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The contribution of structural indices to the modelling of Sitka spruce (*Picea sitchensis*) and birch (*Betula* spp.) crowns

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ABSTRACT

Crown dimensions are important for the quantification of tree interactions in some growth models. This study investigates the potential for structural indices and other spatial measures to improve the prediction of crown radius and crown length for birch (*Betula* spp.) and Sitka spruce (*Picea sitchensis* (Bong.) Carr.) in forests in Wales. Crown dimensions were measured for 125 birch and 154 spruce in six fully stem-mapped research plots. These data were used to test the performance of a crown radius model and a crown length model which estimated crown dimensions on the basis of allometric relationships with stem dimensions. Spatial data from the six plots were used to calculate the structural indices mean directional index, diameter correlation index, species mingling, dbh and height dominance, and dbh differentiation, as well as the Hegyi competition index, and basal area of neighbours and larger neighbours, for each crown measurement sample tree, using various numbers of nearest neighbours. Two non-spatial indices, BAL and BALMOD, were also calculated for all sample trees for comparison. These spatial and non-spatial variables were then incorporated into modified crown dimension models. Model performances, in terms of efficiency and relative bias, were compared to determine whether the inclusion of spatial or non-spatial variables resulted in any improvements over models using tree dimensions alone. Crown length and radius were found to be correlated with most of the spatial measures studied. Models incorporating spatial variables gave improvements in performance over allometric models for every data set, and performed more consistently than models containing non-spatial variables. The greatest improvements were achieved for suppressed birch in unthinned forests which had irregularly shaped and strongly displaced crowns. The spatial variable contributing to the most efficient model for each data set varied widely. This points to the complexity of tree spatial interactions and indicates that there is a great deal of scope for investigating other structural indices and crown dimension model forms.

1. Introduction

The crown of a tree may be defined as "the system of its photosynthetic organs together with the non-photosynthetic organs by which they are physically and physiologically supported, translocating carbohydrates to the stem" (Ottorini et al., 1996, p. 394). Crown dimensions – length, width, surface area or volume – can be used to approximate the scale of the photosynthetic apparatus (e.g. Smith, 1994), which determines the capacity of the tree to produce dry matter (Kozlowski et al., 1991). The sizes, shapes and relative locations of crowns both determine and respond to the shading and constriction effects that characterise above-ground interactions between trees (von Gadow and Hui, 1999). Consequently, crown dimensions have often been used to model competition and growth (e.g. Biging and Dobbertin, 1992; Moravie and Robert, 2003). Such modelling approaches may require information on crown length, radius and possibly profile (shape) as inputs (e.g. Pretzsch et al., 2002) and, as they are rarely measured in forest surveys, these variables must themselves be modelled.

Crown models range in sophistication from simple, deterministic models based on allometric relationships with stem dimensions (e.g. Hasenauer, 1997) to complex models incorporating stochastic elements (e.g. Biging and Gill, 1997), explicitly modelling crown asymmetry (e.g. Cescatti, 1997), or even modelling branch architecture (e.g. Berezovskava et al., 1997). For the purposes of modelling inter-tree interaction, simple models usually suffice (von Gadow, 1996). Allometric models tend to perform well because of the direct dependence of stem growth on crown size, but the intensely spatial nature of tree crown interactions means that variables describing the immediate

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neighbours of a tree may be able to improve model predictions. Simple non-spatial indices can be used to quantify a tree's competitive status within a stand. More sophisticated indices of spatial structure can be used to quantify the regularity of the arrangement of a tree's neighbours, their relative sizes or the degree of species mingling (von Gadow and Hui, 2002; Pommerening, 2002; Aguirre et al., 2003), and stand density in the area immediately surrounding a tree, such as within a radius proportional to tree size, can be measured. All of these factors are likely to influence crown development.

This paper considers approaches to crown modelling suitable for inclusion in single-tree, spatially explicit growth models for Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and birch (silver birch *Betula pendula* Roth and downy birch *B. pubescens* Ehrh.) in Wales. Sitka spruce is the main commercial timber species in Great Britain and birch is a significant contributor to biodiversity in plantation forests (Humphrey et al., 1998). The study focuses on crown length and radius as the most important biometric characteristics of tree crowns. Relationships between these crown dimensions and non-spatial and spatial variables describing local stand density and structure are examined, and crown models incorporating these variables are tested with the aim of improving on the predictions of allometric models. It is hypothesised that models containing non-spatial or spatial variables will be able to account for a greater proportion of variation in crown dimensions than those based on stem dimensions alone, and that spatial models will perform better than non-spatial models because of the structural complexity of the stands studied.

2. Materials and methods

2.1. Data

Data for crown modelling were collected in six permanent research plots in North Wales, covering a range of stand structures (Table 1). These plots were established in three state-owned forests: plots CLG1, CLG2 and CLG7 are located in Clocaenog Forest, plots CYB1 and CYB2 are located in Coed y Brenin, and plot GWY1 is located in Gwydyr Forest. Management input in the sampled stands has been minimal until the recent past, and as a result inter-tree interactions have occurred relatively unmodified by human intervention. In the Coed y Brenin plots, this has led to marked suppression of birch by the more competitive Sitka spruce. In each plot, for all trees equal to or greater than 5 cm diameter outside bark at breast height, 1.3 m (dbh), the species, dbh and height to tree tip (height) were recorded and tree main stem positions were mapped in three dimensions using an electronic theodolite.

Crown measurements were made on random sub-samples of trees in each plot. Altogether 125 birch (in plots CLG7, CYB1, CYB2 and GWY1) and 154 Sitka spruce (in plots CLG1, CLG2, CYB1, CYB2 and GWY1) trees were sampled. For each crown-measured sample tree, two measurements of height and two of height to crown base were made, separated by a horizontal angle of 180°. Crown base was defined as the point at which the lowest live branch left the main stem, excluding epicormic and adventitious shoots and sparsely foliated branches not contiguous with the main part of the crown. Arithmetic mean height and height to crown base were calculated for each tree, and crown length was calculated by subtracting mean height to crown base from mean height.

Eight measurements of crown radius were made for each tree in the cardinal and intercardinal directions, using a vertical sighting tube (Hale, 2004) to sight to the crown margin and a 30 m tape to measure the distance between the centre of the tree bole and the edge of the crown, following the guidelines for the objective identification of the crown edge offered by Ayhan (1977). Quadratic mean (or root mean square) crown radius (Eq. (1)) was calculated for each tree (Hasenauer, 1997), as this gives the most accurate estimate of cross-sectional area (Siostrzonek, 1958)

Table 1
Summary data for permanent research plots

Plot	CLG1	CLG2	CLG7	CYB1	CYB2	GWY1
Location (lat./long.)	53°4′25″N 3°25′53″W	53°4′32″N 3°25′42″W	53°4′7″N 3°25′9″W	52°48′26″N 3°54′1″W	52°48′39″N 3°54′2″W	53°6′16″N 3°49′4″W
Elevation (m.a.s.l.)	390	400	350	210	250	230
Elevation range within plot (m)	9.5	10.1	9.3	6.8	12.3	8.8
Area (ha)	1.00	1.00	1.00	0.10	0.26	1.00
Planting year	1951	1951	1985	1970	1972	1931
Planted crop (species)	SS	SS, LP	SS	SS	SS, RC	SP, SS
Natural regeneration (main species by basal area)	SS	SS, ROW	BI, NS, ROW, WIL	BI, DF, OK, WIL	BI, OK, DF, LP	BI, ROW, OK, WH
Stocking (stems per ha)						
BI	–	–	1,094	1,040	738	177
SS	289	251	172	1,120	1,088	46
Other spp.	–	68	600	500	416	271
Total	289	319	1,866	2,660	2,242	494
Basal area (m^2 per ha)						
BI	–	–	10.2	5.8	5.6	1.0
SS	29.9	27.0	3.1	35.1	31.7	6.0
Other spp.	–	2.7	3.8	3.5	8.1	23.7
Total	29.9	29.7	17.1	44.4	45.4	30.7
Top height (m)						
BI	–	–	11.4	13.8	12.5	7.4
SS	28.6	27.0	11.2	17.3	17.7	27.3

Plot abbreviations are explained in the text. BI is birch (*Betula pendula* Roth, *B. pubescens* Ehrh.), DF is Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), LP is lodgepole pine (*Pinus contorta* Douglas ex Loudon), NS is Norway spruce (*Picea abies* (L.) Karst), OK is oak (*Quercus* spp.), RC is western red cedar (*Thuja plicata* Donn ex D. Don), ROW is rowan (*Sorbus aucuparia* L.), SP is Scots pine (*Pinus sylvestris* L.), SS is Sitka spruce (*Picea sitchensis* (Bong.) Carr.), WH is western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and WIL is willow (*Salix* spp.). Stocking, basal area and top height are reported separately for birch and Sitka spruce. Top height was calculated as the arithmetic mean height of the 100 trees of largest diameter at breast height per hectare, except for GWY1 spruce where there were only 46 spruce per hectare; in this case, the average height of all 23 overstorey trees is given.

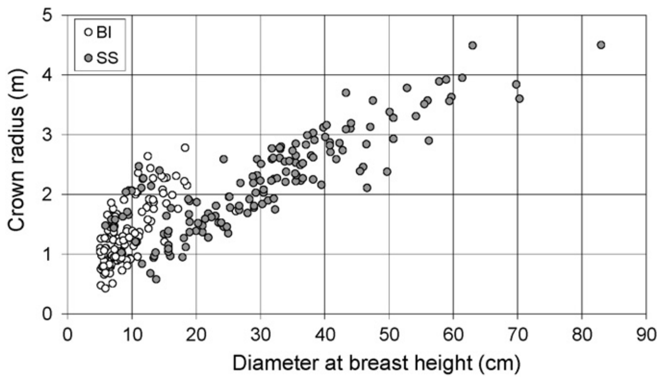

Fig. 1. Scatter plot of crown radius against stem diameter at breast height for all birch (BI) and Sitka spruce (SS) crown measurement sample trees.

for tree interaction modelling.

$$r_{\text{rms}} = \sqrt{\frac{1}{n}\sum_{i=1}^{n} r_i^2} \tag{1}$$

where r_{rms} is the root mean square crown radius (m), r_i the ith crown radius measurement (m) and n is the number of measurements (in this case, $n = 8$). The coefficient of variation of the radius measurements for each sample tree was calculated as a quantification of uniformity in crown shape (Francis, 1986), with a value of zero indicating a perfectly circular crown. In addition, relative canopy displacement, a measure of crown eccentricity defined as "the distance between stem position and canopy centre of mass divided by the mean of the eight canopy extent measurements" (Muth and Bazzaz, 2003, p. 1325), was calculated for each tree. Muth and Bazzaz (2003, p. 1325) state that "a value of zero represents a tree with its canopy centered directly above its stem base. For a canopy the shape of a regular polygon, a value greater than one represents a situation in which the canopy is displaced entirely from the stem base. For the majority of forest trees, relative canopy displacement values tend to range between zero and one, indicating that the canopy is displaced but that the stem base is still positioned at some location beneath the canopy."

Fig. 1 plots crown radius against dbh for all crown measurement sample trees and Fig. 2 plots crown length against height. Data ranges are particularly wide for spruce because of the range of ages and stand densities represented in the permanent research plots. Two broad groups of trees can be recognised in terms of crown radius (Fig. 1). The majority of the spruce conform to an obvious, more or less linear relationship between dbh and crown radius. The birch and the few understorey spruce from CLG2 and GWY1 show a less obvious but steeper linear trend between 5 and 20 cm dbh, demonstrating that these trees have proportionally broader crowns. In the case of the understorey spruce, this is presumably the result of less physical constriction and of increased lateral growth at the expense of apical growth in order to improve light capture. Two distinct trends are also apparent in crown length (Fig. 2); the crowns of trees greater than 20 m in height are proportionally shorter than those of shorter trees. The trees above 20 m height are all planted spruce in plots CLG1, CLG2 and GWY1, and have relatively short crowns presumably because of a lack of thinning in these stands in the past. Initial spacing may have played a role; plots CLG1, CLG2 and GWY1 were established at 1.7 m spacing, whereas CYB1 and CYB2 were planted at 2 m spacing. These trends in crown dimensions indicate that, while there may be strong allometric relationships between stem and crown dimensions, they are also heavily influenced by stand structure.

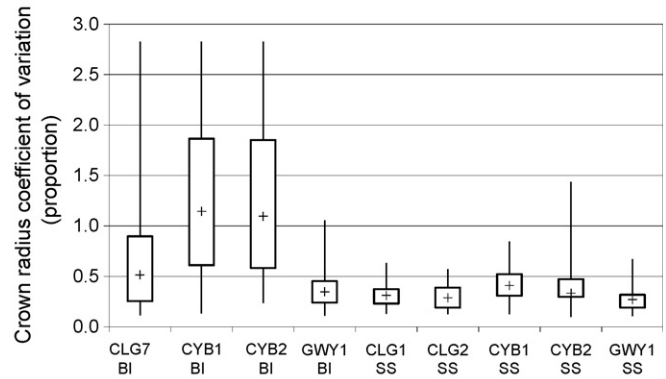

Fig. 3. Medians, minima, maxima and interquartile ranges of crown radius coefficient of variation for all birch (BI) and Sitka spruce (SS) crown measurement samples.

Fig. 3 demonstrates that the relatively suppressed Coed y Brenin birch have far higher coefficients of variation of crown radius than any of the other trees measured. This cannot be ascribed solely to differences in branching patterns between broadleaves and conifers, as the GWY1 birch appear very similar to the spruce data sets; rather, it seems that physical constriction results in considerable crown asymmetry in this species. CYB1 and CYB2 birch also have the highest values of relative canopy displacement (Fig. 4), with medians greater than one (1.12 and 1.04, respectively) suggesting that the crowns of most trees in these data sets are so heavily displaced that no part of the crown is directly above the stem base. These observations suggest that there

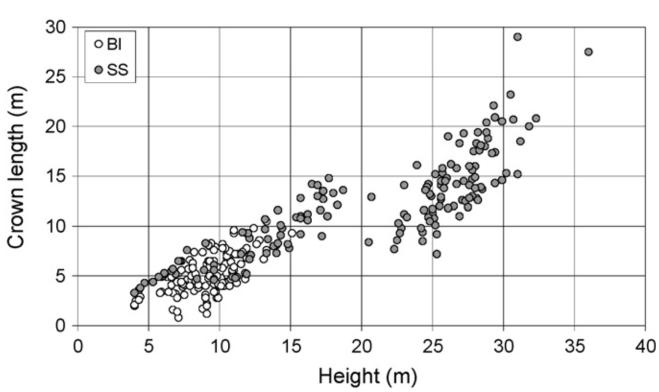

Fig. 2. Scatter plot of crown length against tree height for all birch (BI) and Sitka spruce (SS) crown measurement sample trees.

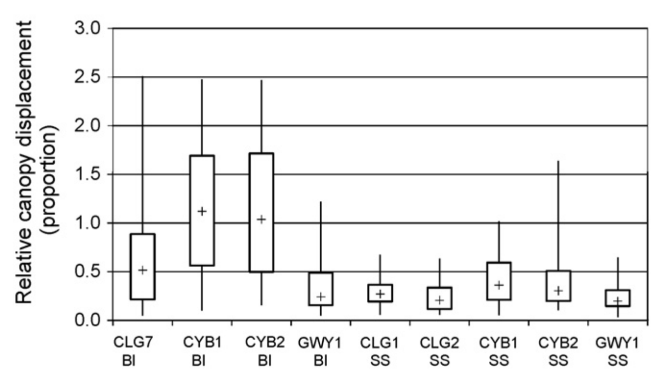

Fig. 4. Medians, minima, maxima and interquartile ranges of relative canopy displacement for all birch (BI) and Sitka spruce (SS) crown measurement samples.

may be some difficulty in modelling these crowns as simple, rotationally symmetrical shapes, but quantifications of spatial interrelations may help.

2.2. Tree crown models

Simple crown models based on dbh and tree height were chosen from seven crown radius models and four crown length models tested in a previous study (Davies, 2006). Models were chosen on the basis of their predictive power, their simplicity, and the ease with which they could be modified to incorporate spatial variables. The crown radius model (Eq. (2)) was modified from one presented by Hasenauer (1997), and the crown length model (Eq. (3)) was modified from a crown base height model presented by Nagel et al. (2002).

$$\hat{r} = e^{a+b\cdot\ln(\text{dbh})} \quad (2)$$

$$\hat{L} = h\cdot e^{-a\cdot(h/\text{dbh})} \quad (3)$$

where $\hat{r}$ is the predicted crown radius (m), $\hat{L}$ the predicted crown length (m), dbh the diameter at breast height (cm), h the tree height (m), e the base of natural logarithms, and a and b are the regression coefficients. Eq. (2) returns positive values of $\hat{r}$ for all values of regression coefficients a and b. For Eq. (3) to return crown length values between zero and tree height, the exponential term should be equal to or less than zero; this is accomplished by constraining the coefficient a to be equal to or greater than zero. These basic model forms were modified to include spatial variables (Eqs. (4)–(7)) so that their relative predictive powers could be compared. The modifier approach was favoured because of its simplicity and parameter parsimony (Vanclay and Skovsgaard, 1997; Schmidt et al., 2006).

$$\hat{r} = e^{a+b\ln(\text{dbh})+cx} \quad (4)$$

$$\hat{r} = e^{a+b\ln(\text{dbh})+c\ln(x+1)} \quad (5)$$

$$\hat{L} = he^{-\max(0,a(h/\text{dbh})+bx)} \quad (6)$$

$$\hat{L} = he^{-\max(0,a(h/\text{dbh})+b\ln(x+1))} \quad (7)$$

where x is the independent variable to be tested, and c is a regression coefficient. Eqs. (4) and (5), like Eq. (2), give positive crown radius values regardless of the values of the regression coefficients. Eqs. (6) and (7) are adapted from Eq. (3) so that the regression coefficients need not be constrained and the directions of crown length relationships with height:diameter ratio (h/dbh) and the independent variables can vary freely.

2.3. Spatial variables

Nine spatial variables were calculated for each crown measurement sample tree. Six spatial diversity indices were calculated (Table 2): mean directional index, MDI (Eq. (8)); species mingling, M (Eq. (9)); diameter dominance, Udbh (Eq. (10)); height dominance, Uh (Eq. (11)); diameter differentiation, T (Eq. (12)); and diameter correlation index, DCI (Eq. (13)). The inclusion of individual tree elevation in the height dominance index, Uh, reflects the importance of topography in determining vertical canopy stratification and dominance (see Table 1 for the elevation ranges observed in the various plots). These spatially explicit structural indices share the same conceptual principles as spatially explicit competition indices. Therefore, the Hegyi competition index, Hg (Table 2, Eq. (14)), was also calculated for each sample tree. The total basal area of all neighbours (BA, m^2) and the total basal area of neighbours of larger dbh than the subject tree (BAL, m^2) were also calculated.

Spatial variables were calculated using several different numbers of nearest neighbours for each subject tree, based on Euclidean distances. All variables were calculated using the three, four, five and seven nearest neighbours (Fig. 5), and diameter differentiation, T, was also calculated for one nearest neighbour. Variables calculated using different numbers of neighbour trees were identified using numerical subscripts. For example, the species mingling index calculated using three neighbours would be written as M_3, and the same index calculated using four neighbours would be written as M_4.

Neighbour selection could result in trees outside plot boundaries being identified as neighbours. Edge correction was therefore required for unbiased estimation of spatial variables. Neither translation nor reflection edge correction (Pommerening and Stoyan, 2006) was deemed suitable, as the height dominance index (Uh) depends heavily on the elevation of individual trees, which could not be objectively modelled beyond plot boundaries. Instead, the random selection of crown measurement sample trees excluded buffer strips (Pommerening and Stoyan, 2006) in each plot. These strips were 10 m wide in the 1 ha plots and 6 m wide in the smaller plots CYB1 and CYB2. In three of the spruce data sets (CLG1, CLG2 and GWY1), however, distances to the seventh nearest neighbours of some reference trees exceeded buffer strip width. This was the case for five reference trees in CLG1, six in CLG2 and four in GWY1; in

Table 2
Individual tree indices used in this study

Index	Diversity of ...	Formula
Mean directional index (Corral-Rivas, 2006)	Tree positions	**(8)** $\text{MDI}_i = \sqrt{\left(\sum_{j=1}^{n}((X_j - X_i)(1/\text{HDist}_{ij}))\right)^2 + \left(\sum_{j=1}^{n}((Y_j - Y_i)(1/\text{HDist}_{ij}))\right)^2}$
Species mingling (von Gadow and Hui, 2002)	Tree species	**(9)** $M_i = \frac{1}{n}\sum_{j=1}^{n} w_j \quad m_j \begin{cases} 1, & \text{species}_i \neq \text{species}_j \\ 0, & \text{otherwise} \end{cases}$
dbh dominance (Aguirre et al., 2003)	Tree dimensions	**(10)** $\text{Udbh}_i = \frac{1}{n}\sum_{j=1}^{n}\text{udbh}_j \quad \text{udbh}_j \begin{cases} 1, & \text{dbh}_i > \text{dbh}_j \\ 0, & \text{otherwise} \end{cases}$
Height dominance (Aguirre et al., 2003)	Tree dimensions	**(11)** $\text{Uh}_i = \frac{1}{n}\sum_{j=1}^{n}\text{uh}_j \quad \text{uh}_j \begin{cases} 1, & h_i + Z_i > h_j + Z_j \\ 0, & \text{otherwise} \end{cases}$
dbh differentiation (Pommerening, 2002)	Tree dimensions	**(12)** $T_i = \frac{1}{n}\sum_{j=1}^{n}\left(1 - \frac{\min(\text{dbh}_i,\ \text{dbh}_j)}{\max(\text{dbh}_i,\ \text{dbh}_j)}\right)$
Diameter correlation index	Tree dimensions	**(13)** $\text{DCI}_i = \frac{\text{dbh}_i \sum_{j=1}^{n}\text{dbh}_j}{n\overline{\text{dbh}}^2}$
Hegyi index (Hegyi, 1974)	Tree dimensions	**(14)** $\text{Hg}_i = \sum_{j=1}^{n}\left(\frac{\text{dbh}_j}{\text{dbh}_i}\frac{1}{\text{HDist}_{ij}}\right)$

i is the reference tree, j is a neighbour tree, n is the number of neighbours, dbh is diameter at breast height (cm), $\overline{\text{dbh}}$ is the arithmetic mean diameter at breast height of all trees in the plot (cm), h is the tree height (m), HDist_{ij} is the horizontal distance between trees i and j (m), and X, Y and Z are Cartesian co-ordinates (m). Values of the species mingling, dbh dominance and height dominance indices (Eqs. (9)–(11)) are distributed between 0 and 1.

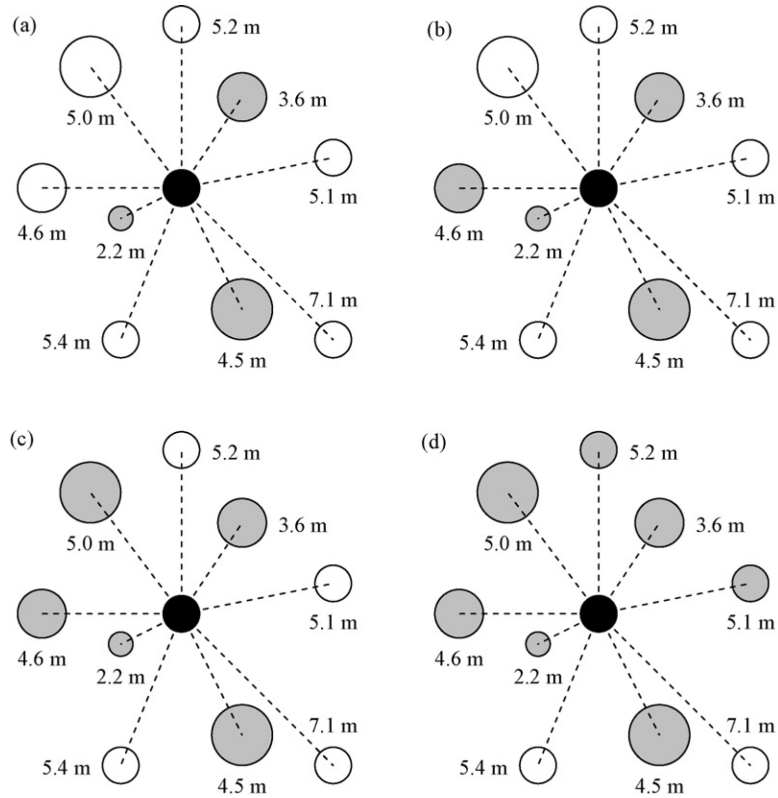

Fig. 5. Selection of the (a) three, (b) four, (c) five and (d) seven nearest neighbours of the reference tree (black circle) based on Euclidean distances, showing the trees identified as neighbours (grey circles) and surrounding trees not identified as neighbours (white circles).

addition, the distance to the fifth nearest neighbour of one reference tree in CLG2 exceeded buffer strip width. To determine whether this resulted in systematic variation in spatial variables, these were examined for significant non-parametric (Spearman's) correlations with the shortest distance to a plot boundary for each sample tree. The relationships observed were not considered sufficiently numerous or consistent to give cause for concern.

Non-parametric (Spearman's) correlation analyses were carried out in SPSS 11.5 (SPSS Inc.) using all data for each species to investigate relationships between crown dimensions and spatial variables.

2.4. Non-spatial variables

Although it was assumed that spatially explicit variables would be required to quantify tree interactions in stands which were, despite their plantation origins, relatively irregular in structure, model tests were also carried out with non-spatial variables for comparison. Two common variables, BAL (Eq. (15)) and BALMOD (Eq. (16)), were calculated for each tree as described by Schröder and von Gadow (1999). BALMOD was originally applied to pure, uniform stands, and includes an index of relative spacing (Eq. (17)) based on stand dominant height. Although most of the stands in this study are mixed and uneven-aged, dominant height was still calculated using data from all trees in each plot, rather than separately by species or cohort, as this was considered to be more representative of the overall stocking of the stands.

$$\mathrm{BAL}_{\mathrm{all},\,i} = \mathrm{BA}_{\mathrm{all}}(1 - p_i) \tag{15}$$

$$\mathrm{BALMOD}_i = \frac{(1 - p_i)}{\mathrm{RS}} \tag{16}$$

$$\mathrm{RS} = \frac{\sqrt{10{,}000/N}}{H} \tag{17}$$

where $\mathrm{BAL}_{\mathrm{all},i}$ is the basal area per unit area of all trees in a given plot larger than reference tree i ($\mathrm{m}^2\ \mathrm{ha}^{-1}$), $\mathrm{BA}_{\mathrm{all}}$ the basal area per unit area of all trees in a given plot ($\mathrm{m}^2\ \mathrm{ha}^{-1}$), p_i the basal area percentile of reference tree i, BALMOD_i the modified BAL for reference tree i, RS the relative spacing index, N the number of trees per unit area for a given plot (stems ha^{-1}), and H is the stand dominant height (m).

As with spatial variables, non-parametric correlations analyses were carried out in SPSS to investigate relationships with crown dimensions.

2.5. Model parameterisation and validation

Data from each crown measurement sample (i.e. all of the birch or spruce for a given research plot) were randomly split into parameterisation and validation data sets of roughly equal size for model testing. In addition, all of the crown measurement data for each species were used to produce a combined data set, randomly split in the same way. For each data set, basic crown models (Eqs. (2) and (3)) and modified models (Eqs. (4)–(7)) were parameterised using Solver (Frontline Systems, Inc.) in Microsoft Excel 2002 (Microsoft Corporation) to minimise the sum of squared errors between measured and predicted values. The modified models were parameterised for all 39 independent variables, the 37 combinations of spatial variables and numbers of nearest neighbours, and the non-spatial variables $\mathrm{BAL}_{\mathrm{all}}$ and BALMOD.

Model validations, comparing observed and predicted values of crown dimensions, were also carried out in Excel, calculating values of model relative bias and efficiency (von Gadow et al., 2003):

$$B\ (\%) = \frac{\sum_{i=1}^{n} (\hat{y}_i - y_i)}{n\bar{y}} \times 100 \quad (18)$$

$$E = 1 - \frac{\sum_{i=1}^{n} (\hat{y}_i - y_i)^2}{\sum_{i=1}^{n} (y_i - \bar{y})^2} \quad (19)$$

where B (%) is relative bias, E the efficiency, $\hat{y}_i$ the ith prediction (modelled crown radius or crown length), y_i the ith observation (measured crown radius or crown length), $\bar{y}$ the mean observation, and n is the number of observations. A t-test was used to determine whether bias was equal to zero. Efficiency values approach one with improving model performance; a value of zero indicates that the model explains no more variation than the mean value alone (von Gadow et al., 2003). Modified models containing spatial variables were ranked for each data set according to efficiency (and relative bias in the case of ties), as were models containing non-spatial variables. The validation results of the best models were compared with those of the basic models to determine whether the inclusion of spatial or non-spatial variables improved model performance.

3. Results

3.1. Relationships between crown dimensions, and spatial and non-spatial variables

The results of correlation analyses are summarised in Table 3. Many factors influence crown dimensions, particularly stand age, stocking density, thinning history, and species, and the interpretation of correlations should be considered in this context. In the plots studied, crown size generally increases with subject tree dominance (Udbh and Uh) and decreases with increasing competitive pressure (as quantified by the Hegyi index, Hg, the basal area of larger trees, BAL, or the non-spatial variables BAL_{all} and BALMOD). There are no significant correlations with MDI, suggesting that the regularity of the arrangement of neighbouring trees does not have a direct or simple effect on crown size. The negative relationships with species mingling (M) in spruce reflect the fact that most of the largest crowns are in plots CLG1 and CLG2, where mingling is minimal, and most of the smallest crowns are in plots CYB1 and CYB2, where mingling is high, but it should be noted that the CYB stands are both younger and more densely stocked than the CLG stands (Table 1). Diameter differentiation (T) is positively correlated with birch crown radius; birch crowns are therefore wider where tree sizes are more heterogeneous, possibly representing the occupancy of different canopy strata. Conversely, spruce crowns are larger in areas where tree sizes are more homogeneous; these negative correlations are strongly influenced by the relatively small naturally regenerated trees in CLG2 and GWY1, which show exceptionally high differentiation with their neighbours. The behaviour of the diameter correlation index DCI is complex. All else being equal, values increase as reference tree size increases. For a given reference tree size, however, they increase as average neighbour size increases, whereas for a given group of reference tree and neighbours they increase as stand mean dbh decreases. The positive relationships observed here between DCI and crown dimensions are likely to be due to the strong dependence of DCI on reference tree dbh (for both birch and spruce, DCI is significantly positively correlated with dbh). The positive correlations between crown dimensions and BA are perhaps counter-intuitive. For a given stand, a larger basal area of neighbouring trees might be expected to indicate a greater level of competition, with a corresponding negative effect on crown size. Over the range of plots sampled, however, the generally positive relationship between BA and crown size simply reflects the fact that the basal area of neighbours tends to be greater in plots where sample trees are larger and more widely spaced.

Table 3
Non-parametric (Spearman's) correlations significant at the 0.05 level between crown dimensions (crown radius, r, and length, L) and spatial and non-spatial variables for birch (BI, 125 trees) and Sitka spruce (SS, 154 trees)

	r_{BI}	L_{BI}	r_{SS}	L_{SS}
MDI_3				
MDI_4				
MDI_5				
MDI_7				
M_3			–	–
M_4			–	–
M_5		–	–	–
M_7		–	–	–
$Udbh_3$	+	+	+	+
$Udbh_4$	+	+	+	+
$Udbh_5$	+	+	+	+
$Udbh_7$	+	+	+	+
Uh_3	+	+	+	+
Uh_4	+	+	+	+
Uh_5	+	+	+	+
Uh_7	+	+	+	+
T_1	+		–	–
T_3	+		–	–
T_4	+		–	–
T_5	+		–	–
T_7	+		–	–
DCI_3	+	+	+	+
DCI_4	+	+	+	+
DCI_5	+	+	+	+
DCI_7	+	+	+	+
Hg_3	–	–	–	–
Hg_4	–	–	–	–
Hg_5	–	–	–	–
Hg_7	–	–	–	–
BA_3	+		+	+
BA_4	+		+	+
BA_5	+		+	+
BA_7	+		+	+
BAL_3		–		
BAL_4		–		
BAL_5		–		
BAL_7		–		
BAL_{all}	–	–	–	–
BALMOD	–	–	–	–

Symbol '+' indicates a positive correlation, '–' a negative correlation.

3.2. Alternative crown radius models

Table 4 shows the maximum efficiency values achieved for the basic crown radius model (Eq. (2)) and modified versions incorporating non-spatial and spatial variables (Eqs. (4) and (5)) for all data sets. Regardless of the modelling approach, efficiency values are generally poorest for CYB1 and CYB2 data sets, particularly for birch. Basic model efficiencies for individual plot data sets are significantly negatively correlated with median crown radius coefficient of variation (Fig. 3) and relative canopy displacement (Fig. 4) at the 0.05 significance level (non-parametric correlations, two-tailed, $n = 9$, $p = 0.030$ and 0.036, respectively), demonstrating that crown radius model performances are poorest in stands where crowns are most irregular in shape and most heavily displaced as a result of suppression. The models with non-spatial variables give slight efficiency gains for five data sets, but in

Table 4
Results of crown radius model tests for birch (BI) and Sitka spruce (SS) data sets, showing for each data set the maximum efficiency achieved by including non-spatial and spatial variables, and the gain in efficiency over the basic model

Data set (and number of trees)	Maximum efficiency (and gain over the basic model)		
	Basic model	With non-spatial variables	With spatial variables
CLG7 BI (50)	0.67	0.67 (+0.00)	0.76 (+0.09)
CYB1 BI (25)	−0.31	−0.19 (+0.12)	0.27 (+0.58)
CYB2 BI (25)	0.02	−2.11 (−2.13)	0.67 (+0.65)
GWY1 BI (25)	0.48	0.56 (+0.08)	0.62 (+0.14)
All plots BI (125)	0.40	0.42 (+0.02)	0.65 (+0.25)
CLG1 SS (50)	0.57	0.55 (−0.02)	0.61 (+0.04)
CLG2 SS (25)	0.49	0.54 (+0.05)	0.57 (+0.08)
CYB1 SS (25)	0.11	−0.11 (−0.22)	0.28 (+0.17)
CYB2 SS (25)	0.26	0.25 (−0.01)	0.47 (+0.21)
GWY1 SS (29)	0.75	0.79 (+0.04)	0.88 (+0.13)
All plots SS (154)	0.75	0.75 (+0.00)	0.77 (+0.02)

Table 5
Crown radius models incorporating spatial variables giving the highest efficiency values for birch (BI) and Sitka spruce (SS) data sets

Data set (and number of trees)	Model form	Independent variable	Efficiency	Relative bias (%)
CLG7 BI (50)	Eq. (5)	Hg_7	0.76	−1.28
CYB1 BI (25)	Eq. (4)	Uh_7	0.27	3.42
CYB2 BI (25)	Eq. (4)	Hg_7	0.67	4.30
GWY1 BI (25)	Eq. (4)	T_3	0.62	1.96
All plots BI (125)	Eq. (5)	BA_7	0.65	2.93
CLG1 SS (50)	Eq. (4)	MDI_5	0.61	0.41
CLG2 SS (25)	Eq. (5)	BAL_7	0.57	0.65
CYB1 SS (25)	Eq. (5)	$Udbh_3$	0.28	7.60
CYB2 SS (25)	Eq. (4)	BA_5	0.47	3.26
GWY1 SS (29)	Eq. (4)	Uh_7	0.88	−4.90
All plots SS (154)	Eq. (4)	Hg_7	0.77	−0.95

some cases actually give worse results than the basic model. Spatial models not only give efficiency gains in all cases, these gains are consistently greater than those for non-spatial models. Gains are especially great for CYB1 and CYB2 birch.

Details of the spatial models giving the highest efficiency values for each data set are shown in Table 5. None of these models is significantly biased at the 0.05 level. The Hegyi index (Hg), height dominance index (Uh) and basal area of neighbours (BA) are the most commonly represented independent variables, and seven is the most common number of neighbours selected. Most variables are not logarithmically transformed. The CLG1 spruce model features the mean directional index, MDI, despite the fact that this variable was not significantly correlated with crown dimensions.

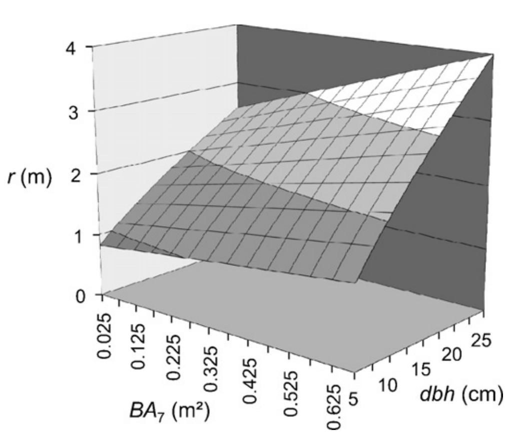

Fig. 6. Crown radius model behaviour for the combined birch data set over the approximate observed range of predictor variables, showing crown radius (r) in relation to reference tree dbh (dbh) and the basal area of the seven nearest neighbours (BA_7).

The models for the two full species data sets are given in Eqs. (20) and (21), and their behaviours are illustrated in Figs. 6 and 7. Both show increases in crown radius with increases in variables which might be expected to represent levels of competition (BA_7 and Hg_7). The spruce crown radius model (Fig. 7) returns extremely high values when both dbh and Hg_7 are high; in practice, however, such high values of Hg_7 are not associated with the larger trees.

$$\hat{r}_{BI} = e^{-1.34520+0.70302\ln(dbh)+0.90728\ln(BA_7+1)} \tag{20}$$

$$\hat{r}_{SS} = e^{-2.17846+0.82286\ln(dbh)+0.10903\,Hg_7} \tag{21}$$

where $\hat{r}_{BI}$ is the predicted birch crown radius (m) and $\hat{r}_{SS}$ is the predicted Sitka spruce crown radius (m).

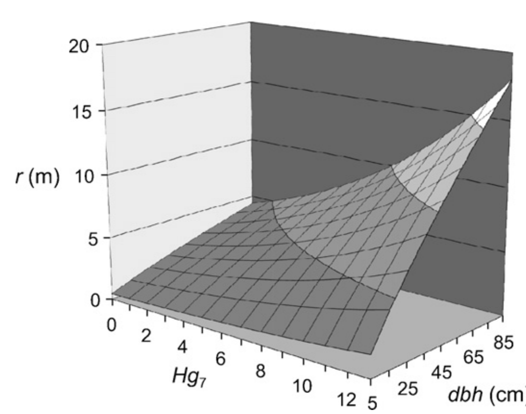

Fig. 7. Crown radius model behaviour for the combined Sitka spruce data set over the approximate observed range of predictor variables, showing crown radius (r) in relation to reference tree dbh (dbh) and the Hegyi index calculated using the seven nearest neighbours (Hg_7).

Table 6
Results of crown length model tests for birch (BI) and Sitka spruce (SS) data sets, showing for each data set the maximum efficiency achieved by including non-spatial and spatial variables, and the gain in efficiency over the basic model

Data set (and number of trees)	Maximum efficiency (and gain over the basic model)		
	Basic model	With non-spatial variables	With spatial variables
CLG7 BI (50)	0.69	0.66 (−0.03)	0.71 (+0.02)
CYB1 BI (25)	0.42	0.62 (+0.20)	0.55 (+0.13)
CYB2 BI (25)	0.31	0.47 (+0.16)	0.53 (+0.22)
GWY1 BI (25)	0.81	0.87 (+0.06)	0.85 (+0.04)
All plots BI (125)	0.59	0.60 (+0.01)	0.61 (+0.02)
CLG1 SS (50)	0.64	0.66 (+0.02)	0.70 (+0.06)
CLG2 SS (25)	0.65	0.70 (+0.05)	0.78 (+0.13)
CYB1 SS (25)	0.54	0.61 (+0.07)	0.63 (+0.09)
CYB2 SS (25)	0.55	0.50 (−0.05)	0.56 (+0.01)
GWY1 SS (29)	0.89	0.92 (+0.03)	0.92 (+0.03)
All plots SS (154)	0.67	0.65 (−0.02)	0.74 (+0.07)

Table 7
Crown length models incorporating spatial variables giving the highest efficiency values for birch (BI) and Sitka spruce (SS) data sets

Data set (and number of trees)	Model form	Independent variable	Efficiency	Relative bias (%)
CLG7 BI (50)	Eq. (6)	BA_7	0.71	4.75
CYB1 BI (25)	Eq. (7)	M_5	0.55	−11.22
CYB2 BI (25)	Eq. (7)	Hg_7	0.53	−8.27
GWY1 BI (25)	Eq. (7)	Hg_7	0.85	3.94
All plots BI (125)	Eq. (6)	BA_7	0.61	−0.01
CLG1 SS (50)	Eq. (7)	Hg_5	0.70	−2.10
CLG2 SS (25)	Eq. (7)	M_3	0.78	5.30
CYB1 SS (25)	Eq. (6)	BAL_3	0.63	9.09
CYB2 SS (25)	Eq. (6)	Uh_3	0.56	1.49
GWY1 SS (29)	Eq. (6)	Hg_7	0.92	3.42
All plots SS (154)	Eq. (6)	BA_5	0.74	2.53

3.3. Alternative crown length models

As with crown radius models, crown length model efficiencies are lowest for CYB1 and CYB2 data sets (Table 6). In general, however, efficiencies are higher than for crown radius models. Non-spatial models give efficiency gains in most cases, and these are greatest for CYB1 and CYB2 birch. Models incorporating spatial variables give gains in all cases, though these are lower than those for non-spatial models for CYB1 and GWY1 birch; again, the greatest gains are for CYB1 and CYB2 birch.

None of the spatial crown length models (Table 7) is biased at the 0.05 significance level. The Hegyi index (Hg) and basal area of neighbour trees (BA) are the most commonly included independent variables, with seven the most common number of neighbours. Approximately half of the models include logarithmic transformation of the spatial variable. Although most of the variables selected can be considered to represent competitive effects or reference tree dominance, the species mingling index features in one birch model and one spruce model, suggesting that crown interactions do not depend on tree size alone.

The models for the species combined data sets are given in Eqs. (22) and (23). Fig. 8 shows the behaviour of the birch model, with crown length increasing with basal area of neighbouring trees (BA_7) and decreasing with height:diameter ratio of the reference tree. Crown length also decreases with height:diameter ratio in the spruce model (Fig. 9) and additionally decreases with basal area of

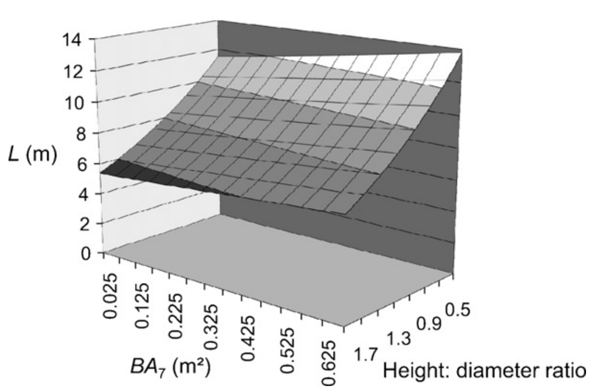

Fig. 8. Crown length model behaviour for the combined birch data set over the approximate observed range of predictor variables, showing crown length (L) of a tree 15 m in height in relation to reference tree height:diameter ratio (height (m) divided by dbh (cm)) and the basal area of the seven nearest neighbours (BA_7). Note that the height:diameter axis has been reversed.

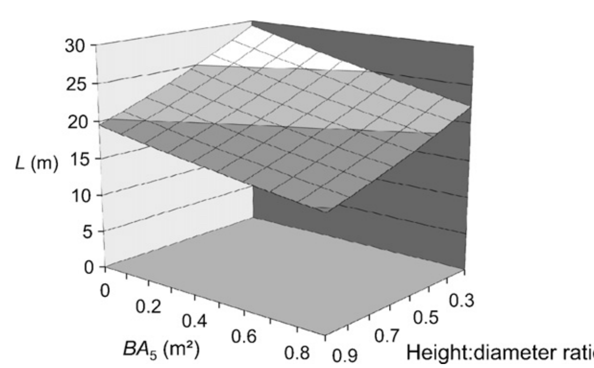

Fig. 9. Crown length model behaviour for the combined Sitka spruce data set over the approximate observed range of predictor variables, showing crown length (L) of a tree 35 m in height in relation to reference tree height:diameter ratio (height (m) divided by dbh (cm)) and the basal area of the five nearest neighbours (BA_5). Note that the height:diameter axis has been reversed.

neighbouring trees (BA_5).

$$\hat{L}_{BI} = he^{-\max(0,\ 0.54513(h/\mathrm{dbh}) - 0.28043 BA_7)} \quad (22)$$

$$\hat{L}_{SS} = he^{-\max(0,\ 0.58557(h/\mathrm{dbh}) + 0.30910 BA_5)} \quad (23)$$

where $\hat{L}_{BI}$ is the predicted birch crown length (m) and $\hat{L}_{SS}$ is the predicted Sitka spruce crown length (m).

4. Discussion

Our results have shown that simple crown radius and crown length models based on stem dimensions alone perform relatively poorly, in terms of model efficiency, in situations where trees are heavily suppressed due to excessive stocking. In these situations, the normally strong relationships between stem and crown dimensions become weaker, and crowns may be very irregular in shape, as quantified by the coefficient of variation of crown radius, and strongly displaced from stem bases, as quantified by relative canopy displacement. In this study, these effects have been particularly pronounced for birch.

Correlation analyses have revealed definite relationships between crown dimensions and a range of spatially explicit and non-spatial indices of stand structure. The inclusion of non-spatial indices can improve model performances in many cases, but greater and more consistent improvements can be achieved using spatially explicit structural indices and other spatial variables. This may indicate that the stands studied are too structurally complex for tree interactions to be modelled using non-spatial variables. Particularly large improvements in model performance have been achieved for the suppressed Coed y Brenin birch data sets. There is still much scope for improvement in the modelling of suppressed crowns, however, as absolute values of model efficiency remain low in some cases, particularly for CYB1 crown radius models. The relationships observed between crown dimensions and spatial variables highlight the intensely spatial nature of crown growth and interactions. It may be that, in the most extreme cases of competition, more sophisticated methods of explicitly modelling asymmetric crown shapes and crown displacement may be required (e.g. Cescatti, 1997; Umeki, 1995).

The variety of models produced for different data sets hints at the complexity of the underlying relationships. All of the spatial variables tested, with the exception of the diameter correlation index, featured in the most efficient models, and no one variable has been shown to be superior in accounting for the interaction of tree crowns. The variability of the models limits their wider use. At present, the most promising models for widespread application are those developed for the combined data sets for each species (Eqs. (20)–(23)). However, as with any models, these should be applied with caution outside the range of their parameterisation data, particularly since the relationships they show with measures of competition or local stand density are generally the reverse of what might be expected within a given stand (Figs. 6–8; cf. Fig. 9).

There is considerable scope for further study in this field. The potential range of model forms, structural indices and neighbour selection methods is vast, and future research may produce robust, effective models that can be applied with confidence across a broad range of stand structures. Most of the spatial variables tested in this study quantify the diversity of tree dimensions, but variables quantifying the diversity of tree positions (mean directional index, MDI) and species (species mingling, *M*) also contributed to viable models and similar indices could be explored. Many existing crown models could be used as the basis for further tests (e.g. Gill et al., 2000; Pretzsch et al., 2002). The models presented in this study are static, and the potential role of spatial diversity indices in dynamic crown models, such as crown base recession models, should also be investigated. Research on heavily suppressed crowns may reveal models that can account for the effects of extreme competition for space and light.

5. Conclusions

This study of the use of spatial diversity indices in crown dimension models has shown that these and other spatial variables can contribute to effective models of crown radius and crown length for birch and Sitka spruce growing in a variety of stand structures, and can yield particularly great gains in model performance in overstocked stands where interactions between crowns are exceptionally intense. The complexity of tree spatial interactions means that, at present, these models are largely stand specific due to their variability, but further work may produce more widely applicable indices and model forms, and may reveal new ways of modelling the crowns of trees facing extreme competition pressure.

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References

Aguirre, O., Hui, G., von Gadow, K., Jiménez, J., 2003. An analysis of spatial forest structure using neighbourhood-based variables. For. Ecol. Manage. 183, 137–145.

Ayhan, H.O., 1977. A crown radius instrument. Scot. For. 31, 67–70.

Berezovskava, F.S., Karev, G.P., Kisliuk, O.S., Khlebopros, R.G., Tsel'niker, Y.L., 1997. A fractal approach to computer—analytical modelling of tree crowns. Trees 11, 323–327.

Biging, G.S., Dobbertin, M., 1992. A comparison of distance-dependent competition measures for height and basal area growth of individual conifer trees. For. Sci. 38, 695–720.

Biging, G.S., Gill, S.J., 1997. Stochastic models for conifer tree crown profiles. For. Sci. 43, 25–34.

Cescatti, A., 1997. Modelling the radiative transfer in discontinuous canopies of asymmetric crowns. I. Model structure and algorithms. Ecol. Model. 101, 263–274.

Corral-Rivas, J.J., 2006. Models of tree growth and spatial structure for multi-species, uneven-aged forests in Durango (Mexico). Ph.D. thesis. University of Göttingen, 135 pp.

Davies, O., 2006. Measuring and Modelling Sitka Spruce (*Picea sitchensis* (Bong.) Carrière) and Birch (*Betula* spp.) Crowns, with special reference to terrestrial photogrammetry. Ph.D. thesis. University of Wales, Bangor, 185 pp.

Francis, J.K., 1986. The relationship of bole diameters and crown widths of seven bottomland hardwood species. USDA Forest Service Research Note SO-328. Southern Forest Experiment Station, 3 pp.

Gill, S.J., Biging, G.S., Murphy, E.C., 2000. Modeling conifer tree crown radius and estimating canopy cover. For. Ecol. Manage. 126, 405–416.

Hale, S., 2004. Managing light to enable natural regeneration in British conifer forests. Forestry Commission Information Note 63. Forestry Commission, Edinburgh, 6 pp.

Hasenauer, H., 1997. Dimensional relationships of open-grown trees in Austria. For. Ecol. Manage. 96, 197–206.

Hegyi, F., 1974. A simulation model for managing jack-pine stands. In: Fries, J. (Ed.), Growth Models for Tree and Stand Simulation. Royal College of Forestry, Stockholm, pp. 74–90.

Humphrey, J.W., Holl, K., Broome, A.C. (Eds.), 1998. Birch in Spruce Plantations: Management for Biodiversity. Forestry Commission Technical Paper 26. Forestry Commission, Edinburgh, 69 pp.

Kozlowski, T.T., Kramer, P.J., Pallardy, S.G., 1991. The Physiological Ecology of Woody Plants. Academic Press, San Diego, 657 pp.

Moravie, M.-A., Robert, A., 2003. A model to assess relationships between forest dynamics and spatial structure. J. Veg. Sci. 14, 823–834.

Muth, C.C., Bazzaz, F.A., 2003. Tree canopy displacement and neighborhood interactions. Can. J. For. Res. 33, 1323–1330.

Nagel, J., Albert, M., Schmidt, M., 2002. Das waldbauliche Prognose – und Entscheidungsmodell BWINPro 6.1 – Neuparametrisierung und Modellerweiterungen.

(The silvicultural decision support system BWINPro 6.1—New parameterisation and model extensions). Forst und Holz 57, 486–493.
Ottorini, J.-M., le Goff, N., Cluzeau, C., 1996. Relationships between crown dimensions and stem development in *Fraxinus excelsior*. Can. J. For. Res. 26, 394–401.
Pommerening, A., 2002. Approaches to quantifying forest structures. Forestry 75, 305–324.
Pommerening, A., Stoyan, D., 2006. Edge-correction needs in estimating indices of spatial forest structure. Can. J. For. Res. 36, 1723–1739.
Pretzsch, H., Biber, P., Ďurský, J., 2002. The single tree-based stand simulator SILVA: construction, application and evaluation. For. Ecol. Manage. 162, 3–21.
Schmidt, M., Nagel, J., Skovsgaard, J.P., 2006. Evaluating individual tree growth models. In: Hasenauer, H. (Ed.), Sustainable Forest Management: Growth Models for Europe. Springer-Verlag, Berlin, pp. 151–163.
Schröder, J., von Gadow, K., 1999. Testing a new competition index for maritime pine in northwestern Spain. Can. J. For. Res. 29, 280–283.
Siostrzonek, E., 1958. Radialzuwachs und Flächenzuwachs. (Radial increment and basal area increment). Forstw. Cbl. 77, 237–254.
Smith, W.R., 1994. An empirical evaluation of a three-dimensional crown model for predicting volume growth. For. Ecol. Manage. 69, 199–209.
Umeki, K., 1995. Modeling the relationship between the asymmetry in crown display and local environment. Ecol. Model. 82, 11–20.
von Gadow, K., 1996. Modelling growth in managed forests—realism and limits of lumping. Sci. Total Environ. 183, 167–177.
von Gadow, K., Hui, G., 1999. Modelling Forest Development. Kluwer Academic Publishers, Dordrecht, 213 pp.
von Gadow, K., Hui, G., 2002. Characterizing forest spatial structure and diversity. In: Björk, L. (Ed.), Sustainable Forestry in Temperate Regions. Proceedings of the SUFOR International Workshop, Lund, Sweden, April 7–9, pp. 20–30.
von Gadow, K., Hui, G.Y., Chen, B.W., Albert, M., 2003. Beziehungen zwischen Winkelmaß und Baumabständen. (Relationship between the Winkelmaß and nearest neighbor distances). Forstw. Cbl. 122, 127–137.
Vanclay, J.K., Skovsgaard, J.P., 1997. Evaluating forest growth models. Ecol. Model. 98, 1–12.