The Distribution of Free Space and Its Relation to Canopy Composition at Six Forest Sites

Roman Dial, Benjamin Bloodworth, Andrew Lee, Patrick Boyne, and Jeffrey Heys

ABSTRACT. Forest canopy free space, element density (clutter), and the distribution and relative abundance of coarse canopy elements were measured at six sites: two boreal (south-central Alaska), two temperate (Washington State and Victoria, Australia), and two tropical (Pacific Costa Rica and Malaysian Borneo). Great clutter, high relative abundance of dead elements, and shallow understory characterized boreal canopies. Presence of dead elements and deep understory characterized temperate sites, sharing clutter profiles that differed in magnitude but not shape from each other. Few dead elements, little obvious zonation, and constant, mid-canopy clutter characterized tropical sites. The neotropical site showed a clear overstory, while the paleotropical site did not. The results motivate three hypotheses: (1) forest canopies of similar latitude and climate have similar structure; (2) canopy zones form cohesive, repeatable structures as "understory" (near-ground nondominant vegetation bounding small free-spaces), "overstory" (high, dominant foliage bounding small free-spaces), "bole zone" (mid-canopy boles bounding the largest free spaces), and "dead zone" (unique to conifer sites and typified by dead elements and upwardly narrowing free-spaces above bole zone); and (3) Australian and paleotropical canopies, regions rich in vertebrate gliders, are an order of magnitude more open (less cluttered) than neotropical and North American canopies, regions poor in gliders. FOR. SCI. 50(3):312–325.

Key Words: Forest canopy structure, latitudinal gradient, forest comparison, gliding vertebrates.

PARKER (1995) DEFINED CANOPY STRUCTURE as the composition, organization, and location of aboveground vegetative structures, as well the interstitial spaces among them. Studies of forest canopy structure traditionally focus on the vegetative elements and their architecture (e.g., Popma et al. 1988, Spies and Franklin 1991, Jack and Long 1992, Van Pelt and North 1996, Koike and Hotta 1996, North et al. 1999). However, the negative

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or "empty space" of forest canopies has also been used to characterize forests (MacArthur and Horn 1969, Terborgh 1985, Lieberman et al. 1989, Connell et al. 1997, Lefsky et al. 1999). This free, open, spatial matrix between foliage, limbs, and boles is where gasses circulate, radiation and precipitation penetrate, and organisms move to disperse and consume. As an example of the role open space may play in organism evolution, global patterns of free space within forest canopies seem to match the distribution of gliding vertebrates. Ease of movement through tall, open stature forests has been hypothesized as a selective agent for gliding locomotion (Emmons and Gentry 1983, Emmons 1995, Dudley and DeVries 1990, Jackson 1999).

Quantifying canopy structure can clarify how solid elements and empty space mediate forest functions. Freiberg (1997), for instance, identified variation in microclimate variables as coincident with solid structure and free space within a Costa Rican *Ficus* crown. Quantifying structure also encourages comparison and contrast of forests (Spies and Franklin 1991, Koike and Hotta 1996, Lefsky et al. 1999, Montgomery and Chazdon 2001, Van Pelt and Nadkarni 2004). The usual measures of canopy structure include maximum canopy height, leaf area index, foliage profiles and volume, as well as statistics of tree allometry, geometry, architecture, and forest "gaps." Canopy gaps are traditionally considered an open space that penetrates from above canopy level to near the ground surface. Lieberman et al. (1989) were among the first to call attention to the fact that gaps exist as more than simple holes penetrating a wooded matrix. Parker (1995) and Connell et al. (1997) replaced the gap/no-gap dichotomy with several kinds of canopy open spaces. Connell et al. (1997) developed a conceptual model dividing the canopy into three tiers and used the presence/absence of vegetation within these tiers to classify eight sorts of openness. Lefsky et al. (1999) used airborne laser technology to measure the strength of laser light reflectance from canopies and so could characterize canopy open space with a continuous measure. Lieberman et al. (1989), Connell et al. (1997), and Lefsky et al. (1999) also used their measures to estimate horizontal variability in their metrics. Despite the handful of developments that have included free space to characterize forests, open space has been cited as a virtually ignored means of putting "the canopy into canopy biology" (Moffett 2001). Lieberman et al. (1989) even suggested that an inclusion of free space measures within the field of forest science would facilitate development of an adequate conceptual framework of forest dynamics.

Our study of free space was motivated by the hypotheses concerning the evolution and global distribution of vertebrate gliders. Emmons and Gentry (1983) proposed that differences in forest structure among continental tropics led to selection for gliding in the paleotropics, where glider diversity is high, and prehensile tails in the neotropics, where gliding vertebrates are absent ("open space hypothesis"). Dudley and DeVries (1990) argued that the greater height of tropical Asian forests was the important factor, more than the type or density of canopy elements. Emmons (1995) modified the open space hypothesis to claim that lack of high, closed canopy connections promotes the evolution of gliding. While American scientists have focused on tropical gliders, Australians have considered the evolution of their rich fauna of temperate marsupial gliders. Jackson (1999) reviewed fossil studies of Australian gliders and pregliders and concluded that the evolution of gliding there coincided with the drying of the Australian continent and the "opening-up" of forests. In Africa, gliding scaly tailed squirrels (Anomaluridae) have been documented to prune small branches along their commonly used flight paths (Kingdon 1997), behavior consistent with the importance placed on open space. Moffett (2000) integrated these hypotheses and conjectured that the tall and sparsely connected forests in tropical Asia provide "large uncluttered spaces" conducive to gliding. Dial (2003) used a mathematical model showing the energy savings of gliding over walking scales linearly with distance traveled, consistent with the open space hypothesis. In this study, we provide quantitative measures of open space and clutter useful for evaluating the open space hypothesis.

We measure the negative, empty, or free space in forest canopies and attempt to find correspondences between the spatial distribution of free space and the composition of canopy elements. Our approach considers a matrix of sample points that constitute a vertical slice of the canopy. From each sample point we measure the distance to and identity of the nearest objects in fixed compass directions (Figure 1). These measures form the basis for estimates of the relative openness and density of forest canopies as a function of height above ground. The results describe canopy structure, free space, and element composition along both vertical and horizontal axes from six native, Pacific sites at three latitudes: two boreal sites from Alaska, and one each from temperate Washington State, temperate Australia, lowland wet Costa Rica, and lowland wet Malaysia.

Methods

Six sites from five Pacific forest types were visited during 2000, 2001, and 2002 in Alaska (AK), Washington (WA), Costa Rica (CR), Australia (AU), and Borneo (MY). Each was sampled by a high, horizontal traverse with a variable numbers of vertical transects suspended from the traverse. Observations were made along these vertical transects at 1- or 2-m intervals (measured using a tape anchored at the ground). Traverse and transect methods have been used previously to sample light environments (Koop and Sterck 1994) and foliage density (Koike and Hotta 1996 and references therein). Five of the six sites were chosen based on the emergent height of co-linear trees. The WA site was selected because it is part of another study (Martha Creek Transect 3, Van Pelt and Nadkarni 2004). We first accessed tall, emergent trees using a combination of single rope and arborist methods (Dial and Tobin 1994). Between these tallest trees we anchored 11-mm diameter static climbing rope as near to the emergents' tops and as tightly as deemed safe, avoiding over-tensioning (Smith and Padgett 1999) in anticipation of an observer's body weight.

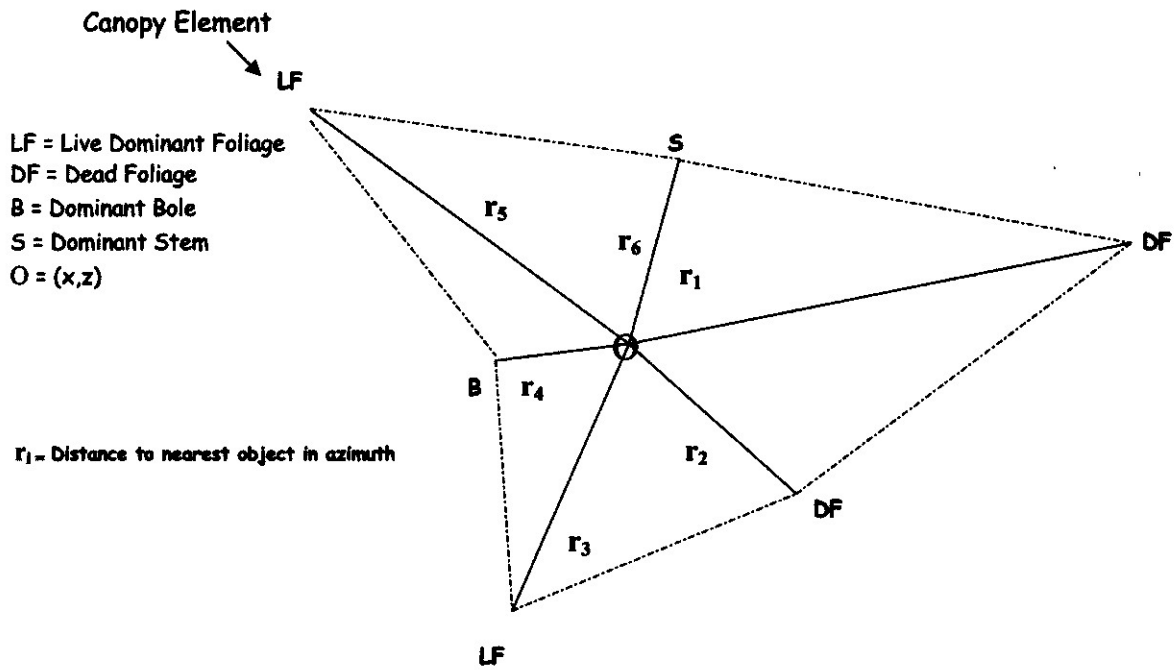

Figure 1. Schematic top view of observation point (*x,z*) where canopy data are collected while suspended from rope *z* meters above the ground and *x* meters from beginning of horizontal traverse. Dashed line indicates polygon used to calculate area, solid lines indicate distances measured.

Support lines running from ground anchors to the emergent anchors prevented rope sag and tree bend.

Sample Sites

Alaska (AK).—The techniques were developed in low-stature forests near Girdwood, south central Alaska (60°59′ N, 149°5′ W) in a relatively depauperate Sitka spruce-western hemlock forest. Because of the latitude, we consider the forest as boreal. Two sites were sampled. The first site ("Spruce-AK"), located at about 70 m above sea level (ASL) on a poorly drained flat, is dominated by Sitka spruce (*Picea sitchensis*), beneath which grow low shrubs of *Echinopanax horridus* and *Alnus*. The tallest individual tree along the traverse was 32 m tall and 0.75 m dbh and aged at 160 years using ring count. Vertical transects were dropped at 5-m intervals along the 70-m traverse for a total of 15 transects sampled at 1-m height increments. A 70-m by 10-m stem map centered below the traverse was used to collect height distributions on all stems >6 cm dbh.

The second boreal site ("Hemlock-AK"), situated on a well-drained shelf at about 150 m ASL, is dominated by western hemlock (*Tsuga heterophylla*), beneath which grow ericaceous shrubs. The tallest individual tree along the traverse was 29 m tall, 0.76 m dbh, and aged at 280 years. Vertical transects were dropped at 5-m intervals along the 55-m traverse for a total of 12 transects sampled at 1-m height increments. In addition, a 60-m by 10-m stem map centered below the traverse was used to collect height distributions of live stems >6 cm dbh.

Washington (WA).—This temperate site was located at 580 m ASL of "Transect 3, Martha Creek" (Van Pelt and Nadkarni 2004) in the Wind River Experimental Forest, Gifford Pinchot National Forest, southern Washington State (45°47′ N, 121°56′ W). This site is a nearly monospecific stand of Douglas-fir (*Pseudotsuga menziesii*), beneath which grow vine maples (*Acer circinatum*). The tallest individual tree along the traverse was 49 m high. Vertical transects were dropped at 5-m intervals along the 115-m traverse for a total of 24 transects sampled at 1-m height increments. R. Van Pelt (University of Washington, Sept. 12, 2001) provided a stem map of the 120-m by 12-m plot, and the height distribution of all stems >6 cm dbh was used to compare to canopy spatial measures.

Australia (AU).—This temperate site was located at approximately 680 m ASL on the Hume Plateau in the Wallaby Creek Catchment Basin of Kinglake National Park, central Victoria, Australia (37°25′ S, 145°11′E) in an approximately 250–300-year-old *Eucalyptus regnans* forest with smaller trees and shrubs of *Olearia agrophylla, Pomaderris aspera, Acacia sp.*, and ferns (Ashton 2000). The tallest and broadest tree along the traverse was 79 m (240 cm dbh), although within 100 m of the sampling traverse grew a 91.6-m *E. regnans,* the tallest known on the Australian mainland (B. Mifsud, Kinglake National Park, Feb. 7, 2002). Vertical transects were dropped at 7-m intervals along the 50-m traverse for 7 total transects sampled at 2-m height increments. The traverse was embedded in a 270-m by 27-m plot established by R. Van Pelt and M. Antoine (University of Washington and Humboldt State University, Feb. 21, 2002).

Costa Rica (CR).—This neotropical site was located at 100 m ASL, northeast of Punta Llorona in Corcovado National Park, southwest Costa Rica (8°35′ N, 83°43′W), in an area identified by Hartshorn (1983) as primary, Pacific lowland tropical wet forest. The tallest tree along the traverse was a 52-m *Brosimum utile*, and the broadest (214 cm dbh, including buttress) was *Vantanea barbouri.* There was

a dense layer of low palm trees. Vertical transects were dropped at 5-m intervals along the 85-m horizontal traverse for 18 total transects sampled at 1-m height increments. While a stem map was drawn, only heights of the four anchor trees were collected.

Borneo (MY).—This paleotropical site was located at approximately 150 m ASL in the Danum Valley Conservation Area, Sabah, Malaysia (4°57′ N, 117°48′ E) in an undetermined but primary-aged dipterocarp forest (Marsh and Greer 1992). The tallest tree along the traverse was a 75-m, 133-cm diameter above buttress (DAB) *Koompassia excelsa;* the broadest was a 73-m, 154-cm DAB *Parashorea malaanonan.* Vertical transects were dropped at 20-m intervals along the 130-m traverse and sampled at 2-m height increments along the 7 transects. Heights of the 11 trees with crowns nearest the traverse were measured by S. Sillett and M. Antoine (Humboldt State University, Apr. 21, 2002).

Definitions

Like Parker (1995), we consider the "forest canopy" to consist of the volume between the ground and the upper surfaces of the tallest trees, including all vegetation (living and dead), soil, suspended water, and interstitial space. We note that the bulk of the canopy volume is not at the upper surface itself ("outer canopy") and we do not address issues of the outer canopy. Instead, we focus on within-canopy traits.

"Canopy elements" are classifications of physical objects, such as boles (trunks and reiterations), stems (limbs and branches), foliage (often taxonomically identified, e.g., palms, maples, herbs), vascular epiphytes, lianas, and litter (dead vegetative elements) as identified by a suspended human observer (as opposed to a remote sensor).

We grouped canopy elements into five coarse types to facilitate cross-site comparisons: "dominant boles," "dominant limbs," "dominant foliage," "nondominant," and "dead." Elements defined as "dominant boles" and "dominant limbs" were reserved for dominant trees (Australian *E. regnans;* North American *P. sitchensis, T. heterophylla, P. menziesii,* and *Populus balsamifera*; any nonpalm, tropical tree); "dominant foliage" was applied to both tree and liana foliage, as it was not reliably differentiated from tree foliage. "Nondominant" elements were any living plant parts that were not dominant tree boles (i.e., trunks), dominant tree or liana foliage, or dominant tree limbs. Nondominants included liana stems (but not foliage), nonwoody palms, epiphytes (both vascular and nonvascular), shrubs, as well as *Acer* at the Martha Creek site, and *Pommaderis, Acacia,* and *Olearia* at the Australian site. "Dead" was applied to any nonliving element.

We will use the word "composition" to refer to a statistical characterization of canopy elements. We define "free space" as the air-filled interstices among canopy elements. For the purposes of this article, we measure "structure" as a linear density of canopy elements ("element density") in units "elements m^{-1}," a metric of and synonym for "canopy clutter." Element density measures how cluttered space is with canopy elements. Canopy clutter differs from "leaf area index" (LAI); we will not attempt to calculate LAI.

In this article, we base our characterizations of forest canopies on clutter (elements m^{-1}), free space area (basal area of a polygonal solid with height either 1 or 2 m), and element composition. In general, we will aggregate and summarize spatial measurements (free space and element density) using medians, because of the sensitivity of means to outliers, or modes (composition). We also present free space samples at horizontal x and vertical z as a point measure at (x,z). A "canopy zone" is a collection of adjacent (x,z) that share a combination of structural, spatial, and elemental features.

Data Collection

Observers carried an Impulse 200 LR laser rangefinder (Laser Technology Incorporated, Englewood, CO) with sighting compass and inclinometer secured to the laser for reference. Observers ascended climbing rope suspended from the traverse and at 1- or 2-m intervals they measured the level (inclination = 0°) distance to the nearest object in equally spaced azimuths (60°, 30°, or 20° intervals). Distance to and identity of nearest object in each of the equally spaced azimuths was recorded at each height. Because the maximum distance of the rangefinder was ~ 500 m, sample points with distances equal to 500 m are omitted from the data. This generally occurred at the top of the vertical transects where we were above the outer canopy. Because outer canopy structure and composition are better studied without rope-based techniques, we provide few measures of the outer canopy.

Data Processing

Spatial Area.—We considered a vertical sample plane as two dimensions, x meters from a reference tree and z meters above the ground, so that each observation point has coordinates (x,z). For each point (x,z), we collected spatial and canopy element data in n different horizontal azimuths, where $n = 6$ for AK and CR, $n = 12$ for AU and MY, and $n = 18$ for WA. We estimated the volume of empty space surrounding this point as the product of an n-sided irregular polygonal area and the transect sampling interval (1 m in AK, CR, and WA; 2 m in AU and MY); however, we report only the area of the polygon $S(x,z)$. The polygon vertices were located at the nearest elements (established by laser) in each of n horizontal azimuths (Figure 1). The spatial area $S(x,z)$ for each n-sided polygon surrounding point (x,z) is estimated as the sum of n adjacent triangles, each with a shared vertex centered at (x,z), and sides congruent to the laser measured distances to the nearest elements, r_i, $i = 1,2, \ldots, n$ (see Figure 1):

$$S(x,z) = 0.5*\sin(\theta)*\sum_{i=1}^{n} r_i*r_{i+1} = 0.25\sqrt{3}*\sum_{i=1}^{6} r_i*r_{i+1}$$

where θ is angle between adjacent distances, r_i and r_{i+1}, with $r_1 = r_{n+1}$. In this article, we present hexagon areas calculated using $n = 6$ radial distances ($\theta = 60°$) for all sites, including WA, AU, and MY, to ensure comparability.

The 18-sided polygons at WA were larger than corresponding hexagons < 887 m^2 (95% of all WA areas) with $S_{18}(x,z) = 10.59 * [S_6(x,z)]^{0.65}$, $r^2 = 0.69$.

Element Composition.—Each point (x,z) also has n observations of nearest elements (see Figure 1), where elements were classed by their status (live or dead), their type (foliage, stem, branch), and taxon/functional group (varied by site), then re-classed using the five coarse element types defined above. Each (x,z) was thus described by a five-dimensional vector counting the number of occurrences of each of the five coarse elements observed from location (x,z). We used a K-means clustering algorithm (SPSS 1998). This classification used initial cluster centers defined by inspection of frequency of elements by height (e.g., Figure 5) to classify each (x,z) into one of five classes named by the predominant (or in the case of the tropical clusters, the second most predominant) coarse element in the cluster center.

Canopy Clutter.—We elected to avoid the MacArthur and Horn (1969) assumptions and equations to estimate leaf or element density at each point (x,z) or to construct relative foliage height profiles, in spite of the fact that their technique (MH) has become the standard method for cross-site comparisons (Lefsky et al. 1999). Our reasoning was that calculating LAI using their method requires distributional assumptions we could not guarantee. Instead of using the MH approach, we constructed element density profiles using a simpler metric, the reciprocal of distance to element, or $1/r_i$, where r_i is the distance to nearest element measured at azimuth i. Thus, if r_i is the distance to a canopy element, then its reciprocal gives the number of elements per unit distance, which we interpret as element density or canopy clutter. For any point (x,z) there are n samples of element density ($n = 6$ for AK and CR, $n = 12$ for AU and MY, and $n = 18$ for WA), which we represent by the median density at (x,z). The collection of median element densities (x,z) across all x and all z then suggests the density of elements across a height section. Because this study was motivated by ideas about openness and clutter of canopies as habitat for gliding animals, rather than as a contribution of LAI estimates, we felt that our index of clutter was better suited than LAI or its related measures.

Results

Free Space

Free space within forest canopies varied vertically (Figures 2 and 3). Figure 2 depicts canopy variation in free space as height sections for each site. To emphasize within-site variation, only relative area is shown. These areas are shown as normalized $\log_{10}[S(x,z)]$, or $\beta = D$ [log(area) − min]/(max − min), with $0 \leq \beta \leq D$. D is the distance between vertical transects (5–20 m), and max and min are the maximum and minimum log(area) observed at each site. In these height section views, small areas are shown as small rectangles and large areas as large rectangles. The dashed horizontal line is the height of the highest tree along the traverse. Because of limited access to the outer canopy, not all sites have large free space (i.e., largest rectangles) at uppermost heights. All six sites have small areas near the ground (smaller areas at Spruce-AK and Hemlock-AK were below 1 m, Bloodworth 2001) and again near the traverse line. Between these regions of small areas are regions of relatively large areas. The temperate sites (AU, WA) and Hemlock-AK have more uniformly large areas in the mid-canopy regions. The tropical sites (MY, CR) and boreal Spruce-AK site show more horizontal heterogeneity in mid-canopy. For example, both the Spruce-AK site and the MY site have regions with large and small spatial areas over the same vertical intervals (compare the third vertical transect from the left with the second from the right at each site). While differing in height, mid-canopy at both the MY and the Spruce–AK sites had a more open, "woodland feel," with substantial overhead sky visible and large areas penetrating two-thirds through the canopy. Hemlock-AK and temperate (WA, AU) sites had a "cathedral feel" at mid-canopy, with less overhead sky visible and more overhead foliage.

In canopy profiles of aggregate measures of space (Figure 3), each forest shows several critical points—local minima or maxima—in median area. These critical points prove useful as references in discussions of element distribution and abundance that follow below. Critical points in the conifer forests (AK, WA) include one spatial minimum near ground (<1 m aboveground at AK sites) and a second minimum at upper-canopy levels, with a spatial maximum at mid-canopy. Across heights there is also some correspondence between stem height abundance and median spatial area (Figure 3, lower panels), best seen at the WA site, less so at the Hemlock-AK site, and least at the Spruce-AK site. Among the conifer sites, the WA and Hemlock-AK sites have similar maxima in mid-canopy space (~500–1,000 m^2), whereas the Spruce-AK site has a substantially smaller maximum (~100 m^2). Mid-canopy open space in the AU and MY sites is substantially larger (~1,000–10,000 m^2) than at any other sites and contrasts sharply with the CR site (~500–1,000 m^2). In vertical profile, spatial distributions seem most similar for the WA and Hemlock-AK sites, with the AU site appearing as a linearly transformed, truncated view of the WA site. The two tropical sites (CR, MY) appear to be as different from each other as they are from the other sites. The MY site is far more open than the CR one in the upper and mid-canopy.

Canopy Clutter

Canopy profiles comparing the six sites (Figure 4) reveal similarities in clutter profiles that correspond to patterns seen in free space. For example, all sites have a local clutter maximum at 1 m. Above this near-ground maximum, clutter decreases to a minimum, then increases again to a maximum at upper-canopy heights. This upper maximum in clutter is greater than the near-ground clutter for all sites except the MY site, illustrating again the openness of this paleotropical site. The two AK sites are similar to each other in the abrupt, steep increase in clutter with height. The two temperate sites (WA, AU) share a similar canopy profile in shape, if not in magnitude, of clutter. Both temperate sites

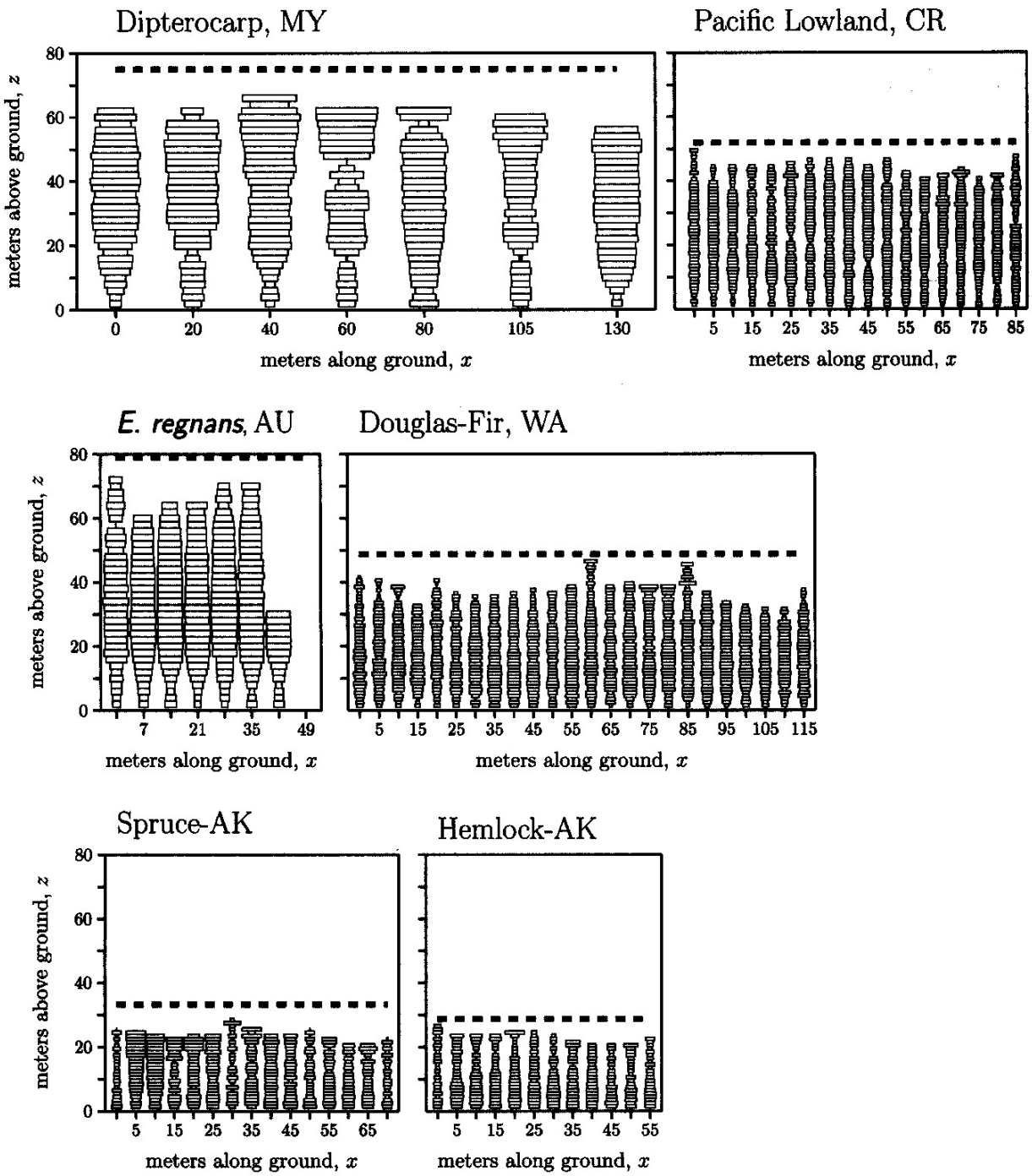

Figure 2. Height sections representing local variation in canopy open space. Each rectangle has width β equal to the normalized log(area) of a hexagon parallel to ground and centered at (x,z), where x is the horizontal distance in meters and z is the meters above ground. Rectangle width $\beta = D[\log(\text{area}) - \min]/(\max - \min)$ is bounded as $0 \leq \beta \leq D$, where D is the distance between vertical transects, and max and min are the maximum and minimum log(area) observed at each site. Rectangle height is equal to vertical sampling interval (1 or 2 m). MY, Danum Valley, Sabah, Malaysia; CR, Corcovado, Costa Rica; AU, Wallaby Creek, Victoria, Australia; WA, Martha Creek, Washington, USA; Spruce-AK, Sitka spruce, Girdwood, Alaska, USA; Hemlock-AK, western hemlock, Girdwood, Alaska, USA.

show a decrease in clutter from the near-ground maximum to a mid-canopy minimum, followed by an abrupt, but not steep (compared with the Alaskan sites), increase to the upper-canopy maximum. The two tropical (CR, MY) sites appear to contrast in their profiles. While both tropical sites have, on average, approximately 0.3 elements m^{-1} at 1 m above the ground, the neotropical site (CR) shows a substantially higher density of elements throughout its canopy.

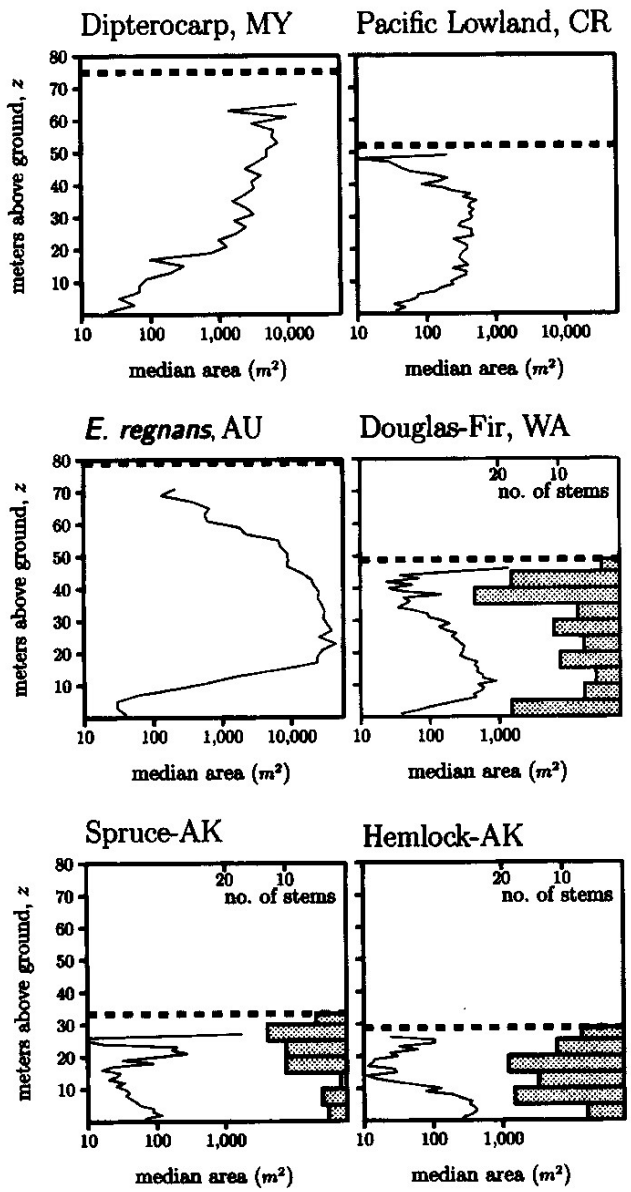

Figure 3. Canopy profiles of median area by height *z* in meters above ground. Dashed lines represent height of tallest tree along horizontal traverses. Washington and Alaska panels show stem height distribution as shaded bars.

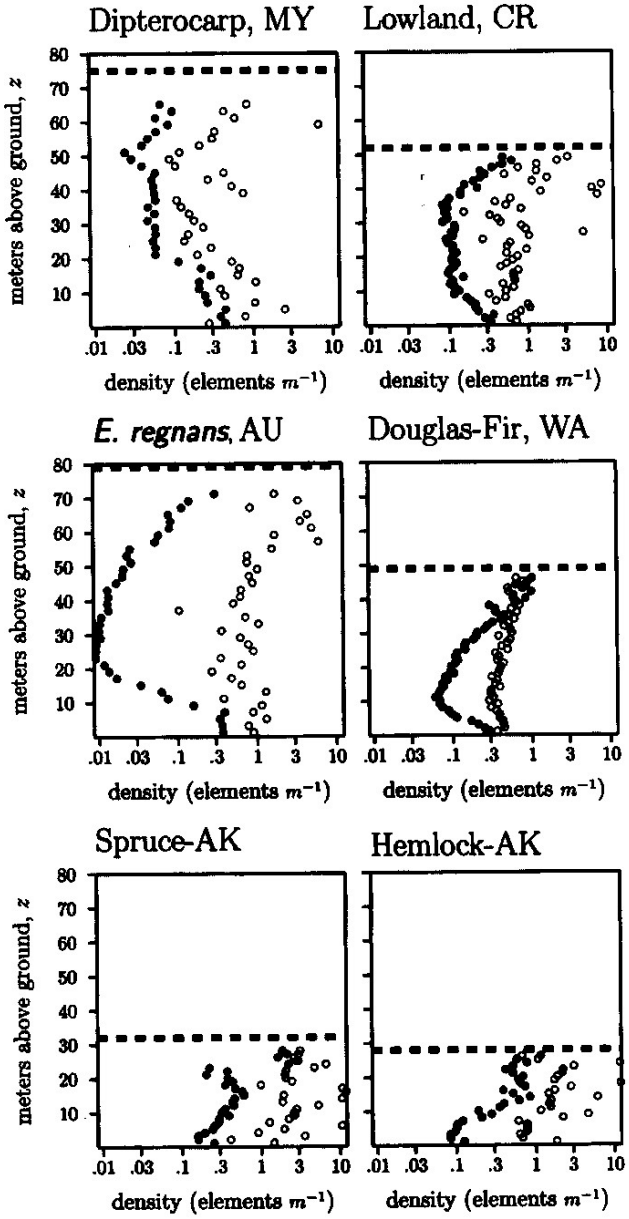

Figure 4. Canopy profiles of median (closed circles) and standard deviation (open circles) of canopy clutter (number of canopy elements per meter) by height *z* in meters above ground. Dashed lines represent height of tallest tree along horizontal traverses.

The median density for the neotropical site at the upper maximum is more than three times the upper maximum for the paleotropical site (MY). Similarly, the mid-canopy minimum is three times greater in the neotropical forest than in the paleotropical one. However, both tropical sites do share a relatively constant density through the mid-canopy, in contrast to the boreal (steep mid-canopy slope) and temperate sites (more gentle mid-canopy slope). The ln(standard deviation) correlates with ln(median density) significantly at all sites but Spruce-AK ($P < 0.005$; site = Pearson's r: WA = 0.84; MY = 0.58; Hemlock-AK = 0.57; AU = 0.46; CR = 0.40; Spruce-AK $r = 0.30$, $P = 0.13$). The Spruce-AK site shows the greatest horizontal variation in element density at most heights and the WA site shows the least. In summary, clutter is bimodal at all sites, with highest element densities near the bottom and the top of the canopy. Among sites, the boreal sites are most cluttered, followed by the WA, CR, and MY sites; the AU site is the least cluttered. The clutter gradient at mid-canopy suggests a latitudinal pattern: flat clutter gradients at low-latitude tropical sites, intermediate gradients at mid-latitude temperate sites, and steep gradients at higher-latitude boreal sites.

Canopy Element Distribution and Relative Abundance

Pooling element observations across all transects for each height at each site (Figure 5) also suggests latitudinal

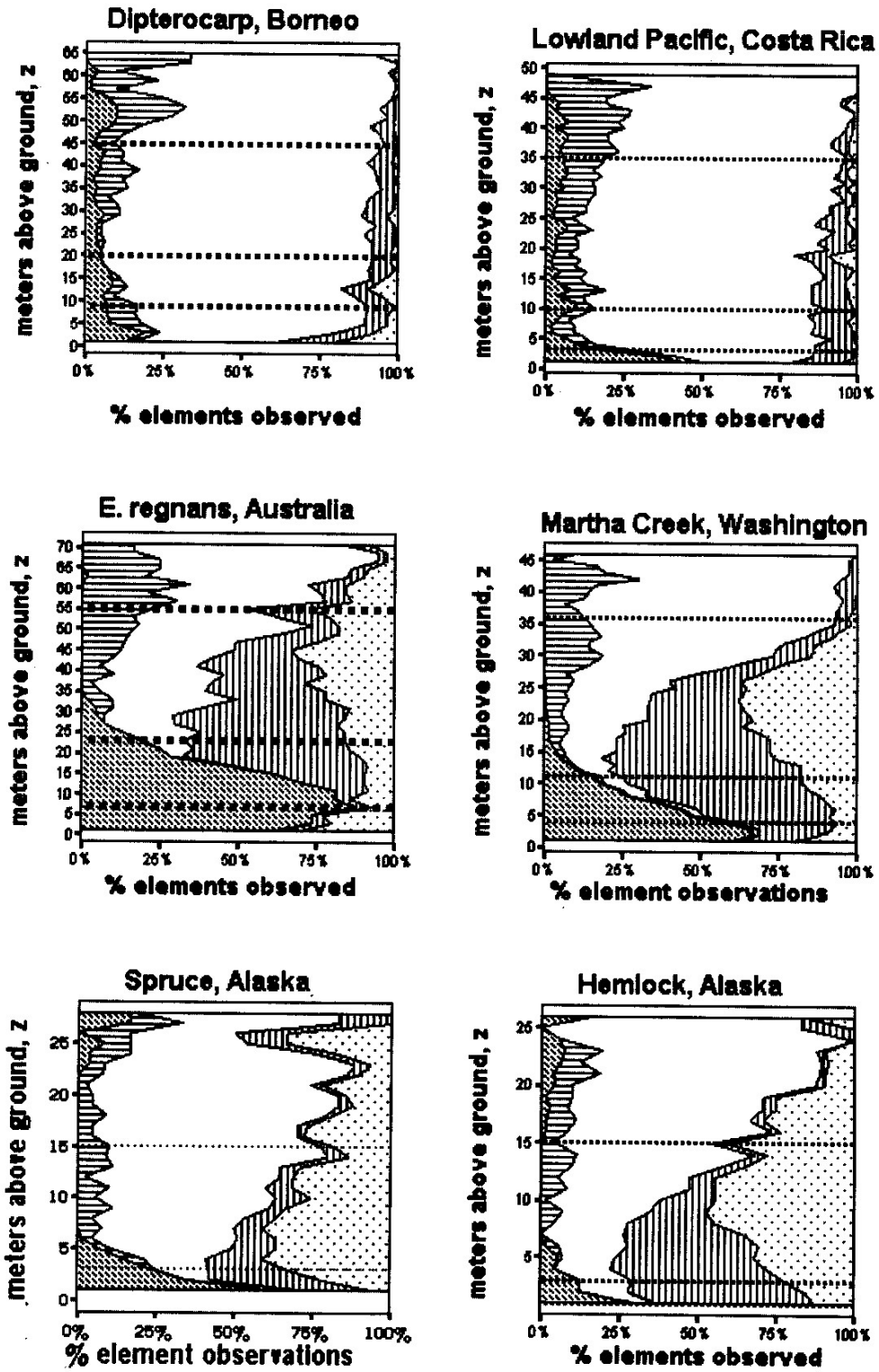

Figure 5. Canopy profiles showing relative abundance of coarse element types by height in meters above ground. Regions defined as follows: white, dominant foliage; dotted, dead elements; vertical stippling, dominant boles; horizontal stippling, dominant limbs; and diagonal stippling, non-dominant elements. Dashed lines represent critical points identified from canopy clutter profiles of Figure 4.

site pairs (Figure 4). The two AK sites alone show a clear bimodal distribution of nondominant elements, with near-ground (herbs and shrubs) and upper-canopy (nonvascular epiphytes) modes. The two temperate sites (WA, AU) show unimodal height distributions for nondominants, where nondominants make up more than half of all observations near ground, and nonzero counts of nondominant elements reach into mid-canopy. Peaks in relative abundance of nondominant elements in both tropical sites (CR, MY) are highest near ground and uniform upward, although there is a noticeable peak for nondominants in the upper canopy of the paleotropical site; the neotropical site has a substantial near ground abundance of small palms. At all sites, nondominant abundance peaks near the ground and corresponds to small areas and high clutter. Dead elements are most abundant in the boreal forests, less abundant in the temperate sites, and rare in the tropical sites. Dead elements at WA are mostly limbs and some boles; in the *Eucalyptus* site, long strips of annually shed bark make up over half of all dead elements. At both temperate and both boreal sites, the peaks in dominant bole relative abundance coincides with the lowest appearance of dominant limbs. These peaks in dominant bole abundance also coincide with mid-canopy free space maxima (Figure 3) and clutter minima (Figure 4). Figure 5 shows the heights of the spatial maxima/clutter minima as mid-canopy dotted lines in the temperate sites and low canopy dotted lines in the boreal sites. Dominant foliage is the most abundant element type at upper-canopy heights for all sites; both tropical sites show a more uniform distribution than either temperate site. The pattern of dominant foliage and bole distributions at the Hemlock-AK site is more similar to the WA site than to the Spruce-AK site.

We used a K-means clustering algorithm (SPSS 1998) to classify like points (x,z) at each site. Inspection of Figure 5 suggested initial clusters that were iteratively adjusted to provide cluster centers corresponding to vector combinations of elements. This method aggregated the element composition observed at each point. Visualized as height sections (Figure 6), these clusters describe horizontal variation in element composition. The tropical sites show substantial horizontal heterogeneity compared to the temperate sites of similar sampling intensity (i.e., MY versus AU, CR versus WA). The Hemlock-AK site shows heterogeneity similar to the WA site. All nontropical sites show a near-ground region of nondominants, an upper-canopy outer-crown region (clusters of mostly dominant foliage), and two intermediate regions, one an inner-crown (clusters of dominant foliage and limbs) and the other a bole region.

Free Space and Composition

Figure 7 presents a composite view of free space and element composition together for each site. In the figure, the modal coarse element class for each height is used to color a regular, hexagonal cylinder. The cylinder has a basal area equal to the median area (for heights with more than one area estimate) and cylinder height equal to 1 m (CR, WA, AK) or 2 m (AU, MY), depending on sampling interval. We call coincidences between element classes and spatial volumes "zones." All sites show two coincidences between element composition and free space volume: (1) an "understory zone" consisting of a nondominant class with a near-ground minimum in free space, and (2) an "overstory zone" consisting of an outer-crown class (i.e., dominant foliage) with an upper-canopy minimum in free space. The boreal and temperate sites show a third coincidence between a bole class and a mid-canopy maximum in free space, a "bole zone." The Hemlock-AK, WA, AU, and CR sites also share a fourth coincidence of an inner-crown class (i.e., dominant limbs and foliage) with narrowing free space. Finally, the North American conifer sites share a fifth coincidence of a dead element class with a tapering spatial volume, above the bole zone and below the inner-crown zone.

Discussion

Latitudinal Patterns

This study suffers from a lack of replication within forest types, as each forest is represented by a single, nonrandomly selected site. Thus the value of any comparison is tempered by questions of representation. The results from all forests sampled suggest a correspondence between aggregate measures of canopy free space and canopy elements (Figures 5 and 7). All six sites share: (1) a relatively homogeneous near-ground region of nondominant foliage bounding relatively small spaces—an "understory"; (2) a second, spatially small, upper zone bounded by tall tree foliage—an "overstory"; and (3) at least one zone of relatively large open space between the two strata, whose composition differed among the sites, but in nontropical sites was bounded by boles—a "bole zone." Beyond these three shared features, the forest structure and composition differ with latitude, possibly due to ecosystem similarities within latitudes, although each latitude is itself represented by only two sites.

The three conifer sites are most similar in free space and element profiles, as might be expected if tree architecture determines canopy structure and canopy structure determines free space. From the free space profiles and height sections, it appears that the Hemlock-AK and Douglas-fir (WA) sites are most similar (Figures 2 and 3). Both have similar-sized open spaces located at the same relative, mid-canopy location, roughly one-quarter of the way to the overstory zone. The observation that both Douglas-fir and hemlock display similar free space and element composition is interesting from the standpoint of classical niche theory, given their frequent coexistence in Pacific Northwest forests and their known light requirements. Douglas-fir is an emergent, early successional heliophile and western hemlock a later successional, shade-tolerant tree. Western hemlock and Sitka spruce may coexist in seemingly identical light environments, yet in the two sites we measured, the negative space they create differs. One interpretation of these speculative observations is that light environment and tree architecture define forest tree niches and coexistence. Indeed, one interpretation of the existence of canopy strata or zones may be the existence of light compensation niches for trees, as developed in the geometric model of Terborgh (1985).

From the perspective of clutter, which more accurately

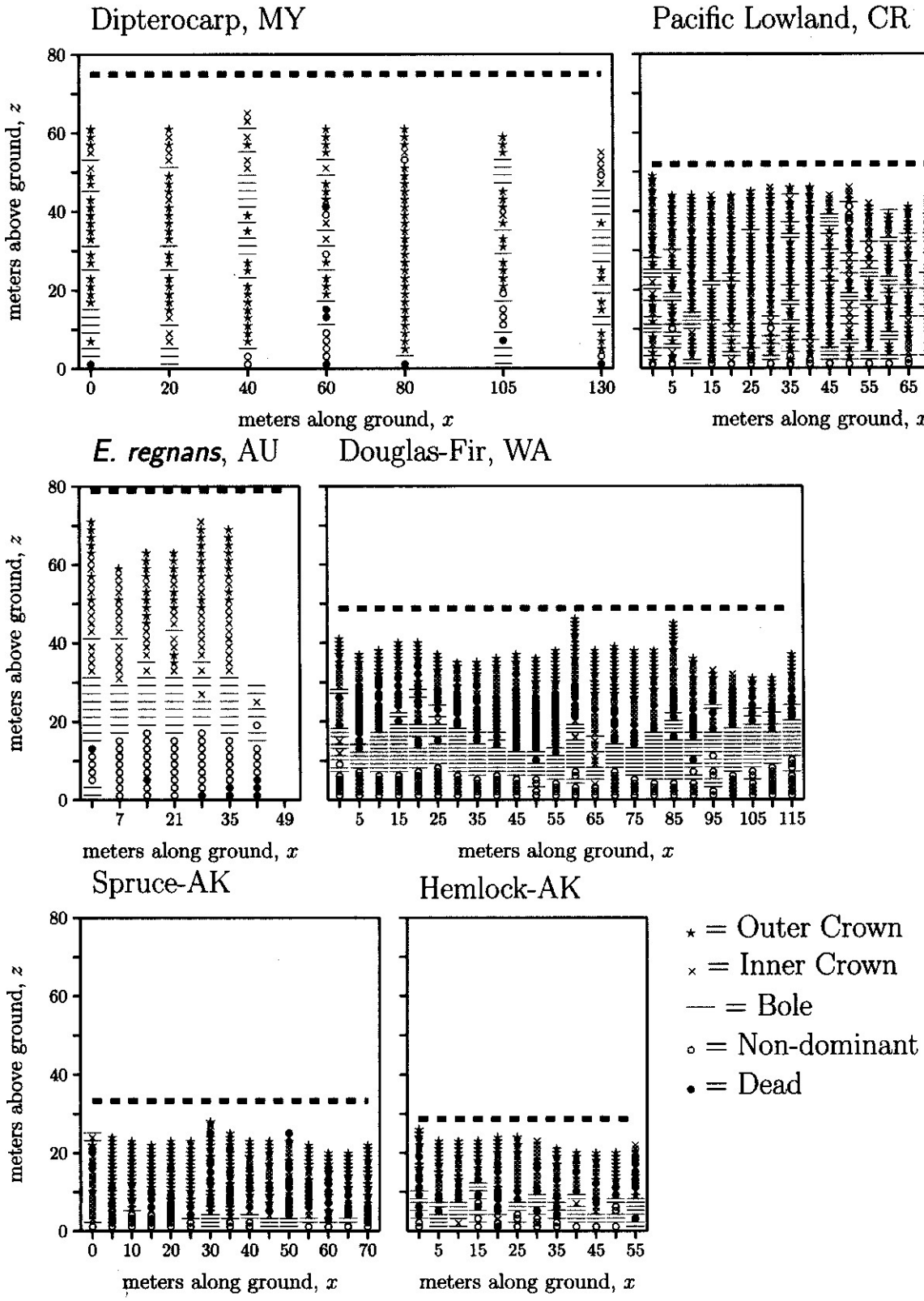

Figure 6. Local variation in canopy element composition at each site. Height sections show results of clustering algorithm used to classify points (*x*,*z*) based on canopy element observations. Symbols correspond to element class: ○, primarily nondominant elements; —, primarily bole elements; ●, primarily dead elements; ×, inner crown (primarily dominant foliage and limbs); ⋆, outer crown (primarily dominant foliage). MY, Danum Valley, Sabah, Malaysia; CR, Corcovado, Costa Rica; AU, Wallaby Creek, Victoria, Australia; WA, Martha Creek, Washington, USA; Spruce-AK, Sitka spruce, Girdwood, Alaska, USA; Hemlock-AK, western hemlock, Girdwood, Alaska, USA. Locations (*x*,*z*) with *x* representing the horizontal distance in meters and *z* representing the vertical distance above ground in meters are shown.

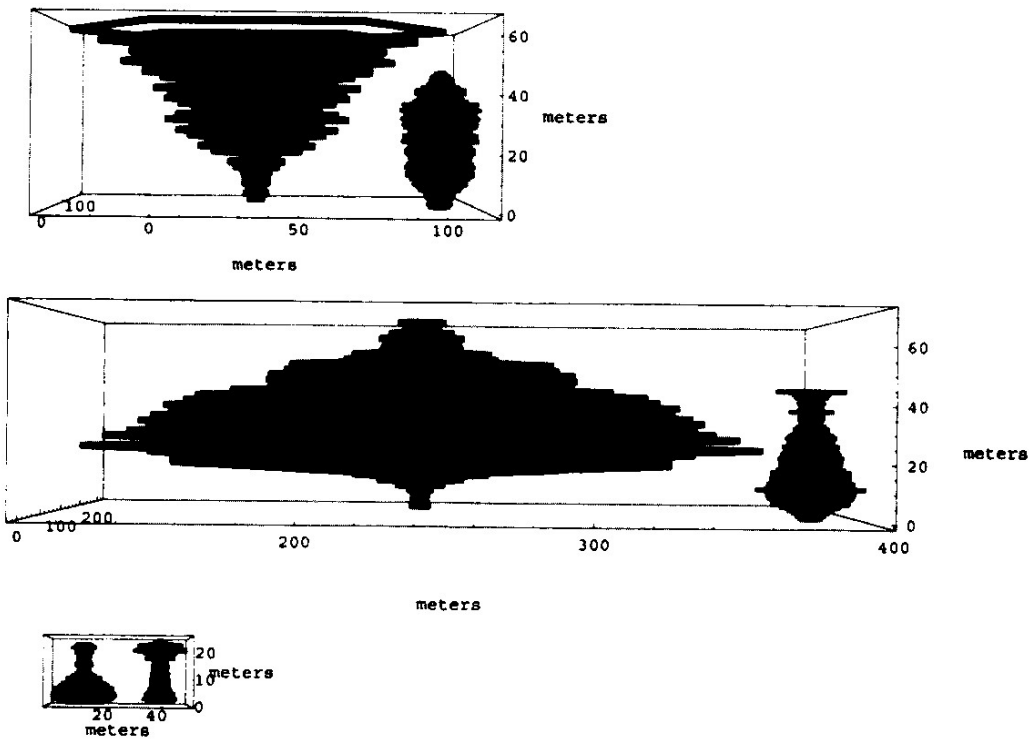

Figure 7. Median free space as a volumetric solid colored by the modal class for that height. Top row: Paleotropical lowland rainforest (Danum Valley, Sabah, Malaysia) on left, neotropical lowland rainforest (Corcovado, Costa Rica) on right. Middle row: Temperate eucalyptus (Wallaby Creek, Victoria, Australia) on left, temperate conifer (Martha Creek, Washington, USA) on right. Bottom row: Boreal hemlock on left, spruce on right (Girdwood, Alaska, USA). Red, primarily nondominant elements; blue, primarily bole elements; black, primarily dead elements; green, inner crown (primarily foliage and limbs); yellow, outer crown (primarily foliage).

captures plant responses to the forest environment than free space, the two boreal sites are most similar in profile and the Douglas-fir site is most similar to the *Eucalyptus* site (Figure 4). The similarity between the *Eucalyptus* and Douglas-fir sites is very interesting to us, as it suggests the possibility of convergent canopy structure reflecting convergent ecosystem function from two differing perspectives. The first perspective is that both temperate sites reflect a similar successional age and response to fire disturbance. Both forest types are subject to aperiodic, temperate latitude drought, typically induced by El Nino Southern Oscillation (ENSO) events (Stewart 1989, Flannery 1999). Both are dominated by very tall (to approximately 90 m), fast-growing, evergreen heliophiles that recruit most densely on catastrophically burned landscapes. While the individual architecture of conifers and eucalypts seems very different, the shape of their forest canopy profiles in area, element density, and vertical distribution of elements are remarkably similar.

An alternative hypothesis for the similarity between the Douglas-fir and *Eucalyptus* sites is motivated by the canopy profiles of element density, distribution, and relative abundance from all six sites (Figures 4 and 5), which break into latitudinal pairs based on clutter profiles at low and mid-canopy. While the profiles of element density at the tropical sites differ substantially from each other in the upper canopy, both tropical sites show a zone of constant element density at mid-canopy (Figure 4). Neither the temperate nor the boreal sites showed such an extensive zone of constant density. This latitudinal pattern is consistent with hypothesized effects of direct sunlight angle, determined by latitude, on canopy structure (Terborgh 1985) and crown depth (Kuuluvainen 1992). Low-angle direct light in the boreal forest leads to deeper crowns on Alaskan spruce and hemlock than in temperate eucalypt or Douglas-fir trees, which in turn are exposed to lower-angle light than tropical forests. This pattern of element density seen across sites may reflect the response of tree architecture to light angle as it varies with latitude. Further studies comparing sites from different biogeographic provinces would help differentiate between hypotheses and motivate new ones.

Free Space and the Evolution of Vertebrate Gliders

The two tropical sites show very different upper-canopy openness (Figures 2, 3, and 7). Above the understory zone, the neotropical site is much less open, by an order of magnitude on average, than the paleotropical one (Figure 3). While both sites show strong understory signatures, defined by a combination of element composition and free space size, only the neotropical site shows a strong overstory signature of small free spaces bounded by dominant foliage along every transect (Figure 2). Like southeast Australia,

Borneo is subject to aperiodic, ENSO drought events (Curran et al. 1999), and the openness of the upper and mid-canopy at both the Australian and the paleotropical sites may be related to ENSO-induced drought.

Emmons and Gentry (1983) first noted the contrast between taxonomic richness of vertebrate gliders in the paleotropics and lack of gliders in the neotropics. They and subsequent authors (Dudley and DeVries 1990, Emmons 1995, Jackson 1999, Moffett 2000) attributed the evolution of gliding in vertebrates to forest structure: tall, open forests are conducive to gliding, while short and cluttered ones are not. In general, tall and/or dry forests will have more open space than shorter, wetter forests. Dry forests tend to be less dense for reasons of moisture stress and fire history. Tall forests tend to be less dense for reasons of self-thinning (White 1991). Hence, tall, dry forests of Australia should be conducive to gliding, as should the tall forests of Borneo. The heights of our two tropical sites are similar to those reported by Dudley and DeVries (1990) for forest heights from other neotropical and paleotropical sites; the height in the Australian site is similar to those reported for other mature *E. regnans* sites (Lindenmayer 2000, Brown 2001). Thus our measures of openness in the tropical and Australian sites may be representative and support the hypothesis that primary neotropical forests have substantially smaller interior spaces than primary paleotropical and tall *Eucalyptus* forests. Indeed, the openness of the Australian and the Bornean sites is striking compared with that of the American sites (Figure 7). In the Australian site, we witnessed three marsupial gliding events from the inner crown to the bole zone in a 2-week period; in Borneo, we witnessed over a dozen gliding events among three species of lizard, one snake, and one mammal in the upper and mid-canopy over a 5-week period. Such openness in the forest interior may also provide habitat for a higher proportion of larger-bodied airborne species in Australia and Asian forests than in the neotropics. The large, dramatic birds and flying mammals of Australia and Borneo—hornbills, fruit pigeons, flying foxes, kookabarras, and cockatoos—are suggestive. Such a study in macroecology (Brown 1995), comparing body size distributions between regional biotas (Dial 2003), is beyond the scope of this article.

Canopy Stratification

A provocative article by Parker and Brown (2000) challenged readers to critically evaluate the use of the word "strata" in canopy science. The analyses in our study seem to indicate that certain vertical patterns in the coincidence of free space and element composition repeat themselves, not only across a forest, but also in other, taxonomically unrelated forests. Our results lend support to the ubiquity of terms such as "overstory" and "understory," and even the introduction of a new term, "bole zone," which may be an important zone for animal movement and dispersal. We avoid using the word "stratum," as it seems to imply a planar layer. Our observations suggest vertical intervals of nontrivial depth—what we call "zones"—occur in a fairly regular sequence from bottom to top, regardless of outer canopy height, but especially in the forests with clear dominants, a pattern long recognized (Richards 1983). Our measures of space and structure are consistent with others finding little evidence for strata or zones in tropical forests, other than overstory and understory (Popma et al. 1988). We have used common zones to compare and contrast forests. We expect that organisms also perceive a canopy structure divided up as functional zones with occasionally sharp changes in gradient slope between zones. Thus, while concepts of canopy strata may not be useful for some applications (Parker and Brown 2000), it seems likely that canopy research will continue to observe canopy zones, or strata, due to the coincidence of multiple gradients (Moffett 2000). Indeed, controversy about the existence of strata in forest canopies seems destined to endure the fate of other dichotomous conceptual issues in ecology. Despite the individual distribution of plant species, vegetative maps will continue to be produced and used, and despite the curve fitting success of null models, many natural communities will still be consider assembled and structured. We feel that use of strata or zones, if objectively detected, carefully delineated, and unambiguously defined, assist in the communication of results and concepts in forest science. In our own work, understory, overstory, and bole zones are clear, vertical intervals with measurable volume, just as the ground and outer canopy are true strata with measurable surface area. Our unpublished measures of canopy light and microclimate also tend to coincide with canopy composition and structure, whether structure is measured in terms of free space or its conceptual inverse, canopy clutter. Measures of light, microclimate, and animal distribution can illustrate the interplay between canopy composition, structure, and processes that result in fairly discrete functional zones within forest canopies.

Caveats

This article has set out to characterize canopy structure in several forests with the aim of comparison and contrast. The results have motivated three hypotheses: (1) forest canopies of similar latitude and climate have similar structure; (2) canopy zones based on coincidence of canopy elements and free space form repeatable structures in tropical, temperate, and boreal canopies (understory, overstory, bole zone, and dead zone); and (3) Australian and paleotropical canopies, rich in vertebrate glider species, are more open and less cluttered than neotropical and North American canopies, regions poor in vertebrate glider richness. However, the techniques used here are limited in several ways. We are unable to fully describe the outer canopy surface. Our calculations of open space are likely gross overestimates. Very distant elements cannot be accurately identified. Most importantly, our samples for each forest type are unreplicated and so our observations actually compare and contrast individual data sets.

Comparison of our data and interpretations for the Martha Creek, WA Douglas-fir site to other data sets for Martha Creek and mature Cascadian Douglas-fir are suggestive with regard to our methods and the WA site. Canopy

volumes estimated using the conic solid approximation method at 5-m intervals (Van Pelt and North 1996, Van Pelt and Nadkarni 2004) show a peak in Douglas-fir canopy volume at 25–30 m above ground and an *Acer* peak at 5 m. The 5-m peak in *Acer* volume is coincident with an abrupt break in our measure of element density (Figure 4) and a peak in nondominant composition (Figure 5). The peak in Douglas-fir volume (Van Pelt and Nadkarni 2004) is approximately 10 m lower than our own estimate of an overstory zone location (35–40 m in Figure 7), coinciding with the location of our dead and inner-crown zones. This is consistent with measures of the foliage-free "bare inner core" of conifers being greatest at largest crown volume (Jack and Long 1992). The location of a crown volume maximum at 26.7 m in an even-aged mature forest (Van Pelt and Nadkarni 2004) would suggest, using the concepts of Jack and Long (1992), that this would be the height of greatest bare inner core. The conic solids of modeled Douglas-fir crowns would have maximal volumes above the bole zone, because the bole zone in general will be below "height to crown base" (Van Pelt and North 1996). Similarly, the maximal volume of the conic solids should be below the outer crown zone, because this latter zone is the conceptual equivalent of the foliated outer shells of the conic solids. Thus our results of space and composition are consistent with a ground-based, conic solid conceptualization and measure of mature Douglas-fir canopy. Similarly, using airborne scanning LIDAR, Lefsky et al. (1999) measured open space in four mature Douglas-fir plots in the H.J. Andrews Experimental Forest, Oregon. The conventional stand attributes Lefsky et al. (1999) provide for their sites are very similar to Martha Creek (e.g., basal areas and maximum height; compare Tables 1 and 2a of Lefsky et al. (1999) with Tables 2 and 3 of Van Pelt and Nadkarni (2004)). Lefsky et al. (1999) found a "closed gap" maximum at mid-canopy between 8 and 15 m, the same location as our free space maximum at the Martha Creek (WA) site. Moreover, Lefsky et al.'s (1999) near-ground mode of their bi-modal "oligotrophic zone" corresponds with our own nondominant zone at less than 5 m above ground. Finally, their "euphotic zone" makes up 50% or more of the total canopy volume at about 35 m and above. Our Figure 7 shows that the outer crown zone begins at approximately the same height above ground. The congruence in canopy structure measures and classifications used here and in Lefsky et al. (1999) and Van Pelt and Nadkarni (2004) suggest our Douglas-fir data, at least, are not idiosyncratic. The congruence among these studies also suggests that LIDAR, the conic solids, and our techniques can agree. Finally, Popma et al. (1988) reported that a 40-m high neotropical lowland wet forest showed no distinct strata, other than a palm layer below ~7 m, which corresponds to our own 5-m nondominant layer at the CR site and lack of cohesive zones other than an overstory.

Nevertheless, we do not know if the similarities between the two temperate sites and between the two tropical sites are due to ecosystem similarities of latitude, successional age, sampling artifact, or some other unknown factor. For example, it is quite possible that an old-growth forest in WA might be more similar to MY or CR in structure and element distribution, and a young stand in MY or CR may be more similar to AU. The methods, analyses, and visualizations described here require a repeated, more rigorous application (i.e., random selection of sites with replication) in other forests of different ages and at similar latitudes to further support hypotheses motivated with the data we have presented. We also hope that sampling height sections for free space and element composition can be satisfactorily integrated with other canopy measures to elucidate canopy functions and processes such as the distribution of biodiversity and light attenuation, precipitation flow, and microclimate moderation by canopy elements. We expect that the techniques of sampling the canopy horizontally, as well as vertically, will lead to further findings that old-growth canopies are more heterogeneous than young canopies, as shown by Van Pelt and Nadkarni (2004) for Cascadian stands, or a congruence between animal use of canopies and their structure and composition. We suggest that quantifying the space within canopies at the level of 50–300-m traverses can help bridge the gap between landscape-scale and individual plant measures of structure and so prove useful for all manner of investigations, from comparing structural characteristics of arboreal animal habitats to understanding forest dynamics.

Literature Cited

ASHTON, D.H. 2000. The environment and plant ecology of the Hume Range, central Victoria. Proc. R. Soc. Victoria. 112:185–278.

BLOODWORTH, B.R. 2001. A comparison of the canopy structure and the vertical distribution of biota in two temperate rainforest groves. M.Sc. thesis, Alaska Pacific Univ., Anchorage, AK. 100 p.

BROWN, J.H. 1995. Macroecology. University of Chicago Press, Chicago, IL. 269 p.

BROWN, B. 2001. The valley of the giants. Focal Printing, Hobart, Tasmania, Australia. 66 p.

CONNELL, J.H., M.D. LOWMAN, AND I.R. NOBLE. 1997. Subcanopy gaps in temperate and tropical forests. Aust. J. Ecol. 22:163–168.

CURRAN, L.M., I. CANIAGO, G.D. PAOLI, D. ASTIANTI, M. KUSNETI, M. LEIGHTON, C.E. NIRARITA, AND N. HAERUMAN. 1999. Impact of El Nino and logging on canopy tree recruitment in Borneo. Science 286:2148–2188.

DIAL, R.J. 2003. Energetic savings and the body size distributions of gliding mammals. Evol. Ecol. Res. 5:1151–1162

DIAL, R.J., AND S.C. TOBIN. 1994. Description of arborist methods for forest canopy access and movement. Selbyana 15:24–37.

DUDLEY, R., AND P. DEVRIES. 1990. Tropical rain forest structure and the geographical distribution of gliding vertebrates. Biotropica 22:432–434.

EMMONS, L.H. 1995. Mammals of rain forest canopies. P.

199–223 *in* Forest canopies, Lowman, M.D., and N.M. Nadkarni (eds.). Academic Press, Boston, MA.

EMMONS, L.H., AND A.H. GENTRY. 1983. Tropical forest structure and the distribution of gliding and prehensile tailed vertebrates. Am. Nat. 121:513–524.

FLANNERY, T.F. 1999. The future eaters. Reed New Holland Press, Sydney, Australia. 423 p.

FREIBERG, M. 1997. Spatial and temporal pattern of temperature and humidity of a tropical premontane rain forest tree in Costa Rica. Selbyana 18:77–84.

HARTSHORN, G.S. 1983. Plants. P. 118–183 *in* Costa Rica natural history, Janzen, D.H. (ed.). University of Chicago Press, Chicago, IL.

JACK, S.B., AND J.N. LONG. 1992. Forest production and the organization of foliage within crowns and canopies. For. Ecol. Manage. 49:233–245.

JACKSON, S.M. 1999. Glide angle in the genus *Petaurus* and a review of gliding in mammals. Mammal. Rev. 30:9–30.

KINGDON, J. 1997. The Kingdon field guide to African mammals. Academic Press, New York. 476 p.

KOIKE, F., AND M. HOTTA. 1996. Foliage-canopy structure and height distribution of woody species in climax forests. J. Plant Res. 109:53–60.

KOOP, H., AND F.J. STERCK. 1994. Light penetration through structurally complex forest canopies: An example of a lowland tropical rainforest. For. Ecol. Manage. 69:111–122.

KUULUVAINEN, T. 1992. Tree architectures adapted to efficient light utilization: Is there a basis for latitudinal gradients? Oikos 65:275–284.

LEFSKY, M.A., W.B. COHEN, S.A. ACKER, G.G. PARKER, T.A. SPIES, AND D. HARDING. 1999. Lidar remote sensing of the canopy structure and biophysical properties of Douglas-fir western hemlock forests. Remote Sens. Environ. 70:339–361.

LIEBERMAN, M., D. LIEBERMAN, AND R. PERALTA. 1989. Forests are not just Swiss cheese: Canopy stereogeometry of non-gaps in tropical forests. Ecology 70:550–552.

LINDENMAYER, D. 2000. Life in the tall Eucalyptus forests. New Holland Publishers, Sydney, Australia. 96 p.

MACARTHUR, R.H., AND H.S. HORN. 1969. Foliage profile by vertical measurements. Ecology 50:802–804.

MARSH, C.W., AND A.G. GREER. 1992. Forest land use in Sabah, Malaysia: An introduction to Danum Valley. Phil. Trans. R. Soc. Lond. B. 128:335–339.

MOFFETT, M.W. 2000. What's "up"? A critical look at the basic terms of canopy biology. Biotropica 32:569–596.

MOFFETT, M.W. 2001. The nature and limits of canopy biology. Selbyana 22:155–179.

MONTGOMERY, R.A., AND R.L. CHAZDON. 2001. Forest canopy structure, canopy architecture, and light transmittance in tropical wet forests. Ecology 82:2707–2718.

NORTH, M., J.F. FRANKLIN, A.B. CAREY, E.D. FORSMAN, AND T. HAMER. 1999. Forest stand structure of the northern spotted owl's foraging habitat. For. Sci. 45:520–527.

PARKER, G.G. 1995. Structure and microclimate of forest canopies. P. 73–106 *in* Forest canopies, Lowman, M.D., and N.M. Nadkarni (eds.). Academic Press, Boston, MA.

PARKER, G.G., AND M.J. BROWN. 2000. Forest canopy stratification—Is it useful? Am. Nat. 155:473–484.

POPMA, J., F. BONGERS, AND J. MEAVE DEL CASTILLO. 1988. Patterns in the vertical structure of the tropical lowland rain forest of Los Tuxtlas, Mexico. Vegetatio 74:81–91.

RICHARDS, P.W. 1983. The three-dimensional structure of tropical rain forest. P. 3–10 *in* The tropical rain forest: Ecology and management, Sutton, S.L., T.C. Whitmore, and A.C. Chadwick (eds.). Blackwell, Oxford University Press, United Kingdom.

SMITH, B., AND A. PADGETT. 1999. On rope—North American vertical rope techniques. National Speleological Society, Huntsville, AL. 382 p.

SPIES, T.A., AND J.F. FRANKLIN. 1991 The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. P. 91–109 *in* Wildlife and vegetation of unmanaged Douglas-Fir forests. Ruggiero, L.F., K.B. Aubry, A.B. Carey, and M.H. Huff (eds.). USDA Forest Service, PNW-GTR-285, Portland, OR.

SPSS. 1998. Statistical package for the social sciences for windows. Release 9.0.0. SPSS, Inc. Chicago, IL.

STEWART, G.H. 1989. The dynamics of old-growth *Pseudotsuga* forests in the western Cascade Range, Oregon, USA. Vegetatio 82:79–94.

TERBORGH, J. 1985. The vertical component of plant species diversity in temperate and tropical forests. Am. Nat. 126:760–776.

VAN PELT, R., AND N.M. NADKARNI. 2004. Development of canopy structure in *Pseudotsuga menziesii* forests in the southern Washington Cascades. For. Sci. 50:326–341.

VAN PELT, R., AND M.P. NORTH. 1996. Analyzing canopy structure in Pacific Northwest old-growth forests with a stand-scale crown model. Northwest Sci. 70:15–30.

WHITE, J. 1991. The allometric interpretation of the self-thinning rule. J. Theor. Biol. 89:475–500.