Methods for evaluating crown area profiles of forest stands[1]

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Abstract: Canopy architectures of five structurally complex forest stands and three structurally simple forest stands in southwest Oregon and the Willamette Valley, Oregon, were evaluated and quantified through crown area profiles. Mixed conifer and mixed conifer–hardwood stands across a range of sites were sampled for crown widths and heights. Crown width and shape equations were derived and used to quantify the stand crown area at incremental heights above the forest floor. Crown area profiles describe the spatial arrangement of aboveground forest vegetation and the total pore spaces between crowns. Plot by plot profiles were combined to produce vertical and horizontal displays of the stand crown area distribution. In complex stands, the forest space was moderately occupied by crowns from the forest floor up to heights over 30 m, producing uniform distributions of between-crown porosity. The structurally complex stands had between-crown porosity values of 70% to 90% for more than 23 vertical metres of canopy, and they had total between-crown porosities of 86% to 91%. The structurally simple stands had between-crown porosity values of 70% to 90% for less than 8 vertical metres of canopy, and they had total between-crown porosities of 69% to 85%. Variances in crown area indicate that variation in horizontal crown area (within heights) was larger in complex stands than in simple stands, but vertical crown areas (between heights) varied less in complex stands. The study provides a basis for discriminating between canopy architectures and for quantifying the porosity of forest canopies.

Résumé : L'architecture du couvert de cinq peuplements à structure complexe et de trois peuplements à structure simple dans le sud-ouest de l'Orégon et dans la vallée de la Willamette (Orégon) a été évaluée et quantifiée en utilisant le profil de surface des houppiers. Les peuplements de conifères mixtes et de conifères en mélange avec les feuillus furent échantillonnés dans différentes conditions de station en mesurant la largeur et la longueur des houppiers. Les équations de largeur et de forme du houppier ont été établies et utilisées pour quantifier la surface des houppiers dans le peuplement à différentes hauteurs au-dessus du sol. Les profils de surface des houppiers décrivent l'arrangement spatial de la végétation au-dessus du sol et la superficie totale correspondant aux espaces vides entre les houppiers. Les profils de l'ensemble des placettes ont été combinés pour produire la représentation verticale et horizontale de la distribution de la surface des houppiers dans le peuplement. Dans les peuplements à structure complexe, l'espace aérien est modérément occupé par les houppiers depuis le niveau du sol jusqu'à plus de 30 m de hauteur avec une distribution uniforme des espaces vides entre les houppiers. La porosité y varie de 70 à 90% sur plus de 23 m de profondeur du couvert et la porosité totale varie de 86 à 91%. Dans les peuplements à structure simple, la porosité varie de 70 à 90% sur moins de 8 m de profondeur du couvert avec une porosité totale de 69 à 85%. La variance dans la surface des houppiers indique que la variation dans l'axe horizontal des houppiers (pour une même hauteur) est plus forte dans les peuplements complexes que dans les peuplements simples, mais la variation dans l'axe vertical (entre les hauteurs) est plus faible dans les peuplements complexes. L'étude fournit une base pour distinguer les différences d'architecture du couvert et quantifier la porosité des couverts forestiers.
[Traduit par la Rédaction]

Introduction

The vertical and horizontal arrangement of the forest canopy is a significant characteristic of forest stand structure. Relationships between stand structure (the spatial arrangement of aboveground vegetation) and wildlife habitat have been of considerable interest and, sometimes, controversy. In particular, some threatened and endangered species, including the northern spotted owl (*Strix occidentalis caurina*), are hypothesized to select habitat with specific structural characteristics (Thomas et al. 1990). Some of the structural characteristics of old forests (such as multilayered, multispecies canopies; dominance by large conifers; large snags; and many fallen logs) are thought to create suitable habitat for the northern spotted owl (Hansen et al. 1991). Similar structural attributes also may be found in varying degrees in young forest stands. Age and species composition alone may not be adequate indicators of preferred habitat (C. Meslow, personal communication).

The forest-canopy portion of stand structure is composed of individual tree crowns; canopy architecture is the spatial arrangement of crowns within the total three-dimensional space of the forest. Crown area profiles (also called canopy profiles or foliage height profiles) have been used to describe canopy architecture in many forest studies. In northern hardwoods,

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Table 1. Descriptions of the structurally complex and structurally simple stands used to develop crown area profiles.

	Complex stands					Simple stands		
Stand description	A	B	C	D	E	F	G	H
Species*	DF, IC, pines, tanoak	DF, IC, pines, Pacific madrone	DF, IC, pines, true firs	DF, IC, pines, true firs	DF, IC, black oak	DF	DF, bigleaf maple	DF
Elevation (m)	536	902	1554	1548	853	290	335	1097
Year thinned	1931	1971	1971	None	None	None	1972, 1985	1975
Stand area (ha)	5.8	3.8	7.4	8.1	3.0	6.5	19.5	4.5
No. measurement plots	21	17	24	25	12	16	25	6
Age range (years)	0–300	0–250	0–300	25–300	0–250	39	52	65–85
Tallest tree measured (m)	61.9	56.1	59.4	57.3	44.8	38.1	42.7	41.1
Plot density (trees/ha)‡								
Mean	1574	2296	1087	1085	885	1030	306	183
Range	79–4660	59–6526	59–5624	91–3958	59–6526	37–2296	32–1302	141–240
Plot basal area (m^2/ha)								
Mean	61	52	48	52	49	43	32	34
Range	38–99	37–76	28–79	30–79	15–77	9–67	9–51	28–41
Site index (m @ 50 years)§	27.1	28.0	27.8	31.2	29.2	38.7	39.9	27.4
Stand density index¶								
Mean	510	491	329	296	387	361	227	209
Range	206–618	178–535	129–629	208–605	92–513	35–634	52–392	167–257

Note: Complex stands were being used by northern spotted owls in southwest Oregon. Stands F and G are younger Douglas-fir stands in the Willamette Valley; stand H is in southwest Oregon.

*DF, Douglas-fir; IC, incense-cedar.

‡Includes trees >4.5 ft (1.4 m) tall; excludes seedlings.

§From Hann and Scrivani (1987).

¶From Reineke (1933).

vertical stratification of the canopy is influenced by the relative shade tolerance and growth rates of species (Guldin and Lorimer 1985). In eastern hardwoods, strong relationships were found between profiles and species composition, age structure, and stand development history (Hedman and Binkley 1988). Crown area profiles are expected to differ between Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands with different disturbance histories (McComb et al. 1993).

Ornithologists have studied connections between stand structure and suitability of stands for arboreal wildlife species. Sturman (1968) found that breeding densities of birds in the San Juan Islands of western Washington were correlated with upper story canopy volume. Mannan and Meslow (1984) compared avian communities in different forest structures in northeastern Oregon. Using Sturman's (1968) methods and ocular estimates, they found that live foliage volume by canopy strata differed between old-growth and managed forests.

We developed sampling methodology and analytical techniques to estimate crown areas and crown area profiles; we also developed methods for sampling and quantifying stand-level canopy architecture. Then we tested these methods in structurally complex stands used by northern spotted owls and in structurally simple stands. Our analysis included quantification of multistoried canopy structure through estimation and graphical display of crown volumes as well as profiles of crown area and canopy porosity.

Methods

Study sites

Five structurally complex stands and three structurally simple stands were selected for study (Table 1). The five complex stands were multiaged and had mixed species compositions. All five were active nesting stands for northern spotted owls and were part of a larger study of stand structure and habitat relationships in southwest Oregon. The complex stands were also chosen to represent a range of plant community types, from low-elevation Douglas-fir – tanoak (*Lithocarpus densiflorus* (Hook. & Arn.) Rehd.) to upper elevation mixed conifer. One of the structurally simple stands was in southwest Oregon and the other two were in McDonald–Dunn Research Forest on the edge of the Willamette Valley. The simple stands were not active nesting sites for spotted owls during the study period.

Stands A and B (Table 1) were multicohort, mixed conifer–hardwood stands. Each had emergent, scattered, older trees (typically ≥150-year-old Douglas-fir, sugar pine (*Pinus lambertiana* Dougl.), or ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.)) that were overtopping denser middle and understories of mixed-aged Douglas-fir, pines, true firs (*Abies grandis* (Dougl. ex D. Don) Lindl. – *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr. species complex), and hardwoods. The two *Abies* species form a morphologically variable hybrid type in southwest Oregon (Franklin and Dyrness 1973), which in this paper shall be referred to as true firs. In stand A the hardwoods were principally tanoak, and in stand B the hardwoods were principally Pacific madrone (*Arbutus menziesii* Pursh). Incense-cedar (*Libocedrus decurrens* Torr.) was found in these stands in both the understory and overstory. Limited salvage of dead and fallen wood was done in stand A in the 1930s. Stand B was thinned in 1971; only scattered older trees judged to be at risk were removed. Both stands had moderate infestations of dwarf mistletoe (*Arceuthobium douglasii* Engelm.).

Stands C and D (Table 1) were mixed conifer stands with no appreciable hardwood component. Species included Douglas-fir, true fir, sugar pine, ponderosa pine, and incense-cedar. Ages of individual trees, measured at breast height, ranged from 0 to 350 years. At least three cohorts were evident in stand C: a sparse overstory of large pines over 150 years old; a more heavily stocked, 60- to 150-year-old mixture of all five species; and an understory of 0- to 30-year-old true fir, Douglas-fir, and incense-cedar. Stand D had two cohorts: an older emergent overstory of Douglas-fir, pines, and incense-cedars; and a younger middle story primarily made up of true firs. Stand D had no seedlings in the heavily shaded and sparsely vegetated understory. Stand C had a greater proportion of Douglas-fir and ponderosa pines, while stand D had a greater proportion of true firs. Dead and diseased overstory trees were removed from stand C in 1971. Stand D had not been thinned. Both stands had moderate infestations of dwarf mistletoe.

Stand E (Table 1) was an even-aged 85-year-old stand of Douglas-fir and incense-cedar that had recently overtopped scattered older California black oak (*Quercus kelloggii* Newb.) (100+ years old). Conifers had invaded open oak woodland after frequent, low-intensity fires had been eliminated. Oaks up to 250 years old were the only "old" trees in this stand. Conifer heights and densities varied in this stand as a result of the heterogeneous competition from oak.

Stands F and G (Table 1) were even-aged Douglas-fir plantations in the McDonald–Dunn Research Forest, Oregon, that were selected as examples of structurally simple stands. Stand F was 39 years old and had not been thinned; its basal area was 42.7 m^2/ha. Stand G was 52 years old and had been commercially thinned twice; its basal area was 32.1 m^2/ha. Stand H (Table 1) was an even-aged (65- to 85-year-old) Douglas-fir stand in southwest Oregon that was intensively thinned from below (i.e., trees in smaller diameter classes were removed) 7 years prior to measurement. The basal area after thinning was about 29.8 m^2/ha, and it had increased to 33.7 m^2/ha by the year of measurement.

Sampling methods

A grid of five measurement plots per hectare was established in each southwest Oregon stand using a random starting point and a random plot-line azimuth. Plots were systematically arranged on the grid, with 45 m between plots and plot lines. Similar grids were used in the McDonald–Dunn Research Forest stands, but at intensities of 1.2 to 2.5 plots/ha.

Each measurement plot included a circular subplot with a fixed 2.37-m radius for measuring trees from seedling height to 10.2 cm diameter at breast height (DBH); a concentric circular subplot with a fixed 4.74-m radius for trees 10.2 to 20.3 cm DBH; and a variable radius plot, using a basal area factor of 20, for trees larger than 20.3 cm DBH.

In the five structurally complex stands, A to E, canopy cover measurements were taken on two perpendicular transects of 30.5 m from each plot center, with the first transect oriented to a randomly chosen azimuth. Horizontal length of conifer, hardwood, or sky was recorded, with the tallest tree type taking precedence. Vertical sightings were taken along the transects using a clinometer as an optical plumb. No canopy cover measurements were made in the structurally simple stands, F, G, and H.

In the five structurally complex stands, 2384 trees were measured for DBH, total height, height to crown base, distance and azimuth to plot center, and latest 5-year radial growth rate. A subsample of 468 trees were measured for crown width at crown base and increment cored at breast height for age. This subsample consisted of the first two plot trees encountered in each 5-cm diameter class, by species, in each stand. Tree heights and crown lengths from crown base to tip were determined using the height pole tangent method (Curtis and Bruce 1968). Crown width was determined as the geometric mean of two crown widths measured perpendicular and parallel to a line from plot center through the tree base.

Data analysis methods

Crown area estimation

Using the subsample of 468 trees, we developed an equation to estimate crown width at crown base for unmeasured trees using the following weighted nonlinear regression:

$$[1] \qquad \mathrm{C\widehat{W}CB} = \mathrm{MCW}\ \mathrm{CR}^{x} + \varepsilon$$

$$x = \alpha_1 \mathrm{CL} + \alpha_2 \frac{\mathrm{DBH}}{\mathrm{THT}}$$

where $\mathrm{C\widehat{W}CB}$ is the estimated crown width at crown base (m); MCW is the theoretical maximum crown width (m) (from Paine and Hann 1982); CR is the crown ratio (crown length/total tree height); ε is an error term; α_1 and α_2 are regression coefficients; CL is the crown length (m); DBH is the diameter at breast height (cm); and THT is the total height (m). This adaptation of the form used by Ritchie and Hann (1985) adds additional terms for stem taper. Weighting with theoretical maximum crown width stabilized the variance across the range of tree sizes. Values for α_1 and α_2 by species are given in Table 2.

Crown taper (shape) equations for conifers were derived from Biging and Wensel (1990), who took measurements from 593 felled trees in northern California. The following derived form was used:

$$[2] \qquad \mathrm{C\widehat{W}h} = \mathrm{C\widehat{W}CB}\left[1 - \frac{h - \mathrm{HTCB}}{\mathrm{THT} - \mathrm{HTCB}}\right]^{\beta} + \varepsilon$$

where $\mathrm{C\widehat{W}h}$ is the estimated crown width at a given height (m); h is height above the forest floor (m); and HTCB is the height to crown base (m). $\mathrm{C\widehat{W}CB}$ is the crown width at crown base, measured in the subsample of 468 trees or estimated with eq. 1. Values for β are as follows: Douglas-fir = 0.402 51; incense-cedar = 0.351 19; ponderosa and sugar pines = 0.392 39; and true firs = 0.502 03 (from Biging and Wensel 1990).

Crown taper equations used for hardwoods were semi-ellipsoidal, based on shapes found for urban hardwood trees (McPherson and Rowntree 1988):

$$[3] \qquad \mathrm{C\widehat{W}h} = \mathrm{C\widehat{W}CB}\left[1 - \left(\frac{h - \mathrm{HTCB}}{\mathrm{THT} - \mathrm{HTCB}}\right)^{2}\right]^{1/2}$$

Crown widths derived from eqs. 2 and 3 were used to calculate horizontal cross-sectional crown area, $\pi(\mathrm{CWh}/2)^2$ (in m^2), at 0.3-m height increments from crown base to tip for each tree. For each plot, crown areas at height were then summed across all trees and multiplied by their expansion factors (the number of trees per hectare each sample tree represented).

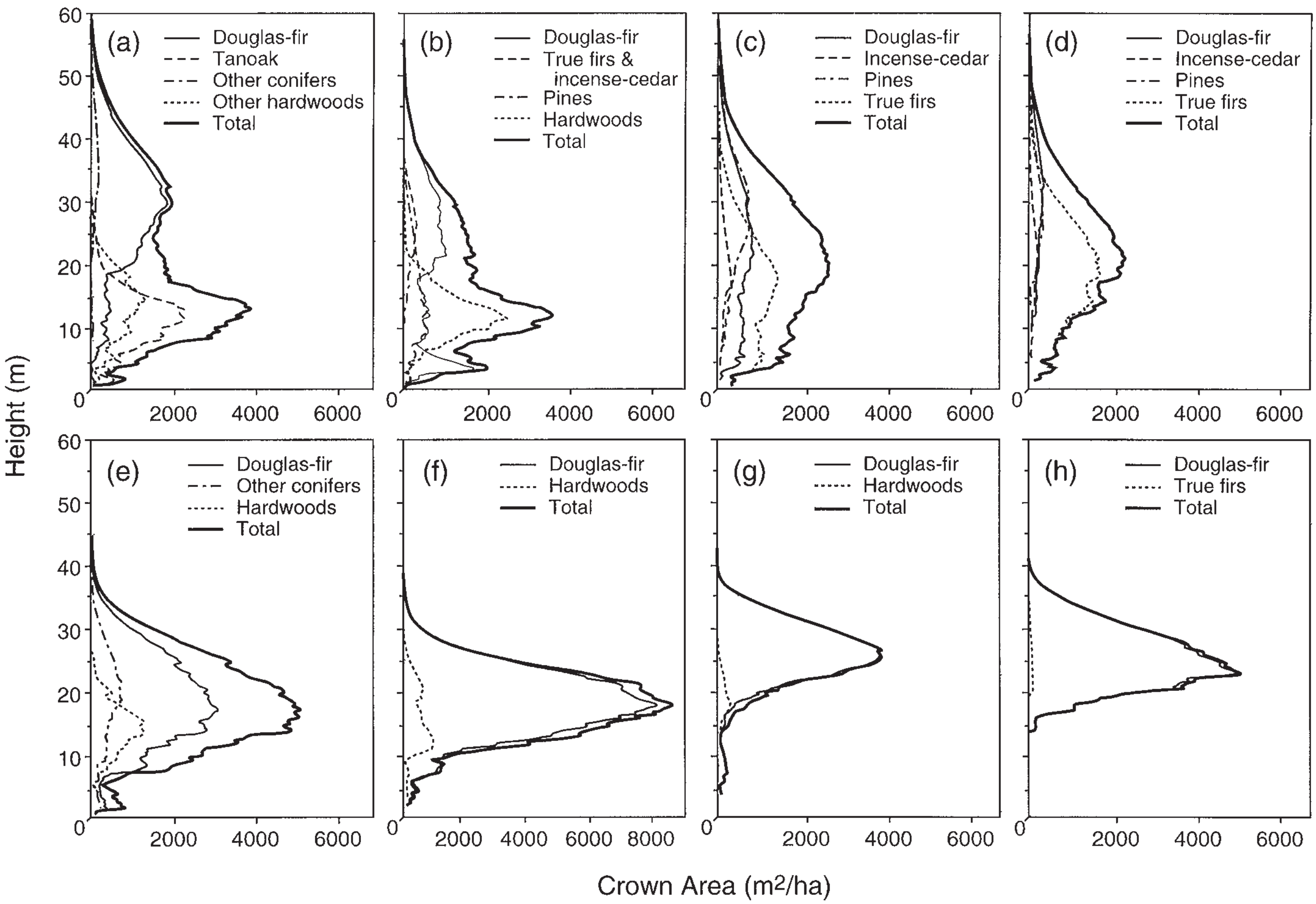
Crown areas at heights (in m^2/ha) may also be expressed as percentages by dividing by 10 000. Crown area percentages

Table 2. Regression coefficients and associated statistics for estimating crown width at crown base.

	No. trees	Crown width (m) Min.	Max.	Mean	α_1	p-value	α_2	p-value	Adjusted R^2
Douglas-fir	152	1.1	17.8	8.2	0.001 733 29	<0.0001	4.554 158	0.026	0.730
Incense-cedar	72	1.9	11.5	6.3	0.002 623 58	<0.0001	0		0.619
Sugar & ponderosa pines	80	3.0	17.5	9.4	0.001 272 21	0.0013	4.381 792	0.046	0.658
True firs	81	1.3	10.2	5.2	0.001 520 58	0.0011	3.339 450	0.085	0.686
Hardwoods	83	0.7	15.9	6.2	0.002 988 09	<0.0001	0		0.453

Note: See text eq. 1 for model form.

Fig. 1. Crown area profiles: mean crown area versus height above the forest floor for stands A to H ((*a*) to (*h*), respectively), by species or species group and total for all species. Note *x*-axis scale change for stand F (Fig. 1*f*).



(of a ha) were used to generate crown area profiles for each sampling plot.

Stand crown volume and stand porosity

Stand crown volumes were calculated as the sum of crown areas at 0.3-m height increments on each tree and expanded to total crown volumes per hectare for each plot; tree crowns were thus modeled as solid objects.

Stand three-dimensional space (in m^3/ha) was calculated as follows:

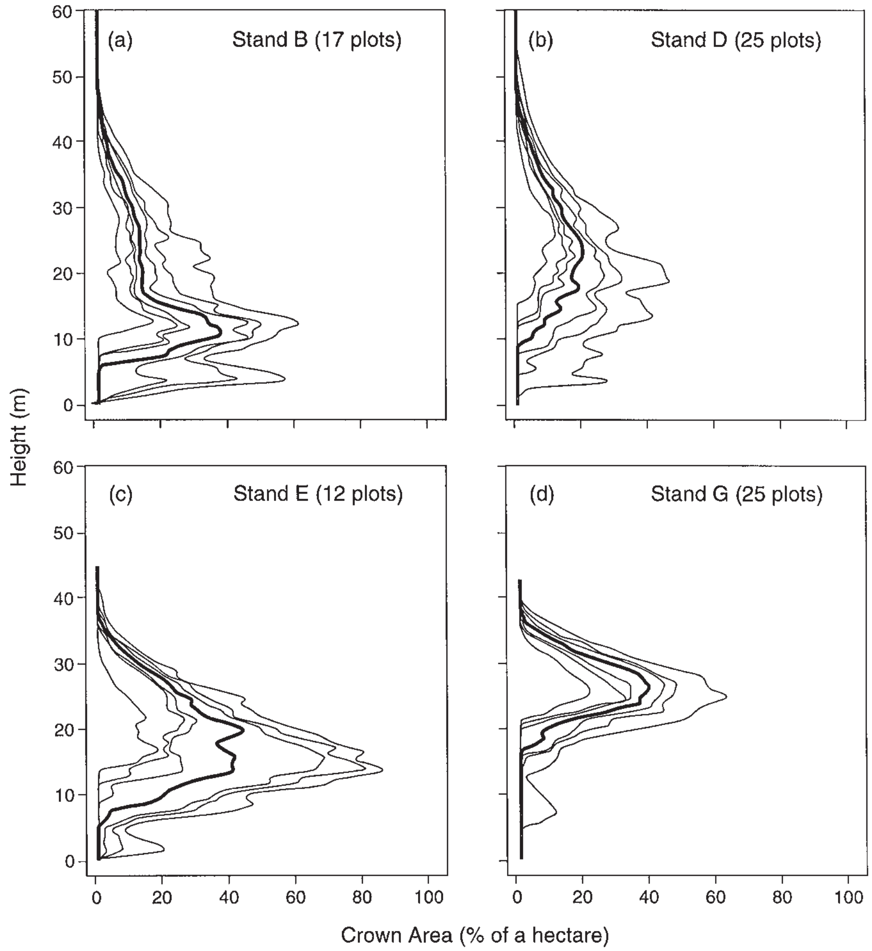
$$\text{[4]} \quad \text{stand space} = (10\,000 \text{ m}^2/\text{ha})\ (\text{stand height})$$

where stand height is the height of the tallest tree measured (m). Porosity of a stand refers to the proportion of void (space between crowns divided by stand space), where that which is not tree crown is void. Porosity was calculated from stand crown volume:

$$\text{[5]} \quad \text{porosity} = \left(1 - \frac{\text{stand crown volume}}{\text{stand space}}\right) \times 100$$

Porosity is thus a proportional measure of a three-dimensional void. Pores in a forest canopy are not isolated, but rather are interconnected capillaries: tubes, tunnels, corridors, or valleys. Trees in a stand have within-crown and between-crown porosity. Only the latter was quantified in this study.

Fig. 2. Density diagrams of crown area profiles: distribution of sample plots with crown area percent at heights above the forest floor for (*a*) stand B, (*b*) stand D, (*c*) stand E, and (*d*) stand G. Lines indicate percentiles of the crown area distributions at heights. The 10th, 25th, 33rd, 50th, 66th, 75th, and 90th percentiles are shown. The dark line is the 50th percentile, or median.



Porosity may also be used in a two-dimensional context, as the area of void per hectare at a given height. In this paper, two-dimensional porosity is called areal porosity:

[6] areal porosity at height h

$$= \left(1 - \frac{\text{stand crown area at height } h}{10\,000 \text{ m}^2/\text{ha}}\right) \times 100$$

The distributions, across stand height, of stand crown area and its proportional inverse, areal porosity, are the numerical foundations of crown area profiles.

Canopy cover percentage

In this report, canopy cover percentage is defined as 100 times the proportion of the area covered by tree crowns as measured at 1.4 m above the forest floor. Tree crowns were treated as entire. This is different from mean crown completeness (Vales and Bunnell 1985), which also takes into account vertical holes within tree crowns.

Results and discussion

Crown area profiles

Crown widths at 0.3-m height increments were used to develop crown area profiles (Fig. 1). These graphical representations of the distribution of stand crown area across stand height are useful in describing individual stands. Similarities between stands with similar canopy architectures are visually evident. Stands A and B both contained multicohort, mixed conifers that were overtopping shade-tolerant hardwoods. Crown area profiles for these two stands are both vertically elongated, and the distributions approach bimodality across height. Both have distinctive peaks at 10 to 12 m, reflecting the large crown areas of the hardwood canopy at that height, and less distinctive peaks at 23 to 30 m, where conifer crowns overtop the shade-tolerant hardwoods (Fig. 1).

Stands C and D (Fig. 1) were both multicohort, mixed conifer stands at upper elevations. Both crown area profiles are vertically elongated with significant crown area between 6 and 36 m. Both profiles peak at about 20 m, reflecting tall heights to crown base for many trees in the stand (Fig. 1). Crowns on understory trees contributed significantly to the canopy architecture in both of these stands, though not to the extent that hardwoods added structure in stands A and B.

Stands E to H were shorter stands without cohorts of emergent older trees. Their profiles show a distinct lack of vertical elongation (Fig. 1), which reflects shorter and roughly similar

Table 3. Porosity and crown area statistics for the eight stands used in this study.

	Complex stands					Simple stands		
	A	B	C	D	E	F	G	H
Mean crown area (m^2)	563	482	506	384	732	1250	453	591
Total crown vol.								
Mean (m^3/ha × 10^3)*	14.12	10.90	12.19	8.92	13.26	19.24	7.83	9.86
SD (m^3/ha × 10^3)*	4.06	3.27	3.91	2.41	5.89	7.02	2.03	1.08
Coefficient of variation	0.29	0.30	0.32	0.27	0.44	0.37	0.26	0.11
Total porosity (%)								
Mean	86.1	88.1	87.5	90.5	81.9	69.1	78.8	85.4
SD	4.01	3.53	4.00	2.57	8.03	11.30	2.90	1.59
Min. mean areal porosity (%)	59.2	62.0	72.1	79.3	51.9	6.8	58	45.3
Ht. at min. mean areal porosity (m)	12.8	12.2	19.2	21.0	15.5	17.1	26.5	22.9
Vertical canopy extent with 70–90% mean areal porosity (m)	30.2	25.3	33.2	23.5	11.6	7.3	7.9	7.6
Height variances (m^2)								
Tree height within plots	55.2	37.9	57.0	59.1	80.9	36.4	27.7	7.4
Tree height between plots(× 10^3)*	10.6	16.3	15.6	15.0	12.4	8.5	5.5	0.1
Crown area variances (m^4 × 10^3)*								
Between heights	193.3	174.1	160.1	108.4	442.7	1731.2	316.1	529.2
Within heights	365.2	236.3	211.1	158.4	505.0	1727.9	159.0	44.6
Canopy cover (%)								
Conifers	40.3	43.3	68.8	86.1	75.1			
Hardwoods	56.3	42.1	0	0	11.4			
Sky	3.4	14.6	31.2	13.9	13.5			

Note: See Table 1 for full description of each stand.
*To obtain actual values, multiply each entry by 10^3.

heights and heights to crown base for most trees within each stand.

The oak component and suppressed conifer understory in stand E added some canopy at heights below 10 m. As this stand developed, conifer height growth rates varied because of uneven competition from the oak overstory. Therefore, the crown area profile is intermediate in shape between the complex and simple stands measured in this study (Fig. 1).

The largest crown areas in this study were found in the youngest stand, stand F, which was 39 years old, even aged, and unthinned. The crown area profile reached maximum crown area at 17.4 m and declined rapidly above and below this height (Fig. 1). At some heights, the horizontal crown area percentages on 17 of the 146 plots in this study exceeded 100%, because crowns intertwine in dense forests. Fourteen of these 17 plots occurred in stand F. The perimeters of crowns were measured to the tips of the branches, but on some trees branch tips may terminate inside the crowns of adjacent trees. Field measurements and subsequent calculations assumed tree crowns were entire and not intertwined. For this reason, stand crown areas were somewhat overestimated, and between-crown space was underestimated. However, field observations indicated that intertwining was slight in most of the stands investigated, perhaps due to the relatively xeric environment of interior southwest Oregon.

Stand G, the 52-year-old, even-aged, thinned stand in the Willamette Valley, exhibited the smallest crown areas of all those studied. As in stand F, the crown area profile peaked strongly, but at a taller height of 26.8 m (Fig. 1). Age and site differences must account for some of the difference in peak crown area heights between stands F and G, but selective removal of shorter trees during thinning in stand G is hypothesized to be the principal causative factor. Scattered bigleaf maple (*Acer macrophyllum* Pursh) added some canopy structure in stand G at heights below 12 m.

The thinning from below in stand H left nearly identically sized trees, increased the stand uniformity, and eliminated most of the canopy below 15 m. Of all the stands studied, stand H exhibited the least plot to plot canopy variation. The crown area profile peaked strongly at 23.2 m (Fig. 1).

Height variances and plot distribution diagrams

Variances of tree heights express vertical heterogeneity in forest canopies. Variances of crown areas between heights also express vertical heterogeneity. These variances are given in Table 3. The tree height variances indicate that the complex stands had large within-plot and between-plot heterogeneity relative to the simple stands. However, variances in crown area (see Table 3) indicate that the between-height (vertical) variation in crown area was lower in complex stands A to D than in the other stands.

The plot distribution diagrams for the crown area profiles of four representative stands (Fig. 2) add plot to plot diversity to the crown area profiles shown in Fig. 1. The four stands displayed in Fig. 2 were chosen to represent diverse canopy structures: stand B, conifer–hardwood; stand D, mixed conifer; stand E, conifer overtopping oak; and stand G, young single-cohort Douglas-fir. The plot distribution diagrams of two complex stands, B and D, show a similar range of crown area percentages by plot across the horizontal scale (within

Fig. 3. Mean areal porosity versus height above the forest floor for stands A to H ((*a*) to (*h*), respectively). Vertical lines outline the range of 70% to 90% mean areal porosity.

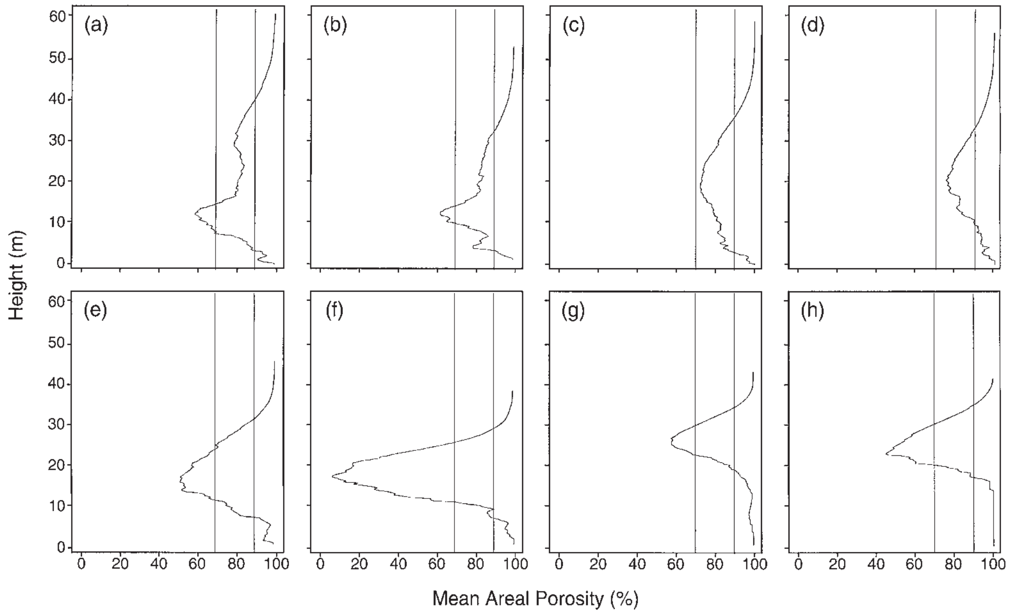
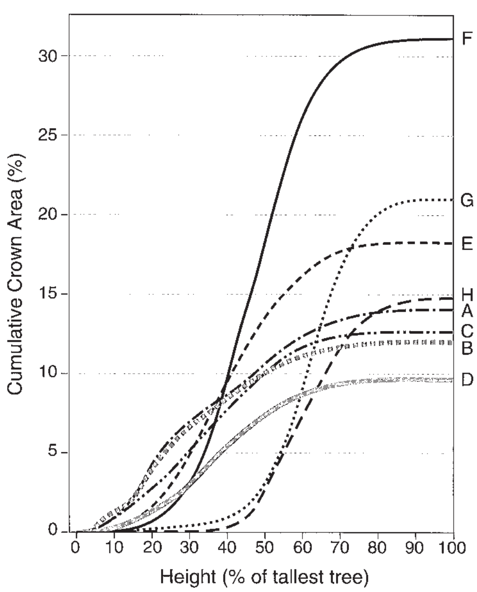


Fig. 4. Cumulative crown area versus height above the forest floor for all species in stands A to H. These functions are equivalent to crown volume below a height expressed as a percentage of the total stand space below that height.



height), but less variation across the vertical scale (between heights) in comparison to stand G.

Stand crown volume and porosity

Mean stand crown volumes per hectare for each stand and their standard deviations are given in Table 3. No clear differentiation between complex and simple stands was evident. Complex mixed conifer–hardwood stands, complex mixed conifer stands, and simple even-aged monospecific conifer stands may have similar stand crown volumes. Stand crown volume may reach maximum values at relatively young ages and remain roughly constant thereafter (Assmann 1970). The largest crown volumes per hectare were found in stand F, which was also the youngest stand; the smallest crown volumes per hectare were found in stand G, which also had the lowest basal area (Table 3). However, for the stands studied, neither age nor basal area was significantly correlated with crown volume.

Total stand porosity means (across plots) and standard deviations are given in Table 3. Again, no clean differentiation between complex and simple stands was evident using this single stand parameter.

Mean areal porosity at heights above the forest floor are shown in Fig. 3. Heights of minimum areal porosity for each stand, the height at which the canopy reaches its maximum closure, are given in Table 3. Also shown in Fig. 3 are vertical grid lines at 70% and 90% areal porosity (roughly the range of mean total stand porosities encountered). The vertical height of canopy with areal porosities in the 70% to 90% range (Table 3) indicates the degree of uniformity within the vertical distribution of pore space.

The distribution of areal porosity across heights was more uniform in the complex stands than in the simple stands (Fig. 3). Four complex stands, A to D, exhibited horizontal crown areas of 1000 to 3000 m^2/ha for approximately 30 m of canopy. This means that for about 24 to 33 m of vertical height, these four stands had 70% to 90% areal porosities (Table 3 and Fig. 3). In contrast, stands F to H had only about 7.6 m of vertical canopy with areal porosities in the 70% to 90% range. Stand E was again intermediate, with 11.6 m of vertical extent in that range. Thus stands A to D had more uniform areal porosity across a longer vertical reach of canopy in comparison to stands E to H. In stands A to D, the forest space was moderately occupied by crowns from the forest floor up to heights over 40 m, producing uniform distributions of between-crown pores.

Cumulative crown area from the ground up was plotted for each stand against height (of the tallest tree measured in that stand) in Fig. 4. The terminus of the plotted lines at the right-hand *y*-axis is the total crown volume percentage of each stand. The total porosity (between crowns) of each stand is 100% minus its terminal value in Fig. 4. This corresponds to the mean total porosity given in Table 3.

Uniform porosity across heights in complex stands is illustrated by the cumulative crown areas in Fig. 4. Stands A to D showed relatively uniform accumulating crown area with increasing heights. This indicates that stands A to D had many medium-sized pores across a wide vertical range. In contrast, stands E to H showed stronger sigmoidal curves. The latter four stands accumulated little crown area near the forest floor and then gained crown area rapidly above crown base heights. Below the crown bases in stands E to H, the forest space was relatively open, occupied only by columnar stems. The foliage was dense at the homologous crown base height, and the canopy was open to the sky at heights a few feet above crown base. In stand F, pores between crowns were large near the forest floor, small from 10 to 20 m, and large again above 20 m.

Canopy cover percentage

Canopy cover was measured in the five complex stands. No trend in canopy cover percentage was evident (Table 3). The percentage of the ground covered by tree crowns may be identical in short and tall stands, even though the crown volumes and porosities of the canopies may differ widely.

Conclusions

Crown area profiles are tools that may be useful in comparing stands and describing wildlife habitat. The objective methods discussed in this paper allow one to quantify canopy characteristics such as crown volume and porosity through their horizontal and vertical distributions.

The stands in this observational case study were not randomly selected, and inferences should not be extended beyond those stands. However, within this set, it is clear that the complex stands had taller and more uniform vertical distributions of canopy than did the structurally simple stands. Further comparisons of randomly selected stands using the methods described may yield insights into the behavior and habitat preferences of birds and arboreal mammals. Large forest birds that live primarily within the canopy, such as northern spotted owls, may use medium-sized between-crown pores as flyways. Canopy conditions that provide access to prey through aerial “tubes,” and also provide overtopping protection from larger predators, may be correlated with the use of such stands by spotted owls. That is, stands with pores that are relatively permeable to spotted owls but not to their predators may be preferred habitat. Stands that are not easily permeable to spotted owls, or that are equally permeable to their predators, may not be preferred habitat.

Further investigation of canopy porosity, both within and between crowns, may provide additional insights into niche selection by arboreal animals. Coupling the methods described in this paper with forest growth and yield models may improve analyses of the changes in the canopy as stands develop and aid prediction of the effects of proposed silvicultural treatments on canopy architecture.

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