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Individual-tree distance-dependent growth models for uneven-sized Norway spruce

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Individual tree selection (ITS) is one option to manage uneven-sized forest ecosystems. However, scientifically based field guidelines adapted to ITS and economic profitability are rare, often because there is a lack of suitable tree models to use in growth and treatment simulations. The objective of this study is to develop individual-tree distance-dependent growth models focusing on Norway spruce dominated uneven-sized stands. Three models of different complexity, but with the same structural basis, are presented, followed by some examples of growth patterns for the subject trees. The data include 1456 trees (307 sample trees) collected from five sites in southern Sweden. The basic model (S) depends on subject tree size as the predictor, the second model (SD) adds distance to competitors as a predictor, and the third model (SDC) adds crown ratio as a predictor to the structure. R^2_{Adj} increases with number of predictors from 0.48 to 0.58 to 0.62. The levels of RMSE improve accordingly from 5.02 cm^2 year^{-1} (S) to 4.43 cm^2 year^{-1} (SD) and 4.26 cm^2 year^{-1} (SDC). The present calibration range and model structures primarily make the models suitable for management simulation of individual-tree selection of Norway spruce in southern Sweden. The format of the models allows for further extension with additional predictors and calibration data with greater coverage.

Introduction

Uneven-sized forest management with individual tree selection (ITS) is one way to accommodate diverse expectations from various stakeholders. However, increased application of ITS is, in many regions, hindered by the paucity of scientifically based field guidelines. Currently there are relatively few tree growth models available that are appropriate for the ITS scenario analyses required to develop optimal field recommendations.

ITS is generally understood as a practice in which trees are individually selected for harvest in a compromise between set management aims, e.g. silvicultural, economic or ecological (Pommerening and Murphy 2004; Spinelli et al. 2016). In ideal case, the corresponding field operations follow a science-based protocol of selection guidelines or rules, defined in accordance with the management goals for the forest.

In the context of resource use efficiency (Binkley 2004), ITS guidelines that optimize round wood value production are of interest. This aim implicates that the field selection analysis shall evaluate whether a tree group, which is competing for the same resources as the subject tree, will perform better or worse if the subject tree is selected for harvest or not. This decision involves many dimensions, of which a central part is the ability to forecast individual tree growth of residual trees depending on the decision taken.

The task of defining an appropriate structure for an individual-tree growth model, adapted to the specified requirements, involves compromises between conflicting interests, including model complexity to achieve biological realism (Buchman and Shifley 1983), and model simplicity to allow for flexibility and relevance in field applications (Pacala et al. 1996; Robinson and Monserud 2003). Theory-oriented approaches support more flexible representation of data (Weiskittel et al. 2011) and are potentially less sensitive to extrapolation beyond the observed data range (Pretzsch 2009; Weiskittel et al. 2011) compared with more pure statistical methods. At the other end, theoretical complexity should be constrained to the level at which input and output variables are compatible with units available for the field user (Pukkala and Miina 1998; Pretzsch 2009).

Distance-dependent models (Munro 1974) are adequate tools for quantifying the variation in stand structure, which enables precise prediction of single tree growth (Bella 1971; Mitchell 1975; Daniels et al. 1986; Pukkala 1989; Canham et al. 2004; Pretzsch 2009, p. 310). With distance-dependency incorporated, the model can be used to analyze spatial impact on ITS. Results from distance-dependent models are also easier to transform into useable field guidelines than those from distance-independent models (Pukkala and Miina 1998).

Tree age should not be included as a predictor for growth in uneven-sized stands, due to large variances, both within stands

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(Peng 2000; Vanclay 2012) and within diameter-classes (Tarasiuk and Zwieniecki 1990). Instead, tree size is the most appropriate predictor of tree growth in structurally diverse stands (Shiue 1962; Zeide 1993; Pukkala et al. 2009). It is furthermore crucial that growth models intended for ITS application are calibrated with data from representative diverse stand structures (Pukkala et al. 2009; Lundqvist 2017).

The majority of the tree-growth models developed for Norway spruce (*Picea abies* (L.) Karst.) and Fennoscandia are distance-independent (Näslund 1935; Jonsson 1980; Söderberg 1986; Holte and Solberg 1989; Hynynen et al. 2002; Andreassen and Tomter 2003; Pukkala et al. 2009; Elfving and Nyström 2010; Pukkala et al. 2013; Bianchi et al. 2020a). Regarding the few existing distance-dependent models, some rely on tree age as predictor (Pukkala et al. 1998; Vettenranta 1999) and others are calibrated exclusively on even-sized stands (Pukkala 1989; Tham 1989; Pukkala and Kolström 1991; Pukkala et al. 1994). An exception is Bianchi et al. 2020b) who presented a distance-dependent model for southern Finland and ITS. This model has a statistical polynomial structure, which makes it relatively complex in terms of number of predictor variables. Therefore, based on the existing limited range of models, there is room for additional spatial models with a stronger focus on theoretical simplicity.

The model variables in an individual-tree growth model need to describe at minimum two core processes: (1) the subject tree growth potential and (2) the growing space available due to competition (Zeide 1993; Hasenauer 2006). Concerning the first part, the tree growth potential, Zeide (1993) found that it could in turn be broken down into two opposing components. The first positive component represents the innate tendency towards exponential multiplication, associated with the biotic potential. The second opposing component represents the constraints imposed by internal self-regulatory mechanisms (and, if not separated, also by external factors associated with competition, limited resources and damage). The decline component is traditionally based on tree age but Zeide (1993) also proposed a general formula based on tree size. The differential form of the logistic function is an example of an equation that meets the above criteria. It was first used for tree growth modelling by Mackinney (1937). An alternative but similar differential equation, with a closed-form solution, has recently been developed by Lohmander (2017).

The influence of competition from a neighbouring tree (the second process) should be a decreasing function of the distance between the neighbour and the subject tree and an increasing function of the size of the neighbour (Weiner and Solbrig 1984). A wide spectrum of distance-dependent methods has been proposed for weighting competitor influence (Dale et al. 1985; Biging and Dobbertin 1992; Burkhart and Tomé 2012). Most studies report no clear trends regarding which competition index that displays the best performance (Alemdag 1978; Weiner and Solbrig 1984; Daniels et al. 1986; Pukkala 1989; Biging and Dobbertin 1995; Miina and Pukkala 2002; Rivas et al. 2005). Some studies, however, indicate that size-distance indices are superior (Tomé and Burkhart 1989; Biging and Dobbertin 1992; Filipescu and Comeau 2007).

Weiskittel et al. (2011, p. 26) presented an overview of the considerations necessary for including a size-distance index in a growth model: (1) decide on a size attribute, (2) determine which trees are competitors, (3) define a relative size estimate, and (4) introduce a method of weighting competitor influence.

The most common variables used as size attribute are diameter at breast height (dbh), and basal area at breast height (Burkhart and Tomé 2012, p. 210). Competitors are generally identified by application of a fixed rule determining whether a neighbouring tree is a competitor or not (Soares and Tomé 1999; Pretzsch 2009, p. 295). The identification with a fixed rule results in unwanted edge effects, which are likely to influence model performance (Martin et al. 1977). One strategy to smooth out distinct edges and simultaneous weight competitor influence is to use non-linear distance functions with a defined asymptote (Soares and Tomé 1999; Elfving and Jakobsson 2006). The relative size of competing trees is most often expressed by the ratio of competitor size to subject tree size (Hegyi 1974; Martin and Ek 1984; Biging and Dobbertin 1992).

Previous research indicates that indices of competition often fail to explain major parts of the variation introduced by local competition (Soares and Tomé 1999) and the performance of individual indices varies according to forest type and forest conditions (Burkhart and Tomé 2012, p. 228).

Norway spruce is the most important commercial tree species in southern Fennoscandia, and as a secondary tree species it is well suited for uneven-sized forest management and ITS. The objective of this study is to develop individual-tree distance-dependent growth models focusing on Norway spruce dominated uneven-sized stands on fertile sites in southern Sweden. Furthermore, the model shall be constructed with components backed by theoretical reasoning and aim for structural simplicity, high accuracy, and facilitate for spatial ITS management analyses.

Three basal area increment models with different levels of complexity, but with the same structural basis, are presented, followed by some examples of subject tree growth patterns depending on the influence of competitor distance, competitor tree size, subject tree crown ratio, and subject tree size.

Methods

Calibration data

Five separate plots in southern Sweden were selected for collection of calibration data. Selected sites represent uneven-sized Norway spruce dominated stands, medium to fertile site quality, without thinning treatments in the last 10-year period, see Table 1. Other species were present, the main one being Scots pine (*Pinus sylvestris*). All the stands are a result of natural regeneration. Past management input ranged from active selection cutting to laissez-faire cultivation with self-promoted tree size diversification, see Figure 1.

One square plot per site, 60 × 60 m, was measured. Positions were recorded for all trees with diameter at breast height (dbh) above 6 cm, using Postex equipment (Haglöf) which employs ultrasound and triangulation for distance measurements. Coordinates were measured from nine circular sample plots per site, evenly distributed in a grid. The nine sub-plots were inter-fitted into one global coordinate map by ordinary least square regression of double-measured coordinate reference points, defined by

Table 1 Model training data sets.

	Measure	Mosshult	Romperöd	Simontorp	Öveshult	Lilla Norrskog
Site	Latitude (°)	57°08	56°19	56°21	56°37	57°18
	Altitude (m)	190	100	120	210	270
	Site index (SI)[a]	G31	G30	G31	G30	G29
Stand	Number of stems (st ha^{-1})	920	654	612	726	488
	Basal area (m^2 ha^{-1})	38	30	30	32	32
	Mean dbh (cm)	19.3	20.1	22.1	20.8	25.6
	Proportion of Norway Spruce	0.63	0.58	0.74	0.83	0.62
	Time since last cutting (years)	>50	44	10	>30	>10
	Self-thinning ratio	0.18	0.07	0.05	0.1	0.03
Sample trees	Number of sample trees	57	43	68	74 (71)[b]	65
	Mean dbh (cm)	24.2	23.2	22.6	23.6	20.9
	SD dbh (cm)	13.4	12.6	12.2	10.8	13.3
	Max dbh (cm)	60.5	51.5	51.5	50.9	51.2
	Min dbh (cm)	6.8	6.1	6.4	5.9	6.0
	Mean growth (cm^2 $year^{-1}$)	6.50	8.07	8.14	6.80	9.52
	SD growth (cm^2 $year^{-1}$)	6.13	7.13	7.14	5.07	8.85
Revision	Period	2012–2016	2012–2016	2013–2017	2013–2017	2013–2017

Stand measures based on trees with dbh (diameter at breast height) > 6 cm. Species proportions based on basal area. Self-thinning ratio represents number of trees that have died within the last 10 years divided by number of living trees. SD = standard deviation. [a]SI = height at age 100, according to the Swedish system (Hägglund and Lundmark 1977). [b]The model that incorporates crown ratio included 71 of the sample trees.

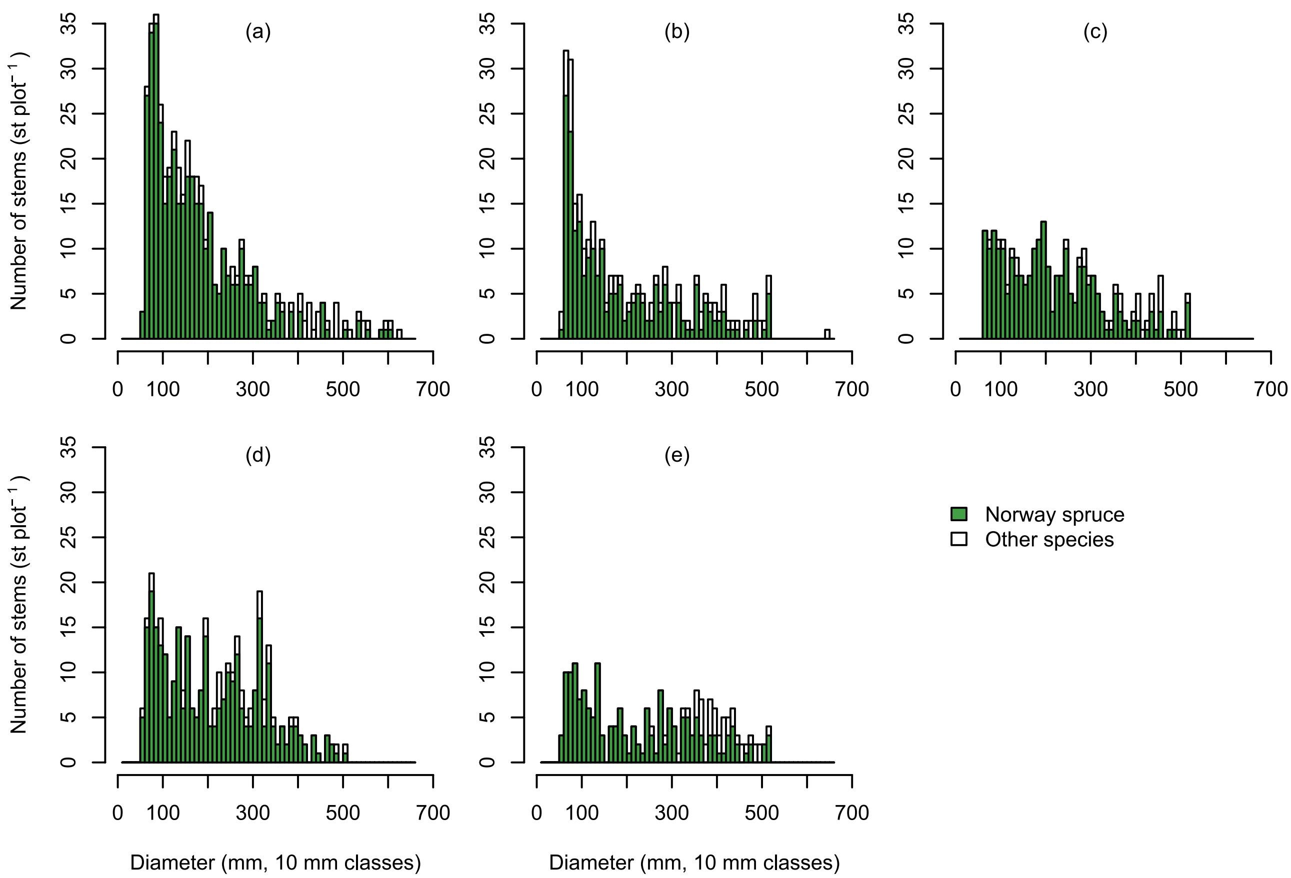

Figure 1 Diameter distribution histograms for the calibration data plots, (a) Mosshult, (b) Romperöd, (c) Simontorp, (d) Öveshult and (e) Lilla Norrskog.

sticks placed along the sub-plot borders. As a consequence of the circular shape of the sub-plots, some additional trees, adjacent to the 60 × 60 m square, were recorded and used for the calibration. The resulting total data set, from the five sites, consisted of 1456 live tree positions. Data on species and cross-calipered dbh was collected for all trees. At one of the sites, tree positioning was also undertaken using a terrestrial laser (Leica P40), which indicated a systematic underestimation of the Postex distances by 1–3 per cent and a random variation of 4 cm (1 SD).

Sample trees ($n = 307$) were selected for additional data collection and later use as subject trees in the model calibration. The selection used stratified random sampling, based on tree variables within four fixed sub-divisions of dbh-classes. The selection within each strata was made subjectively on the basis of two-dimensional plots of preliminary competition variables and maximizing the coverage in these plots. Examples of such variables are tree diameter, summed basal areas of all trees within a certain radius or basal area of larger spruce within a certain radius. Only trees with complete records of competitor tree positions within 10 m were selected as sample trees. The additional data from the sample trees covered tree height, crown length, crown width and annual ring width from the last 5 years. Ring widths were measured from increment cores extracted from the north side at breast height (corresponding calendar years are referred to as revision period in Table 1), using an LINTAB 6 device (RinnTech). Mean measurement error was estimated to 0.016 mm, of which 38 per cent is explained by technical error and the remaining part is due to intra ring width variations and shrinkage. To be included in the data set, the sample trees also had to meet the following criteria: (1) no detected root rot within the sapwood, (2) a live top shoot, and (3) no visible damage that could impair growth and that has been caused by factors other than tree competition.

To prepare the data set for calibration of the model the tree diameters at the start of the growth period had to be estimated. To do this, the ring widths of the last 5 years were used to calculate the total diameter growth for each sample tree. From this, simple linear regression was used to estimate diameter growth as function of tree diameter. The regression model was then used to reduce the diameter of all trees except the sample trees. For the sample trees, the year ring measurements were used directly.

Modelling

The selected model structure can be described as of ‘grey box’ type (Pretzsch 2009, p. 428), built up by structures that can, to some extent, be explained by biological or physical phenomena. The first part represents the internal growth potential of the subject tree and follows the structure suggested by Lohmander (2017), see equation (1). The expression consists of two terms describing the biotic potential and the constraints due to increasing size (Zeide 1993).

$$\frac{dx_i}{dt} = a_1 x_i^{0.5} + a_2 x_i^{1.5} \tag{1}$$

where $\frac{dx_i}{dt}$ is the basal area increment of subject tree $\boldsymbol{i}$ (cm^2 year^{-1}), $\boldsymbol{x}$ is basal area (m^2) and the parameters $\boldsymbol{a}$ are regression coefficients. The exponent 0.5 of the first term (the biotic potential) is defined by proportions between tree diameter (square root of the basal area), vertical crown projection area and basal area growth. The second term, the internal growth constraint, is a relative share multiplier, defined by the difference between 1 and a fitted proportion of the basal area, $\mathbf{1}-\boldsymbol{bx}$. Hence, $\frac{dx_i}{dt} = a_1x^{0.5}(1 - bx) = a_1x^{0.5} - a_1bx^{1.5}$ (Lohmander 2017).

The second part, the competition index (**CI**), adds external growth restriction to the first internal growth part due to inter-tree competition based on size-distance indices (see equation (2) for the fundamental structure). The formula is a development from the general structure described by Burkhart and Tomé (2012, p. 210).

$$\mathrm{CI}_i = \sum_{j \neq i}^{n} x_j \, g\left(x_i, x_j\right) \, f\left(R_{ij}\right) \tag{2}$$

where **CI** is defined as the sum of the basal area $\boldsymbol{x}$ of all competitor trees, weighted by a size weighting function ($g(x_i, x_j)$) and by a distance weighting function ($f(R_{ij})$), in relation to each competitor tree $\boldsymbol{j}$. From the assumptions above, candidate formulae for CI were created and evaluated separately. For the distance weighting function, $f(R_{ij})$, three requirements were set:

1. The effect of competition shall decrease with distance, i.e. $\frac{df(R)}{dR} \leq 0$.
2. The decrease with distance must be strong enough so that the competition from trees close to the subject tree is more important than the total competition from trees far away. Expressed formally, this means that there should exist a distance, $\boldsymbol{d}$, probably in the range of 4–10 m, for which the area integral $\int_0^d f(R) \cdot 2\pi R \cdot dR$ is greater than $\int_d^\infty f(R) \cdot 2\pi R \cdot dR$. In other words, for a tree in a forest with reasonably even stem distribution, the summed competition from trees within the distance of $\boldsymbol{d}$ is more important than the sum of the competition from all other trees in the forest.
3. Getting closer to the subject tree, the weighting function shall approach a maximum value asymptotically, i.e. $\lim_{R \to 0} f(R) = k$ and $\frac{df(0)}{dR} = 0$.

Once the basic **CI** formula was selected, it was further developed and fitted simultaneously with the complete growth model. Please refer to Olsson and Fagerberg (2019) for further details.

The candidate formulae of the total model expressions were evaluated in the first development phase with adjusted R^2, statistical properties of the regression parameters and residual analysis. In a second phase, when the main part of the model structure was formulated, 10-fold cross-validation was also employed. For the cross-validation, the total sample was randomly divided into ten groups of equal numbers of subject trees. From this grouping, ten different training samples were created by omitting one test group in each sample; i.e. each test group contained unique observations where each observation is used only once for validation. The model was then fitted to each of these training samples and the performance was studied with the excluded validation group (residual plots and RMSE), see Figure 2. Furthermore, the sample-to-sample-variation of the parameter values were standardized and analyzed (Figure 3). Empirical studies have shown that 5- to 10-folds is optimal to yield test error rate

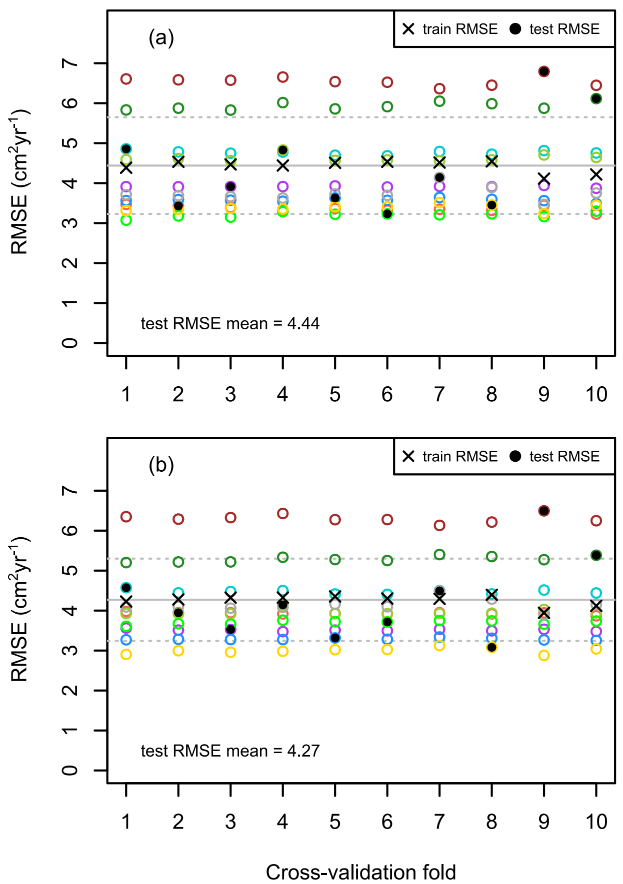

Figure 2 RMSE per cross-validation fold with (a) the SD-model and (b) the SDC-model (included predictors; S = tree size, D = inter-tree distance, and C = crown ratio). Lines represent test RMSE values; grey solid = mean, grey dotted = standard deviation. Test sets are indicated as empty circles with a unique colour per sample when they are part of the training set. Cross indicates training set mean value. Differences between training and test RMSE means are 0.01 for the SD-model and 0.01 for the SDC-model (training RMSE d.f. ≥ 273, test RMSE d.f. ≥ 30).

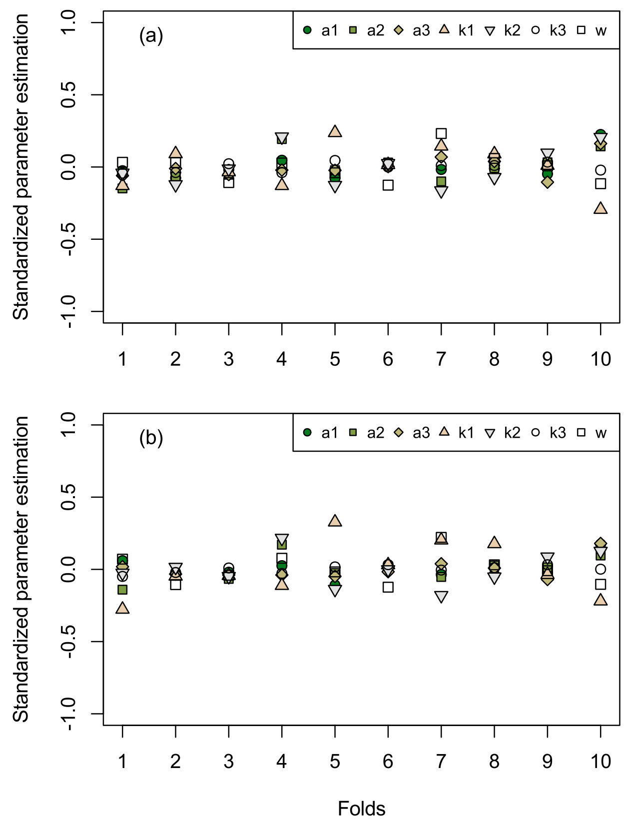

Figure 3 Fitted parameter estimates per cross-validation fold, standardized as relative deviation from mean, (a) SD-model and (b) SDC-model (included predictors; S = tree size, D = inter-tree distance and C = crown ratio).

estimates with a balanced trade-off between high bias and high variance effects (James et al. 2013).

Three model alternatives were developed with different numbers of predictor variables: (1) with the predictor subject tree size (S); (2) with the predictors tree size and distance to competitors (SD); and (3) with the predictors tree size, distance to competitors and crown ratio of the subject tree (SDC), see equations (3)–(5).

$$\mathrm{S}: \frac{dx_i}{dt} = a_1 x_i^{0.5} + a_2 x_i^{1.5} = x_i^{0.5}\,(a_1 + a_2 x_i) \tag{3}$$

$$\begin{aligned}\mathrm{SD}: \frac{dx_i}{dt} &= a_1 x_i^{0.5} + a_2 x_i^{1.5} + a_3 x_i^{0.5}\left(\sum_{j\neq i} x_j \left(\frac{x_j}{x_i}\right)^{k_2} e^{-\left(\frac{R_{ij}}{k_3}\right)^2} w_j\right)^{k_1} \\ &= x_i^{0.5}\left(a_1 + a_2 x_i + a_3\left(\sum_{j\neq i} x_j \left(\frac{x_j}{x_i}\right)^{k_2} e^{-\left(\frac{R_{ij}}{k_3}\right)^2} w_j\right)^{k_1}\right)\end{aligned} \tag{4}$$

$$\begin{aligned}\mathrm{SDC}: \frac{dx_i}{dt} &= \mathrm{CR}\cdot a_1 x_i^{0.5} + \mathrm{CR}\cdot a_2 x_i^{1.5} + \mathrm{CR}\cdot a_3 x_i^{0.5} \\ &\quad \times \left(\sum_{j\neq i} x_j \left(\frac{x_j}{x_i}\right)^{k_2} e^{-\left(\frac{R_{ij}}{k_3}\right)^2} w_j\right)^{k_1} \\ &= \mathrm{CR}\cdot x_i^{0.5}\left(a_1 + a_2 x_i + a_3\left(\sum_{j\neq i} x_j \left(\frac{x_j}{x_i}\right)^{k_2} e^{-\left(\frac{R_{ij}}{k_3}\right)^2} w_j\right)^{k_1}\right)\end{aligned} \tag{5}$$

where **CR** is the living crown ratio of total tree height (living crown length is defined by the lowest living branch). ***w*** is a parameter used for competitor tree species other than spruce (if spruce then ***w*** = 1). R_{ij} is the distance between the subject tree ***i*** and competitor tree ***j*** (m). Linear parameters are indicated by ***a***, while non-linear parameters are indicated by ***k***.

The fitting of the models was accomplished in two steps. The first step applied a hierarchical setup using the Matlab function nlinfit (a numerical iterative function for non-linear least square regression) to estimate the non-linear parameters. For each call by nlinfit, the linear parameters, a_1 to a_3, were estimated analytically by standard linear least squares inside the call-back function. In this step, each site was allocated a unique value of

Table 2 Observation data for the even-sized test set.

	Measure	1Thin C3/C24	3Thin C3
Site	Latitude (°)	56°33	56°33
	Altitude (m)	110	110
	Site index (SI)[a]	G32/G33	G32
Stand	Number of stems (st ha^{-1})	2089/2511	756
	Basal area (m^2 ha^{-1})	21.1/31.0	26.4
	Mean dbh (cm)	10.9/12.2	20.5
	Proportion of Norway Spruce	1	1
	Time since last cutting (years)	–	9
Sample trees	Number of sample trees (st)	396	64
	Mean dbh (cm)	11.6	20.8
	SD dbh (cm)	3.2	5.0
	Max dbh (cm)	19.4	30.1
	Min dbh (cm)	3.4	7.4
	Mean growth (cm^2 year^{-1})	5.5	10.6
	SD growth (cm^2 year^{-1})	4.1	7.5
Revision	Period	1987–1993	2010–2020

Initial conditions of two trial plots C3 and C24 represent first thinning (1Thin) and the later revision of C3 represents third thinning (3Thin). For 1Thin, some of the stand measures and the Site index are presented per plot. SD = standard deviation. [a]SI = height at age 100, according to the Swedish system (Hägglund and Lundmark 1977).

a_1, but all other parameters remained shared. In the second step, all other parameters were fixed and a single common value of a1 was estimated using standard linear least squares fitting.

The two-step parameter fitting was chosen since it was found that it resulted in less variation of the parameter estimates in the cross-validation tests; i.e. it was considered as more robust compared with the single step approach, see discussion below.

Performance in even-sized stands

The performance of the SD-model was also tested in even-sized stand conditions. Data from the Skogaby trial site in the southwest of Sweden, which is run under the auspices of the Swedish University of Agricultural Sciences, was used. Three trial plots were divided into two groups representing the stand development stage before first thinning (1Thin) and before third thinning (3Thin), respectively, see Table 2. Each plot is 30 × 30 m, surrounded by a 10 m zone in which the same treatment as the central plot is applied. The plots were established by planting and the 3Thin stand was thinned 17 and 9 years before the start of the revision period. The SDC model was assumed to perform similar to the SD model in even-sized stands, therefore it was not tested.

Results

Adjusted coefficient of determination (R^2_{Adj}) increased from 0.48 to 0.58 when the size-distance index was added to the model (Table 3), while adding the predictor crown ratio resulted in a further moderate improvement to 0.62. Consequently, model performance follows the degree of complexity; however, the level of unexplained variation is only slightly improved when the crown ratio variable is added on top of distance weighting (Figure 4). The validity of the models, expressed as RMSE, improves according to the same pattern, with lower errors the more predictors that are included; 5.02 cm^2 year^{-1} (S); 4.43 cm^2 year^{-1} (SD); and 4.26 cm^2 year^{-1} (SDC). Corresponding RMSE mean values for the test-folds in the cross-validation are almost identical (Figure 2). The residual analyses show no systematic trends related to any of the predictor variables. However, the mean residuals calculated per site (Table 4) indicate that site quality differences represent a considerable part of the unexplained variation. As expected, residual variation is heteroscedastic and increases with predicted growth level (Figure 5). Predicted growth per observation, site and model is displayed in Figure 6. With crown ratio added, residual variation remains, to a large extent, unaffected except for a faintly visible improvement for the most productive trees.

When the SD model was tested on even-sized stands the results indicated a general and systematic overestimation of approximately 5–6 cm^2 year^{-1} (Figure 7).

For the purpose of visualizing the competition effects, annual ring widths based on the SDC-model are shown for a theoretical tree group, where one variable at time is changed, see Figure 8. Comparing the ranges of impact, the crown ratio is the variable that has the largest impact on radial growth, followed by distance to large competitors. The distance to large competitors has a distinct impact on all subject tree sizes, with more pronounced effects the smaller the subject tree and the shorter the distance. The size of large competitors also displays noticeable effects, more clearly seen for small subject trees. Annual ring widths are fairly stable for subject trees between 10 and 40 cm dbh with a rapid decrease in smaller trees.

Discussion

The model structure chosen is based on a few hypotheses about the growth potential of the tree and the impact of competition

Table 3 Regression statistics of the S-, SD- and SDC-models (included predictors; S = tree size, D = inter-tree distance, and C = crown ratio) based on the complete calibration set.

Parameter	S			SD			SDC		
	Estimate	*t*-value	*P*-value	Estimate	*t*-value	*P*-value	Estimate	*t*-value	*P*-value
a_1	43.76	33.7	<0.001	106.6	92.8	<0.001	154.4	104.5	<0.001
a_2	-18.13	-0.95	0.344	-149.1	-5.5	<0.001	-212.2	-5.7	<0.001
a_3				-118.2	-7.7	<0.001	-142.7	-4.1	<0.001
k_1				0.501	2.2	0.029	0.357	1.5	0.128
k_2				0.276	3.1	0.002	0.325	2.7	0.008
k_3				5.033	10.5	<0.001	4.918	9.6	<0.001
w				0.482	3.5	<0.001	0.637	3.6	<0.001
RMSE	5.02			4.43			4.26		
MSE	25.2			19.7			18.2		
R^2_{Adj}	0.481			0.588			0.622		

RSME and MSE were calculated consistently for all models by dividing the residual sum of squares by *n*. R^2_{Adj} = coefficient of determination adjusted for the number of predictors.

Table 4 Site and model specific statistics of the S-, SD- and SDC-models (included predictors; S = tree size, D = inter-tree distance, and C = crown ratio).

Site	Mean residual			Adj R^2		
	S	SD	SDC	S	SD	SDC
Mosshult	-2.3	0.1	0.1	0.45	0.73	0.76
Romperöd	0.4	-1.1	-0.8	0.52	0.55	0.66
Simontorp	0.1	-0.4	-0.5	0.51	0.58	0.55
Öveshult	-1.7	-1.5	-1.2	0.26	0.4	0.38
Lilla Norrskog	2.3	2.2	1.9	0.5	0.61	0.68

Mean residuals (cm^2 $year^{-1}$) and adjusted R^2 (Adj R^2).

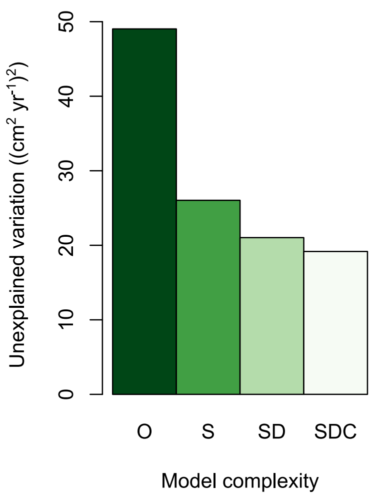

Figure 4 Unexplained variation depending on model complexity. O represents variance (S^2) of the observations. S, SD, SDC represent test mean square error (MSE) of models S, SD and SDC, respectively (included predictors; S = tree size, D = inter-tree distance and C = crown ratio). Degrees of freedom are equal to *n* in all estimates.

(see section Modelling). If the first two terms, represented by model S, are solved as a differential equation, see Lohmander (2017), the explicit solution shows that annual diameter increment is almost constant as long as the trees are moderately sized. This increment capacity then decreases as the tree grows larger and the internal processes require an increasing proportion of the collected resources. Since the model is expressed as basal area growth this behaviour may not be obvious when just looking at the expression.

The third term, the competition index, is regarded as the sum of the basal area of competitor trees, but with weighting factors for the different competitors and an exponent (k_1) on the summed competition. When the third predictor variable (**CR**) was added, the best result was achieved when it was included as a multiplier in all three terms. This can be viewed as a scaling of the complete model, but of course, the values of parameters change to adopt for this.

The competition index

Basal area was selected as the unit to quantify competition since it produced less parameter variation compared with using dbh. The competition term also includes the square root of the basal area of the subject tree ($x_i^{0.5}$, corresponding to dbh). This is because it was found that the summed competition

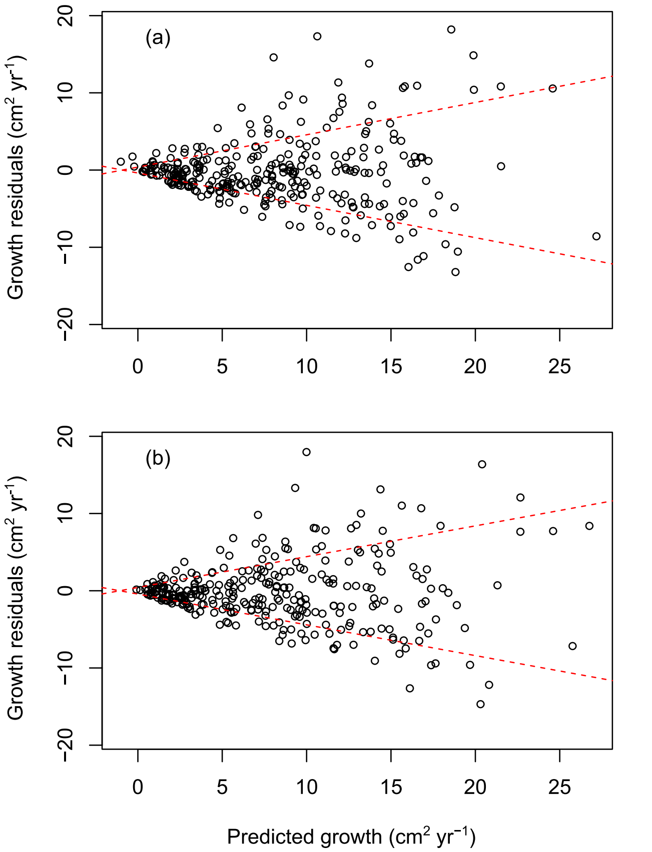

Figure 5 Growth residuals plotted against predicted growth, with (a) the SD-model ($n = 307$) and (b) the SDC-model ($n = 304$) (included predictors; S = tree size, D = inter-tree distance, and C = crown ratio). Lines indicate ±1 SD (red dotted), calculated with linear regression of accumulated RMSE values where each accumulation step is represented by the mean value within a window of 15 observations.

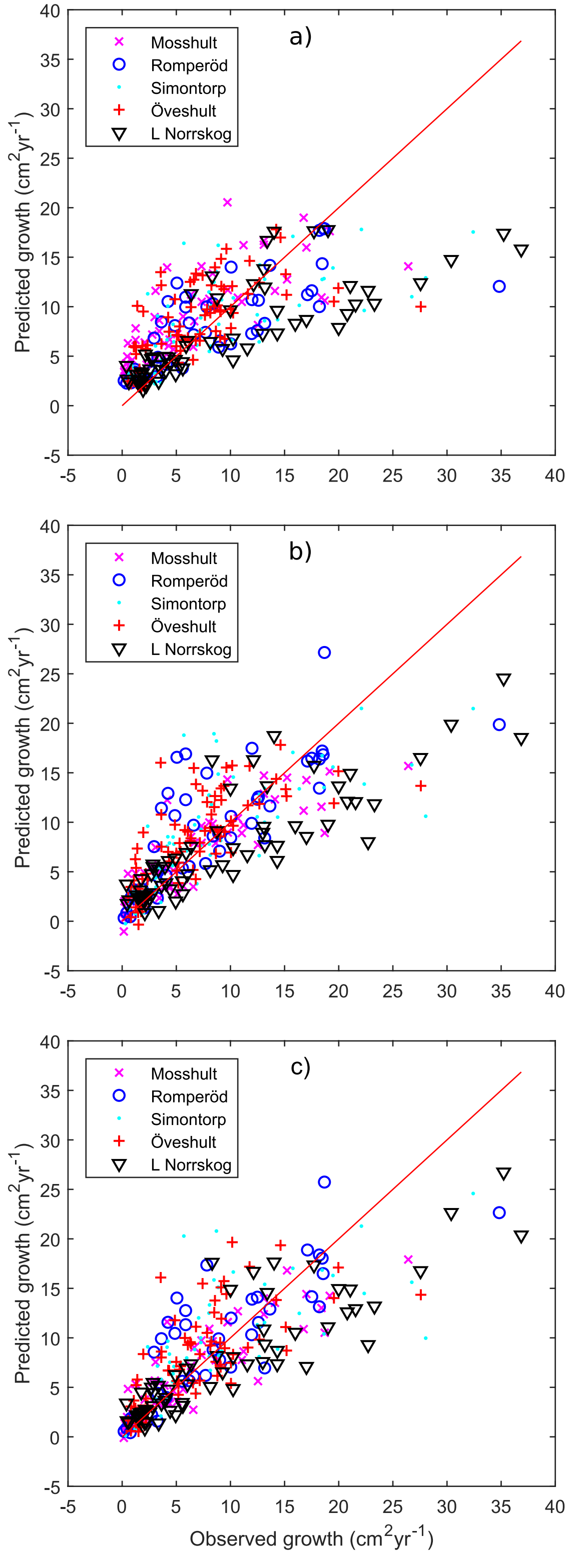

Figure 6 Predicted growth plotted against observed growth presented per model and site (a) S-model, (b) SD-model and (c) SDC-model (included predictors; S = tree size, D = inter-tree distance and C = crown ratio). The red line indicates perfect prediction.

resulted in a certain reduction of the annual ring width, rather than a certain reduction of the basal area growth. The effect of competitor tree species on the inter-tree competition was considered by the weight (w) (≤ 1) which reduces this effect from species other than spruce. The data available do not support unique weighting factors for the different species. The estimates of w support previous findings stating that competition from other species results in less growth reduction than competition from spruce (Pukkala et al. 2009, 2013). In this study, competition influence from other species was allocated weights of 48 per cent (SD) and 64 per cent (SDC) compared with spruce.

The parameter k_1 (0.50 and 0.36) exhibits a decreasing competition impact per unit (basal area) with increasing levels of competition. This effect was less significant when crown ratio was added to the model. The parameter k_2 adjusts the relative size estimate of competitors. In some other studies, only competition from larger trees is included (Lorimer 1983; Pukkala and Kolström 1987). This kind of approach assumes a one-sided competition (Burkhart and Tomé 2012, p. 215) that results in a step

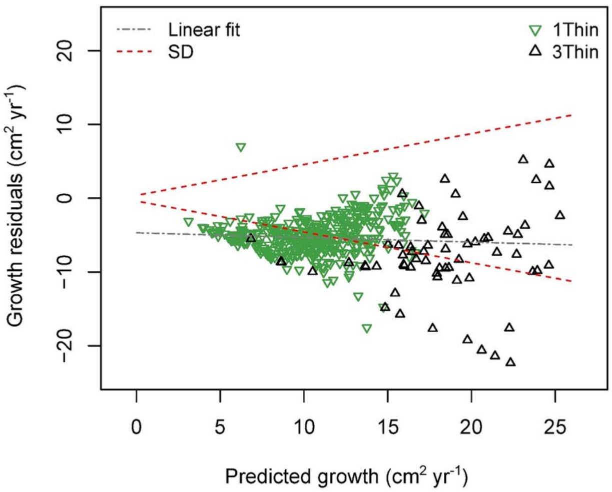

Figure 7 Growth residuals based on test observations from first-thinning (1Thin) and third-thinning (3Thin) even-sized stands, from simulations with the SD-model (included predictors; S = tree size and D = inter-tree distance), displayed against predicted growth. Trendline from linear regression of both subsets; $y = -4.69 - 0.06x$ (P-value = 0.09). Red dotted reference lines display the standard deviation lines from the SD-model calibration (Figure 5).

change in the weighting of competitors when the size of a competitor exceeds the subject tree. This study in contrast, assumes a two-sided continuous relation $(\frac{x_j}{x_i})^{k_2}$. Estimated k_2-values (0.276 and 0.325) increase weight for competitors larger than the subject tree while the effect is reverse for smaller competitors.

The function chosen for distance weighting, $e^{-(\frac{R}{k3})^2}$, was used by Elfving and Jakobsson (2006) in a similar context. For this function, no fixed distance for defining the competition range is required. This is illustrated by the area integral in Figure 9, which has passed 98 per cent of its maximum value at $2k_3$. Common spatial functions reported in the literature are often based on the formula $\frac{1}{R_{ij}}$ (Hamilton 1969; Hegyi 1974; Martin and Ek 1984; Canham et al. 2004), which is problematic in this respect because the area integral keep growing towards infinity at a constant rate. It should also be noted that the area integral of the weighting function ($\int_0^\infty f(R)\cdot 2\pi R\cdot dR$) sums to $\pi\cdot k_3^2$, i.e. k_3 could be interpreted as a characteristic radius representing the range of competition. In this case, k_3 is approximately 5.0 m for both models; i.e. the competition influence is about 50 per cent at 5 m and close to 0 per cent at 10 m. This is in line with the results of Miina and Pukkala (2000). They optimized the fixed search radius for Norway spruce competitors in Finland with a distance-dependent competition index based on vertical angles (Pukkala and Kolström 1987). Optimum value was 10 m but reducing the radius down to 6 m only resulted in minor reduction in predictability.

Parameter estimation

The parameter estimation proved to be more robust in a two-step approach. This procedure was necessary due to the site-to-site-variation in both site fertility and average competition. Since the variation in fertility is not resolved by the model, variations in growth that are truly due to differences between sites could falsely have affected the competition parameters if they had been estimated in one single step. By allowing for site specific growth potentials (unique a_1) in the first step when setting the competition parameters, this bias is eliminated. In the second step, a common value of a_1 can then be set with the other parameters fixed.

As can be seen in Figure 5, the data is heteroscedastic. This means that the parameter estimates could be biased to produce a better fit in the area of high residuals (faster growing trees) at the expense of the fit in the area of lower variance. The standard methods to handle this are to include variance weighting (Zuur et al. 2009) or transformation of the response variable. However, careful analyses of residuals together with cross-validated estimations of RMSE and model parameters did not expose any significant non-symmetrical behaviour, thus supporting the position that the parameters are not biased. Secondly, the higher variance is associated to high growth and large tree diameter, which means that trees of high economic importance are given a high weight in the regression. Consequently, if the heteroscedasticity has had an effect on the estimation, valuable trees have got higher prediction accuracy at the expense of non-commercial tree prediction, which is an acceptable effect when the models are applied to management simulation. Therefore, the heteroscedasticity was left without action.

Model performance

The cross-validation shows small differences between training and test-fold mean values of RMSE, indicating stable model performances. Some individual folds display larger deviations, particularly folds 9 and 10 (Figure 2). However, tree-group-to-tree-group variation is much larger than fold-to-fold variation. Thus, even for the folds with the largest deviations, the RMSE of the same tree group is not significantly worse when it is used as test sample compared with when it is part of the training sample. Therefore, it can be concluded that the model structure is robust to stochastic sample variation.

The validity of the models is difficult to compare with previous research since few corresponding models exist covering a similar geographical range. The model references that do exist also often have an empirical/statistical approach and do not express a clear intention to strive towards simplicity and few predictors. The distance-dependent model presented by Bianchi et al. 2020b) serves as the most relevant reference, although it is a statistical model that depends on 10 predictor variables. They presented a lower RMSE from cross-validation (3.21 cm). The other distance-dependent models (Tham 1989; Pukkala and Kolström 1991; Pukkala et al. 1994; Pukkala et al. 1998; Vettenranta 1999) presents R^2-values ranging between 0.57 and 0.82. The distance-independent tree models that are calibrated with uneven-sized stands and without age as a predictor (Andreassen and Tomter 2003; Pukkala et al. 2009; Pukkala et al. 2013; Bianchi et al. 2020a) display R^2-values (when present) ranging from 0.49 to 0.88. Given that the models SD and SDC of this study are relatively simple (2 or 3 input measures), do not involve any distance-independent stabilizing stand measures, and are

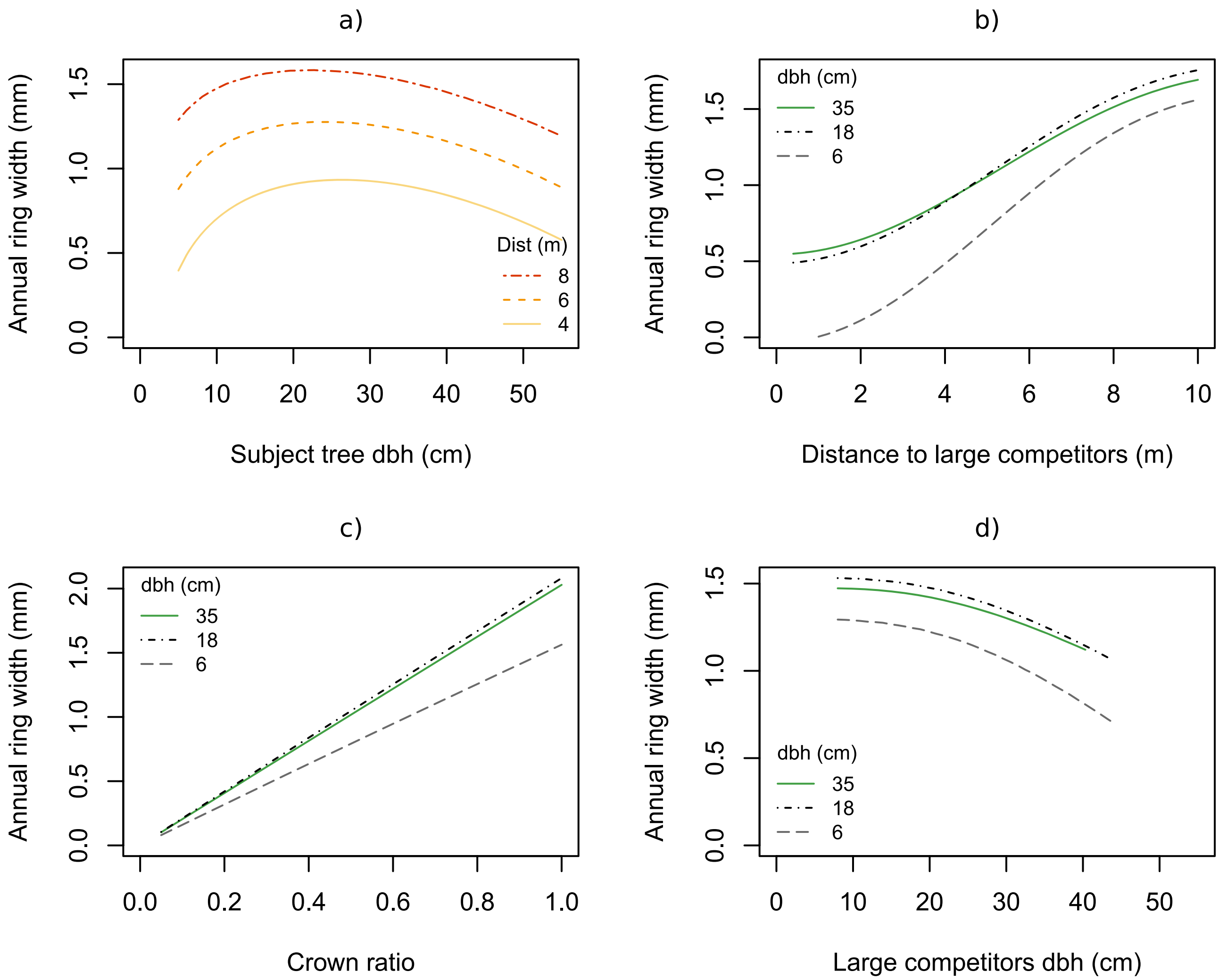

Figure 8 Subject tree annual ring widths from an uneven-sized growth competition case, calculated with the SDC-model (included predictors; S = tree size, D = inter-tree distance, and C = crown ratio). All diagrams represent the same group of competing trees with settings kept constant except for the respective *x* variable displayed, i.e. (a) subject tree dbh (diameter at breast height), (b) distance to large competitors, (c) crown ratio and (d) dbh of large competitors. Tree group start setting; total basal area = 20 m^2/ha, crown ratio = 0.6, number of large competitors = 4, dbh of large competitors = 35 cm, dbh of small competitors = 8 cm, all trees are Norway spruce and all competitors are located 6 m from the subject tree. Group basal area is kept constant by adjusting the number of small competitors according to the sizes of the large trees (initial number of small competitors depending on subject tree dbh are 29, 43 and 48, respectively). Dist is distance between large competitors and the subject tree.

ultimately motivated by spatial ITS optimization aims, the performance appears to be satisfactory compared with existing models.

Some research suggests that distance-dependent models are able to reliably predict growth in stand types outside the range of the calibration data (Clutter et al. 1983; Vanclay 1994). This study, however, indicates systematic simulation bias for applications in even-sized structures when calibration is done with uneven-sized data.

Given the data used for the calibration, the model can be expected to be valid for uneven-sized Norway Spruce in Swedish boreal conditions at latitude 56°–58° and medium to fertile site qualities. The proportion of other species should be moderate (<40 per cent). Since the models depend on spatial information, general use is hampered by limited access to coordinate set data, but the rapid technical development within forest mensuration can be expected to remove that shortage in the future. The spatial model format, in which competition is defined with both distance and tree size, enables unlimited ITS management analyses since all the options for creating cost-efficient field recommendations with different combinations of metrics are still available. With access to spatial models, future research will resolve whether distance-dependent information is necessary for optimal ITS management, or if it is sufficient to rely on non-spatial growth models.

Future model development

This study shall primarily be considered as a pilot study based on a limited data set. Considering the presented results and

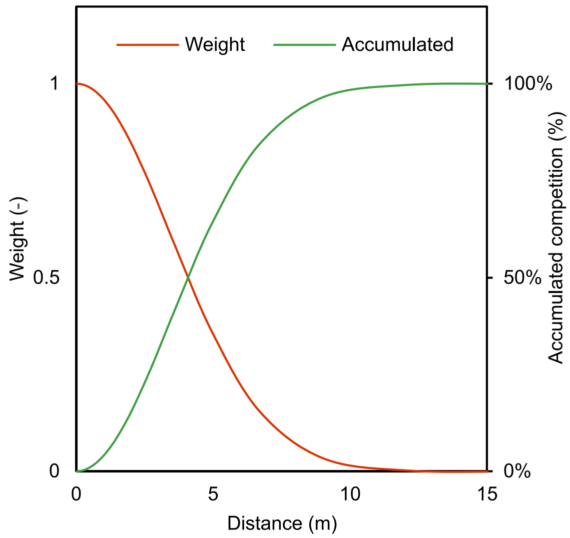

Figure 9 The distance weighing function and its area integral displayed as relative accumulated competition, assuming an even spatial distribution of competitor basal area.

the partly theoretical approach, the models should be suitable for further extension with additional predictors and calibration data with greater coverage. Following the results of Forrester (2021), the candidates for a fourth and a fifth predictor are, in the same order, variables indicative of site quality and treatment. Apart from broadening the geographical area and developing models for additional species, species-specific calibration of the parameter (*w*) would also make the models applicable to a wider range of situations.

Model performance could potentially be refined if a more representative measure for the crown ratio was applied. Since crown length was measured from the height of the lowest living branch, an inevitable consequence is that stem sections with only fragmented coverage of green needles are in many cases included in the living crown. Estimates that more accurately represent the capacity of the canopy to absorb light could probably improve model prediction, e.g. by defining living crown base as height to the lowest whorl with at least three living branches (Burkhart and Tomé 2012, p. 100). Another option for developing the model structure is to incorporate subject tree size as a predictor for the distance weighting function. Pretzsch (2009, p. 296) points out that a defined search radius is only adequate for a certain tree size. In the current distance function, weight is solely decided by the distance regardless of subject tree size.

Conclusion

The distance-dependent models presented are well suited for application in simulation studies of uneven-sized stand structures. Specifically, the calibration range and model structure make them appropriate for use within management simulation of individual-tree selection of Norway spruce dominated stands in southern Sweden. The model structure allows for management optimization of influential selection criteria such as subject tree target diameter, subject tree crown ratio, competitor distance and competitor tree size. The format of the models should make them suitable for further extension with additional predictors and calibration data with greater coverage.

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Conflict of interest statement

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Data availability

The data underlying this article are available in SND [Swedish National Data Service], at https://doi.org/10.5878/6tkj-tb97.

References

Alemdag, I. 1978 Evaluation of some competition indexes for the prediction of diameter increment in planted white spruce. *Information Report Forest Management Institute (Canada). no. FMR-X-108* Canadian Forestry Service, Dept. of the Environment. Ottawa, p. 39.

Andreassen, K. and Tomter, S.M. 2003 Basal area growth models for individual trees of Norway spruce, Scots pine, birch and other broadleaves in Norway. *Forest Ecol. Manag.* **180**, 11–24.

Bella, I.E. 1971 A new competition model for individual trees. *For. Sci.* **17**, 364–372.

Bianchi, S., Huuskonen, S., Siipilehto, J. and Hynynen, J. 2020a Differences in tree growth of Norway spruce under rotation forestry and continuous cover forestry. *Forest Ecol. Manag.* **458**, 117689.

Bianchi, S., Myllymaki, M., Siipilehto, J., Salminen, H., Hynynen, J. and Valkonen, S. 2020b Comparison of spatially and nonspatially explicit nonlinear mixed effects models for Norway spruce individual tree growth under single-tree selection. *Forests* **11**, 1338.

Biging, G.S. and 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. and Dobbertin, M. 1995 Evaluation of competition indices in individual tree growth models. *For. Sci.* **41**, 360–377.

Binkley, D. 2004 A hypothesis about the interaction of tree dominance and stand production through stand development. *Forest Ecol. Manag.* **190**, 265–271.

Buchman, R.G. and Shifley, S.R. 1983 Guide to evaluating forest growth projection systems. *J. For.* **81**, 232–254.

Burkhart, H.E. and Tomé, M. 2012 *Modeling Forest Trees and Stands*. 1st edn. Springer Science & Business Media, p. 457.

Canham, C.D., LePage, P.T. and Coates, K.D. 2004 A neighborhood analysis of canopy tree competition: effects of shading versus crowding. *Can. J. For. Res.* **34**, 778–787.

Clutter, J.L., Fortson, J.C., Pienaar, L.V., Brister, G.H. and Bailey, R.L. 1983 *Timber management: a quantitative approach*. 1st edn. John Wiley & Sons, Inc., p. 333.

Rivas, J.J.C., González, J.G.Á., Aguirre, O. and Hernández, F.J. 2005 The effect of competition on individual tree basal area growth in mature stands of *Pinus cooperi* Blanco in Durango (Mexico). *Eur J Forest Res* **124**, 133–142.

Dale, V., Doyle, T. and Shugart, H. 1985 A comparison of tree growth models. *Ecol. Model.* **29**, 145–169.

Daniels, R.F., Burkhart, H.E. and Clason, T.R. 1986 A comparison of competition measures for predicting growth of loblolly pine trees. *Can. J. For. Res.* **16**, 1230–1237.

Elfving, B. and Jakobsson, R. 2006 Effects of retained trees on tree growth and field vegetation in *Pinus sylvestris* stands in Sweden. *Scand. J. For. Res.* **21**, 29–36.

Elfving, B. and Nyström, K. 2010 *Growth Modelling in the Heureka System*. Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, p. 97.

Filipescu, C.N. and Comeau, P.G. 2007 Competitive interactions between aspen and white spruce vary with stand age in boreal mixed woods. *Forest Ecol Manag* **247**, 175–184.

Forrester, D.I. 2021 Does individual-tree biomass growth increase continuously with tree size? *Forest Ecol Manag* **481**, 118717.

Hamilton, G. 1969 The dependence of volume increment of individual trees on dominance, crown dimensions, and competition. *Forestry* **42**, 133–144.

Hasenauer, H. 2006 Concepts within tree growth modeling. In *Sustainable Forest Management*. H., Hasenauer (ed.). Springer, pp. 3–17.

Hegyi, F. 1974 A simulation model for managing jack-pine stands. In *Growth Models for Tree and Stand Simulation*. J., Fries (ed.). Department of Forest Yield Research, Royal Collage of Forestry, pp. 74–90.

Holte, A. and Solberg, B. 1989 A test of the accuracy of two individual tree growth functions for Picea abies. *Scand. J. Forest Res.* **4**, 247–257.

Hynynen, J., Ojansuu, R., Hökkä, H., Siipilehto, J., Salminen, H. and Haapala, P. 2002 *Models for Predicting Stand Development in MELA System*. Metsäntutkimuslaitos.

Hägglund, B. and Lundmark, J.-E. 1977 Site index estimation by means of site properties. *Stud For Suec* **138**, 1–38.

James, G., Witten, D., Hastie, T. and Tibshirani, R. 2013 *An Introduction to Statistical Learning*. 1st edn. Springer, p. 426.

Jonsson, B. 1980 *Functions for Long-term Forecasting of the Size and Structure of Timber Yields*[in N. Sweden]. Avdelningen for Skogsuppskattning och Skogsindelning, Swedish University of Agricultural Sciences, p. 121 Rapport.

Lohmander, P. 2017 A general dynamic function for the basal area of individual trees derived from a production theoretically motivated autonomous differential equation. *Iran J. Manag. Stud.* **10**, 917–928.

Lorimer, C.G. 1983 Tests of age-independent competition indices for individual trees in natural hardwood stands. *Forest Ecol. Manag.* **6**, 343–360.

Lundqvist, L. 2017 Tamm Review: Selection system reduces long-term volume growth in Fennoscandic uneven-aged Norway spruce forests. *Forest Ecol. Manag.* **391**, 362–375.

Mackinney, A.L. 1937 Construction of yield tables for nonnormal loblolly pine stands. *J. Agric. Res.* **54**, 531–545.

Martin, G., Ek, A. and Monserud, R.A. 1977 Control of plot edge bias in forest stand growth simulation models. *Can. J. For. Res.* **7**, 100–105.

Martin, G.L. and Ek, A.R. 1984 A comparison of competition measures and growth models for predicting plantation red pine diameter and height growth. *For. Sci.* **30**, 731–743.

Miina, J. and Pukkala, T. 2000 Using numerical optimization for specifying individual-tree competition models. *For. Sci.* **46**, 277–283.

Miina, J. and Pukkala, T. 2002 Application of ecological field theory in distance-dependent growth modelling. *Forest Ecol. Manag.* **161**, 101–107.

Mitchell, K.J. 1975 Dynamics and simulated yield of Douglas-fir. *For. Sci.* **21**, a0001–z0001.

Munro, D.D. 1974 Forest growth models-a prognosis. In *Growth Models for Tree and Stand Simulation*. J., Fries (ed.). Department of Forest Yield Research, Royal College of Forestry, pp. 7–21.

Näslund, M. 1935 Ett gallringsförsök i stavagranskog. In *Reports of the Swedish Institute of Experimental Forestry*. Swedish Institute of Experimental Forestry, pp. 651–725.

Olsson, J.-O. and Fagerberg, N. 2019 En avståndsberoende tillväxtmodell på trädnivå för gran: -en preliminär modell baserad på två skiktade bestånd i Götaland. In *Arbetsrapport*. Department of Forestry and Wood Technology. Linnaeus University, p. 15.

Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A. Jr., Kobe, R.K. and Ribbens, E. 1996 Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecol. Monogr.* **66**, 1–43.

Peng, C. 2000 Growth and yield models for uneven-aged stands: past, present and future. *Forest Ecol. Manag.* **132**, 259–279.

Pommerening, A. and Murphy, S. 2004 A review of the history, definitions and methods of continuous cover forestry with special attention to afforestation and restocking. *Forestry* **77**, 27–44.

Pretzsch, H. 2009 *Forest Dynamics, Growth, and Yield*. 1st edn. Springer-Verlag, p. 664.

Pukkala, T. 1989 Prediction of tree diameter and height in a Scots pine stand as a function of the spatial pattern of trees. *Silva. Fenn.* **23**, 83–99.

Pukkala, T. and Kolström, T. 1987 Competition indices and the prediction of radial growth in Scots pine. *Silva. Fenn.* **21**, 55–67.

Pukkala, T. and Kolström, T. 1991 Effect of spatial pattern of trees on the growth of Norway spruce stand. *Silva. Fenn.* **25**, 117–131.

Pukkala, T., Lähde, E. and Laiho, O. 2009 Growth and yield models for uneven-sized forest stands in Finland. *Forest Ecol. Manag.* **258**, 207–216.

Pukkala, T., Lähde, E. and Laiho, O. 2013 Species interactions in the dynamics of even- and uneven-aged boreal forests. *J. Sustain. Forest* **32**, 371–403.

Pukkala, T. and Miina, J. 1998 Tree-selection algorithms for optimizing thinning using a distance-dependent growth model. *Can. J. For. Res.* **28**, 693–702.

Pukkala, T., Miina, J., Kurttila, M. and Kolström, T. 1998 A spatial yield model for optimizing the thinning regime of mixed stands of *Pinus sylvestris* and *Picea abies*. *Scand. J. For. Res.* **13**, 31–42.

Pukkala, T., Vettenranta, J., Kolström, T. and Miina, J. 1994 Productivity of mixed stands of *Pinus sylvestris* and *Picea abies*. *Scand. J. For. Res.* **9**, 143–153.

Robinson, A.P. and Monserud, R.A. 2003 Criteria for comparing the adaptability of forest growth models. *Forest Ecol. Manag.* **172**, 53–67.

Shiue, C. 1962 Measuring and predicting growth for all-aged stands. In *Tree Growth*. T.T., Kozlowski (ed.). The Ronald Press Company, pp. 385–400.

Soares, P. and Tomé, M. 1999 Distance-dependent competition measures for eucalyptus plantations in Portugal. *Ann. For. Sci.* **56**, 307–319.

Spinelli, R., Magagnotti, N., Pari, L. and Soucy, M. 2016 Comparing tree selection as performed by different professional figures. *For. Sci.* **62**, 213–219.

Söderberg, U. 1986 *Functions for forecasting timber yield: increment and form height of individual trees of native tree species in Sweden*. Ph.D. dissertation. Swedish University of Agricultural Sciences.

Tarasiuk, S. and Zwieniecki, M. 1990 Social-structure dynamics in uneven-aged Scots pine (*Pinus sylvestris*) regeneration under canopy at the Kaliszki Reserve, Kampinoski National Park (Poland). *Forest Ecol. Manag.* **35**, 277–289.

Tham, Å. 1989 Prediction of individual tree growth in managed stands of mixed *Picea abies* (L) Karst, and *Betula pendula* Roth & *Betula pubescens* Ehrh. *Scand. J. For. Res.* **4**, 491–512.

Tomé, M. and Burkhart, H.E. 1989 Distance-dependent competition measures for predicting growth of individual trees. *For. Sci.* **35**, 816–883.

Vanclay, J.K. 1994 *Modelling forest growth and yield: applications to mixed tropical forests*. CAB International, p. 537.

Vanclay, J.K. 2012 Modelling continuous cover forests. In *Continuous Cover Forestry*. T., Pukkala, K., von Gadow (eds.). 2nd edn. Springer, pp. 229–241.

Weiner, J. and Solbrig, O.T. 1984 The meaning and measurement of size hierarchies in plant populations. *Oecologia* **61**, 334–336.

Weiskittel, A.R., Hann, D.W., Kershaw, J.A. Jr. and Vanclay, J.K. 2011 *Forest Growth and Yield Modeling*. 1st edn. John Wiley & Sons, p. 415.

Vettenranta, J. 1999 Distance-dependent models for predicting the development of mixed coniferous forests in Finland. *Silva. Fenn.* **33**, 51–72.

Zeide, B. 1993 Analysis of growth equations. *For. Sci.* **39**, 594–616.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. and Smith, G.M. 2009 *Mixed Effects Models and Extensions in Ecology with R*. Springer, p. 579.