

Analyzing Canopy Structure in Pacific Northwest Old-Growth Forests with a Stand-Scale Crown Model

Abstract

In forests, the canopy is the locale of critical ecosystem processes such as photosynthesis and evapotranspiration, and it provides essential habitat for a highly diverse array of animals, plants, and other organisms. Despite its importance, the structure of the canopy as a whole has had little quantitative study because limited access makes quantification difficult and integration of detailed measures of many individual tree crowns is necessary. A model is presented for simulating the crown architecture of individual trees in the Pacific Northwest to analyze their collective influence on canopy structure at the stand scale. The model uses ground-based measurements of tree height, height to crown base, and crown radii. Crown shapes are modeled as solid geometric shapes based on these measures. Two examples are used to illustrate the model's applications: an estimation of the vertical distribution of foliage in an old-growth Douglas-fir/western hemlock forest; and an estimation of understory light conditions in an experimental gap, made by applying ray tracing technology to a model of the overstory tree crowns. Both examples illustrate how the model can increase detail in the description of canopy structure. Further application and future testing of the model will help refine its precision.

Introduction

The forest canopy has been hailed as one of the last biological frontiers and the greatest source of species diversity in forests (Erwin 1982, Schowalter 1988, Lesica and Antibus 1991, Terborgh 1985, 1992, Wilson 1992). Canopies are critical elements of the forest ecosystem from numerous viewpoints. They modify both meso- and micro-climate, affect regional evaporation, cloud condensation, and temperature fluctuations (McNaughton 1989, Harr 1982, Chen 1991). The canopy is the exchange site for atmospheric gases, precipitation, and particulate interception (Hutchinson et al. 1986, Campbell and Norman 1989, Gao and Li 1993). In old-growth forests of the Pacific Northwest, the complex canopy structure has been recognized as essential for many species of wildlife, arthropods, and epiphytes (several articles, this issue). Research in forest canopies has been limited, however, by both the logistical problems of accessing the tall tree crowns, and the heterogeneous structure of the canopy environment. Despite numerous studies of canopy processes and species diversity, the structure of the canopy remains poorly understood and has rarely been quantitatively analyzed.

Other studies of canopy structure have examined the fine scale of individual tree crown architecture (Massman 1982) or large-scale canopy cover for a watershed or landscape (Cohen and

Spies 1992, Wu and Strahler 1994). Detailed measures of branch patterns and leaf orientation can be used to assess shade tolerance or branch architecture (Hutchinson et al. 1986, Canham 1988), but these measures are specific to the structure of individual trees or the canopy process under study (Norman and Campbell 1989). Aerial photography and satellite imagery are used to examine changes in canopy cover with succession or disturbance (Cohen et al. 1990, Nel et al. 1994, Nilson and Peterson 1994), but they do not provide detailed information on the internal structure of the canopy.

Measures of canopy structure at intermediate spatial scales are not well developed because stand-scale analysis requires direct measurement of many tall, complex tree crowns. In mature and old-growth forests, accessing and measuring a sufficient sample of tree crowns to describe a stand's canopy structure is difficult. In spite of these difficulties, a three-dimensional stand-scale measure of canopy structure is needed for at least three reasons: this scale is necessary to link processes operating across fine (individual tree architecture) and coarse (remote measures of large-scale canopy cover) scales of structure; many arboreal wildlife species may respond to canopy structure at this scale; and land management monitoring and planning often occur at the stand scale.

A direct method of modeling the canopy structure of old-growth forest stands in the Pacific

Northwest is presented in this paper. The model is used to quantitatively describe the vertical distribution of crown foliage within a stand and associated effects on the amount of light in the understory. Estimates of individual crown volumes are made from ground-based measures of tree height, height to the live crown, crown shape, and crown diameter. Although these methods were developed in coniferous old-growth forests, the techniques should be applicable to other forest types, to successional stages where canopy structure may be less complex, or both. As research activities in forest canopies increase, standardized methods for quantitatively analyzing canopy structure are needed. This model is presented as a preliminary approach toward measuring stand-scale canopy structure while the model's accuracy is tested further.

Approaches to Measuring Canopy Structure

Canopy Structure and Tree Age

Canopy structure refers to the spatial arrangement of tree stems, branches and foliage within a forest. As forest stands develop, the vertical and horizontal distribution of the canopy becomes more heterogeneous, and its measurement becomes more difficult. In young stands of trees, particularly conifers, canopy structure is fairly homogeneous and growth patterns are predictable. Models of individual trees can predict annual branching patterns, branch angles, and leader and branch extension lengths with some accuracy for young trees (Hamilton 1969, Horn 1971, Hatch et al. 1975, Halle et al. 1978). Growth and yield models, such as OREGANON (Hann et al. 1992), can provide good estimates of a tree's crown growth, including responses to thinning mortality.

As trees age, however, they become taller and their crowns longer, more complex, and more idiosyncratic. Trees in an old-growth forest are products of hundreds of years of individual responses to disturbance, competition, injury, light availability and quality, and other stochastic events. For each tree, the sum of these collective differences creates a unique, complex, crown shape that is difficult to predict or model (Canham 1988, Young and Hubbell 1991). In conifer forests, the canopy may begin as a fairly uniform band of cone-shaped crowns, and develop into a multi-layered array of polymorphous crown shapes. Maps

of the foliage distribution in individual old-growth Douglas-fir trees at the H.J. Andrews Experimental Forest in central Oregon showed that the crown shape of each tree was unique and irregular (Pike et al. 1977, Massman 1982).

Scale and Access

Canopies are studied at many different scales depending on the arboreal species or process. From landscapes to stands to individual trees to branches, the scale of interest determines the detail at which canopy structure should be measured (Kruijt 1989). Researchers interested in fine-scale processes are not concerned with the unique shape of each old-growth tree crown. When canopy-dwelling arthropods are being studied, for example, foliage distribution on a single branch can be examined for habitat use and availability (Winchester, this issue). For studies of photosynthesis and particulate interception, canopy structure may require a map of foliage or branch distribution within a single crown. When working at these scales, direct access to the canopy is possible using towers, lifts, or rope techniques developed by urban arborists. Although these systems are time consuming to establish, they afford precise measurements of crown components.

Landscape ecologists and foresters interested in canopy structure on a watershed or regional scale rely on remote imagery from airplanes and satellites (Woodcock et al. 1990, Wu and Strahler 1994). Remote methods eliminate access problems and increase the canopy sample size, but also decrease detail. Digital satellite imagery has been used to classify forest stands by age class across landscapes, by using the reflectance signal of canopies, (Morrison 1989). Digital imagery or videography from low-flying aircraft can distinguish individual tree crowns, shadows and the openness of a stand (Cohen et al. 1990).

Remote imagery provides valuable large-scale images of changes in canopy structure with age or disturbance, but it provides little information about the interior canopy environment. In forests with multiple crown layers, high foliage densities, or irregular crown cover, measures of only the outer canopy surface provide little information about canopy structure. Assessing canopy structure at the stand scale requires integration of numerous measures of individual tree architecture. Measurements must include more than a

sample of a few tree crowns, but must provide greater detail than can be obtained from a remote image of the canopy's upper surface. This compromise between sample size and detail, along with problems accessing mature forest canopies, has often led to the use of indirect measures of canopy structure, such as light transmission.

The amount of light in a forest is influenced by the density and distribution of canopy foliage (Anderson 1963, Horn 1971, Reifsnyder et al. 1971). The percentage of full sunlight that reaches the forest floor is a broad measure of foliage density. The most common methods of measuring light penetration, however, integrate the incoming light over the whole sky (Reifsnyder et al. 1971, Hutchinson et al. 1980, Oberbauer et al. 1988, Chazdon and Pearcy 1991) providing little information regarding the distribution of light as a function of canopy structure. Fisheye photographs can help isolate the direction of incoming light (Evans and Coombe 1959, Anderson, 1963, Horn 1971, Canham et al. 1990); however, each photo represents only a single location, making stand-scale analysis difficult. A larger scale measure of canopy structure that does not use light transmission is leaf area index (LAI), a measure of the number of foliage layers over a given area of forest floor, provides a stand-level index of foliage quantities (Waring et al. 1982). All of these techniques, however, provide little detailed information on canopy structure because they do not measure how foliage is spatially distributed (Oker-Blom and Kellomaki 1982, Chason et al. 1991).

Canopy Structure in Pacific Northwest Old-Growth Forests

Pacific Northwest old-growth forests have tall, multilayered canopies, which are difficult to access and structurally complex. Much of the old growth below 1000 m in elevation is dominated by Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*). These forests can be up to 80 m tall, with foliage distributed throughout (Franklin and Waring 1980), so that the amount of understory light provides little information about foliage distribution in the canopy. The trees may be tall but are generally not very wide. Branch lengths seldom exceed 8 m and the upper canopy tends to have distinct crowns because of branch abrasion.

To confound matters, the amount of light reaching the forest floor may not reflect the canopy structure directly overhead. In the Pacific Northwest (at latitudes from 44 to 58°), sun angles are oblique during most of the growing season. Analyses of fisheye photos reveal that significant amounts of light filter through a Pacific Northwest forest canopy at 45 degrees or more off vertical (Figure 1a and 1b) (Easter and Spies 1994). Flat projections of tree crowns used to model canopy effects on understory light may work well in low-latitude tropical forests or short-stature, broadleaf temperate forests (e.g., Runkle 1992), but they do poorly in the Pacific Northwest.

For Pacific Northwest old-growth forests, measurement of the location and crown dimensions of individual trees can be integrated to provide a stand-scale description of canopy structure. Ground-based measurement is a practical compromise between direct measurements of a few branches and remote, large-scale sampling of a forest's outer canopy cover. With ground-based measures, an observer can quickly and directly measure the individual tree parameters that collectively describe the density and distribution of a stand's canopy foliage. Treating each tree crown as a simple geometric shape is possible, thus making canopies of complex, old-growth stands relatively easy to model in three dimensions.

Although treating crowns as solids may be inappropriate at fine scales, such simplification can provide a three-dimensional map of generalized tree crowns that collectively approximate stand-scale structure. For example, this level of structure modeling might help assess foraging conditions for an owl which flies between rather than through crowns. Although this model is a simplification of a complex canopy environment, it is a step toward the three-dimensional analysis necessary to understand the influence of canopy structure on arboreal processes and species diversity.

Measuring Canopy Structure: Crown Model Technique

Data for model development were collected in a Douglas-fir / western hemlock old-growth forest at the Wind River Experimental Forest in the southern Washington Cascade Range. The site is a relatively flat, moderately productive forest that originated 400-500 years ago (Franklin and DeBell

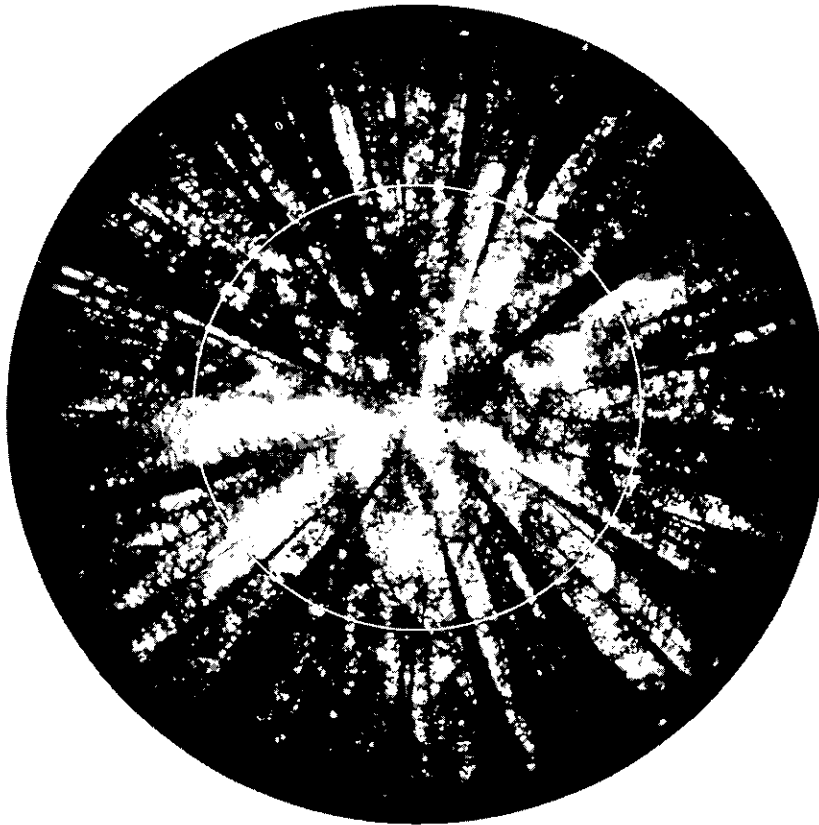


Figure 1a. Hemispherical photograph (fisheye photo) taken in a closed portion of an old-growth Douglas-fir/western hemlock forest. The center of the image is directly above the camera, and the white circle represents 45 degrees below vertical. Note that significant light penetration occur at angles greater than 45 degrees.

1988). The forest stand is near the upper limits of the western hemlock zone (Franklin and Dyrness 1973), with an understory tree layer dominated by Pacific silver fir (*Abies amabilis*), Pacific yew (*Taxus brevifolia*) and western hemlock. No detectable major disturbance has occurred since stand initiation, resulting in a multilayered forest. The largest trees are Douglas-firs up to 60 m tall and from 275-500 years old (Franklin and Waring 1980), and the western hemlocks occupy all strata from seedlings to old trees (Figure 2).

All trees taller than 50 cm were mapped for use in the spatially explicit model. This height was chosen because small seedlings can be ephemeral; population numbers do not stabilize until understory trees become well established (Van

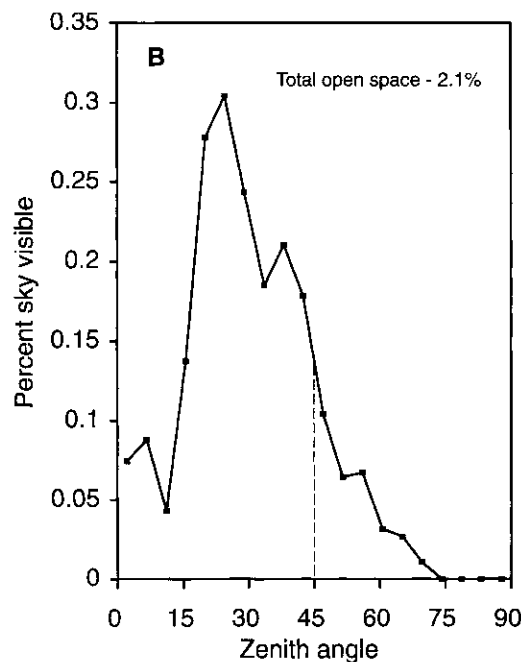


Figure 1b. The distribution of open space for the image in 1a. Maximum light penetration is at 25 degrees.

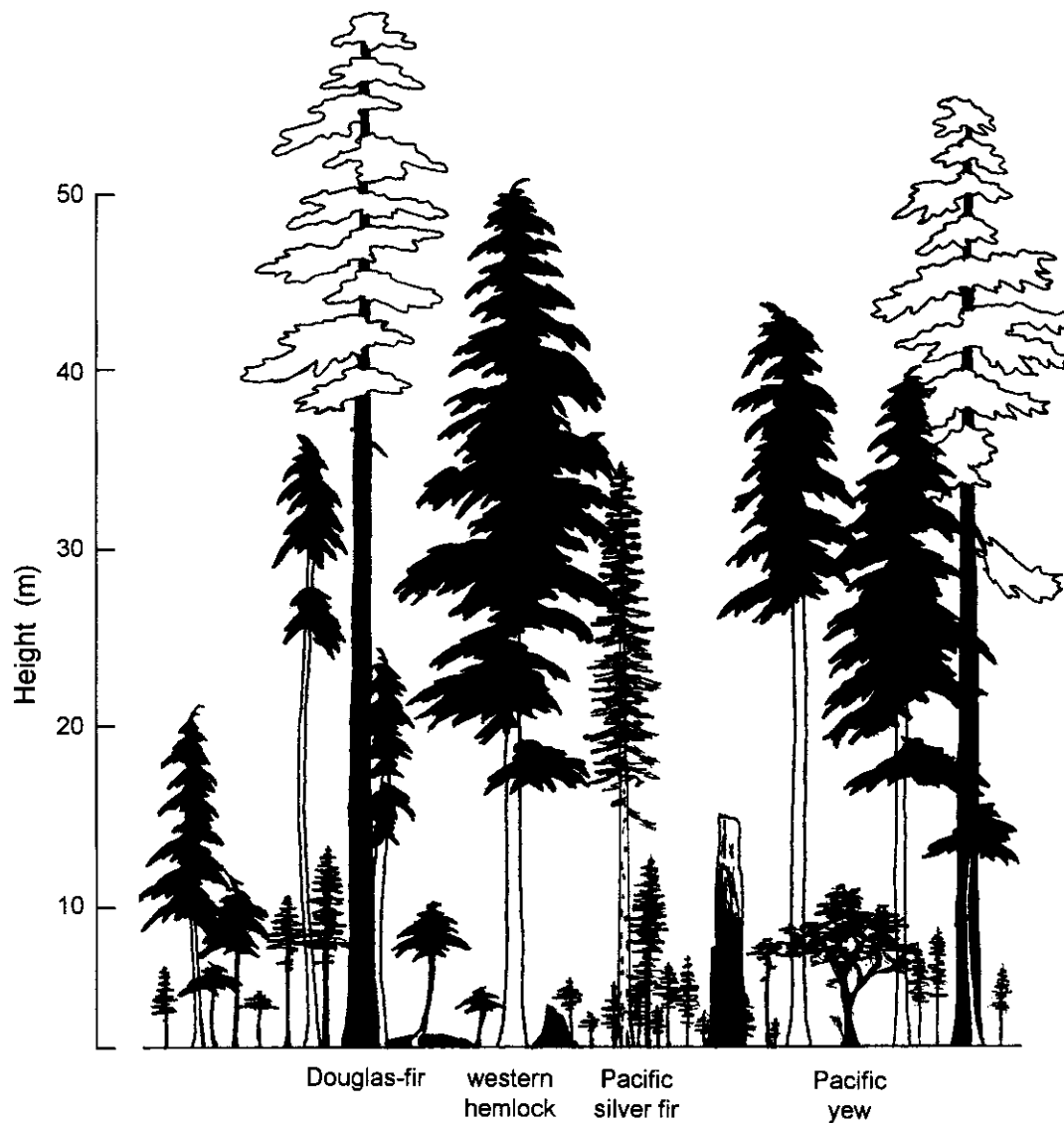


Figure 2. 50 x 20 m cross section of the study site at the Wind River Experimental Forest. Note the diversity of tree heights and the vertical distribution of the foliage.

Pelt, unpublished). Each crown was characterized by measuring the tree's height and height to the crown base, mapping the crown projection or measuring four crown radii, and assigning a crown shape (Figure 3). If a detailed view of the lower crown is required, height to crown base could be replaced by a value for the height to partial crown, the height to full crown, and the compass directions of the partial crown (North 1993).

Two 400 m transects were placed in interior portions of the forest. Trees greater than 5 cm in

diameter at breast height (dbh) were mapped in a 20 m wide band centered on the transect line. Each of these trees was identified to species and also measured for total tree height, height to crown base, and crown radii. Trees taller than 50 cm were sampled in a 2 m wide transect centered on the same transect line. Although time permitted tree height measurements for only 85% of the trees, regressions of dbh by species on the 1429 measured trees were used to estimate the remainder (Table 1).

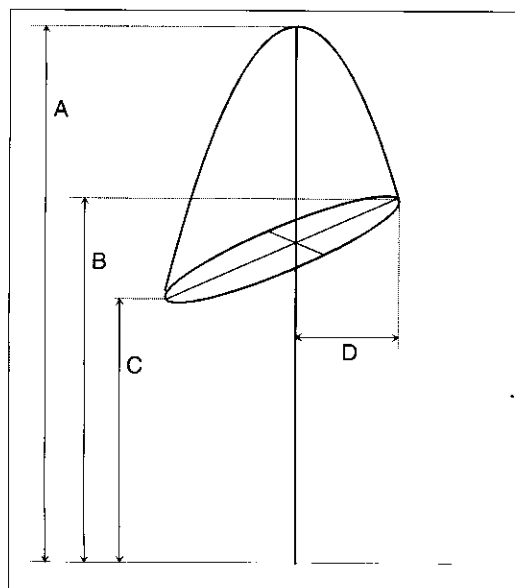


Figure 3. The variables required for the crown model: a, the tree height; b, height to full crown base; c, height to partial crown; d, four crown radii.

Data were also collected in a 0.2 ha circular gap in the Experimental Forest. This gap was cut as part of a larger study looking at the effects of experimental canopy removal on the forest understory (Van Pelt et al. 1992). All trees taller than 50 cm were mapped in a 0.4 ha area centered on the gap, and measurements for each tree followed the protocol used for the transect samples.

Crown Shape

For model construction, the crown of each sample tree was classed as one of several solid geometric shapes. No single shape can be applied to all trees because old-growth crowns are unique and irregular. Several simple forms, however, can be applied to most tree crowns.

Cones are perhaps the most commonly used shape for modeling conifers because they are easy to describe mathematically and are conformable to many crown shapes (Figure 4). In addition, most conifers and many broadleaf trees have conical shapes for the first several decades of their lives, and indeed many retain this shape for several hundred years (Horn 1971).

Cylinders are another group of geometric shapes that could be used to simulate certain tree crowns. Tall, closed canopy forest trees often develop deep, narrow crowns best represented by cylindrical shapes. Although young conifers are generally not flat topped, emergent old-growth trees can develop flat tops when they have stopped growing in height. The calculations for cylinders are simple and this shape should not be overlooked for appropriate situations.

Paraboloids are versatile shapes that are adaptable to a wide variety of crowns. These shapes can be used for trees that have either the deep crowns of main canopy trees, or the short, wide crowns of suppressed understory trees. In either case, the widest part of the crown is at or near the bottom of the crown, which makes paraboloids an appropriate choice.

Ellipsoids (including prolate and oblate spheroids) or truncated ellipsoids are similar to paraboloids in that they also approximate some old-growth tree crowns. A half-ellipsoid looks similar to a paraboloid of equal height and width, yet the paraboloid is narrower at all heights except for the bottom. Old-growth Douglas-firs often have ellipsoidal crowns, with the widest part of the crown low but not at the crown base.

Geometric shapes for each crown were selected in the field after viewing crown shape from several angles. All Douglas-fir tree crowns in this study were modeled as truncated ellipsoids, and all other trees are modeled as paraboloids. To

TABLE 1. Regression equations used to predict height from dbh for the trees used in the crown model; 1429 trees were used to develop the equations.

Species	Predicting equation	N	adj r^2
<i>Tsuga heterophylla</i>	$Ht = 50.863 * (1 - e^{-(.022 * DBH)^{1.512}})$	693	0.947
<i>Abies amabilis</i>	$Ht = 45.59 * (1 - e^{-(.028 * DBH)^{1.539}})$	468	0.958
<i>Pseudotsuga menziesii</i>	$Ht = 136.389 * (1 - e^{-(.003 * DBH)^{0.6965}})$	149	0.746
<i>Taxus brevifolia</i>	$Ht = 17.542 / (1 + (5.367 * e^{-(.006 * DBH)}))$	119	0.604

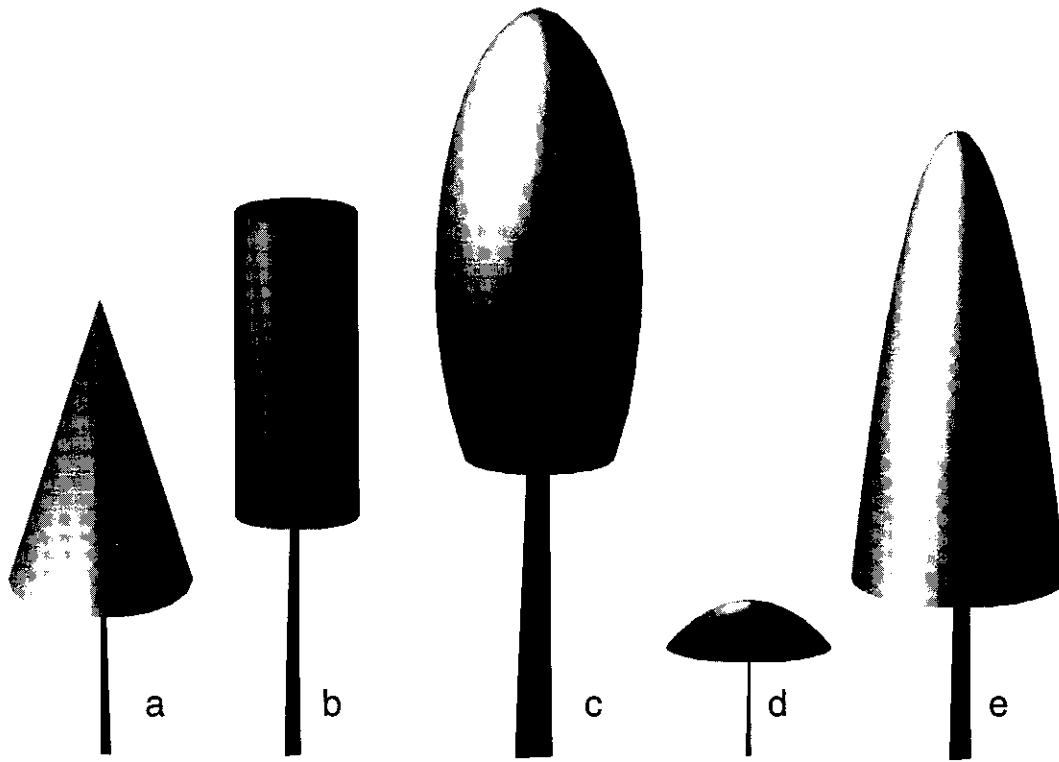


Figure 4. Potential crown shapes used in the model. from left to right: cone, cylinder, ellipsoid, paraboloid (wider than tall), and another paraboloid (taller than wide).

qualitatively assess the fit between actual crown shape and selected geometric shapes, photographs of 13 trees were digitally scanned. Two-dimensional silhouettes of the crowns were compared with the geometric shape selected in the field (Figure 5). The geometric shapes exclude irregular, lower branches and long branch tips, and fill in crown gaps where branches are missing.

The selected geometric shape, crown length, and crown radii were used to model the crown shape and height of each tree at its specific X-Y location along the transect. The resulting stand model closely approximates crown locations using specific height and position measurements, but it simplifies crown shape as a geometric solid.

Applications of the Crown Model

The following two examples illustrate how the model can be used to describe canopy conditions. The first estimates the vertical distribution of foliage based on measurements from the 20 x 400

m transects. This estimate is presented only to illustrate the model's capabilities because we do not have an exact measure of the real foliage distribution. The second example is a spatially explicit application that estimates understory light surrounding the experimental canopy gap. In this application, a subset of the model's results from specific locations are compared to fisheye photographs taken at the same locations.

Application I: Vertical Distribution of Foliage

The crowns for all trees along the transect were modeled and then horizontally sliced at 5 m height intervals. Crown cross-sectional area and volume were calculated for each tree at each interval. Frustum volumes were summed by species for each 5 m layer to estimate the vertical distribution of crown foliage. These data are presented in Figure 6 in two ways; graph A shows the total crown volume / ha at each height for each species;

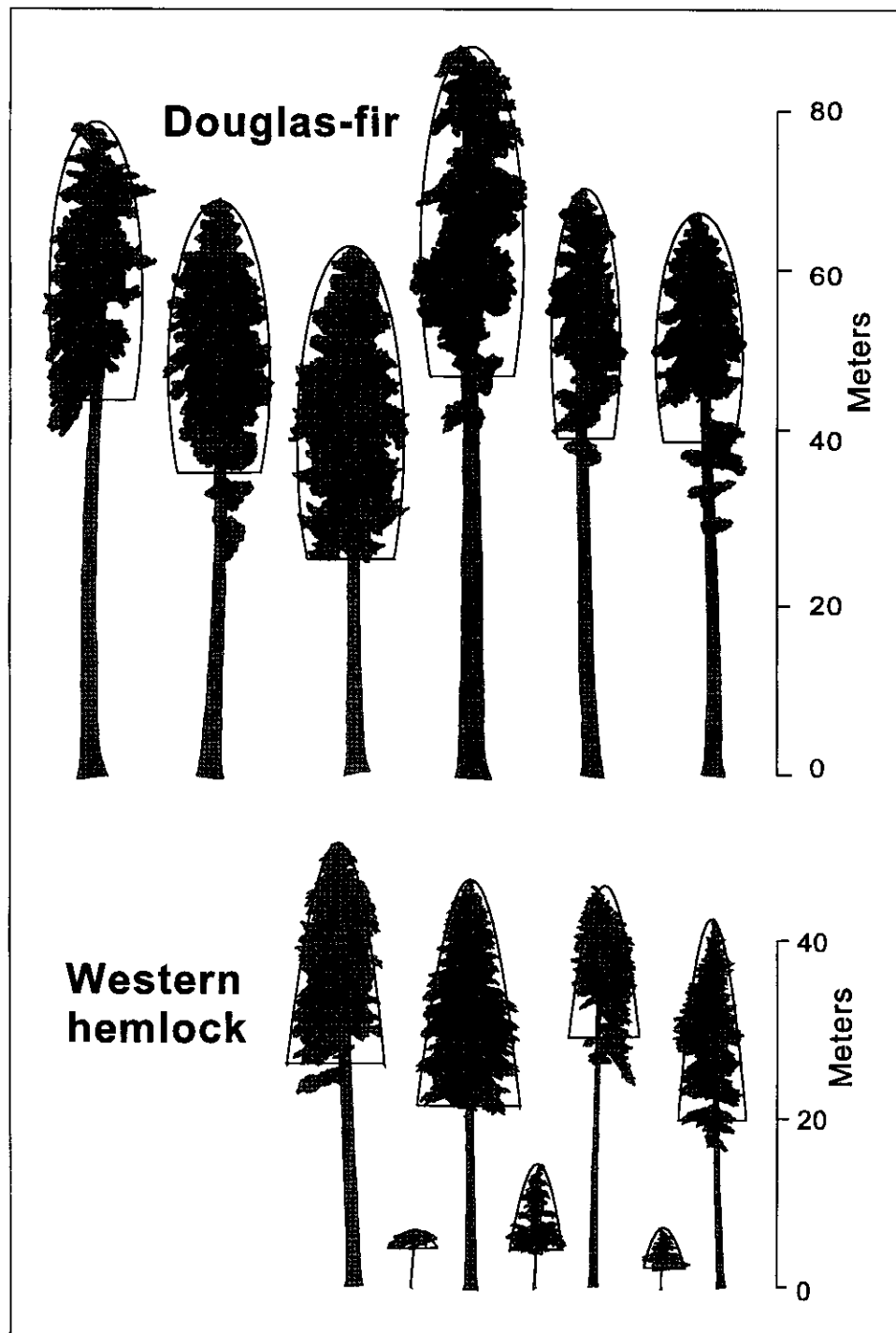


Figure 5. Top: Six photographic silhouettes of old-growth Douglas-fir trees with a truncated ellipsoid overlaid to show the model's approximation of the actual crown shape. Bottom: Seven photographic silhouettes of old-growth western hemlock trees with parabolic shapes overlaid to show the versatility of paraboloids for modeling a diversity of crown structures.

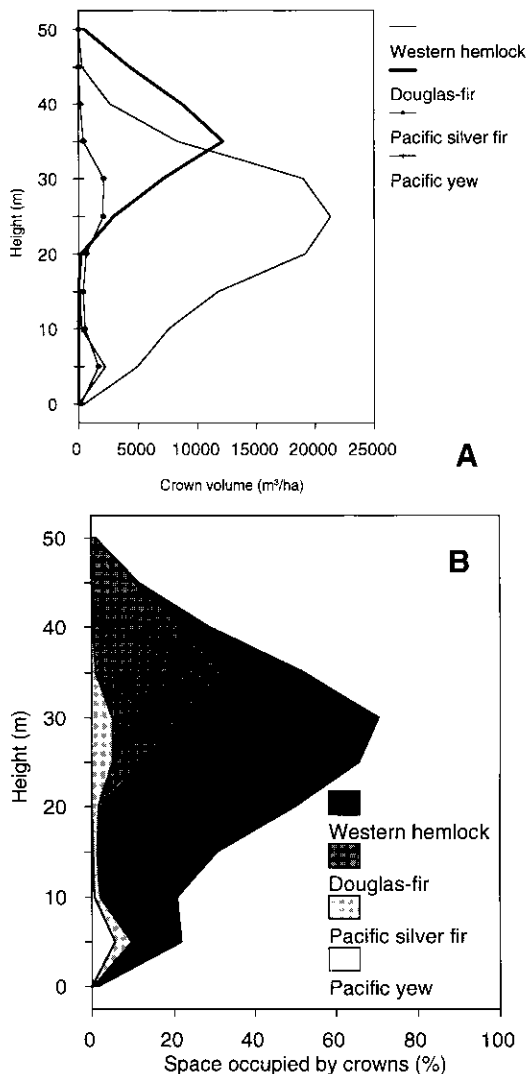


Figure 6. Vertical foliage distribution for the forest at Wind River: A, for each species individually in cubic meters per hectare; and, B, by species (individual shades), or total stand (outer boundary) as a percent of total available open space.

graph B is an area graph showing the total three-dimensional space occupied by each species by height interval.

The model helps visualize foliage distributions that cannot be measured with above-canopy remote imagery or understory light conditions. Slicing the canopy clearly showed that the highest density of foliage was between 20 and 42 m. Yet even in this vertical zone, 40% of the canopy space

is open. Shade-intolerant Douglas-fir extends and dominates the upper canopy environment, providing most of the crown volume above 43 m. In total volume, however, the stand is dominated by western hemlock and in the lower canopy most of the space is occupied by hemlock crowns. In this stand, although large Douglas-fir may punctuate the outer canopy, most of the canopy structure is determined by the density and distribution of subdominant, shade-tolerant species.

Application II: Using the Crown Model to Estimate Light Reaching the Forest Floor

Hemispherical (fisheye) photography can be used to estimate the amount of light penetrating a canopy. Through the use of the crown model and a computer animation technique called ray tracing, a computerized equivalent of fisheye photos can be generated. From a selected point, the visible hemisphere's tree crowns are drawn by using the model, and the animation technique presents an overhead view from the ground. This view, similar to a fisheye photo, can be analyzed and the amount of visible open sky can be calculated. The ray tracing program (POV-RAY 2.0, 1993) models the light through the canopy by mathematically placing a camera, light source, and objects in three-dimensional space using ASCII text definitions. A window of a given resolution is defined and the program then calculates the path of light rays from each pixel back to the light source based on the reflective nature of the objects. Although ray tracing is commonly used for detailed photorealistic images, its accurate rendering of objects in three-dimensional space makes it useful for scientific illustration.

The canopy's effect on understory light was explored using the ray tracing techniques and crown models to simulate the canopy. To estimate light distribution throughout the 0.4 ha plot containing the experimental gap, ray-traced images were generated for 204 stations placed 4 m apart in each gap. A radial grid, like those used in fisheye photo analysis (Rich 1989), was imposed on each ray-traced image. By using the grid, the total percentage of open sky in each image was calculated. Each cell in the grid is analyzed for the percentage of the cell blocked by tree crowns, and cell percentages are summed over the image. The image for the gap center is shown in Figure 7A. This process is repeated for all images

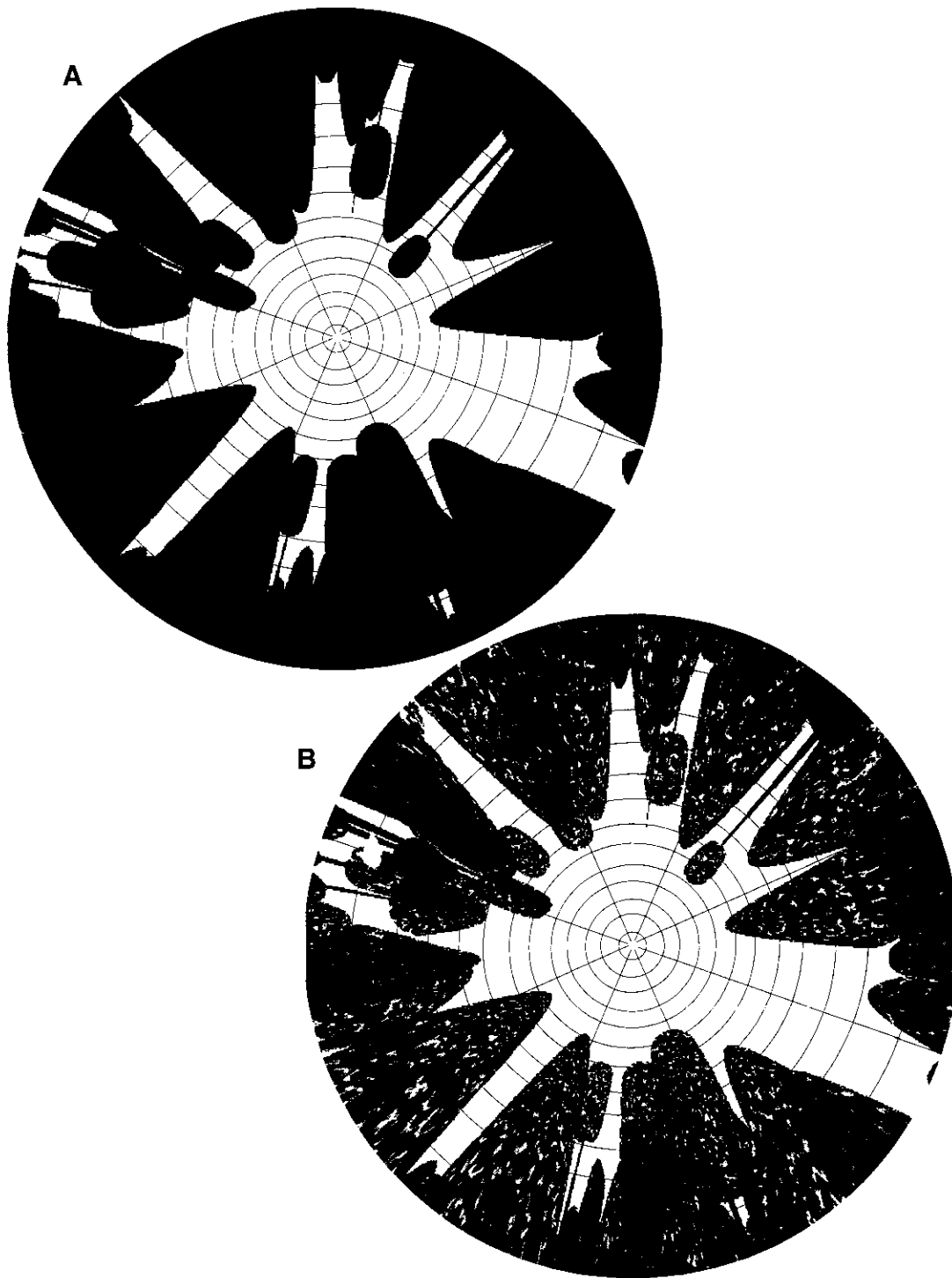


Figure 7. A, A simulated fisheye image taken from the center of a 0.2 ha opening in the Wind River old-growth forest (120 degree aperture); and B, the same image but with transparent textures added to more closely approximate actual conditions. Transparent textures were calibrated with a subset of actual hemispherical photos.

generated for each location and kriging is used to spatially interpolate the light distribution between the 204 stations.

A more accurate simulation of the light distribution can be made by using texturing techniques within the ray tracing program. Texturing lets the tree crowns transmit light in a more realistic manner. A subset of fisheye photographs taken from the Experimental Forest were used to calibrate tree transparency in the model. Figure 7B shows where this was done for the same location as Figure 7A.

To evaluate how well this application of the crown model simulates light transmission, comparisons of ray-traced images and fisheye photographs from the same location were made for 10 stations in two experimental gaps at Wind River. The fit between actual and predicted values of open sky were significant when summed either by zenith angles or by *azimuth* direction (Table 2).

TABLE 2. Regression statistics for comparisons of actual fisheye photos with simulated fisheye photos. For the zenith angle regressions, N = 20; for *azimuth* direction, N = 8. All values are significant.

Plot	Location	Zenith angle		Azimuth direction	
		r ²	p value	r ²	p value
1	17 m N	0.988	<0.001	0.576	0.018
1	14 m N	0.992	<0.001	0.799	0.002
1	Center	0.997	0.001	0.789	0.004
1	14 m S	0.473	0.001	0.897	<0.001
1	28 m S	0.962	<0.001	0.928	<0.001
2	25 m N	0.999	<0.001	0.786	0.002
2	13 m N	0.998	<0.001	0.966	<0.001
2	Center	0.989	<0.001	0.972	<0.001
2	13 m S	0.919	<0.001	0.817	0.001
2	25 m S	0.982	<0.001	0.851	0.001

Once the entire array of locations has an image, surface maps of the distribution of open sky by percentage throughout the gap were generated using a geographic information system (ARC/INFO, v. 6.1.2, 1993). This can be combined with a model of the amount of diffuse radiation distributed across the sky to estimate the total amount of diffuse radiation that is penetrating the canopy. The ratio of this to the total amount of diffuse radiation in an unobscured sky is known as Indirect Site Factor (ISF). The ISF is a measure of

diffuse light conditions in the understory, which in our example occurs at the center of the opening (Figure 8A).

To investigate the influence of latitude on understory light distribution, sun-paths throughout the growing season were modeled. This measure provides an idealized value (i.e. no cloud cover) of direct light conditions in the gap (Figure 8b). The maximum direct light possible over the entire year (Direct Site Factor, DSF) is 0.325 and is shifted 17 m north of the gap center. The 0.325 value means that 32.5 percent of the possible direct light reaches that spot, given no clouds or haze. The shift indicates that light filtering through tall Pacific Northwest forests influences understory conditions at an oblique angle to the forest floor. Simple vertical or horizontal measures will not give an accurate assessment of tree response to canopy gaps, because the changes may be completely shifted out of the gap. This result is similar to that presented by Canham et al. (1990), who modeled gaps as cylinders at the same latitude.

Discussion

The measure of an ecological model is its ability to accurately illuminate complex processes at the expense of some simplification. Powerful computers and new statistical techniques have made three-dimensional modeling of the forest canopy possible. Yet these models will always be built on some simplified measurements of canopy structure determined by the selection of scale and access method.

Because the model is a simplification of a complex structure, the model is meant for stand-scale research, not for detailed analyses. Crown shapes are treated as solids in this model, yet foliage density within a single crown is actually distributed as a foliage shell of variable thickness (Jensen and Long 1982). For young trees and shade-tolerant old trees, the inside of the shell is an area of high shade and is thus largely photosynthetically inactive. Old trees, however, have unique branching patterns and can develop very open crowns. At the stand scale this variability is minimized, but more detailed models will be needed if a closer examination of forest structure is required. For old-growth tree crowns, attaining the next higher level of detail is a major step that will require modeling tree crowns through their individual branches. Such a model would require numerous

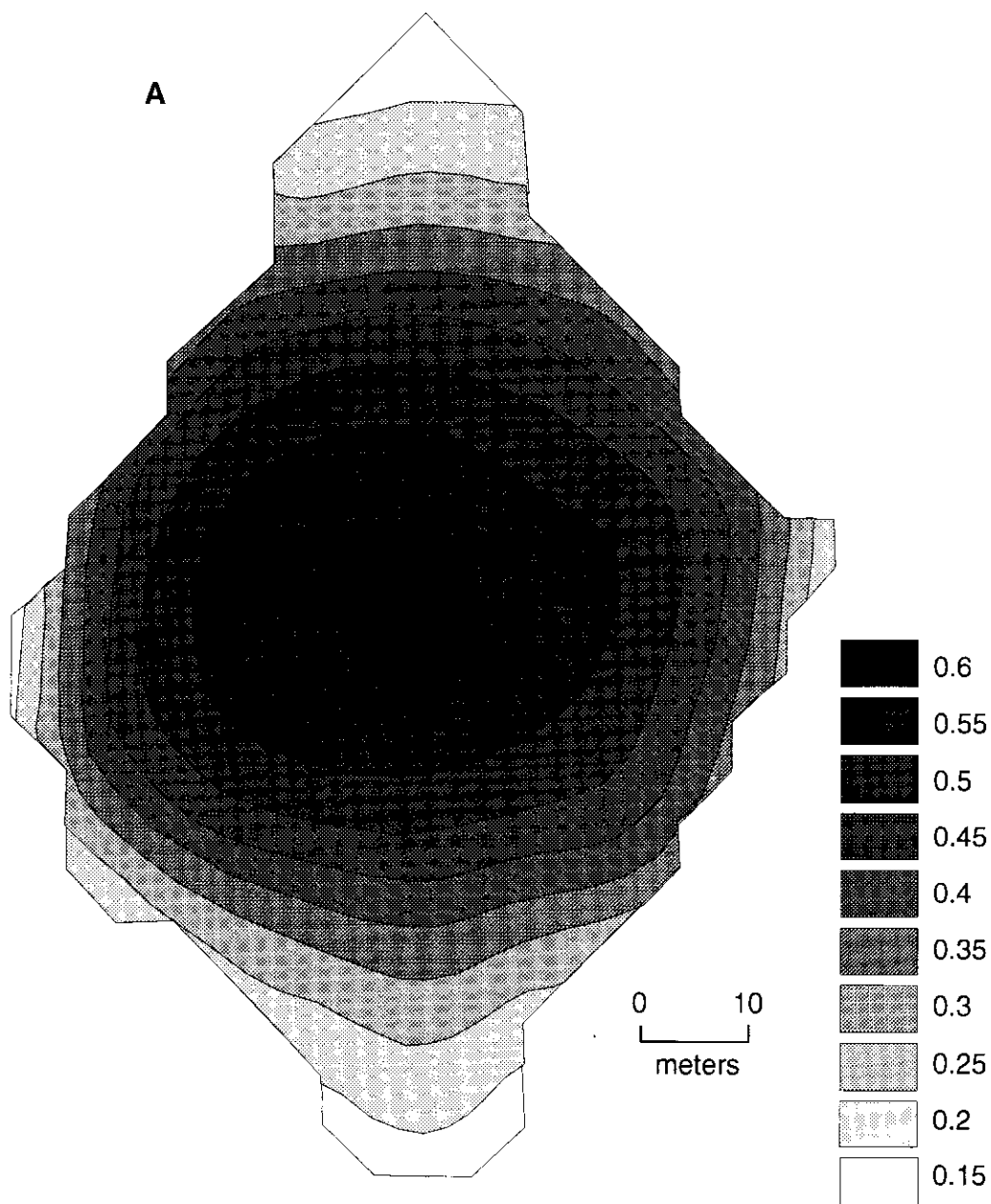
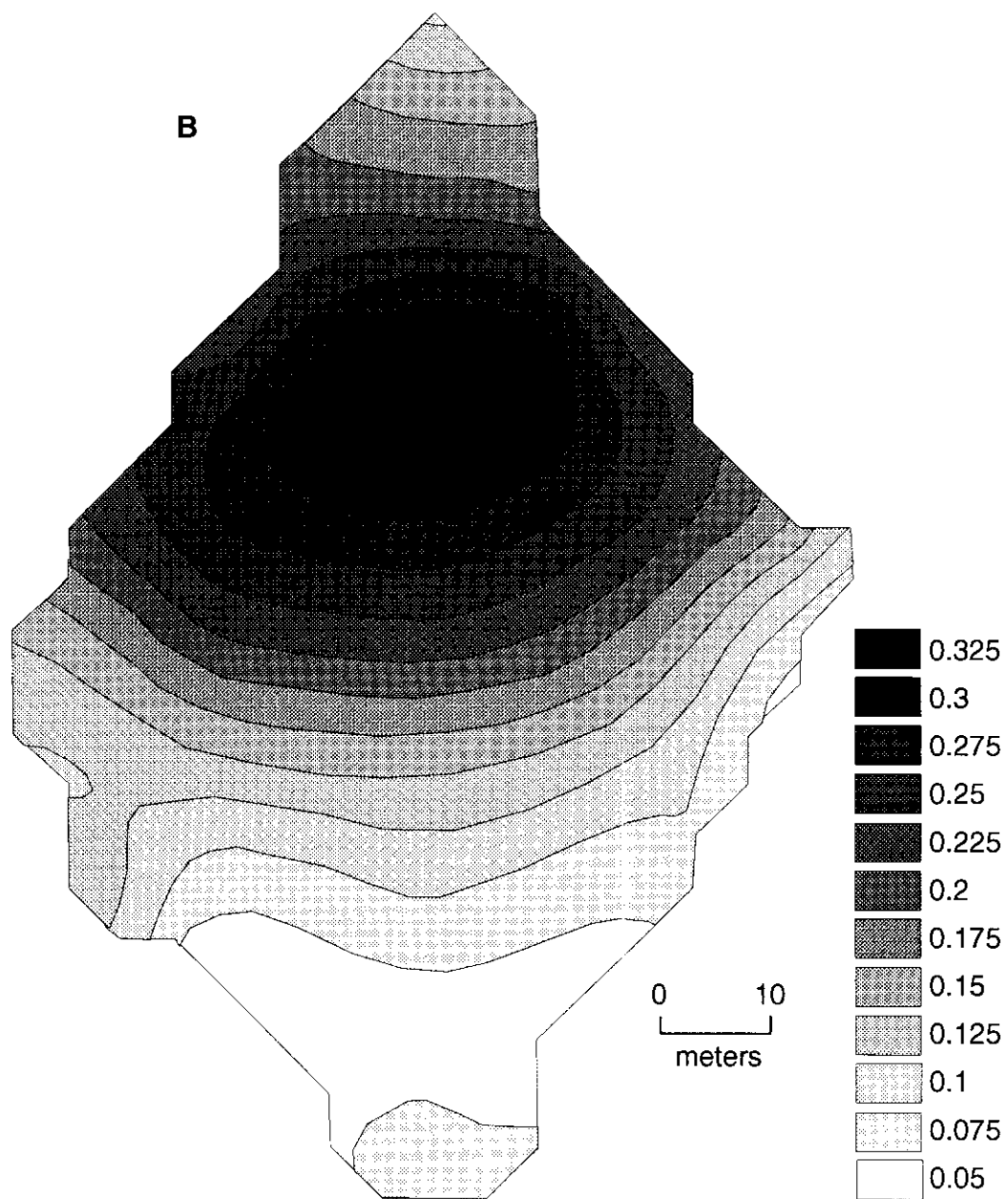


Figure 8. A, Results of the diffuse light model. Indirect Site Factor for a 0.4 ha area surrounding the 0.2 ha gap. The outer boundary is the limit of the plot and the irregular white line represents the crown projections of the remaining canopy trees. The gap center has the highest ISF. B, A direct light model showing the percentage of possible direct sun (Direct Site Factor, DSF) over the course of a growing season. This analysis makes no predictions for clouds or haze. The maximum value is shifted 17 m north of gap center.



measurements within individual crowns, rather than a few easily measured crown dimensions.

The applications presented describe two of the many potential uses of this model to stand-scale research. Two applications illustrate how crown volumes are vertically distributed and how crowns affect light penetration. The next logical step for this application is to combine the vertical distribution with horizontal spacing of trees to come up with a three-dimensional analysis of crown distribution. A corollary to this approach is an analysis in three dimensions of the open space within the forest canopy. For arboreal species such as the northern flying squirrel (*Glaucomys sabrinus*) or the northern spotted owl (*Strix occidentalis caurina*), the amount and distribution of open space may be important to movement or foraging success (Carey 1985, Rosenberg and Anthony 1992).

The computer-generated hemispherical photos also have wide applicability. Not only can large areas be analyzed once the stand parameters have been mapped, but analysis of canopy openness at various vertical locations is easily accomplished, an aspect that has limited canopy photography from the ground. Simulations of proposed harvesting activities is yet another application of the light model. Selective logging, green-tree retention, strip cutting, and other forestry practices can be simulated under current and future conditions.

At present the accuracy of the model is difficult to assess because there is no absolute measure of canopy structure. Unlike ground-level forest structure, the canopy environment does not readily imply a standard unit of measure. A stand's basal area is easily sampled because tree boles are discrete structures. Tree crowns, however, can be considered a fractal shape (Zeide 1993) because their dimensions will change depending on the size of the sample unit. Any model's representation of the canopy is relative to the scale it works at and the size of its smallest sample unit. The crown model presented is for stand-scale assessment of canopy structure using individual tree crowns which are treated as simple geometric solids. Given these parameters we believe the model can help visualize patterns in canopy struc-

ture which could further a more analytical exploration of the canopy environment.

Conclusion

Studies of forest structure have often focused on tree stems, and the function and composition of the immediate environment near the ground. In a plant community where the vegetation is 30 to 80 m tall, however, many of the dynamic ecological processes and biodiversity will occur in the arboreal environment about which little is known. Before the ecological interactions of species and processes can be linked with their environment, a measure of the aggregate crown or stand-scale structure is needed. This measure would have at least three benefits: until most of the species and complex interactions of an ecosystem are well studied, measures of structure must often serve as a surrogate measure of function or biotic diversity; for experimental design and sampling, researchers need to know how the canopies of different stands are distinct and what factors make them so; and most monitoring, planning, and management of forests are at the stand scale. A measure of canopy structure that uses ground-based methods would provide foresters with a means of comparing canopy environments between different stands.

In this paper, we present a method for modeling old-growth forest canopies at the stand scale using ground-based measures. This technique is based on easily measured crown dimensions and can aid in three-dimensional analysis of forest processes. Two applications of the model were used to examine the vertical distribution of foliage and understory light levels in a Pacific Northwest old-growth forest. The model indicates that much of the foliage mass in the old-growth sample stands is dominated by shade-tolerant, subcanopy species, and that light conditions for a point on the forest floor are more influenced by the canopy's structure at an oblique angle than the tree crowns directly overhead. We believe the model can help researchers analyze the complex structure of the overstory environment as they explore the ecology of the canopy frontier.

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