees. Their branch plot-based approach yielded information on substrate characteristics that our method does not generate (e.g., branch angle and direction), but their sample sizes were very small relative to ours in terms of number of stems inventoried.

Previous studies conducted in structurally simple

between mean throughfall volume at a given sample location and the cylinder depth of all tree structural components (Figure 8). Because epiphytes are always associated with branches, and because nearly all branches in the primary forest were associated with epiphytes, these two component types were nonindependent, and we were not able to dis-

plantation forests have detected relationships between throughfall interception and ground-based measurements of forest structure: e.g., proximity to adjacent tree stems (Ford and Deans 1978, Johnson 1990, Bouten et al. 1992); crown surface area projections (Ford and Deans 1978). These two-dimensional and ground-based techniques appear to describe the structurally simple secondary forest and young, evenly spaced monospecific canopies in plantation forests, but may not be useful for older, naturally regenerated coniferous forests such as those at our study site.

The vertical canopy cylinder transects provided a strong predictive relationship with throughfall in a structurally complex, old-growth forest. The technique estimated the quantity of canopy material located within the cylinder in a nondestructive way. The strong correlation between canopy height and throughfall volume demonstrated that the ability to establish strong quantitative relationships between throughfall and canopy structure in these forests requires measurements at the within-canopy scale. The tight relationships we found between a relatively narrow cylinder diameter and throughfall volume at a given point across multiple rainfall events implies that a relatively small portion of the canopy affects the amount of rainfall that reaches a given point on the forest floor. Future research should focus on identifying the specific canopy structural elements responsible for these patterns, which may require experimental and microcosm work in the laboratory and field.

The availability of near-total access to the 3-D volume of the forest provided by the canopy crane was key to identify patterns relating to structure and function. The cost of such a tool is admittedly high, both in initial outlay and in maintenance. However, the structural data generated by studies such as this can be reused in conjunction with other functional attributes of the same forest (e.g., pollutant deposition, light penetration, atmospheric turbulence) if the data are made available in forms that are conducive to spatially explicit comparison and syntheses (North et al. 2004). Ongoing efforts to facilitate these activities are being carried out in collaborative work by canopy researchers and database scientists (Nadkarni and Cushing 2001). The ability to rapidly and accurately measure canopy structure will lead to an improved ability to predict functional processes such as atmospheric interception and retention of matter and energy and could lead to improved forest management.

The spatial distribution of throughfall can also affect the physical and biological heterogeneity of the ecosystem, e.g., the density of herbaceous understory vegetation (Anderson et al. 1969), soil water spatial patterns (Durocher 1990, Bouten et al. 1992), and the distribution of fine roots in the soil (Ford and Deans 1978). Relationships have also been documented between the spatial patterns of throughfall and various measurements of canopy structure, e.g., tree location (Johnson 1990, Loustau et al. 1992), crown projections (Ford and Deans 1978), and canopy openness (Anderson et al. 1969). In all of these studies, the forests were young and even-aged (14–50 years old), and all but the latter consisted of a single species that was planted in rows. The relatively homogeneous structure of these forests precluded the need

for detailed within-stand structural measurements such as the ones we made in this study because the individual crowns could be considered uniform. Due to high structural heterogeneity of naturally regenerated older forests, it is probable that structural measurements are required at the scale of individual trees or even within crowns to describe canopies in sufficient detail to explain relationships between canopy structure and throughfall.

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