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Modeling canopy structure and heterogeneity across scales: From crowns to canopy

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Abstract

Canopy studies have been limited in ecological investigations due to problems of canopy accessibility, and the lack of efficient sampling and modeling methods. The primary objective of this study was to develop an efficient modeling approach to describe the 3-dimensional, hierarchical structure of individual crown shells within stands and corresponding canopy patches. Crown shells were modeled based on crown ratio, maximum cardinal radius, vertical position, and shape. Canopies were represented by adding unique crowns to simulated point patterns of trees of known aggregation as measured by Pielou's index of nonrandomness. Canopy patches were delineated at multiple horizontal and vertical scales using the ARC/INFO geographic information system (GIS). The patterns of canopy patches are clearly variable and scale dependent. Canopy patterns become more diverse at broader horizontal scales, and change greatly from the lower to the upper canopies. The modeling approach used in this study has general utility in characterizing 3-dimensional canopies of many types of forests. © 1997 Elsevier Science B.V.

Keywords: Crown; Canopy; Simulation; GIS; Scale; Spatial pattern

1. Introduction

Canopy architecture reflects the summation of growth (branch and foliage development), resource competition (e.g., for light, space), and disturbance processes (e.g., blowdown, fire) sustained over the life of a forest. As the upper interface between forests and the atmosphere, forest canopies receive and release energy through photosynthesis, respiration, and evapotranspiration. Furthermore, canopies buffer the forest interior from external disturbances. Various studies have suggested that canopy structure is one of the key variables influencing many forest ecosystem structures and functions, such as spatial heterogeneity and temporal dynamics of understory vegetation, patterns in regeneration mosaics, and microclimatic variation (Spies and Franklin, 1989; Nadkarni and Longino, 1990; Runkle, 1991; Chen and Franklin, 1996). The complexity and dynamics of forest canopies have a direct influence on the overall structure and function of an ecosystem (Schowalter, 1988; Norman and Campbell, 1989; Parker et al.,

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1992). As such, understanding the form and development of canopy architecture will lead to an improved understanding of forest ecosystem properties.

Despite their critical ecological role, our knowledge of forest canopies has advanced slowly relative to other areas of forest ecology. Current understanding is far from adequate, not only because of access problems, but also because of the requisite volume of primary data that must be collected and analyzed (Parker et al., 1992). Because forest canopies are composed of multiple crowns, a logical approach to studying their structure is to observe all crowns, including their spatial position, size, and shape. This type of approach was suggested and used by Horn (1971), Norman and Campbell (1989), and Koop (1989) with field mapping of tree architecture at small scales. Using architectural analysis, these researchers successfully provided insight into a number of phenomena, including growth phases, stand vigor, and the effects of perturbation. However, these researchers did not perform quantitative analyses, probably because of limited techniques and tools. Geostatistics and geographic information systems (GIS) allow researchers to: (1) show canopy structures at different scales, both horizontally and vertically, and (2) analyze how canopy structure and composition change at different scales by combining the information database using GIS.

The goal of this study was to develop an efficient modeling approach to quantify the 3-dimensional structure of a canopy by: (1) developing a 3-D model of crown shells; (2) simulating a canopy by adding unique crowns to a simulated point pattern of trees of known aggregation; and (3) examining, using GIS, the hierarchically patterned, vertical and horizontal canopy structure generated from the model. Studying forest canopies by modeling crown size, shape, and location at various spatial scales is accurate and efficient. This approach could be developed further to link with other ecological models to study the relationship between 3-dimensional canopy structure and other ecosystem processes.

2. Modeling approach

Forest canopies were modeled and analyzed by simulating spatial point patterns of stems and constructing 3-dimensional crown shells for a number of predefined sub-populations (defined in this study as a group of stems of the same species). Necessary input variables include stand density, species composition, diameter distribution of each species, spatial patterns of stems, and crown shapes and dimensions (Fig. 1).

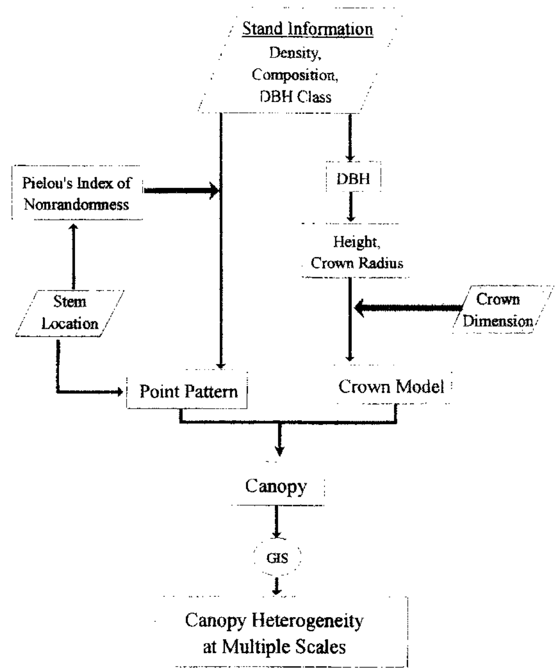


Fig. 1. Flow chart for the modeling process. The input includes stand information, a set of tree location data to estimate Pielou's index of nonrandomness, and the crown information. The modeling output is then used as an input for GIS (we use ARC/INFO) to analyze the canopy heterogeneity at multiple scales.

2.1. Point pattern and diameter distribution

There are numerous highly developed methods for simulating spatial point patterns (Daniels et al., 1979; Diggle, 1983; Moeur, 1993). In this study we utilize an approach that takes a flexible, generalized distribution function which includes different generating processes such as random, clustered, and uniform. The parameters needed for the function are chosen to generate various spatial patterns. An index of nonrandomness (Pielou, 1959) was used in this study:

$$\alpha = c\bar{x} \quad (1)$$

where $\bar{x}$ is the mean squared distance between a random point and a target stem, c is the density parameter expressed as the average number of stems per circle of a unit radius. The population is claimed to have a random [when $\alpha = (n-1)/n$], aggregated [when $\alpha > (n-1)/n$], or uniform [when $\alpha < (n-1)/n$] distribution, where n is the number of distances measured.

Daniels et al. (1979) used the Pearson type XI distribution as the basis for generating patterns of known aggregation, as measured by Pielou's index of nonrandomness. The cumulative density function of the Pearson type XI distribution is:

$$F_x(x) = 1 - \left(1 + \frac{c}{k}x\right)^{-k} \quad (2)$$

where k is a heterogeneity parameter that may be estimated by Pielou's index of nonrandomness:

$$k = \alpha/(\alpha - 1)$$

The squared distances from random points to nearest trees were then simulated by the following equation:

$$x = \frac{k}{c}\left[(1-u)^{-1/k} - 1\right] \quad (3)$$

where u is a random number from a uniform [0,1] distribution.

Trees are located on the perimeters of a series of nonoverlapping circles with radii $r = x^{1/2}$ centered on the random points. Actual coordinates of the trees are determined by fixing their positions on the circumference of the generated circles and their angles (θ) from the random points (Fig. 2). The point pattern generated by this approach is random, clustered, or uniform according to different combinations of c and α values.

We calculated α values based on field data from a spruce-fir forest. Detailed field sampling of this spruce-fir forest was conducted in a 100 m × 200 m plot by Chen (1986) at the Changbaishan Natural Reserve (CNR) which is on the slope of a dormant volcano in northeast China (42°01′ N and 128°05′ E). The spruce-fir forest is about 250 years old, and is typical of those commonly found in high elevation areas of the west Pacific Crest, between 1100 and 1700 m elevation in the CNR. Annual precipitation in the area is 600–900 mm. Greater than 60% of the yearly rainfall occurs in summer (June–August). Average annual temperature is −7.3–4.9°C. Soils are mountain brown coniferous soil. The dominant tree species include white spruce (*Picea jezeoensis*), fir (*Abies nephroleptis*), and birch (*Betula ermanii*). Other common species are larch (*Larix olgensis*), mountain ash (*Sorbus pohuashanensis*), and several maple species (*Acer spp.*). Data collected in Chen's study included a stem map of all trees > 6 cm in diameter at breast height (DBH), species, height, crown ratio, and crown radius in each of 4 cardinal directions for individual trees. Chen and Bradshaw (1996) concluded that there were unique point patterns for different size classes and species of trees.

In this study, the α values in Eq. (1) were calculated based on these data for each sub-population (3 evenly divided DBH classes for spruce, and 2 evenly divided classes for other species groups). We assumed that the point patterns of each sub-population were independent of each other.

The Weibull function was used to simulate diameter distributions and to compute the number of stems for each DBH class. The cumulative density function of the Weibull distribution is:

$$F(\mathrm{DBH}) = 1 - e^{-((\mathrm{DBH}-a)/b)^c} \quad (4)$$

where a is the smallest tree diameter in the stand, b is the scaling parameter that ensures 63% of the tree diameters are between 'a' and 'b', and c is the shape parameter of the function (Arvanitis and Reich, 1991). The a, b, and c parameters were estimated based on Chen's field data (Fig. 3). Individual tree size (DBH) was assigned by the following equation:

$$DBH = a + b[-\ln(1-u)]^{1/c} \quad (5)$$

when $u \approx u(0,1)$.

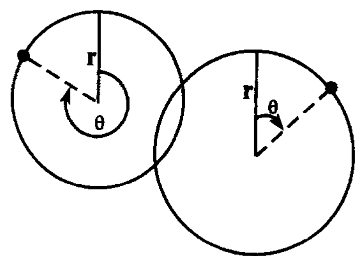


Fig. 2. Determinations of tree positions were made by fixing distances (r) and the azimuth (θ) from random points which are the center of circles. Points on the perimeters of circles represent trees (modified from Daniels et al., 1979).

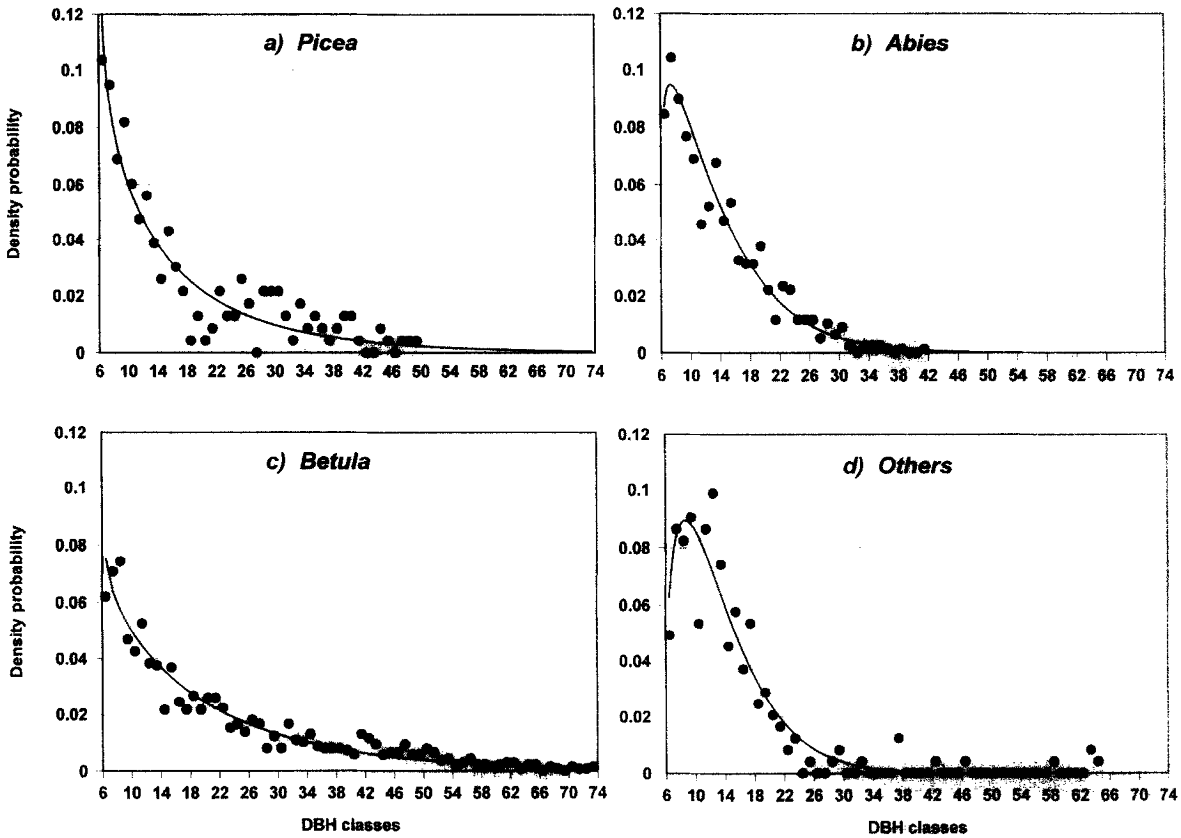


Fig. 3. Simulated DBH distributions of four species using a Weibull function. The data were collected by Chen in an old-growth spruce-fir forest at the Changbai Mountain Biosphere Reserve (42°01′N and 128°05′E) in northeast China. The parameter values are listed in Table 1.

2.2. Crown shell

A canopy is composed of a set of crowns of individual trees. Three-dimensional canopies are characterized by first constructing individual crown shells. We simulated a crown shell by modeling the vertical shape of a crown in four cardinal directions, and by developing a continuous elliptical cross-section from crown base to top. The crown shell model in this study was simplified by assuming that: (a) all trees have upright stems; and (b) the are maximum radii are only at cardinal directions. In reality, there are tree crowns with large vertical gaps between branches which were not represented explicitly in the model. Different shapes and vertically asymmetric profiles, based on the four cardinal directions, were modeled by modifying the equation of crown shell proposed by Horn (1971):

$$\left(\frac{l_i - Z}{l_i}\right)^{e_{1i}} + \left(\frac{r_i}{R_i}\right)^{e_{1i}} = 1 \text{ when } Z \le l_i \quad (6)$$

$$\left(\frac{Z - l_i}{L_i - l_i}\right)^{e_{2i}} + \left(\frac{r_i}{R_i}\right)^{e_{2i}} = 1 \text{ when } Z > l_i \quad (7)$$

where R_i is the maximum crown radius at direction i ($i = 1$, 2, 3, and 4 corresponding to east, north, west, and south, respectively), L_i is the crown length at direction i, l_i is the length at direction i from tree top to the vertical position at which R_i was found, r_i is the crown radius along direction i at any height, Z is the length from tree top to the vertical position at

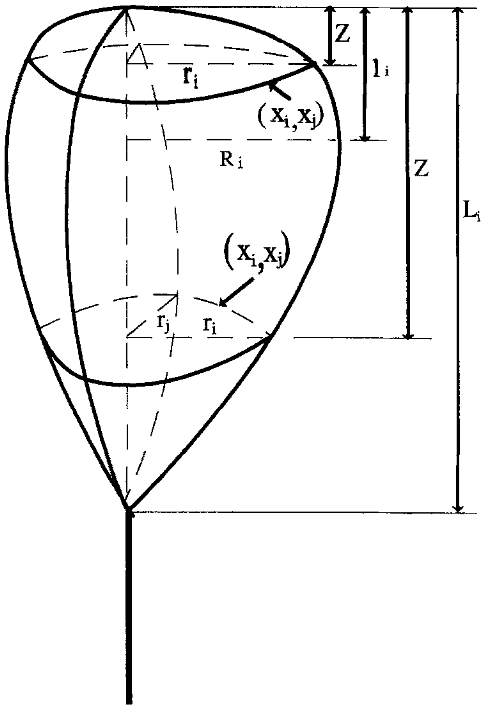


Fig. 4. Parameters and variables used in the crown shell model in a 3-dimensional view of crown architecture.

which r_i was found, and e_{1i} and e_{2i} are the shape parameters at direction i controlling the vertical changes in radius (Figs. 4 and 5).

Four vertical profiles were transversely crosscut at various vertical heights to generate a set of transverse, smooth asymmetry-round-shape polygons that consist of four truncated ellipses, using elliptical equations:

$$\left(\frac{x_i}{r_i}\right)^2 + \left(\frac{x_j}{r_j}\right)^2 = 1 \quad (8)$$

where (x_i, x_j) is the coordinate point on the crown shell at level Z, and r_i, r_j are the cardinal radii perpendicular to each other. Both i and j represent four cardinal directions ($i = 1, 2, 3$ and 4; $j = 1, 2, 3$ and 4, respectively, yet $i \neq j$ in Eq. (8) (Fig. 4). The values of r_i and r_j were derived from Eqs. (6) and (7). Data describing crown polygons at different heights for different species and/or size classes were generated and imported to an ARC/INFO GIS system to explore 3-dimensional canopies and analyze spatial heterogeneity across the stand. To simplify the simulation, we took the averages for the four cardinal measurements, thus the four cardinal curves of Eqs. (6) and (7) are assumed to be the same in this paper.

2.3. Parameter estimation

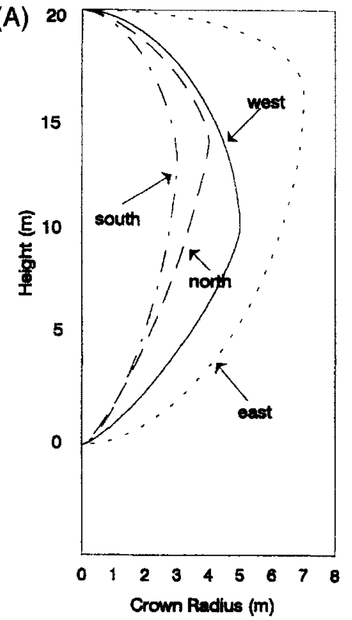
The stand information collected by Chen (1986) in an old-growth spruce-fir forest was used to estimate the parameters needed for the model (i.e., Eqs. (1)–(7)), including: stand density, species composition, diameter distribution, Pielou's index of non-randomness, DBH-height relationship by species, crown ratio by species, and DBH-crown radius relationships (Table 1). Linear and nonlinear regression models were applied using SAS to predict tree height and crown radii by species, using an exponential equation (Chen, 1986), and diameter distribution us-

Table 1
Stand information for simulation and parameters used for model input in a 9 ha Spruce-fir forest

Species	Spruce	Fir	Birch	Others
Stand information				
Density (tree/ha)	947.5	184.2	105.3	79.0
Composition (%)	53.0	29.0	9.0	9.0
DBH				
Minimum (cm)	6.0	6.0	6.0	6.0
Maximum (cm)	74.0	42.0	50.0	64.7
b^*	15.2783	8.2151	10.8735	8.2112
c^*	0.9350	1.1364	0.8612	1.2998
Pielou's index (α)				
DBH class 1	1.151	1.225	2.119	1.592
DBH class 2	1.501	2.376	1.758	1.571
DBH class 3	1.214			
Crown				
Crown ratio	0.74	0.85	0.78	0.68
MRL/Crown length	0.70	0.66	0.33	0.50
e_1^*	1.2	1.5	3.0	2.0
e_2^*	3.0	3.0	1.5	2.0

b^* and c^*: Weibull function parameters.
MRL*: The length from the tree top to where maximum crown radius occurs.
e_1^* and e_2^*: Shape parameters for upper and lower crown shells, respectively.

(A)



Parameters used for simulation of the 3-D crown shell

	East	North	West	South
l_i (m)	4	6	10	7
L_i (m)	20	20	20	20
R_i (m)	7	4	5	3
e_1	2.2	1.5	1.8	1.7
e_2	1.8	1.3	1.3	1.5

(B)

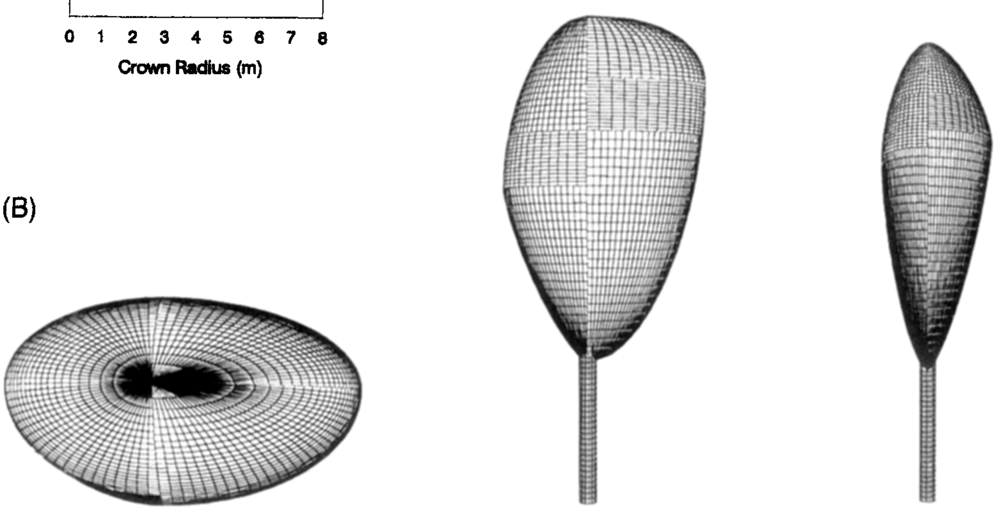


Fig. 5. 3-Dimensional crown architecture from the crown shell model. The table in this figure shows the parameters which are used to obtain the crown shell as in (A) and (B). (A) shows the different shapes of crown shell curves at cardinal directions and (B) shows that the crown shell is asymmetric.

ing a Weibull function (Eq. (5)). Model parameters were independently estimated for four species groups: spruce, fir, birch, and all others. The model was designed to take flexible inputs of plot size, number of species and size classes (i.e., sub-populations), and other parameters included in Table 1. The outputs are a series of ASCII files containing crown projections or cross-section data for GIS analysis by species, diameter, or height. In this study, we simulated a 300 m × 300 m (9 ha) stand based on these parameters (Table 1). The size was selected to mimic a small harvesting unit in forestry practice (i.e., ca. 22 acres).

2.4. Generation of 3-dimensional canopies

An ARC/INFO polygon coverage was imported from the ASCII files for each sub-population. The 3-dimensional structure of a forest canopy was expressed as a series of canopy projections or cross-section maps (i.e., 2-D) from the bottom to the top of the canopy, including 9 projection coverages of plane view (one for each sub-population) and 45 cross-section coverages at 5 heights above the ground: 2, 6, 10, 14, 18 m. The advantages of using GIS are that canopy patches can be viewed and summarized by overlaying two or more coverages to generate new information on canopies (e.g., canopy gaps).

Five grid coverages with grain sizes of 4, 16, 64, 256 and 1024 were also generated to explore scale changes in canopies in this 9 ha plot. These grid coverages were then overlaid with canopy coverages to examine the changes in canopy characteristics across multiple grid sizes (i.e., scaling). Canopy gaps, defined as areas not occupied by crowns, were selected in an INFO database to describe the spatial distribution of gaps within the stand. We examined the effects of stand density and stem distribution on both the number of canopy patches occupied by tree crowns of different species and the sizes of canopy coverages at different spatial resolutions and heights.

The Shannon index (H') is a reliable measurement for system diversity (i.e., canopy structural diversity) (Turner and Ruscher, 1988). In this study, we calculated H' as:

$$H' = -\Sigma p_i \ln p_i \quad (9)$$

where p_i is the proportion of the total canopy coverage that is in sub-population i. Higher H' values indicate greater diversity of the composition of canopy patches in the cell. Means and standard deviations were calculated for each grid size and plotted against size to explore the changes in canopy heterogeneity with grid sizes.

3. Model applications

We compared the total gap area of the simulated and actual stands only because the computer generated stand (9 ha) is larger than the field sampling stand (2 ha). The proportion of the simulated stand in canopy gaps is 19.58% as compared to 19.60% for the actual stand.

3.1. Horizontal patterns

There are physical connections among tree crowns over a very large area of the canopy (Fig. 6). Calculations from the database generated from ARC/INFO

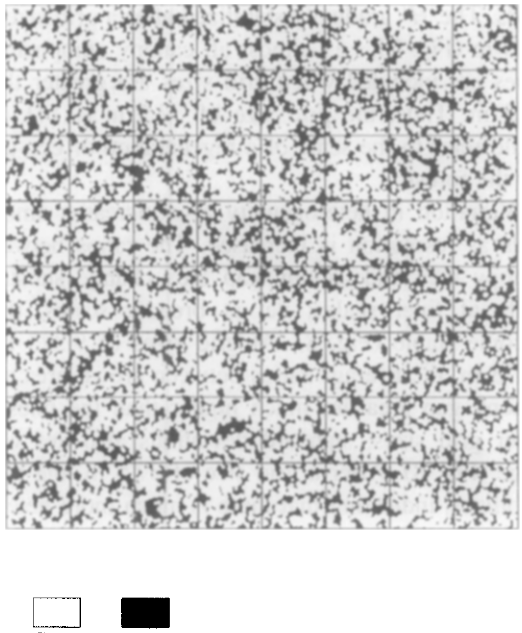


Fig. 6. Simulated canopy projection of a stand of 9 ha. The grid in the figure has a cell size 37.5 m. It can be seen that canopy and gap patches are different at different grid sizes. Sometimes the crown is connected, and sometimes we could see nested crowns within large gaps.

showed that, within the 9 ha (300 m × 300 m) stand, about 78.9% of canopy area is connected. Thus the number of canopy gap patches (1002) is much greater than the number of canopy patches (104). Except for one large canopy patch, all canopy patches seemed to be nested within canopy gaps. Moreover, canopy gaps are also connected and cover very large areas (up to 356 m^2). The ratio of canopy area to gap area is 4.11.

We used the Shannon index to demonstrate the diversity of the canopy (Eq. (9)). The canopy composition was more diverse at broader scales (Fig. 7). Finer scales may include only one crown type or canopy gap; as the grid size increases, the number of crown types increases until all types are included. Because the crown composition changed dramatically among cells at the finer scales, the standard deviation of the Shannon index was much larger at finer scales than at the broader scales. Canopy composition stabilized at broader scales and there was little difference in the canopy composition among grids. The H' gradually stabilized after a grid size of 37.5 m (Fig. 7), i.e., almost all canopy composition types are included when grid sizes are greater than 37.5 m. Thus, the grid size of 37.5 m (0.141 ha) could refer to the scale of a regeneration or eco-unit for the forest.

Variation in heterogeneity also increases among cells as resolution is increased. The ratios between canopy area and canopy gap area change substantially at finer scales; yet at broader scales, they become stable (Fig. 8). At grid sizes of 9.375 and 18.75 m, the average ratios between crown area and canopy gap area are much higher than the ones at other grid sizes; standard deviations also are very large (Fig. 8). After a grid size of 37.5 m, the ratio stabilizes, indicating that there is much more heterogeneity when comparing patch changes at finer scales.

The structure of canopy patches and canopy gap patches is mainly affected by: (a) the density of trees; (b) tree locations; (c) the species composition; and (d) the shape and size of the crown. Because there is higher heterogeneity at finer scales, we used the smallest grid size (9.375 m) to analyze how these factors affect canopy patches. At a grid size of 9.375 m, the average tree density is 11.6 trees per grid, with a range of 5 to 20. At this grid size, tree density was the main factor affecting canopy patch size and the number of canopy patches, i.e., the greater the number of trees, the larger the canopy area (Fig. 9A), yet there was a smaller number of canopy patches (Fig. 9B) because the trees are highly connected. When tree densities are the same or similar, the spatial pattern of trees affects the number and size of canopy patches (Fig. 9A–B). When tree density is low and trees are clustered, canopy area is large within the grid. Yet when tree density is high and trees are clustered, the canopy area within each grid decreases (Fig. 9A). When tree density is low, the spatial pattern of trees greatly affects the number of canopy patches; yet when density is high, there are no obvious effects of spatial patterns on the number of canopy patches (Fig. 9B).

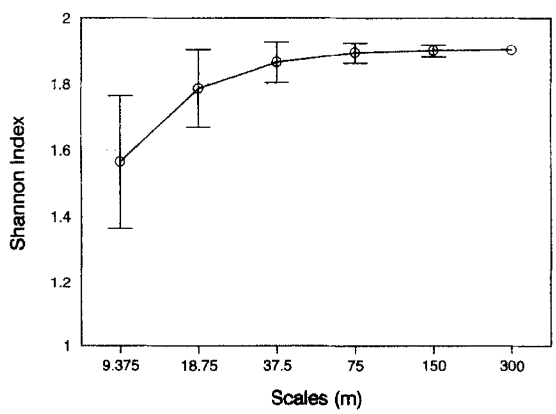


Fig. 7. The diversity of the canopy composition at different grid sizes, calculated using the Shannon index. Circles are the average value of Shannon indices at different grid sizes. Bars are the standard deviations of Shannon indices at different grid sizes.

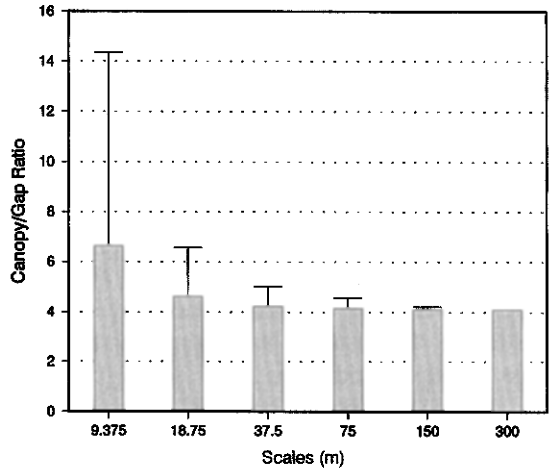
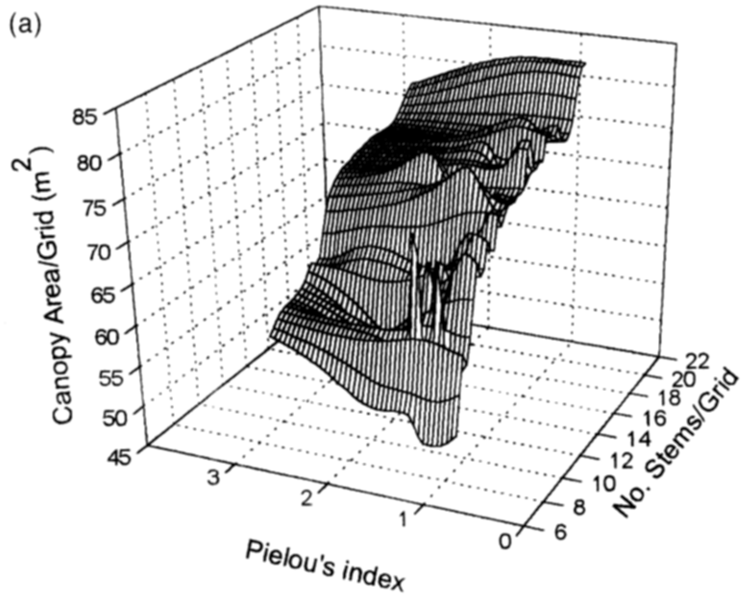


Fig. 8. The average and the standard deviation of the ratio between canopy and gap areas at different grid sizes. The line bars show that the canopy patch structures change dramatically at finer scale.

3.2. Vertical changes

Crown intersections at tree heights of 2, 6, 10, 14 and 18 m are shown in Fig. 10. Species composition and the structure of canopy patches differ significantly between the lower and higher parts of crowns. In addition, the number of species and the size of the crowns decrease dramatically at both the lowest and greatest heights. At 18 m, there is only one species, spruce (Fig. 10). Yet at mid canopy height (6–10 m), species composition is much more diverse, and the



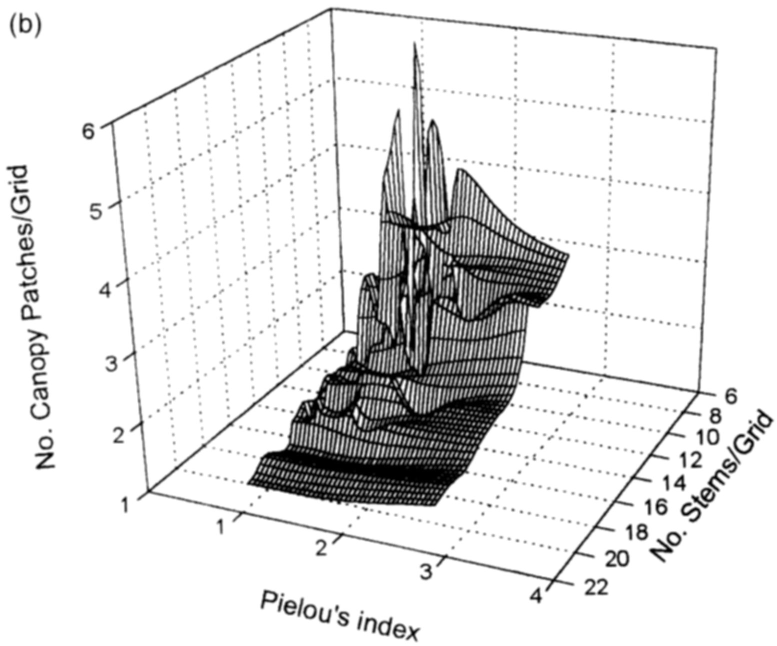


Fig. 9. To see how the canopy size and the density in each grid are affected by the density of trees and Pielou index. (A) The relationship between canopy area within each grid, Pielou index (α), and the number of trees within each grid. When $\alpha = 1$, trees are randomly distributed, when $\alpha > 1$, trees are clustered, and when $\alpha < 1$, trees are uniformly distributed. (B) The relationship between the number of canopy patches within each grid, Pielou index (α), and the number of trees within each grid. α value has the same interpretation as in A.

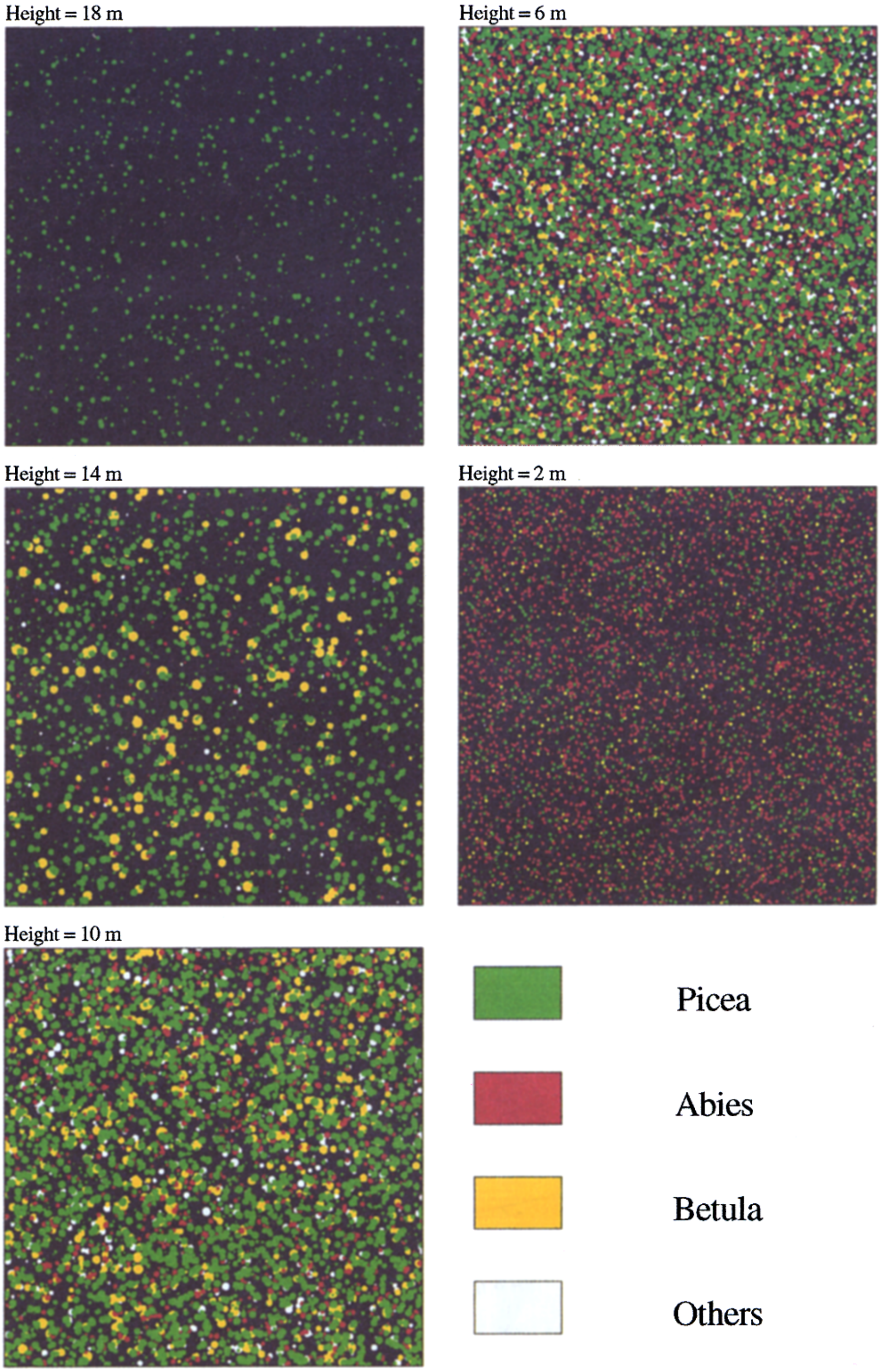


Fig. 10. Crown intersections at different tree heights. Notice that there could be intersections at any height if necessary which means that the whole vertical structure could be presented using ARC/INFO.

size of canopy patches becomes much larger (Fig. 10).

The areas of canopy and gap patches change

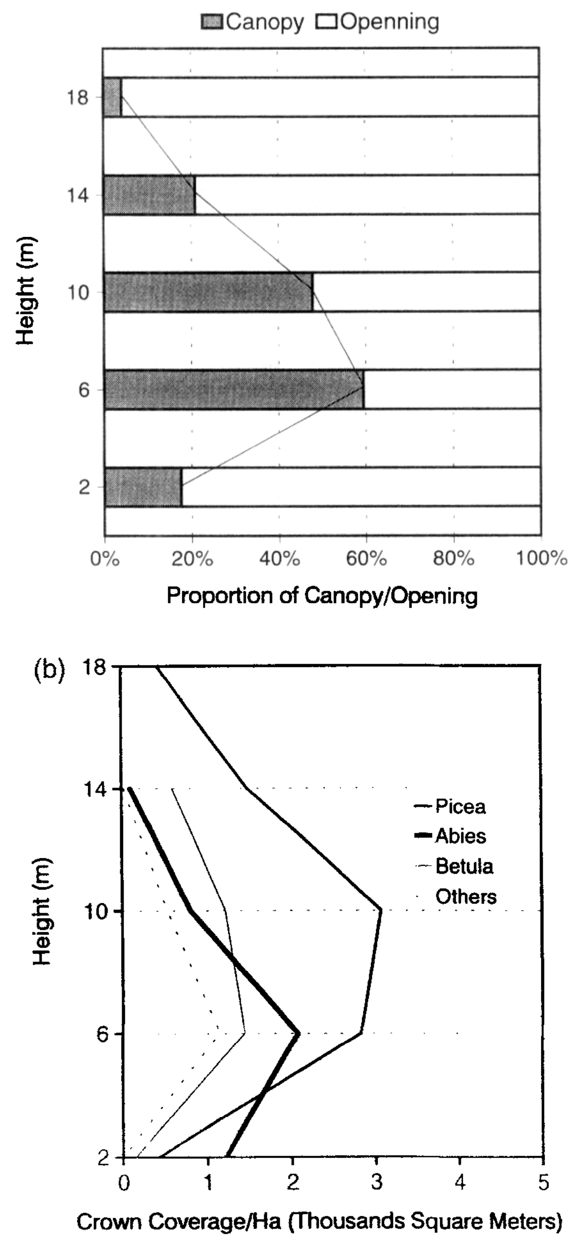


Fig. 11. (A) Crown and gap areas at different tree heights using information from the data file generated automatically by ARC/INFO. (B) Crown areas of different species at different heights, from which we determine how the crown of each species are distributed vertically.

greatly from the lower to the upper canopy (Fig. 11A). Crown coverages of the different species change dramatically at different heights (Fig. 11B). Spruce is the main component of the whole canopy structure, especially at heights of 6, 10 and 14 m. The canopy areas of fir are larger at 2 and 6 m, but they decrease quickly above 14 m. This means that firs have relatively lower crowns than other species in this forest. For birch, canopy areas are larger at 6 and 10 m.

The patterns of canopy patches are clearly variable and scale dependent. The canopy composition becomes more diverse at broader scales and changes greatly from the lower to the upper canopies. The modeling approach used in this study has general use in characterizing 3-dimensional canopies of many types of forests.

4. Discussion

Patch models of the JABOWA (Botkin et al., 1972) and FORET (Shugart and West, 1977) genre, which are broadly used to describe dynamic processes of forests, are vertically explicit only in describing foliage distribution, and assume uniform horizontal distribution of foliage in each patch. In the latest variants of these patch models, foliage is distributed uniformly along a cylinder of variable heights to represent relative crown depth, (e.g., FORSKA, Prentice and Leemans, 1990). Plot sizes in these patch models need to correspond to the width of the crowns (typically 100 to 1000 m^2). The canopy model developed in this study provides horizontal resolution, so plots can have any size without losing details in foliage distribution. This would enable patch models to be run at any spatial scale without the problem of interaction among small plots.

Patterns of canopy gaps at various heights in canopies can be related to light and microclimate environment and hence to tree vigor and regeneration. The term 'gap' as used here refers to an area within the forest where the canopy (leaf height of tallest stems) is noticeably lower than in adjacent areas (Runkle, 1985, 1991). Most definitions also restrict gaps to the areas directly under the canopy gap although additional areas sometimes may be included (e.g., the 'expanded gap' which extends to the bases of canopy trees bordering the gap; Runkle, 1985, 1991). In this study, the delineation of the gap was expanded to three dimensions.

This research will provide useful information on the interrelationships between structural attributes and processes of ecosystems. The equations of the crown shell model can broadly describe various crown shapes especially asymmetric ones. The model can also simulate different spatial patterns at multiple scales. It could be linked with other dynamic models to predict the growth and death of trees and succession, or linked to disturbance models focusing on fire, harvesting, wind throw, and thinning. These linkages can be explored at multiple scales to determine how pattern-process relationships vary among scales. For example, the model developed in this study can be closely related to other ecosystem studies, such as those predicting ecosystem dynamics with canopy interaction information, light distribution in and under the forest canopies, spatial heterogeneity and temporal changes of understory vegetation, patterns in regeneration mosaics, and microclimatic variation in the forest. In forest management, thinning has been widely used to promote tree growth, increase wood production and quality, and maintain ecosystem diversity and stability (Koop, 1989). Using the model developed in this study, one can evaluate the influences of silvicultural alternatives, such as thinning, partial harvests, or aggregation across the stands.

The canopy composition has more diversity at broader scales. When the grid size is equal to or larger than 37.5 m, H′ gradually stabilized, suggesting a minimum grid size of 37.5 m is needed to include all canopy composition types. Thus, the grid size of 37.5 m (0.141 ha) could refer to the scale of a regeneration or eco-unit. The size of a regeneration unit in natural forests in Europe seldom exceeds the diameter equal to one or two tree heights (Korpel, 1982; Koop, 1989). In a wide variety of transects from all over the world, Oldeman (1989) distinguishes regeneration units of about similar size. The grid size of 37.5 m matches the diameter of one or two tree heights for spruce-fir forests in CNR. Considering the standard deviation of diversity, a grid size equal to or larger than the grid size of 37.5 m is needed to include the whole canopy composition.

5. Conclusion

The structures of the canopy and of canopy gaps are mainly affected by: (a) the density of trees, (b) tree locations, (c) species composition, and (d) the shape and size of the crowns. In other words, species composition and the shape and size of the crowns affect canopy structure. Tree density is the main factor affecting crown areas and the number of canopy patches. When tree densities are the same or similar, the spatial pattern of trees affects the number and size of canopy patches. Species composition and the structure of canopy patches change substantially at the lower and higher parts of crowns. In addition, the number of species included and the sizes of the crowns decrease significantly between the lower and higher parts of crowns. Yet at the middle height, species composition is much more complicated, and the size of the canopy patches becomes much larger. In short, the canopy structure changes dramatically at different scales, not only horizontally, but also vertically. Different scales need to be used for different research purposes. There is greater heterogeneity at finer scales. Patches delineated vertically can be useful in understanding and predicting ecological processes.

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