Structure and asymmetry of tree crowns in relation to local competition in a natural mature Scots pine forest

Seppo Rouvinen and Timo Kuuluvainen

Abstract: This study examined the effect of local competition, as determined by the number, size, and spatial distribution of neighboring trees, on crown base height, crown width, and crown asymmetry of trees growing in a natural mature Scots pine (Pinus sylvestris L.) forest in eastern Finland. Local competition was described with competition indices. Crown asymmetry was characterized as the distance and direction from the stem center to the visually estimated crown mass center. Nonspatial and spatial models for crown base height and crown width were derived, as well as a spatial model for the horizontal distance from the crown mass center to stem base position. The effect of neighbors on the direction of crown mass center from stem base position was studied using the center of competition and the widest free angle free of competitors closer than 5 m. The derived spatial models for crown base height and crown width, taking local competition into account, were only slightly better than the nonspatial models. This was because diameter at breast height and tree height, the independent variables used in the nonspatial models, described quite well the conditions of local competition for a tree. The spatial model for crown base height was 2.22% units (adjusted $R^2$) better than the nonspatial model. Correspondingly, the spatial model for crown width was 1.77% units better than the nonspatial model. Crown asymmetry characteristics were measured for 57% of the trees. The spatial model for the distance to the crown mass center could only explain about 10% of the total variation of the dependent variable. The model for the direction of the crown mass center from stem base position showed that the variables describing direction of local competition, i.e., the competition center and the widest free angle, could not adequately explain the direction of asymmetry. One reason for this was that tree crowns showed plastic responses to the prevailing asymmetry of solar radiation geometry. Therefore, the directional distribution of the crown asymmetry was strongly weighted toward southern and southwestern directions, i.e., the directions of most abundant incoming solar radiation. We suggest that the detected developmental plasticity in crown asymmetry was affected both by the directionality of solar radiation geometry and by that of local competition, which is influenced by the number, size, and spatial distribution of close competitors.

Résumé : Cette étude examine l’effet de la compétition locale déterminée par le nombre, la taille et la distribution spatiale des arbres voisins sur la hauteur de la base du houppier, ainsi que la largeur et l’asymétrie du houppier des arbres poussant dans une forêt naturelle mature de pin sylvestre (Pinus sylvestris L.) dans l’est de la Finlande. La compétition locale est décrite par des indices de compétition. L’asymétrie du houppier est caractérisée par la direction et la distance entre le centre de la tige et le centre de gravité du houppier estimé visuellement. Des modèles non spatiaux et spatiaux pour la hauteur du houppier et la largeur du houppier sont dérivés, ainsi qu’un modèle spatial pour la distance horizontale entre le centre de gravité du houppier et la base de la tige. L’effet des voisins sur la direction du centre de gravité du houppier à partir de la base de la tige est étudié à l’aide du centre de la compétition et du plus grand angle libre exempt de compétiteurs à moins de 5 m. Les modèles spatiaux dérivés pour la hauteur de la base du houppier et la largeur du houppier et qui tiennent compte de la compétition locale sont légèrement supérieurs aux modèles non spatiaux. Ceci s’explique par le fait que le diamètre à hauteur de poitrine et la hauteur de l’arbre, les variables indépendantes utilisées dans les modèles non spatiaux, décrivent relativement bien les conditions de compétition locale d’un arbre. Le modèle spatial de la hauteur de la base du houppier est supérieur de 2,22% unités ($R^2$ ajusté) au modèle non spatial. De la même façon, le modèle spatial de la largeur du houppier est supérieur de 1,77% unités au modèle non spatial. Les caractéristiques de l’asymétrie du houppier sont mesurées sur 57% des arbres. Le modèle spatial de la distance au centre de gravité du houppier explique seulement 10% de la variation totale de la variable dépendante. Le modèle de la direction du centre de gravité du houppier à partir de la base de la tige montre que les variables qui décrivent la direction de la compétition locale, c’est-à-dire le centre de compétition et le plus grand angle libre, n’expliquent pas adéquatement la direction de l’asymétrie. Ceci provient du fait que le houppier réagit de façon plastique à l’asymétrie qui domine dans la géométrie du rayonnement solaire. De ce fait, la distribution directionnelle de l’asymétrie du houppier est fortement débordée vers les directions sud et sud-ouest, c’est-à-dire les directions où le rayonnement solaire a la plus forte incidence. Nous suggérons que la plasticité dans le développement de l’asymétrie du houppier est affectée à la fois par le caractère directionnel de la géométrie du rayonnement solaire et de la compétition locale qui est influencée par le nombre, la taille et la distribution spatiale des compétiteurs immédiats.
Introduction

The growth of a tree is determined by the size, form, and functioning of its crown (Ford 1985). In a broad sense, crown structure is an expression of the spatial pattern of resource acquisition (Harper 1985; Ishizuka 1984). However, a tree crown does not only serve as a resource collector but also as a defense against adverse physical forces and competitive interference of neighboring trees (Waller 1986). In this respect, the role of aerial architecture is emphasized by the notion that the link between physiological properties and competitive effectiveness is often less distinct than the link between competitiveness and structural traits (Caldwell 1987). Competition can be defined as a reciprocal negative interaction between two trees through direct interference (e.g., wind abrasion) or indirect exploitation of shared resources (Connell 1990). Particularly, competition for radiation is suggested to play a central role in determining the growth and development of trees and tree crowns (e.g., Schulze and Chapin 1987).

The crown structure of most trees develops by serial repetition of organs. According to this view, a tree can be regarded as an integrated complex of modules, usually shoots (Sprugel et al. 1991). The area and spatial distribution of foliage determine the amount of light interception, which has been suggested to be linearly related to biomass production (Cannell et al. 1987; Stenberg et al. 1994). On the other hand, architectural traits are ultimately determined by carbon allocation, which is expressed as plastic modifications of crown structure according to the local growing environment. This plasticity is important, since it helps trees to adjust to the heterogeneity of light availability and to intercept light more efficiently (Ishizuka 1984; Franco 1986; Sorrensen-Cothern et al. 1993).

 morphological plasticity of trees has been regarded as a species-specific ecological strategy. For example, in tropical forests, crown asymmetry seems to be more a rule than an exception (Young and Hubbell 1991; Young and Perkocha 1994). On the other hand, coniferous trees, with their monopodial growth habit and rigid architecture, have been suggested to allow only limited flexibility in growth (Waller 1986). However, some observations point out that this is not necessarily always the case (Umeki 1995).

Knowledge on crown structure is needed in several types of forest ecological research, e.g., in modeling the spatial distribution of radiation in the forest understory (Pukkala et al. 1993), in predicting the susceptibility of trees to wind and snow damage, and in visualizing tree and stand structures (Leersnijder 1992). In addition, the structure of tree crowns and forest canopies affects the reflection of solar radiation, which forms the basis for acquiring information on forest ecosystems using remote sensing techniques.

To increase our understanding of how tree populations are organized and how they develop, we should know how crown structure, resource acquisition, and spatial competitive interactions are related to each other (Ford and Sorrensen 1992). The spatial pattern of trees obviously strongly affects among-tree competition for light (Kuuluvainen and Pukkala 1987; Kuuluvainen 1992). It has also become clear that in tree populations, most of the competitive interference occurs between close neighbors (Weiner 1984; Kenkel 1988; Kenkel et al. 1989). Thus, crown asymmetry should be most distinct in forests exhibiting clustered tree distribution. There is evidence, derived using simulation models, that tree-scale spatial interactions have profound large-scale effects on ecosystem-level properties, like biomass accumulation and community composition in forests (Pacala and Deutschman 1995).

The purpose of this study was to examine how the spatial pattern of trees and the consequent local competition environment are related to crown structure and crown asymmetry in a natural mature Scots pine (Pinus sylvestris L.) forest. First, spatial models for crown width and crown base height were derived and compared with nonspatial models. Second, it was tested whether crown asymmetry could be predicted by the competition environment of a tree. Third, the derived models were used in simulations to illustrate the effect of the spatial pattern of trees on crown base and crown width.

Material and methods

Study area

The study area is situated in the northern part of the Petkeljärv National Park in eastern Finland (62°36′N, 31°11′E). The national park was founded in 1956 and is now part of the Karelian biosphere area founded in 1992 under the Man and Biosphere (MAB) program of UNESCO. The Petkeljärv National Park, which belongs to the southern boreal vegetation zone (Ahti et al. 1968), is the most important nature conservation area of esker landscape in North Karelia and one of the most notable in Finland. The interlobate formation chain consists of a sinusous ridge, side ridges, and hummocks and a deltaic ice-marginal enlargement (Lyytikäinen 1982).

The study area was located in the northern part of the national park, on a topographically rather homogenous area, which is some distance away from the hiking trails. The area is located approximately 152 m above sea level. In 1993 the mean temperature was 1.7°C and the annual precipitation 665 mm (Anonymous 1994). The understory vegetation is mainly composed of dwarf shrubs (Vaccinium vitis-idea L., Vaccinium myrtillus L., Calluna vulgaris (L.) Hull), moses (Pleurozium schreberi (Brid.) Mitt, Hylocomium splendens (Hedw.) Br., Sch. & Gmb., Dicranum spp.), and lichens (Cladonia spp.) The site was classified under the Vaccinium type (rather poor fertility) according to the Finnish site classification system (Cajander 1909).

The age of the dominant tree layer, composed mostly of Scots pine was 150–200 years. There were also scattered individuals of birch (Betula pendula Roth and Betula pubescens Ehrh.), Norway spruce (Picea abies (L.) Karst.), aspen (Populus tremula L.), and willow (Salix caprea L.). From these, only birch cooccurred with pine in the dominant canopy layer. Pollen analysis of peat samples taken from a small bog close to the study area (analysis not shown) suggests that swidden cultivation has occurred in the area in the past (see also Simola 1995). Also, small-scale selective logging may have occurred in some parts of the park before protection in 1956. However, the forest in the studied area had probably developed all of its life span void of human influence, since there were no signs of logging activity.

Measurements

A spatial mapping of tree locations and measurement of dimensions of trees taller than 0.3 m was carried out over an area
of 4 ha (200 × 200 m). Because diameter at breast height (DBH) and crown width were not measured for smaller trees, only living trees taller than 10 m were used in this study. The tree mapping and measurement of tree dimensions were carried out with a field station tachymeter (model Nikon 520), which is a geodetic device for accurately measuring vertical and horizontal angles and distances. From these measurements the locations and dimensions of physical objects, seen through the high-quality optics of the device, can be determined using simple arithmetics. The tachymeter itself is composed of specialized optics and a microprocessor, which is connected to a data logger and its microprocessor. Distance measurements are based on infrared beam reflectance between the main device and a movable prism. For the computation of tree dimensions, we developed the program MEKRI (Rouvinen et al. 1997). The program calculates the dimensions of trees in the microprocessor of the data logger before storing the data. Altogether, the study material consisted of 2550 trees (Table 1; Fig. 1). The measured tree variables were coordinates, diameter at 1.3 m (DBH), height, crown width, and crown base height.

When a tree crown was noticeably asymmetric, the location \((x, y)\) of the crown mass center (needles and branches) was visually estimated from underneath the crown and measured using the tachymeter prism (Fig. 2). Although this procedure involves some subjectivity, the pattern and particularly the direction of asymmetry were fairly easy to detect. This was because of “crown shyness,” i.e., there was always some space between adjacent crowns. Crown asymmetry was measured from 1437 trees. To quantify crown asymmetry, the distance and direction between stem base center and crown mass center were computed from the measured coordinates \((x, y)\) of these variables (Fig. 2). If a tree was fairly symmetric, the crown mass center was assumed to be in the same place as the stem base center.

### Competition indices used

The local competition environment of a tree was described with 16 different competition indices (CI). Most of them were based on the distances, diameters, and heights of neighboring trees (Pukkala and Kolström 1987). Eight of the indices were sums of the angles from a tree to its neighbors. To quantify crown asymmetry, the distance and direction between stem base center and crown mass center were computed from the measured coordinates \((x, y)\) of these variables (Fig. 2).

1. Hopkins (1954) and Clark & Evans (1954) showed that most

### Table 1. Characteristics of 2550 trees and values of two grouping indices in the study area (Hopkins is the grouping index of Hopkins (1954) and Clark & Evans is the grouping index of Clark and Evans (1954)).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mean</th>
<th>Min.</th>
<th>Max.</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>DBH, cm</td>
<td>23.80</td>
<td>6.00</td>
<td>56.30</td>
<td>7.71</td>
</tr>
<tr>
<td>Height, m</td>
<td>22.06</td>
<td>10.10</td>
<td>31.80</td>
<td>4.67</td>
</tr>
<tr>
<td>Crown width, dm</td>
<td>28.51</td>
<td>6.00</td>
<td>81.00</td>
<td>10.53</td>
</tr>
<tr>
<td>Crown base, m</td>
<td>14.01</td>
<td>0.50</td>
<td>23.90</td>
<td>3.75</td>
</tr>
<tr>
<td>Hopkins</td>
<td>1.11</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Clark &amp; Evans</td>
<td>1.03</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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among-tree interactions occurred at a very local scale (<4 m) (see also Kenkel et al. 1989). Accordingly, when computing the angle sums, as well as other indices, only trees growing closer than 5 m from the focal tree were taken into account. A 5 m wide buffer zone delimited the study area. Trees in the buffer zone were used in calculating competition indices, but not as focal trees in the modeling of crown dimensions.

When trees growing in the buffer zone were excluded, 2200 pine trees were left for modeling. The location of the crown mass center was measured for 1251 of those trees. They were then used in models to determine the direction of the crown mass center. We used 1447 pine trees in models for the distance of the crown mass center from the stem base, after adding 196 systematically selected trees (every fifth tree) that had been considered to have a symmetric crown. This was done to estimate the effect of only slightly asymmetric crowns, which could not be measured due to methodological problems.

The basic form of the horizontal angle sum was defined as

\[ CI_1 = \sum_{j=1}^{n} \alpha_j \]

where \( \alpha_j = \arctan\left(\frac{d_j}{L_{ij}}\right) \) if \( L_{ij} \leq 5 \) m, else \( \alpha_j = 0 \) (radians); \( \alpha_j \) is the horizontal angle (radians), \( d_j \) is the DBH (centimetres) of the competitor, and \( L_{ij} \) is the distance (m) between the subject tree and the competitor.

The horizontal angle sums were calculated in three ways: (1) taking into account all trees within 5 m (CI1, eq. 1; Fig. 3), (2) taking into account only trees with a DBH larger than the focal tree (CI2), and (3) multiplying the angle by the ratio of the diameters of the neighbor and subject trees (CI3). In addition, a horizontal angle sum was calculated, where diameters were replaced by crown widths (CI4). This sum was used in modeling the crown base and the horizontal distance of the crown mass center from the stem base.

The basic form of the vertical angle sum was defined as (Fig. 4)

\[ CI_5 = \sum_{j=1}^{n} \beta_j \]

where \( \beta_j = \arctan\left(\frac{h_j}{L_{ij}}\right) \) if \( L_{ij} \leq 5 \) m and \( h_j > h_i \), else \( \beta_j = 0 \) (radians); \( \beta_j \) is the vertical angle (radians), \( h_j \) is the height (metres) of the subject tree, \( h_i \) is the height (metres) of the competitor, and \( L_{ij} \) is the distance (metres) between the subject tree and the competitor.

In addition to this method, the vertical angle sums were calculated in three different ways (CI6–CI8): (1) considering trees that were taller than 80% of the focal tree height (Fig. 4b), (2) taking into account trees that were taller than half of the focal tree height, and (3) taking into account trees taller than the focal tree. Competition indices based on diameters and distances of the subject tree and competitors (CI9–CI12, see Appendix) were also tested.

Two competition indices were calculated so that the relative size of the subject tree was taken into account (CI13 and CI14, see Appendix). The widest angle from the subject tree, denoted as the free angle, was determined by taking into account all trees nearer than 5 m (ANG). The free angle was also determined by taking into account only trees nearer than 5 m with a diameter greater than 80% of the subject tree diameter (ANG08). Characteristics of these competition indices for 2200 pines are shown in Table 2.

The above defined competition indices were used to model crown base height and crown width. To model the location of the crown mass center in relation to that of the stem base, the location of the center of competition was computed (1) as the simple arithmetical mean of the neighbors’ coordinates and as the mean weighted by (2) the diameters of competitors, (3) the square of the diameters of competitors, (4) the diameter and distance to competitors, and (5) the square of the diameter and the inverse of the distance to competitors (CC1–CC5, see Appendix).

It was then assumed that the crown mass center of the subject tree was located symmetrically on the opposite side of the

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**Fig. 3.** Principle for the computation of the horizontal angle sum. \( \alpha_i \) is the horizontal angle from the subject tree to the competitor, \( d_j \) is the DBH of the subject tree, \( d_j \) is the DBH of the competitor, and \( L_{ij} \) is the distance between the subject tree and the competitor.

**Fig. 4.** Principle for two (\( a \) and \( b \)) vertical angle sums. (\( a \)) CI5; (\( b \)) CI6, \( \beta_i \) is the vertical angle from the subject tree to the competitor, \( h_i \) is the height of the subject tree, \( h_j \) is the height of the competitor, and \( L_{ij} \) is the distance between the subject tree and the competitor.
Table 2. Characteristics of the 2200 trees (preparation material for the models of the crown base and crown width).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mean</th>
<th>Min.</th>
<th>Max.</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>DBH, cm</td>
<td>24.22</td>
<td>6.00</td>
<td>56.30</td>
<td>7.56</td>
</tr>
<tr>
<td>Height, m</td>
<td>22.40</td>
<td>10.10</td>
<td>31.80</td>
<td>4.41</td>
</tr>
<tr>
<td>Crown width, dm</td>
<td>28.21</td>
<td>6.00</td>
<td>81.00</td>
<td>10.30</td>
</tr>
<tr>
<td>Crown base, m</td>
<td>14.41</td>
<td>3.50</td>
<td>23.90</td>
<td>3.34</td>
</tr>
<tr>
<td>ANG, degrees</td>
<td>170.49</td>
<td>49.00</td>
<td>360.00</td>
<td>71.40</td>
</tr>
<tr>
<td>ANG08, degrees</td>
<td>217.60</td>
<td>49.00</td>
<td>360.00</td>
<td>90.38</td>
</tr>
<tr>
<td>CI1, rad</td>
<td>13.34</td>
<td>0.00</td>
<td>36.34</td>
<td>5.88</td>
</tr>
<tr>
<td>CI2, rad</td>
<td>6.76</td>
<td>0.00</td>
<td>31.48</td>
<td>5.86</td>
</tr>
<tr>
<td>CI3, rad</td>
<td>14.81</td>
<td>0.00</td>
<td>100.96</td>
<td>9.26</td>
</tr>
<tr>
<td>CI4, rad</td>
<td>6.83</td>
<td>0.00</td>
<td>32.18</td>
<td>5.84</td>
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<tr>
<td>CI5, rad</td>
<td>3.68</td>
<td>0.00</td>
<td>18.26</td>
<td>3.19</td>
</tr>
<tr>
<td>CI6, rad</td>
<td>4.10</td>
<td>0.00</td>
<td>17.32</td>
<td>2.44</td>
</tr>
<tr>
<td>CI7, rad</td>
<td>12.93</td>
<td>0.00</td>
<td>37.13</td>
<td>5.80</td>
</tr>
<tr>
<td>CI8, rad</td>
<td>1.89</td>
<td>0.00</td>
<td>16.94</td>
<td>2.23</td>
</tr>
<tr>
<td>CI9, cm·m⁻¹</td>
<td>41.82</td>
<td>0.00</td>
<td>119.27</td>
<td>19.31</td>
</tr>
<tr>
<td>CI10, m⁻¹</td>
<td>2.03</td>
<td>0.00</td>
<td>19.19</td>
<td>1.54</td>
</tr>
<tr>
<td>CI11, m⁻²</td>
<td>1.02</td>
<td>0.00</td>
<td>53.64</td>
<td>1.82</td>
</tr>
<tr>
<td>CI12, m⁻¹</td>
<td>2.72</td>
<td>0.00</td>
<td>85.19</td>
<td>3.99</td>
</tr>
<tr>
<td>CI13, —</td>
<td>0.90</td>
<td>0.18</td>
<td>1.64</td>
<td>0.23</td>
</tr>
<tr>
<td>CI14, cm²·m⁻²</td>
<td>30.73</td>
<td>0.00</td>
<td>79.31</td>
<td>13.26</td>
</tr>
</tbody>
</table>

Crown asymmetry
The modeling of crown asymmetry was divided into two tasks. First, the horizontal distance of the crown mass center from the stem base position was modeled using the least sum of squares method. DBH, height, their logarithms and square roots, competition indices, and horizontal arithmetic distance to the center of competition were tested as independent variables. A stepwise method was used to select preliminary independent variables and the final models were fixed afterwards.

Second, modeling of the direction of the crown mass center was done by comparing the measured and predicted directions (using formulas CC1–CC5, ANG, and ANG08) as follows:

\[ 4 \text{ Difference} = |\text{Direction}_{\text{measured}} - \text{Direction}_{\text{predicted}}| \]

Equation 4 was used to examine the effect of competitors on the direction of the crown mass center.

Since the directions of the crown mass centers are circular in nature, circular statistics were used for analyzing the data (Batschelet 1981). We used the Rayleigh test to determine the randomness of angle distributions for the orientation of crown asymmetry, circular correlation analysis to examine the relationships between angular distributions, circular–linear correlation to determine if the distance of the crown mass center from the stem base position was related to the direction of crown asymmetry, and the Mardia–Watson–Wheeler test to determine if the measured and the predicted (modeled) angle distributions of crown asymmetry direction differed from each other (see Batschelet 1981). All these methods assume independence of observations, which was not necessarily fulfilled. Therefore the results obtained using circular statistics must be interpreted with some caution.

The randomness was tested using the Rayleigh test. In this test the length of the mean vector is measured. The rectangular coordinates of the mean vector are (e.g., Batschelet 1981)

\[ 5 \ \bar{x} = \frac{1}{n} \left( \cos \phi_1 + \cos \phi_2 + \ldots + \cos \phi_n \right) \]

\[ 6 \ \bar{y} = \frac{1}{n} \left( \sin \phi_1 + \sin \phi_2 + \ldots + \sin \phi_n \right) \]

where \( n \) is number of the observations and \( \phi \) is angle. From these quantities the length of the mean vector (\( m \)) is calculated as follows:

\[ 7 \ m = \left( \bar{x}^2 + \bar{y}^2 \right)^{\frac{1}{2}} \]

The null hypothesis is that the angles are randomly distributed and the test statistic is the mean vector length as defined by eqs. 5, 6, and 7. The critical values for the Rayleigh test are tabulated in Batschelet (1981).

When determining the true circular correlation coefficient, both positive and negative correlations must be examined simultaneously. Positive correlation implies that as one of the paired angles increases, so does the other. Negative correlation implies that when one of the paired angles increases, the other
decreases. Because the angles (measured and predicted) were not randomly distributed (Rayleigh test), the correlation was calculated using the rank correlation formulas (e.g., Batschelet 1981). The proper circular correlation coefficient is the larger of the two calculated, i.e.

\[ r = \max(r_+, r_-) \]

where \( r_+ \) refers to positive correlation and \( r_- \) to negative correlation; \( r^2 \) was used as a test statistic (Batschelet 1981).

Circular-linear correlation was used to examine if the distance of the crown mass center from the stem base position was related to the direction of crown asymmetry (crown mass center). The Mardia-Watson-Wheeler two-sample test was used to test whether the measured and predicted (modeled) angle distributions differed significantly from each other (Batschelet 1981).

Simulation of the effect of the spatial pattern of trees on crown structure at the stand level

The derived models for crown structure and simulated forests representing different spatial structures were used to examine the effect of the spatial distribution of trees on the crown structure at the stand level. The model stands were generated with the HAVU program (Pukkala et al. 1994). The program generates different spatial distributions of trees by using given stand characteristics as input information. For every tree, DBH, height, age, and coordinates are derived using simultaneous equations (Pukkala et al. 1994).

We generated regular, Poisson-distributed, and grouped forest stand plots with 600 stems/ha to study the effect of the spatial distribution of trees on crown base height and crown width (see Fig. 9). Stand age in the model stands was set as 100 years, dominant height at 27 m, and stand basal area at 30 m²·ha⁻¹. Crown base height and crown width for each tree were predicted by spatial models developed in this study.

Results

Direction and location of the crown mass center

Fifty-seven percent of the mapped Scots pine trees had crowns that were asymmetric enough to facilitate the measurement of a separate crown mass center. The frequency distribution of the directions of the crown mass centers was not random (Rayleigh test, \( p < 0.001 \)) but strongly weighted toward southern, southwestern, and western directions (mean angle 228°) (Fig. 5). However, there was no directionality in the distribution of the distances of crown mass center from stem base positions (circular-linear correlation analysis, results not shown) (Fig. 6). The mean horizontal distance of crown mass center from stem base position was 45.6 cm, considering only trees with this crown asymmetry characteristic.

Models for crown base height

The best nonspatial model (with one independent variable) for crown base height was as follows (model 1):

\[
\begin{align*}
\hat{h}_c &= \text{Constant} + \text{Height} \\
\text{Constant} &= 2.086, \quad \text{t-value} = 8.242, \quad \text{Adj. } R^2 = 0.528 \\
\text{Height} &= 0.550, \quad \text{t-value} = 49.643, \quad \text{RMSE} = 2.291 \text{ m} \\
\end{align*}
\]

\( F_{(1,2198)} = 2464.388 \)
Correspondingly, the nonspatial model with two independent variables was as follows (model 2):

<table>
<thead>
<tr>
<th>Variable</th>
<th>Coefficient</th>
<th>t-value</th>
<th>Adj. $R^2$</th>
<th>RMSE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>-0.071</td>
<td>-0.296</td>
<td>0.630</td>
<td>2.029 m</td>
</tr>
<tr>
<td>DBH</td>
<td>-0.263</td>
<td>-24.603</td>
<td>1.967</td>
<td>1.967 m</td>
</tr>
<tr>
<td>Height</td>
<td>0.941</td>
<td>52.944</td>
<td>0.137</td>
<td>0.137</td>
</tr>
</tbody>
</table>

The competition index $Cl_6$ is the vertical angle sum (see Appendix). The sign of the competition index indicates that the more local competition there is, the higher the crown begins. The model indicates that when the competition index reaches its maximum value, the crown base is about 4.4 m higher than in the situation without competition, assuming a constant DBH and tree height.

The model residuals show no meaningful trends or any lack of variance homogeneity or normality when plotted against predicted crown base heights (Fig. 7a). Standard errors of the residual values (SE) are, however, quite high.

**Models for crown width**

The best nonspatial model with one independent variable for crown width was as follows (model 4):

<table>
<thead>
<tr>
<th>Variable</th>
<th>Coefficient</th>
<th>t-value</th>
<th>Adj. $R^2$</th>
<th>RMSE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>3.599</td>
<td>7.336</td>
<td>0.557</td>
<td>6.855 dm</td>
</tr>
<tr>
<td>DBH</td>
<td>1.016</td>
<td>52.557</td>
<td>0.243</td>
<td>6.520 dm</td>
</tr>
</tbody>
</table>

Models 4 and 5 indicate that the bigger the DBH is, the wider is the crown. Model 5 also depicts that the more slender is the tree, the narrower is the crown.

The best spatial model for crown width was as follows (model 6):

<table>
<thead>
<tr>
<th>Variable</th>
<th>Coefficient</th>
<th>t-value</th>
<th>Adj. $R^2$</th>
<th>RMSE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>14.832</td>
<td>14.597</td>
<td>0.617</td>
<td>6.374 dm</td>
</tr>
<tr>
<td>DBH</td>
<td>1.318</td>
<td>32.969</td>
<td>0.226</td>
<td>6.646 dm</td>
</tr>
</tbody>
</table>

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<td>32.969</td>
<td>0.226</td>
<td>6.646 dm</td>
</tr>
</tbody>
</table>

The competition index $Cl_6$ is based on diameters and distances of the subject tree and competitors (see Appendix). The second competition index (ANG08) is the widest free angle, where only neighbors with a diameter greater than 80% of the diameter of the subject tree were taken as competitors. The
signs of the competition indices show that competition acts to make crowns narrower (CI₉), and the availability of space (as reflected by ANG08) acts to make crowns wider.

The residuals of model 6 show that it agrees quite well with the assumptions of the regression model (Fig. 7b). There are no systematic trends in the residuals as a function of predicted crown widths.

Spatial model for the horizontal distance of the crown mass center from the stem base position

Only a spatial model (model 7) was derived for the horizontal distance of the crown mass center from the stem base location:

<table>
<thead>
<tr>
<th>Variable</th>
<th>Coefficient</th>
<th>t-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>dist. =</td>
<td>-0.038</td>
<td>-0.933</td>
</tr>
<tr>
<td>DBH</td>
<td>0.147</td>
<td>10.445</td>
</tr>
<tr>
<td>CI₈</td>
<td>0.270</td>
<td>5.511</td>
</tr>
<tr>
<td>CI₇</td>
<td>-0.168</td>
<td>-7.281</td>
</tr>
<tr>
<td>CI₆</td>
<td>0.048</td>
<td>6.656</td>
</tr>
</tbody>
</table>

The competition indices included in model 7 are based on the vertical angle sum (CI₈), horizontal angle sum (CI₇), and diameters and distances of the subject tree and competitors (CI₆) (see Appendix).

The model is rather poor in terms of statistical characteristics (Adj. R², RMSE, sₑ, and F-value). In addition, the interpretation of the competition indices and the whole model is rather difficult. Residuals of the model are divided evenly on both sides of the zero line (Fig. 7c).

Model for the direction of crown asymmetry

Seven different indices (CC₁–CC₅, ANG, and ANG08) were used in predicting the direction of the crown mass center. The results obtained using these indices are presented in Tables 3 and 4. When using eq. 4, we can see that the best prediction for the direction was obtained when the coordinates of the competition center were derived as the weighted average of the competitors’ coordinates (index CC₅) (Table 3). Comparing the results of the models with measured results with regard to mean angles and circular correlation coefficients confirms that index CC₅ was the best (Table 4). However, in all cases the positive correlation coefficient was larger than the negative correlation coefficient and the test statistic r² showed that the correlation was significant at the p < 0.001 level (i.e., correlation differs from zero).

The predicted angles using index CC₅ showed a trend toward southwest directions, although not nearly as strong as that for the observed data (see Fig. 5). The Rayleigh test values for the measured and predicted (index CC₅) distributions were 0.332 and 0.080, respectively, indicating that neither of the angle distributions was random (p < 0.001). The mean angle for the data predicted using index CC₅ was 227° and that of the measured data 228° (Table 4).

Testing the models

The spatial models for crown base height and crown width (models 3 and 6) were tested by dividing the whole-sample tree material into two populations, so that every second tree was used to derive new models and the remaining trees were used as test material. The RMSE’s of the test material were 1.977 m for crown base height and 6.370 dm for crown width. The sₑ’s were 0.138 for crown base and 0.229 for crown width. These characteristics were quite similar to the RMSE’s and sₑ’s of models 3 and 6, derived from the whole tree material.

For testing the derived models for crown mass center, we divided our study area into four equally sized square parts (100 × 100 m) and predictions for the positions of crown mass centers were computed using models 7 (horizontal distance of the crown mass center from the stem base location) and CC₅ (direction of the crown mass center from the crown base position) for the four square plots (20 × 20 m) situated in the center of each 1-ha plot. After calculating the predicted positions, crown maps were drawn for these plots and compared with the crown maps based on measurements (Fig. 8). The circular correlation coefficients computed for the measured and predicted angle distributions were rₑ = 0.486 and rₑ = 0.167 and so rₑ = 0.486 and rₑ = 0.237. With a preassigned significance level of 0.001, we can conclude that rₑ differs significantly from zero. Thus, in these four plots the relationship between measured and predicted angle distributions shows a weak positive correlation. The Mardia–Watson–Wheeler test indicated that we could not reject the null hypothesis, i.e., the measured and predicted (using index CC₅) angle distributions did not differ from each other (Table 4).

The Pearson’s product moment correlation coefficient for the measured and predicted (with model 7) distance of the crown mass center from the stem base location was 0.180.

Based on these analyses, we can conclude that the used models could not adequately predict the asymmetry characteristics of crowns.

Effect of the spatial pattern of trees on crown structure

The derived models for crown structure and simulated forests representing different spatial structures were used to examine the effect of the spatial distribution of trees on the crown structure at the stand level. We generated regular, Poisson-distributed, and clustered forest stand plots with 600 stems/ha (Fig. 9). Two grouping indices were calculated to describe the degree of aggregation of the three model stands generated by the HAVU program. The index of Clark and Evans (1954) was 1.65 for the regular stand, 1.14 for the Poisson-distributed stand, and 0.82 for the grouped stand. The values of the Hopkins index (1954) were 0.21, 0.58, and 1.42, respectively.

The mean crown base slightly increased with increasing grouping of trees (Fig. 10a). However, the difference was quite small, only about 0.8 m between the regular and grouped stands. The mean crown width slightly decreased with increasing grouping of trees (Fig. 10b). This effect was more pronounced than in the case of the crown base and the difference in crown width between the regular and grouped stands was about 0.4 m.

These results agree with expectations. According to the models, competition increases crown base height and decreases crown width. Competition may be increased through stand density or grouping of trees. The simulations showed that grouping of trees had an effect on crown base and crown width.

Discussion

Our first purpose was to examine the effect of size, number, and spatial distribution of local competitors (trees within a 5-m
radius from the subject tree) on crown base height and crown width of trees growing in a natural mature Scots pine forest in eastern Finland. Local competition was described with different kinds of competition indices. Our second purpose was to examine the effect of local competition on crown asymmetry, determined as the distance and direction of the crown mass center from the crown base position.

Nonspatial and spatial models for crown base and crown width were derived, as well as a spatial model for the horizontal distance of the crown mass center from the stem base position. The effect of neighbors on the direction of the crown mass center from the stem base position was studied using the center of competition and the widest free angle devoid of competitors. Although we initially computed many competition indices to describe the effect of local competition by neighbors, only some of them were useful to be included in the models (models 3, 6, and 7).

The derived spatial models for crown base and crown width were only slightly better than nonspatial models, all having DBH and tree height as independent variables. The spatial model for crown base (model 3) was 2.22% units (Adj. \( R^2 \)) better than the nonspatial model (model 2). Correspondingly, the spatial model for crown width (model 6) was 1.77% units better than the nonspatial model (model 5). This indicates that direct information on competition, as described by competition indices, could only slightly improve the models for these crown characteristics. The most important reason for this is that DBH and height together describe already quite well the conditions of local competition in a tree stand: the more slender a tree was, the more intense was the local competition, and vice versa. However, if one knew the spatial relationships of trees through time, the explanatory value of spatial data might be greater than considering spatial relationships at one point in time.

Simulated forest stands were used to examine the effect of the spatial distribution of trees on crown base height and crown width at the stand level. Compared with actual measurements in real stands, simulation has the advantage that stand properties can easily be controlled. When interpreting the obtained results, it must be kept in mind that only one stand density (600 stems/ha) was used. The results of the simulations proved to be logical. Crown base was on average highest in the grouped stand, where distances between trees within groups were short and local competition was high. In stands with regular and Poisson tree distributions, crown bases were lower. Crowns were on average widest in the regular stand where crowns of individual trees have maximum space to grow horizontally in all directions. In the Poisson stand and especially
in the grouped stand, the growth of crowns was restricted due to grouping of trees. The models for the direction of crown mass center from stem base position showed that the computed center of competition and the widest free angle could only explain to a limited extent the directionality of crown asymmetry. The observed data showed a strong trend toward southwest directions, i.e., the directions of most abundant incoming solar radiation. This mechanism also explains the asymmetry of predicted angle distribution, since the predictions were only computed for trees with asymmetric crowns. Thus, these findings support the hypothesis that in northern latitudes, tree crowns show plastic responses in crown shape to the prevailing asymmetric solar radiation geometry (Ilvessalo 1967) in order to increase the crown surface area receiving direct solar radiation (see also Kuuluvainen 1992). This also means that among-tree shading and competition for light are closely linked to the direction of the close competitors. In conclusion, our results suggest that the observed crown asymmetry is the result of both the flexibility of crown development in relation to solar radiation geometry and the asymmetry of local competition caused by the number, size, and spatial distribution of close competitors. The results obtained cannot be explained by the direction of winds in the district because dominant wind direction is from the southwest (Tammelin 1991). Thus, if wind were to be responsible for the detected crown asymmetry, the opposite direction of asymmetry to that found in this study should occur. Factors like slope were not examined (e.g., Umeki 1995), but this factor probably had no significant effect, since the topography of the study area was rather flat.

The spatial model for the distance of the crown mass center could only explain about 10% of the total variation of the dependent variable. One reason for this is the confounding effect of solar radiation geometry on crown shape. Another reason could be the relative subjectivity in the measurement of the crown mass center. Taking into account the crown asymmetry due to solar radiation geometry might have improved the models describing crown asymmetry. It is also evident that factors like tree age and history of the competition environment, which could not be taken into account, have an effect on crown structure and may thus confound the relationship between metric crowns are those with free growing space in southwest directions and close competitors in other directions, while trees having competitors in southwest directions do not develop as strong crown asymmetry in other directions, where crown surfaces are shaded from direct radiation. The models for the direction of crown mass center from stem base position showed that the computed center of competition and the widest free angle could only explain to a limited extent the directionality of crown asymmetry. The observed data showed a strong trend toward southwest directions, i.e., the directions of most abundant incoming solar radiation, while in predicted (modeled) data the same trend was evident but much weaker. What can be the mechanism behind these patterns? We suggest that the trees with markedly asym-
crown structure and the present competition environment (e.g., Heikinheimo 1953; Waller 1986).

It is noteworthy that in the studied Scots pine forest, almost two thirds of the measured trees had a clearly asymmetric crown. Thus, judged from the present data, crown asymmetry appears to be very common in natural mature Scots pine forests, which have regenerated naturally and undergone the natural self-thinning process. Although not examined in the present study, it is likely that crown asymmetry increases the range of branch characteristics available for, e.g., epiphytic lichens as well as the overall structural complexity of the canopy layer. For example, the complex spatial arrangement of trees and the gappiness of the canopy layer (see Fig. 1) obviously allow specific branches (especially those growing on northeast sides of gaps receiving direct sunlight) to grow much older and bigger (see Fig. 2a) compared with a situation with a more even spatial distribution of trees, as is often the case in managed forests. This may have an effect on epiphytic lichen communities, which are known to play important roles in forest ecosystems. For example, in northern Swedish spruce forests, Esseen and Renhorn (1996) found that epiphytic lichen mass was strongly related to mass, diameter, and age of branches. There is an apparent need for further studies on crown asymmetry as a structural characteristic of natural forest canopies and its contribution to both functional and ecological diversity in forest ecosystems.

Acknowledgments
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References


Appendix

Formulas for competition indices used and for the center of competition. For explanations of symbols, see Figs. 3 and 4. Index i denotes the subject tree and j the competitor, n is the number of competitors inside a 5-m radius from the subject tree, and g denotes the basal area of a tree (in CI13 and CI14).

Horizontal angle sums:

\[ CI_1 = \sum_{j=1}^{n} \arctan(d_i/L_{ij}) \]

\[ CI_2 = \sum_{j=1}^{n} \arctan(d_j/L_{ij}), \quad d_j > d_i \]

\[ CI_3 = \sum_{j=1}^{n} (d_i/d_j)\arctan(d_j/L_{ij}) \]

\[ CI_4 = \sum_{j=1}^{n} \arctan(d_i/L_{ij}), \quad h_j > h_i \]

Vertical angle sums:

\[ CI_5 = \sum_{j=1}^{n} \arctan(h_j/L_{ij}), \quad h_j > h_i \]

\[ CI_6 = \sum_{j=1}^{n} \arctan((h_j - 0.8h_i)/L_{ij}), \quad h_j > 0.8h_i \]

\[ CI_7 = \sum_{j=1}^{n} \arctan(h_j/L_{ij}), \quad h_j > h_i/2 \]

Competition indices based on diameters and distances of the subject tree and the competitor:

\[ CI_9 = \sum_{j=1}^{n} \frac{d_j}{L_{ij}} \]

\[ CI_{10} = \sum_{j=1}^{n} \frac{d_i}{L_{ij}} \]

\[ CI_{11} = \sum_{j=1}^{n} \frac{d_j}{L_{ij}^2} \]

\[ CI_{12} = \sum_{j=1}^{n} \frac{(d_i/d_j)^2}{L_{ij}} \]

Competition indices based on the relative size of the subject tree:

\[ CI_{13} = \frac{d_i}{\sum_{j=1}^{n} g_j} + \frac{\sum_{j=1}^{n} d_ig_j}{\sum_{j=1}^{n} d_j} \]

\[ CI_{14} = \frac{\sum_{j=1}^{n} g_j}{\Pi \times 5^2} \]

The location of the center of competition:

\[ CC_1: \bar{x}_j = \frac{\sum_{j=1}^{n} x_j}{n}, \quad \bar{y}_j = \frac{\sum_{j=1}^{n} y_j}{n} \]

\[ CC_2: \bar{x}_j = \frac{\sum_{j=1}^{n} d_jx_j}{\sum_{j=1}^{n} d_j}, \quad \bar{y}_j = \frac{\sum_{j=1}^{n} d_jy_j}{\sum_{j=1}^{n} d_j} \]

\[ CC_3: \bar{x}_j = \frac{\sum_{j=1}^{n} d_j^2x_j}{\sum_{j=1}^{n} d_j^2}, \quad \bar{y}_j = \frac{\sum_{j=1}^{n} d_j^2y_j}{\sum_{j=1}^{n} d_j^2} \]
\[ \bar{x}_j = \frac{\sum_{i=1}^{n} d_j x_i (1/L_{ij})}{\sum_{j=1}^{n} d_j/L_{ij}}, \quad \bar{y}_j = \frac{\sum_{i=1}^{n} d_j y_i (1/L_{ij})}{\sum_{j=1}^{n} d_j/L_{ij}} \]

\[ \bar{x}_j = \frac{\sum_{i=1}^{n} d_j x_i^2 (1/L_{ij})}{\sum_{j=1}^{n} d_j/L_{ij}}, \quad \bar{y}_j = \frac{\sum_{i=1}^{n} d_j y_i^2 (1/L_{ij})}{\sum_{j=1}^{n} d_j/L_{ij}} \]