Forest Systems
24(2), e023, 13 pages (2015)
eISSN: 2171-9845
http://dx.doi.org/10.5424/fs/2015242-05742
Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria (INIA)

RESEARCH ARTICLE

OPEN ACCESS

Analysis of Individual Tree Competition Effect on Diameter Growth of Silver Birch in Estonia

Kobra Maleki[1*], Andres Kiviste[1] and Henn Korjus[1]

[1] *Estonian University of Life Sciences, Institute of Forestry and Rural Engineering, Department of Forest Management, Kreutzwaldi 5, Tartu 51014, Estonia*

Abstract

Aim of study: The present study evaluates a set of competition indices including spatially explicit indices combined with different competitor selection approaches and non-spatially explicit competition indices. The aim was to quantify and describe the neighbouring effects on the tree diameter growth of silver birch trees.

Area of study: Region throughout Estonia.

Material and methods: Data from the Estonian Network of Forest Research Plots was used. After quantifying the selected indices, the best non-spatial indices and spatial indices (combined with neighbour selection methods) were separately devised into a growth model as a predictor variable to assess the ability of the diameter growth model before and after adding competition measures. To test the species-specific effect on the competition level, the superior indices were recalculated using Ellenberg's light indicators and incorporated into the diameter growth model.

Main results: Statistical analyses showed that the diameter growth is a function of neighbourhood interactions and spatial indices were better growth predictors than non-spatial indices. In addition, the best selections of competitive neighbours were acquired based on the influence zone and the competition elimination angle concepts, and using Ellenberg's light values had no significant improvement in quantifying the competition effects.

Research highlights: Although the best ranking spatial competition measures were superior to the best non-spatial indices, the differences were negligible.

Keywords: Competition indices; zone of influence; stem diameter increment; *Betula pendula* Roth.

Citation: Maleki, K., Kiviste, A., Korjus, H. (2015). Analysis of Individual Tree Competition Effect on Diameter Growth of Silver Birch in Estonia. Forest Systems, Volume 24, Issue 2, e023, 13 pages. http://dx.doi.org/10.5424/fs/2015242-05742.

Received: 12 Feb 14. **Accepted**: 08 Apr 2015

Funding: This study was supported by the Institutional Research Funding IUT21-04 (B21004MIMK) and Estonian Science Foundation Grant ETF8890.

Competing interests: The authors have declared that no competing interests exist.

Correspondence should be addressed to Kobra Maleki: kobra.maleki@emu.ee

Introduction

Competition among individual trees is a fundamental ecological process that plays a major role in population dynamics, survival, growth and species replacement (Peet & Christensen, 1987). By definition, competition is ''an interaction between the individuals, leading to a reduction in the survival, growth and reproduction of the competing individuals" (Begon et *al*., 1996). Several case studies have been conducted in ecology and forestry to develop, improve or modify different competition indices (*CI*s). Such indices quantify the competition level for an individual tree and are classified into two major groups of non-spatially explicit indices (e.g. Biging & Dobbertin (1995) and Schröder & Gadow (1999)) and spatially explicit indices (e.g. Hegyi (1974) and Alemdag (1978)). Non-spatial indices are functions of stand level variables, or of the initial dimensions of the trees, and therefore do not require the trees coordinates. Whenever spatial indices are used to measure the influence of local neighbours on a central tree (the subject tree), the dimensions and the relative location of neighbour trees are required for the computation (Tomé & Burkhart, 1989; Corral Rivas *et al*., 2005).

For several species and forest conditions, the effectiveness of different *CI*s on tree diameter or basal area growth has been examined (Munro, 1974; Martin & Ek, 1984; Pukkala & Kolström, 1987; Holmes & Reed, 1991; Contreras *et al*., 2011). Since several aspects of stand density and neighbour sizes influence the tree growth, non-spatial *CI*s with simple structures are

parsimonious to quantify the competitive status of trees in each stand. On the other hand, as ecology is spatial (Berger & Hildenbrandt, 2000), therefore by increasing the interval distance, the negative interaction of neighbours will decrease and spatial *CI*s take the explicit description of tree spacing into account. Additionally the identity of neighbouring species is an important factor in the characterization of their competitive effect (Bella, 1971; Zhao *et al*., 2006). Competition can occur among *conspecific* individuals, plants of same species, and *hetero-specific* individuals, plants of different species, termed *intraspecific* and *interspecific* competition, respectively. The competition behaviour of different species can be differentiated by using Ellenberg *et al*.'s system (1991). It is the most widely used indicator species system, which compares the response of different species to edaphic and climatic parameters, such as light, temperature, moisture and nitrogen at a 9-point scale for each.

To investigate the effect of competition on the diameter growth of trees, we focused our study on silver birch *(Betula pendula* Roth*)*. Silver birch occurs naturally in northern temperate and boreal forests and it is an essential ecological and commercial broadleaved tree species (Hynynen *et al*., 2010). As a pioneer tree species (Fischer *et al*., 2002), birch is light demanding, and if it grows as a dominant tree with low competitive effects of neighbours, in a stand with relatively wide spacing, birch maintains its vitality and vigorous growth (Hynynen *et al*., 2010). In Estonia, birch is the second most abundant tree species in terms of forest cover (31.2%) and the coverage is expanding (Yearbook of Forest, 2013). A few attempts have been made to study birch growth related to the negative interaction of tree competitive status in stands (Jõgiste, 1998; Prévosto *et al*., 1999; Andreassen & Tomter, 2003; Damgaard & Weiner, 2008; Kaitaniemi & Lintunen, 2010).

The main objective of this study was to investigate the adequacy of different spatial and non-spatial *CI*s to explain single-tree silver birch diameter growth in Estonia. Further objectives were to find the best competitor selection method for Estonian birch stands and evaluate the differences in competitive ability of different species by employing Ellenberg's species-specific light indicator values. Specifically, we hypothesized that (i) the *CI*s contribute to explain diameter increments in silver birch; (ii) spatial indices perform better than non-spatial indices; (iii) selecting the potential competitors based on the concept of the influence zone is superior to variable competition zone radii; and (iv) considering the species-specific competition improves the ability of spatial indices to account for growth variability.

Materials and methods

Study data

The study was carried out in Estonia, which lies on the eastern shores of the Baltic Sea across the Finnish gulf (lat. 57.3°-59.5° N, long. 21.5°-28.1° E). Average temperatures range from 16.3°C to 18.1°C in July and from -3.5°C to -7.6°C in February. Average annual precipitation increases from west to east within a range of 600-700 mm. In this study, data from the Estonian network of forest research plots (ENFRP) was used. ENFRP was established during the period 1995–2004 and covers Estonia entirely (Kiviste & Hordo, 2002). The permanent plots were circular with a radius of 10, 15, 20, 25 or 30 m depending on the stand age and density and as a rule, every plot had at least 100 trees in the overstory. For the current study, we benefit the data from 121 silver birch dominated research plots (where more than 65% of the number of trees were birches) consisting of 16,186 trees with 5-year measurement intervals.

Within each plot the azimuth, the distance from plot centre, the diameter at breast height (*d),* and the defects of each tree were assessed. For every fifth tree, and for dominant and rare tree species, the tree height and the height to the live crown base were also measured. Since the height records of all trees were required for some calculations, based on the height-diameter model developed by Kiviste *et al*. (2003), all unmeasured tree heights were estimated.

Species composition of all trees within the studied plots was 67% silver birch, 24% Norway spruce and 9% of several other species (see Table 4). Plots were established in managed and even-aged forests, and if there was a thinning operation in the time period between the plot measurements, they were excluded. Table 1 summarizes main stand variables of study plots and Fig.1 shows the dynamics of average height, basal area, and quadratic mean diameter.

Table 1. Main characterization of the birch dominated permanent plots*

	A	N	d_g	id_5	h	SI_{100}	BA
Minimum	18	223	3.80	0.00	5.60	15.28	3.40
Mean	34	2378	11.88	1.34	14.38	25.76	18.16
Maximum	90	5471	36.00	6.90	32.50	34.10	36.60
Standard deviation	13.80	1465	5.70	0.77	5.61	4.09	5.84

* *A*, stand age (year); *N*, the number of trees per hectare; d_g, the quadratic mean diameter at breast height of trees (cm); i_{d5}, the 5-year tree diameter increment (cm); h, average stand height (m); SI_{100}, site index at reference age 100 years (m); *BA*, stand basal area (m^2ha^{-1}).

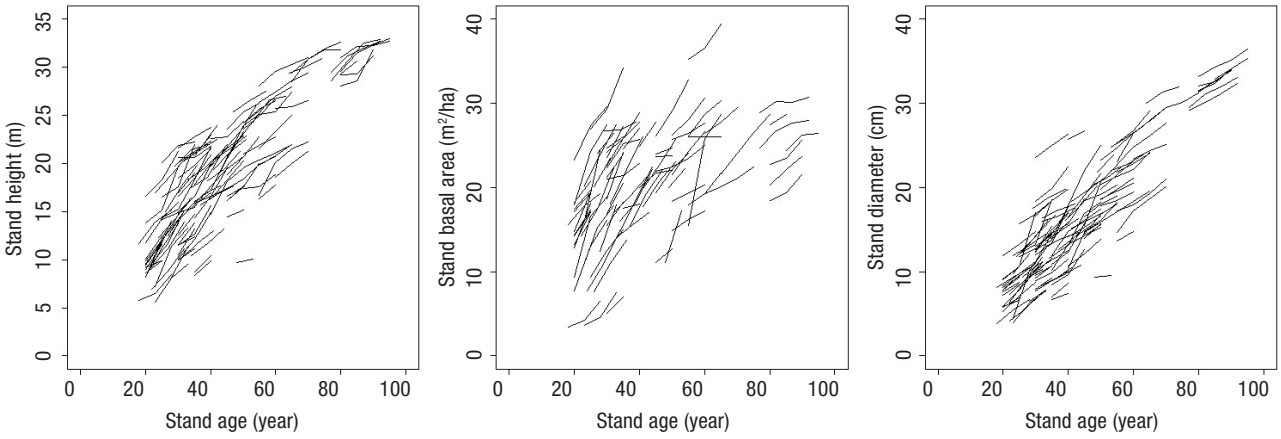

Figure 1. The dynamics of average height (left), basal area (middle), and quadratic mean diameter (right).

Competition indices

The competition for each subject tree was quantified using 18 different *CI*s, consisting of 7 non-spatial and 11 spatial indices (Table 2). The indices described below were selected from the literature, taking into consideration the available tree variables for this study, and their simplicity to describe the competition situation of a tree, as it is difficult to understand the statistical qualities of an index with the combination of several primary variables (Weiglet & Jolliffe, 2003).

The first seven indices in Table 2 are non-spatial indices. In a plot, $BA\text{-}g_j$ *CI* proposed by Steneker & Jarvis (1963), is the sum of the basal area (g) of the neighbouring trees j for a subject tree i (m^2 ha^{-1}); *BAL* presented by Wykoff *et al*. (1982) is the sum of the basal area of trees larger than the subject tree (m^2 ha^{-1}). *Sdr* sums up the d of neighbours divided by the subject tree d in the plot (ha^{-1}). The index dr_g calculates the ratio of the diameter of the subject tree to the quadratic mean diameter of the plot (Hamilton, 1986) and *BAr* is another form of *Sdr* that considers g instead d. The index *BALr* is the ratio of *BAL* to the cumulative basal area of the plot (Vanclay, 1991) and finally *BALMOD* (Schröder & Gadow, 1999) modifies *BALr* by dividing it into the relative spacing index as following:

$$RS = \frac{\sqrt{S/N}}{H_{Dom}} \quad (1)$$

where S is plot area (m^2), N is the number of trees on plot, and H_{Dom} is the stand dominant height (m) (mean height of hundred thickest trees per hectare (Assmann, 1970)).

The next three competition indices *Sl, SOr* and *SOdr* in Table 2 are so-called influence-zone overlap indices, which assume that a horizontal circle surrounding the subject tree can represent the active competition area, and that competition occurs where neighbouring trees overlap their influence zone with the subject tree's influence zone. The radius of these circles is thought to be equal to the expected growing space of open-grown trees, and usually is a function of tree size (Corral Rivas *et al*., 2005).

Finally, the last eight indices in Table 2 are size-ratio spatial *CI*s. The idea of this type of indices was derived from the hypothesis that competition effect has positive relationship with the size of neighbouring trees and negative relationship with their distance from the subject tree (Tomé & Burkhart, 1989). For spatial indices of *Heg* (Hegyi, 1974), *Almdg* (Alemdag, 1978), *Sdrl1* (Lorimer, 1983), *Sdrl2* (Martin & Ek, 1984), and *SBAr* (Daniels *et al*., 1986) the diameter at breast height performs as a tree size indicator. *SAng1* (Lin, 1974) is the sum of horizontal angles. Since the average elevation angle of the brightest region of the sky over the growth season can be approximated by angle of 45° (Stadt & Lieffers, 2000), the 45° gauge was employed for this index. The index *SAng2* sums up the horizontal angles originating from the subject tree centre and spanning the diameter of each competitor (Rouvinen & Kuuluvainen, 1977), and *SdrAng* calculates the sum of the horizontal angles multiplied by the ratios of the diameter of the competitors and the subject trees (Fig. 2).

Methods of competitor identification (*SM*)

As well as the mathematical formulation, the value of a competition index depends on the method used to

Table 2. The list of competition indices tested to use in the tree diameter growth model*

Index	Sources	Equations
Non-spatially explicit indices		
BA-g$_j$	Steneker & Jarvis (1963)	$\sum_{j\neq i}^{n}(g_j)\Big/S$
BAL	Wykoff *et al*. (1982)	$\sum_{d_i<d_j}^{n}(g_j)\Big/S$
Sdr	Lorimer (1983)	$\left(\left(\sum_{j\neq i}^{n}d_j\right)\Big/d_i\right)\Big/S$
dr$_g$	Hamilton (1986)	d_i/d_g
BAr	Corrona & Ferrara (1989)	$\left(\left(\sum_{j\neq i}^{n}g_j\right)\Big/g_i\right)\Big/S$
BALr	Vanclay (1991)	$\sum_{j\neq i}^{n}(g_{j;dj>d_i})\Big/G$
BALMOD	Schröder & Gadow (1999)	$\left[\left(\sum_{d_i<d_j}^{n}(g_j)\Big/G\right)\right]\Big/RS$
Spatially explicit indices		
Sl	Staebler (1951)	$\sum_{j\neq i}^{n}l_{ij}$
SOr	Gerrard (1969)	$\sum_{j\neq i}^{n}(O_{ij}/CZ)$
SOdr	Bella (1971)	$\sum_{j\neq i}^{n}\left((O_{ij}\cdot d_j)/(CZ\cdot d_i)\right)$
SBAr	Daniels et al. (1986)	$\left((d_i^2\cdot N_c)\Big/\sum_{j\neq i}^{n}d_j^2\right)$
Heg	Hegyi (1974)	$\sum_{j\neq i}^{n}\left(d_j/(d_i\cdot l_{ij})\right)$
SAng1	Lin (1974)	$2\sum_{j\neq i}^{n}\arctan\left(d_j/2l_{ij}\right)$
SAng2	Rouvinen & Kuuluvainen (1977)	$\sum_{j\neq i}^{n}\arctan\left(d_j/l_{ij}\right)$
SdrAng	Rouvinen & Kuuluvainen (1977)	$\sum_{j\neq i}^{n}\left((d_j/d_i)\cdot\arctan\left(d_j/l_{ij}\right)\right)$
Almdg	Alemdag (1978)	$\sum_{j\neq i}^{n}\left\{\pi\left[(l_{ij}\cdot d_i)/(d_i+d_j)\right]^2(d_j/l_{ij})\Big/\sum(d_j/l_{ij})\right\}$
Sdrl1	Lorimer (1983)	$\sum_{j\neq i}^{n}\left((d_j/d_i)\Big/\sqrt{l_{ij}/CZR}\right)$
Sdrl2	Martin & Ek (1984)	$\sum_{j\neq i}^{n}(d_j/d_i)\cdot\exp\left((16\cdot l_{ij})/(d_i+d_j)\right)$

*N_c, number of competitor trees; d_i, subject tree *d* (cm); d_j, competitor tree *d* (cm); d_g, basal area weighted plot diameter (cm); l_{ij}, distance between the competitor *j* and the subject tree *i* (m); *G*, basal area of the trees within the plot (m^2ha^{-1}); g_i, basal area of subject tree *i* (m^2ha^{-1}); g_j, basal area of competitor tree *j* (m^2ha^{-1}); *CZR*, the radius of influence zone (m); *RS*, relative spacing index of plot; O_{ij}, crown overlap between the neighbour tree *j* and the subject tree *i* (m^2); *CZ*, the area of influence zone (m^2); *S*, plot area (ha).

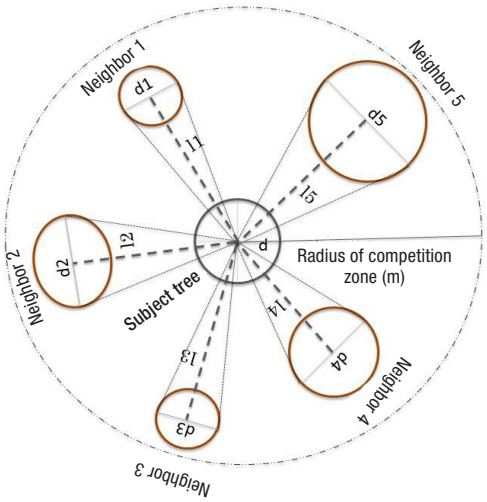

Figure 2. Schematic of the horizontal angles originating from the subject tree centre and spanning the diameter (at breast height) of each competitor tree within the competition zone used to calculate indices *Sang2* & *SdrAng; *dx* is the diameter at breast height (cm), *lx* is the distance between the subject tree and its competitors (m).

define competitors for the subject tree (Bigging & Dobbertin, 1992). Among different proposed methods to choose the potential competitors, we tested four approaches. The first two approaches, approaches 1 and 2, were based on the concept of an influence-zone that assumes an imaginary circle whose centre is constituted by the subject tree (Staebler, 1951) and trees inside this circle are competitors. The last two approaches, approaches 3 and 4, identified competitors based on variable competition zone radii, often weighted by dimensions of the subject tree and its neighbours (Daniels, 1976; Ford & Diggle, 1981):

1. The radius of influence zone was defined as a fraction of the stand's average height for each plot; $CZR_{0.4h}$ was set equal to 0.4 average height of plot (Sims *et al*., 2009).
2. Based on Lee & Gadow (1997) the influence zone radius was calculated using the following equations:

$$CZR_k = k \cdot \sqrt{\frac{10000}{N}} \quad (2)$$

where CZR_k is dynamic radius, N is the number of trees per hectare, and k is a constant number. The function $\sqrt{\frac{10000}{N}}$ calculates average distance between the neighbours. The values of k equal to two (CZR_{k2}) and three (CZR_{k3}) multiply this distance by two and three, respectively to define *CZR*. Within the influence zone, trees were considered to be active competitors if $d_j \geq 0.3d_i$ (where d_j is d of competitor and d_i is the d of subject tree) and they were beyond the crown projection of other competing trees, considering a competition elimination angle of 30˚ (*CEA*=30˚).

3. The *Bitterlich method* (1952) was used to identify the competitors in variable plot radii samplings. BAF_1, BAF_2 and BAF_4 tested three basal area factors (*BAF*) equal to 1, 2 and 4 $m^2\,ha^{-1}$, respectively. A tree was considered a competitor if its distance to the subject tree was:

$$l_{ij} \leq d_i \cdot \sqrt{\frac{50}{BAF}} \quad (3)$$

where l_{ij} is the distance between the subject tree i and the neighbouring tree j and d_i is the diameter of the subject tree. The values of *BAF* equal to 1, 2 and 4 correspond to the opening angles of β =1.15˚, 1.62˚ and 2.30˚, respectively. Therefore, when the *BAF* values and boundary angles increase, fewer trees meet the criteria for being considered as competitors (Lorimer, 1983; Tomé & Burkhart, 1989).

4. Finally, the *reserved search-cone method* (Pretzsch, 2009) or angular height method (Richards *et al.,* 2008) applied height angle from the base of the subject tree to identify the competing neighbours. For a search-cone opening angle β, set up at the stem base of the subject tree, competitors are neighbouring trees whose heights are greater than a critical distance, determined as the following:

$$l_{ij} < \frac{h_i}{\tan(90\text{-}\beta/2\ )} \quad (4)$$

where l_{ij} is the distance between the subject tree and the competitor tree, and h_i is the subject tree height. If the apex of the reversed search-cone is at the crown base height of the subject tree (cbh_j) then a neighbouring tree with height h_j is a competitor when:

$$l_{ij} < \frac{h_i - cbh_i}{\tan(90 - \beta/2)} \quad (5)$$

We tested the opening angle β equal to 100˚, 80˚, and 60˚, respectively where the apex was set up either at the stem base (SCH_{100}, SCH_{80} and SCH_{60}) or at the crown base height ($SCHCr_{100}$, $SCHCr_{80}$ and $SCHCr_{60}$).

In all the above-mentioned methods, in order to avoid the interference from the competitive effects of non-measured trees beyond the plot borders, we computed *CI*s only for interior trees on each plot where the neighbours' information was available for them. After determining the competitors, we calculated the spatially explicit *CI*s for each subject tree. Four spatially explicit *CI*s (*Sl*, *SOr*, *SOdr,* and *Sdrl1*) were based on the influence zone concept and only the first two approaches of competitor selection ($CZR_{0.4h}$ and CZR_k) were applicable to quantify the mentioned indices. Moreover, the allometric crown radius model, (developed by Lang *et al*., 2007) was used to calculate the crown radius that was required for quantifying indices *SOr* and *SOdr* as well as fitting the Eqs. (7) and (8):

$$R_{cr} = 0.5\left[a_1 d + \frac{a_2 d}{h}\right] \quad (6)$$

where R_{cr} is the crown radius (m), d and h are the diameter at breast height (cm) and the total height of the tree (m) respectively, and a_1 and a_2 are estimation parameters (Table 3).

Table 3. The values of parameters for the used allometric crown model for main tree species

Species	Parameters	
	a_1	a_2
Pinus sylvestris	0.1060	0.6150
Picea abies	0.0830	1.0620
Betula sp.	0.1340	0.9460
Populous termula	0.1370	0.8940
Alnus incana	0.0223	1.1700
Alnus glutinosa	0.1340	1.2300

Statistical and comparative analyses of competition indices

Preliminary analysis was carried out to pre-select adequate *CI* candidates to include in our growth model. As suggested by Pedersen *et al*. (2013) we applied the Spearman rank correlation (Spearman's *rho*) to characterize the relationship between the 5-year tree diameter increment (i_{d5}) and the competition indices. The Spearman correlation is able to consider potential nonlinear trends frequently seen in growth and competition studies, besides it is valid for the data size larger than 10 (Siegel, 1956) which was applicable to our data. The existence of a pairwise relationship between i_{d5} and *CI*s was proved using the *t-test*. Based on the Spearman rank correlation results, the four best *CI*s (two non-spatial and two spatial *CI*s) were selected for further analyses.

Then, we constructed a linear multiple regression model (Wimberly & Bare, 1996; Jõgiste, 2010) between i_{d5} (cm) and some predictor variables that influence diameter growth. In a preliminary assessment, *nonlinear extra sum of square method* (Bates & Watts, 1988) was applied to evaluate the effect of plots on growth. For this purpose, we considered the simple model of diameter growth as a function of tree diameter. In order to differentiate the study plots, we introduced dummy variables to the defined simple model. Then, we compared the two mentioned models using *F-test* and a significant effect of plots was detected (F=8.56; P<0.0001). Therefore, predictor variables presenting the initial stand status were also included in the growth models (Eqs. (7) and (8)). Additionally, for each combination of selected variables, the variance inflation factors (VIF) were calculated to certify that our multiple models were not influenced by multicollinearity amongst explanatory variables. We only implemented the combination of variables with VIFs<10 (Soares & Tomé, 2001; Corral Rivas *et al*., 2005). Eventually, the growth model was fitted by improvising some initial stand variables along with the tree variables.

$$\left[\left(\sum_{d_i<d_j}^{n}\left(g_j\right)\Big/ G\right)\right]\Big/ RS \quad (7)$$

In order to evaluate the efficiency of the chosen *CI*s to improve the prediction ability of growth function, the numerical value of each of those indices, two non-spatial *CI*s and two spatial *CI*s, was independently added to the previous growth function:

$$i_{d5} = b_0 + b_1(d) + b_2(cr) + b_3(RS) + b_4(dr) + b_5(SI_{100}) + b_6(CI) \quad (8)$$

where b_k are coefficients to be estimated, i_{d5} is the 5-year tree diameter increment (cm), d is the subject tree diameter at breast height (cm) that integrates the past competitive interactions (Soares & Tomé, 1999), *cr* is the ratio between the crown width and the tree height that depicts the vigour of trees of similar size (Schröder *et al*., 2002). The relative diameter *dr* is the ratio between the subject tree diameter and the quadratic mean diameter of the stand that represents the dominance of the subject tree in relation to other trees in the stand, *RS* is the stand relative spacing, and SI_{100} is the stand site index. Nilson (2005) model was used to estimate the average height of the stands at reference

age 100 years (m) and *CI* is the competition measure for the subject tree. *R* statistical software version 3.1.2 (*R* Development Core Team, 2014) was employed to carry out all the required analyses for this research.

Before proceeding with the subsequent analyses, the existence of any correlation among residuals was explored. For this purpose, the growth model was fit using the *lme* function from the *nlme* package in *R* as following:

$$i_{d5} = X\beta + Zu + \varepsilon \quad (9)$$

For the recent linear mixed effect model, i_{d5} is the dependant variable; *b* is a vector of fixed effects consisting of the same explanatory variables of Eq. (7); *u* is a vector of random effects including tree, plot, and growth interval (measurements); *e* is a vector of random errors; *X* and *Z* are design matrices relating the 5-year diameter growth to fixed and effect random effects, respectively. The previous and recent models were compared in terms of *AIC* (Akaike's Information Criterion) where $\Delta AIC = AIC_{\text{multiple model}} - AIC_{\text{mixed model}}$. In addition, to ensure that there was not any remaining within-group correlation, the recent model was checked with an auto-regressive structure (*AR1*). The mixed effect models, those with and without auto-regressive structures, were compared using *ANOVA* (analysis of variances).

The relative quality of growth functions, with and without *CI*s, were estimated using R^2 (Adjusted-R^2), the root mean square error (*RMSE*, calculated using the *rmse* function for the model residuals in *R*), *AIC* and Akaike weights (AIC_w). The probability that model is the best with the lowest expected information loss is illustrated by the smallest value of *AIC* and the biggest AIC_w (Wagenmakers & Farrell, 2004). Additionally, the performance and the contribution of each *CI* to the growth model were assessed with the mean square error reduction (*MSER*).

$$MSER = 100\left(1 - \frac{MSE_8}{MSE_7}\right) \quad (10)$$

where MSE_7 and MSE_8 are the mean square errors of models 7 and 8, respectively.

Finally, the efficiency of *CI*s in different stand stages and the contribution of different species in the competition load of a subject tree were evaluated. Stand development stages were defined by the age of the silver birch, as the dominant tree species. First, to differentiate the effect of different neighbouring species on competition, tree diameters were weighted differently. For that purpose, tree diameters were multiplied by their corresponding Ellenberg's species-specific light transmission coefficients (Ellenberg *et al*., 1991) from one (plants in deep shade) to nine (plants in full light); then, the selected spatial *CI*s were recalculated using the new weighted diameters. Table 4 provides the Ellenberg's light values for more frequent tree species in Estonia. Finally, subject trees were divided into three subdivisions of young (<35 years), middle-aged (35-69 years) and old stands (≥70 years). For each age group, the regression analyses for the selected *CI*s and tree diameter growth were repeated separately.

Table 4. The Ellenberg's species-specific light coefficients for more frequent tree species in Estonia

Species	Ellenberg's values
Fraxinus excelsior, *Acer platanoides*, *Ulmus glabra*	4
Alnus glutinosa, *Tilia cordata, Picea abies, Salix fragilis*	5
Populus tremula, *Alnus incana*, *Sorbus aucuparia*	6
Betula pendual, *Pinus sylvestris, Quercus robur*	7
Juniperus communis	8

Results

In Table 5 the Spearman's rank correlation coefficients between the tree diameter growth and non-spatial *CI*s and also the combination of spatially explicit *CI*s and the competitor selection methods are presented. Table 5 shows that the competitor selecting approaches significantly affect the growth prediction ability of spatial indices and the competition selection methods of CZR_{k3}, $CZR_{0.4h}$ and SCH_{60} demonstrated greater values of Spearman's *rho*, respectively. Among different spatial indices in these three neighbours selecting methods, *SdrAng* and *Heg* were well correlated with diameter increment. However, the values of *rho* for *Heg* were slightly lower than *SdrAng*. None of the alternatives of *Bitterlich method* (BAF_1, BAF_2 and BAF_4) showed to be an appropriate selection method of competitors. Furthermore, *BAL* and *BALMOD* as the best non-spatial *CI*s did not perform better than the superior spatial indices *SdrAng* and *Heg*. The results presented in Table 5 are based on the analyses of 2,742 subject trees that were presented in different neighbours' selection methods and 18 different non-spatial and spatial *CI*s are quantified and available for them.

The comparison of the linear mixed effect models and the linear multiple models detected the improve-

Table 5. The Spearman's rank correlation coefficients between the 5-year tree diameter increment and competition indices for a sample of 2,742 subject trees presenting in different neighbours' selection methods

	Plot	$CZR_{0.4h}$	CZR_{k2}	CZR_{k3}	BAF_1	BAF_2	BAF_4	SCH_{100}	SCH_{80}	SCH_{60}	$SCHCr_{100}$	$SCHCr_{80}$	$SCHCr_{60}$
Non–spatial indices													
BA–g$_j$	–0.160	–	–	–	–	–	–	–	–	–	–	–	–
BAL	**–0.598**	–	–	–	–	–	–	–	–	–	–	–	–
Sdr	–0.320	–	–	–	–	–	–	–	–	–	–	–	–
dr$_g$	–0.435	–	–	–	–	–	–	–	–	–	–	–	–
BAr	–0.436	–	–	–	–	–	–	–	–	–	–	–	–
BALr	–0.469	–	–	–	–	–	–	–	–	–	–	–	–
BALMOD	**–0.558**	–	–	–	–	–	–	–	–	–	–	–	–
Spatial indices													
Sl	–	–0.285	–0.273	–0.306	–	–	–	–	–	–	–	–	–
SOr	–	–0.225	–0.217	–0.279	–	–	–	–	–	–	–	–	–
SOdr	–	–0.334	–0.292	–0.381	–	–	–	–	–	–	–	–	–
SBAr	–	–0.578	–0.531	–0.590	–0.196	–0.164	–0.098	–0.491	–0.528	–0.551	–0.475	–0.530	–0.532
Heg	–	**–0.623**	–0.504	**–0.650**	–0.241	–0.193	–0.165	–0.456	–0.483	**–0.597**	–0.423	–0.459	–0.481
SAng1	–	–0.359	–0.319	–0.375	–0.214	–0.182	–0.171	–0.303	–0.306	–0.350	–0.282	–0.303	–0.322
SAng2	–	–0.409	–0.363	–0.417	–0.237	–0.231	–0.219	–0.386	–0.378	–0.390	–0.330	–0.348	–0.384
SdrAng	–	**–0.641**	–0.606	**–0.656**	–0.499	–0.430	–0.386	–0.591	–0.598	**–0.616**	–0.579	–0.600	–0.614
Almdg	–	–0.411	–0.368	–0.408	–0.086	–0.065	–0.074	–0.092	–0.228	–0.374	–0.282	–0.289	–0.227
Sdrl1	–	–0.522	–0.501	–0.531	–	–	–	–	–	–	–	–	–
Sdrl2	–	–0.302	–0.225	–0.363	–0.157	–0.131	–0.120	–0.210	0.175	–0.311	–0.135	–0.179	–0.219

ment in linear mixed effect regressions in terms of *AIC*, but the *ANOVA* comparison between the mixed effect models, with and without an auto-regressive structure, did not show significant remaining within-group correlation (P-value>0.05). Subsequently, the growth model was fit into linear mixed effect regression (Eq. (9)) with no auto-regressive structure for further analyses in this study. All explanatory variables used for Eq. (7) were considered as mixed effects and proved significant (P-value<0.05), also *VIF* indicated no problem with multiclollinearity, all values being less than eight. In order to test the contribution of selected *CI*s, they were devised into the recent growth model.

Table 6 illustrates the statistical measures of mixed effect models, including R^2, *RMSE*, *MSER*, *AIC*, AIC_w, and also *DAIC*. The indices comparisons were done for different sample size of subject trees based on each neighbour selection method. Generally, the contributions of *CI*s were significant but not very large in magnitude, and among the *CIs* added to the model, *SdrAng* presented the most significant contribution, no matter which competitor selection method was used. After that, *Heg* was found to be important in efficiency to improve the growth model. Non-spatial *CI*s of *BAL* and *BALMOD* showed less contributions to the growth model than the spatial indices, except for SCH_{60} where *BAL* appeared slightly better than *Heg CI*.

The results of analyses for different age groups (Table 7) demonstrated that competition had stronger prediction ability in younger stands, and spatially *CI*s proved to be better than non-spatial ones. As shown in Tables (6) and (7), the Ellenberg's light values performed a slight improvement for some models in order to describe the species-specific effect. The profiles of the R^2 and *AIC* did not show considerable variation between the two methods of calculating selected spatial *CI*s, with and without Ellenberg's values (Table 6). However, statistical measures for young stands viewed a slight improvement for including species-specific values in competition quantifications (Table 7).

Table 6. Contribution of the competition indices to tree diameter growth model

SM	Model	R^2	RMSE (cm)	MSER (%)	AIC	AIC_w	ΔAIC
CZR_{k3} (8265 subject trees)	*No CI*	0.564	0.432	–	6183.70	0.000	249.64
	Heg	0.604	0.422	4.831	5903.26	0.000	328.23
	$Heg^{Ellenberg}$	0.605	0.422	4.796	5894.69	0.002	346.67
	SdrAng	0.607	0.419	6.114	5883.26	0.447	157.43
	$SdrAng^{Ellenberg}$	0.607	0.419	6.107	5882.89	0.551	183.95
	BAL	0.592	0.422	4.627	5992.51	0.000	349.88
	BALMOD	0.589	0.422	4.791	6011.89	0.000	377.56
$CZR_{0.4h}$ (6426 subject trees)	*No CI*	0.521	0.471	–	4019.22	0.000	312.57
	Heg	0.569	0.451	8.469	3574.45	0.000	336.94
	$Heg^{Ellenberg}$	0.571	0.449	9.364	3560.08	0.001	363.55
	SdrAng	0.579	0.451	8.700	3485.58	0.779	374.01
	$SdrAng^{Ellenberg}$	0.578	0.451	8.656	3488.11	0.220	343.83
	BAL	0.567	0.460	4.759	3592.26	0.000	381.02
	BALMOD	0.567	0.461	4.576	3596.89	0.000	371.91
SCH_{60} (3840 subject trees)	*No CI*	0.485	0.435	–	1325.51	0.000	74.17
	Heg	0.544	0.424	4.758	1184.29	0.003	152.40
	$Heg^{Ellenberg}$	0.544	0.424	4.845	1182.60	0.008	133.32
	SdrAng	0.548	0.419	7.239	1174.16	0.544	128.65
	$SdrAng^{Ellenberg}$	0.548	0.419	7.324	1175.17	0.328	95.03
	BAL	0.546	0.416	8.627	1177.25	0.116	168.91
	BALMOD	0.542	0.419	7.262	1187.65	0.001	177.81

**Heg* and *SdrAng* are spatial indices without including the species-specific values. $Heg^{Ellenberg}$ and $SdrAng^{Ellenberg}$ are corresponding spatial indices including Ellenberg's species-specific values for three different neighbour selecting methods. *BAL* and *BALMOD* are non-spatial indices, for the subject trees of same data set used for analyses in each competitor selecting method.

Discussion

Computing the correlation coefficient of tree growth, and determining the efficiency of *CI*s when added to a tree growth model, have been widely used (Burkhart & Tomé, 2012). In the current study, adding the *CI*s to the growth model slightly improved the model, which can be partially due to the inclusion of relative dimensions of the trees in model. Relative dimensions measure the hierarchical position of the subject tree within the stand, and indirectly indicate the competitive status of the trees (Burkhart & Tomé, 2012).

Results from comparing different *CI*s proposed that spatial *CI*s of *SdrAng* and *Heg* were the best indices suitable to quantify the competition status of birch trees, respectively. Several studies (Castagneri *et al*., 2008; Contreras *et al*., 2011) have reported that *SdrAng* can describe a greater proportion of the investigated variation in growth models. Also, *Heg* demonstrated superior performance to non-spatial *CI*s in many studies (Alemdag, 1978; Pukkala & Kolström, 1987; Holmes & Reed, 1991; Mailly *et al*., 2003). The indices of *SdrAng* and *Heg* assign greater weight to the closer and bigger competitor trees (Wimberly & Bare, 1996) and it was following along the Cole & Lorimer (1994) hypothesis that noticeable competitive stress occurs by immediate competitors surrounding the subject tree crown.

The results we obtained for non-spatial *CI*s showed that *BAL* and *BALMOD* improved the predictive ability of Eq. (9), although in a smaller amount than when using the *CI*s of *SdrAng* or *Heg. S*ome studies including *BAL* or *BALMOD* found an improvement (large or modest) in model performance (e.g. Biging & Dobbertin, 1995; Corral Rivas *et al*., 2005). However, similar to our study, several other studies suggested that spatial measures provided more precise growth prediction (Boivin *et al*., 2010; Contreras *et al*., 2011), and to the contrary, many studies did not report

Table 7. Contribution of the competition indices to tree diameter growth in different age groups

Age group	Model	SM								
		CZR_{k3}			$CZR_{0.4h}$			SCH_{60}		
		rho	AIC	AIC_w	rho	AIC	AIC_w	rho	AIC	AIC_w
Young stands	*Heg*	–0.625	3908.56	0.008	–0.611	2594.14	0.000	–0.559	2608.35	0.000
	Heg^{Ellenberg}	–0.633	3906.50	0.023	–0.619	2593.95	0.000	–0.573	2604.73	0.001
	SdrAng	–0.694	3902.25	0.190	–0.655	2575.26	0.337	–0.669	2597.93	0.033
	SdrAng ^{Ellenberg}	–0.714	3899.43	0.779	–0.671	2573.91	0.663	–0.694	2591.17	0.966
	BAL	–0.618	3920.17	0.000	–0.578	2615.14	0.000	–0.602	2612.23	0.000
	BALMOD	–0.586	3918.31	0.000	–0.570	2609.71	0.000	–0.594	2612.72	0.000
Middle-aged stands	*Heg*	–0.522	3603.31	0.011	–0.480	2497.72	0.022	–0.376	2041.02	0.061
	Heg^{Ellenberg}	–0.496	3605.24	0.004	–0.458	2498.98	0.012	–0.353	2043.01	0.023
	SdrAng	–0.614	3595.05	0.673	–0.600	2494.53	0.108	–0.534	2035.80	0.835
	SdrAng ^{Ellenberg}	–0.583	3596.59	0.312	–0.565	2495.22	0.076	–0.481	2040.52	0.079
	BAL	–0.564	3636.79	0.000	–0.549	2493.38	0.191	–0.475	2050.31	0.001
	BALMOD	–0.566	3636.18	0.000	–0.565	2491.12	0.592	–0.486	2047.96	0.002
Old stands	*Heg*	–0.442	587.34	0.034	–0.382	308.67	0.016	–0.311	260.53	0.003
	Heg^{Ellenberg}	–0.402	590.46	0.007	–0.311	308.97	0.014	–0.300	261.92	0.002
	SdrAng	–0.544	585.59	0.081	–0.515	306.99	0.037	–0.492	253.44	0.110
	SdrAng ^{Ellenberg}	–0.498	587.77	0.027	–0.455	311.24	0.004	–0.463	256.76	0.021
	BAL	–0.603	581.52	0.618	–0.589	302.36	0.379	–0.532	252.03	0.222
	BALMOD	–0.507	583.47	0.233	–0.504	301.62	0.549	0.518	249.91	0.642

any superiority of spatial indices to non-spatial ones (Soares & Tomé, 1999; Stadt *et al*., 2007; Roberts & Harrington, 2008). The superiority of size-ratio *CI*s of *SdrAng* and *Heg* that used the *d* as indicator of size was probably because of the actual correlation between the subject tree's diameter increment and its *d* (Holmes & Reed, 1991); however, the strength of competitive stress explained by such correlations might be unclear (Brand & Magnussen, 1988; Larocque, 2002).

While non-spatial *CI*s are simple functions of the stand or a tree's dimensions, the selection of the neighbours that affect the growth of a subject tree is of crucial importance when calculating spatial indices. Concerning the competitor selection methods, the best results were acquired with those based on the influence zone and competition elimination angle concepts. Several studies showed that the competition status of a tree could potentially vary depending on the radius of influence zone (Pukkala & Kolström, 1987; He & Duncan, 2000; Nanami *et al*., 2005). The CZR_k was a multiple of average distance between the trees in the plot and highly affected by stand density. In our study plots, considering *k* equal to three and *CEA* equal to 30° proved to be a good fit to select the adequate number of active competitors. Although some studies (e.g. Alvarez *et al*. 2003) found better results using a different angle gauge, the angle gauge of 30° provided satisfactory results in some other studies (e.g. Lee & Gadow, 1997; Corral Rivas *et al*., 2005; Zhang *et al*., 2009).

The next superior competition selection approach, $CZR_{0.4h}$, was simple in practice and in accordance with studies showing that, the optimal influence zone radius strongly depended on the tree's initial dimensions (D'Amato & Puettmann, 2004; Sims *et al*., 2009). Considering the third suitable competitor selection method, similar to several other studies, the opening angle of 50°-60° performed well (Biging & Dobbertin, 1995; Pretzsch, 2009; Oheimb *et al*., 2011) where bigger angles (80° and 100° in this study) mainly de-

creased the merit of the search-cone method used to detect the competitors (Richards *et al*., 2008). In contrast to the CZR_{k3}, the two methods of $CZR_{0.4h}$ and SCH_{60} gave more weight to tree height than distance, and since in our study, there was a lack of height measures for all trees, the selecting system of CZR_{k3} was preferable to identify competitors for central trees.

Despite the fact that the identity of neighbouring species is an important factor in the characterization of their competitive effects (Bella, 1971; Zhao *et al*., 2006; Kaitaniemi & Lintunen, 2010; Bošelá *et al*., 2013), no significant improvement appeared in recalculating the selected indices using Ellenberg's light values except for young trees. One possible explanation is that in our study plots about two-thirds of the trees analysed were birch with the same light factors. Consequently, giving weight to different species did not significantly change the values of measured competition. In addition, *interspecific* competition mainly caused by Norway spruce appeared inferior due to differences in temporal growth patterns and shade-tolerance (Tahvanainen & Forss, 2008; Hynynen *et al*., 2011). Furthermore, the influence of competition on diameter growth was not strongly impacted by the number of species in the local neighbourhood as suggested by Oheimb *et al*. (2011). The slight improvement in young stands might be due to the nature of Ellenberg's light values that refer to the preferences of the early stage of the tree life cycle. During the early stage, when light-demanding birch trees rapidly occupy regeneration areas, Norway spruce tends to appear more shade-tolerant; consequently, weighting them differently in competition measures is justified. Moreover the performance of *CI*s changed slightly by stand development. In young stands spatial indices performed better while in older stands, non-spatial indices showed superior results. In the early stage, pioneer birches grow quite fast and vigorously (Hynynen *et al*., 2011), and spatial *CI*s explain competition effects better in dense young stands, since they account for the short distances between the neighbouring trees, that are competing for resources. In older stands, due to mortality induced by different factors, including competition (Sims *et al*., 2009), the number of trees decline and non-spatial *CI*s are adequate for competition studies.

The overall results of this study provided a better understanding of competition in birch stands. Although spatial *CI*s performed better than non-spatial *CI*s, the reported differences between the spatial and non-spatial indices are relatively small. The spatial indices require tree attributes and locations, and the recording of such information is expensive and time consuming. Therefore, we suggest applying the spatial indices only when studying the competition in the natural development of young stands, where the stands are usually dense, because these types of indices give more weight to trees that are closer to the subject tree. In the middle-aged and old managed stands, an efficient measure of competition is possible by employing the non-spatial indices that do not require as many field measurements.

Acknowledgements

We are sincerely grateful and would like to thank our guest professor, Arne Pommerening, who has kindly contributed recommendations and ideas for this research project.

References

Alemdag IS, 1978. Evaluation of some competition indexes for the prediction of diameter increment in planted white spruce / by I.S. Alemdag. Forest Management Institute, Ottawa, Canada.

Alvarez MF, Barrio M, Gorgoso F, Alvarez JG, 2003. Influencia de la competencia en el crecimiento en sección en Pinus radiata D. Don. Invest Agrar Sist Rec For 12(2): 25–35.

Andreassen K, Tomter SM, 2003. Basal area growth models for individual trees of Norway spruce, Scots pine, birch and other broadleaves in Norway. For Ecol Manag 180: 11-24.

Assmann E, 1970. The Principles of Forest Yield Study, Pergamon Press, Oxford, UK.

Bates DM, Watts DG, 1988. Nonlinear regression analysis and its applications. Wiley, New York. http://dx.doi.org/10.1002/9780470316757

Begon M, Harper JL, Townsend CR, 1996. Ecology: individuals, populations and communities. Blackwell Science, New York. http://dx.doi.org/10.1002/9781444313765

Bella IE, 1971. A New Competition Model for Individual Trees. For Sci17: 364-372.

Berger U, Hildenbrandt H, 2000. A new approach to spatially explicit modelling of forest dynamics: spacing, ageing and neighbourhood competition of mangrove trees. Ecol Model 132: 287-302. http://dx.doi.org/10.1016/S0304-3800(00)00298-2

Biging GS, 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 GS, Dobbertin M, 1995. Evaluation of Competition Indexes in Individual Tree Growth-models. For Sci 41: 360–377.

Bitterlich W, 1952. Die Winkelzählprobe. Forstw Cbl 71: 215–225. http://dx.doi.org/10.1007/BF01821439

Boivin F, Paquette A, Papaik MJ, Thiffault N, Messier C, 2010. Do position and species identity of neighbours matter in 8-15-year-old post-harvest mesic stands in the boreal mixedwood? For Ecol Manag 260: 1124-1131.

Bošelá M, Petráš R, Šebeň V, Mecko J, Marušák R, 2013. Evaluating competitive interactions between trees in mixed

forests in the Western Carpathians: Comparison between long-term experiments and SIBYLA simulations. For Ecol Manag 310, 577-588.

Brand DG, and Magnussen, S. 1988. Asymmetric, two-sided competition in even-aged monocultures of red pine. Can J For Res 18: 901–910. http://dx.doi.org/10.1139/x88-137

Burkhart HE, Tomé M, 2012. Modeling Forest Trees and Stands. Springer Netherlands, Dordrecht. http://dx.doi.org/10.1007/978-90-481-3170-9

Castagneri D, Vacchiano G, Lingua E, Motta R, 2008. Analysis of intraspecific competition in two subalpine Norway spruce (Picea abies (L.) Kast.) stands in Paneveggio (Trento, Italy). For Ecol Manag 255: 651–659.

Cole WG, Lorimer CG, 1994. Predicting tree growth from crown variables in managed northern hardwood stands. For Ecol Manag 67: 159–175.

Contreras MA, Affleck D, Chung W, 2011. Evaluating tree competition indices as predictors of basal area increment in western Montana forests. For Ecol Manag 262: 1939-1949.

Corral Rivas JJ, Álvarez González JG, Aguirre O, Hernández FJ, 2005. The effect of competition on individual tree basal area growth in mature stands of Pinus cooperi Blanco in Durango (Mexico). Eur J For Res 124: 133–142. http://dx.doi.org/10.1007/s10342-005-0061-y

D'Amato AW, Puettmann KJ, 2004. The relative dominance hypothesis explains interaction dynamics in mixed species Alnus rubra/Pseudotsuga menziesii forests. Ecol 92: 450–463. http://dx.doi.org/10.1111/j.0022-0477.2004.00888.x

Damgaard C, Weiner J, 2008. Modeling the growth of individuals in crowded plant populations. Plant Ecol 1: 111-116. http://dx.doi.org/10.1093/jpe/rtn008

Daniels RF, 1976. Simple competition indices and their correlation with annual loblolly pine tree growth. For. Sd. 22: 454-456.

Daniels RF, Burkhart HE, Clason TR, 1986. A comparison of competition measures for predicting growth of loblolly pine trees. Can J For Res 16: 1230-1237. http://dx.doi.org/10.1139/x86-218

Ellenberg H, Weber HE, Düll R, Wirth V, Werner W, Paulissen D, 1991. Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobotanica, 18: 1–248.

Fischer A, Lindner M, Abs C, Lasch P, 2002. Vegetation dynamics in central European forest ecosystems (near-natural as well as managed) after storm events. Folia Geobot 37: 17-32. http://dx.doi.org/10.1007/BF02803188

Ford ED, Diggle PJ, 1981. Competition for Light in a Plant Monoculture Modelled as a Spatial Stochastic Process. Annals of Botany 48: 481-500.

Hamilton DA, 1986. A logistic model of mortality in thinned and unthinned mixed conifer stands of Northern Idaho. For Sci 32(4): 989–1000.

He F, Duncan RP, 2000. Density-dependent effects on tree survival in an old-growth Douglas fir. For Ecol 88: 676–688.

Hegyi F, 1974. A simulation model for managing jackpine stands, In: Fries, J. (Ed.), Proceedings of IUFRO meeting S4.01.04 on Growth models for tree and stand simulation, Royal College of Forestry, Stockholm, Sweden.

Holmes MJ, Reed DD, 1991. Competition indices for mixed species northern hardwoods. For Sci 37: 1338-1349.

Hynynen J, Niemisto P, Vihera-Aarnio A, Brunner A, Hein S, Velling P, 2010. Silviculture of birch (Betula pendula Roth and Betula pubescens Ehrh.) in northern Europe. Forestry 83: 103-119. http://dx.doi.org/10.1093/forestry/cpp035

Hynynen J, Repola J, Mielikäinen K, 2011. The effects of species mixture on the growth and yield of mid-rotation mixed stands of Scots pine and silver birch. For Ecol Manag 262: 1174-1183.

Jõgiste K, 1998. Productivity of mixed stands of Norway spruce and birch affected by population dynamics: a model analysis. Ecol Model 106: 77-91. http://dx.doi.org/10.1016/S0304-3800(97)00183-X

Jõgiste K, 2010. A basal area increment model for Norway spruce in mixed stands in Estonia. Scan J For Res 15: 97–102. http://dx.doi.org/10.1080/02827580050160529

Kaitaniemi P, Lintunen, A. 2010. Neighbor identity and competition influence tree growth in Scots pine, Siberian larch, and silver birch. Annals of For Sci 67: 604. http://dx.doi.org/10.1051/forest/2010017

Kiviste A, Hordo M, 2002. Eesti metsa kasvukäigu püsiproovitükkide võrgustik (Network of permanent forest growth plots in Estonia) Forestry Studies 37: 43-58.

Kiviste A, Nilson A, Hordo M, Merenakk M, 2003. Diameter Distribution Models and Height-Diameter Equations for Estonian Forests. Modelling Forest Systems 169-179.

Lang M, Nilson T, Kuusk A, Kiviste A, Hordo M, 2007. The performance of foliage mass and crown radius models in forming the input of a forest reflectance model: A test on forest growth sample plots and Landsat 7 ETM+ images. Remote Sensing of Environment, 110(4): 445-457. http://dx.doi.org/10.1016/j.rse.2006.11.030

Larocque GR, 2002. Examining different concepts for the development of a distance-dependent competition model for red pine diameter growth using long-term stand data differing in initial stand density. For Sci 48: 24–34.

Lee WK, Gadow Kv, 1997. Iterative Bestimmung von Konkurrenzbaeume in Pinus densiflora Bestaenden (Iterative selection of competitor trees in Pinus densiflora stands). Allg. For. Jagdztg 168: 41-45.

Lin JY, 1974. Stand growth simulation models for Douglas-fir and western hemlock in the northwestern United States, in: Fries J. (Ed.), Growth Models for Tree and Stand Simulation, Royal Coll. For., Stockholm, Sweden. Pp. 02–118.

Lorimer CG, 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. For Ecol Manag 6: 343–360.

Mailly D, Turbis S, Pothier D, 2003. Predicting basal area increment in a spatially explicit, individual tree model: a test of competition measures with black spruce. Can J For Res 33: 435-443. http://dx.doi.org/10.1139/x02-122

Martin GL, Ek AR, 1984. A Comparison of Competition Measures and Growth Models for Predicting Plantation Red Pine Diameter and Height Growth. For Sci 30: 731-743.

Munro DD, 1974. Forest growth models –a prognosis. in J. Fries (ed.): Growth models for tree and stand simulation. Royal Coll. For., Res. Notes 30, pp. 7-21. Stockholm, Sweden.

Nanami S, Kawaguchi H, Yamakura T, 2005. Sex ratio and gender-dependent neighbouring effects in Podocarpus nagi,

a dioecious tree. Plant Ecol 177: 209-222. http://dx.doi.org/10.1007/s11258-005-2210-2

Nilson A, 2005. Generalization of height growth as difference equations fit for estimating the site index of stands. Metsanduslikud Uurimused 43: 173-184.

Oheimb vG, Lang AC, Bruelheide H, Forrester DI, Wäsche I, Yu M, Härdtle W, 2011. Individual-tree radial growth in a subtropical broad-leaved forest: The role of local neighbourhood competition, For Ecol Manag 261: 499–507.

Pedersen RØ, Næsset E, Gobakken T, Bollandsås OM, 2013. On the evaluation of competition indices -The problem of overlapping samples. For Ecol Mang 310: 120-133.

Peet RK, Christensen NL, 1987. Competition and tree death. BioScience 37: 586-595. http://dx.doi.org/10.2307/1310669

Pretzsch H, Biber P, Ďurský J, 2002. The single tree-based stand simulator SILVA:construction, application and evaluation. Forest Ecol Manage 162: 3–21. http://dx.doi.org/10.1016/S0378-1127(02)00047-6

Pretzsch H, 2009. Forest Dynamics, Growth and Yield. Springer-Verlag Berlin Heidelberg, Germany. http://dx.doi.org/10.1007/978-3-540-88307-4_1

Prévosto B, Coquillard P, Gueugnot J, 1999. Growth models of silver birch (Betula pendula Roth.) on two volcanic mountains in the French Massif Central. Plant Ecol 144: 231-242. http://dx.doi.org/10.1023/A:1009858508312

Pukkala T, Kolström T, 1987. Competition indices and the prediction of radial growth in Scots pine Silva Fenn 21: 55-76.

R Development Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. http://www.R-project.org.

Richards M, McDonald AJS, Aitkenhead MJ, 2008. Optimisation of competition indices using simulated annealing and artificial neural networks. Ecol Model 214: 375–384. http://dx.doi.org/10.1016/j.ecolmodel.2008.03.008

Roberts SD, Harrington CA, 2008. Individual tree growth response to variable-density thinning in coastal Pacific Northwest forests. For Ecol Manag 255: 2771-2781.

Rouvinen S, Kuuluvainen T, 1997. Structure and asymmetry of tree crowns in relation to local competition in a natural mature Scot pine forest. Can J For Res 27: 890–902. http://dx.doi.org/10.1139/x97-012

Schröder J, Gadow Kv, 1999. Testing a new competition index for Maritime pine in north western Spain. Can J For Res 29: 280-283.

Schröder J, Rodriguez R, Vega G, 2002. An age-independent basal area increment model for Maritime pine trees in northwestern Spain. For Ecol Manag 157: 55–64.

Siegel S, 1956. Nonparametric Statistics for the Behavioral Sciences. McCraw-Hill, New York.

Sims A, Kiviste A, Hordo M, Laarmann D, Gadow K v, 2009. Estimating tree survival: a study based on the Estonian Forest Research Plots Network. Annales Botanici Fennici 46: 336-352. http://dx.doi.org/10.5735/085.046.0409

Soares P, Tomé M, 1999. Distance-dependent competition measures for eucalyptus plantations in Portugal. Ann. For. Sci, 56: 307-319. http://dx.doi.org/10.1051/forest:19990405

Soares P, Tomé M, 2001. A tree crown ratio prediction equation for eucalypt plantations. Ann For Sci, 58: 193-202. http://dx.doi.org/10.1051/forest:2001118

Stadt KJ, Lieffers VJ, 2000. MIXLIGHT:A flexible light transmission model for mixed-species forest stands. Agricultur Foest. Meteorol. 102: 235–252. http://dx.doi.org/10.1016/S0168-1923(00)00128-3

Stadt KJ, Huston C, Coates KD, Feng ZL, DaleMRT, Lieffers VJ, 2007. Evaluation of competition and light estimation indices for predicting diameter growth in mature boreal mixed forests. Annals of For Sci 64: 477-490. http://dx.doi.org/10.1051/forest:2007025

Staebler GR, 1951. Growth and spacing in an even-aged stand of Douglas-fir. Master's thesis, University of Michigan, USA.

Steneker GA, Jarvis JM, 1963. A preliminary study to assess competition in a white spruce-trembling aspen stand. For. Chron. 39: 334–336. http://dx.doi.org/10.5558/tfc39334-3

Tahvanainen T, Forss E, 2008. Individual tree models for the crown biomass distribution of Scots pine, Norway spruce and birch in Finland. For Ecol Manag 255: 455-467.

Tomé M, Burkhart HE, 1989. Distance-Dependent Competition Measures for Predicting Growth of Individual Trees. For Sci 35: 816-831.

Vanclay JK, 1991. Mortality functions for north Queensland rainforests. J. Tropical For Sci 4: 15–36.

Vitas A, 2011. Seasonal Growth Variations of Pine, Spruce, and Birch Recorded by Band Dendrometers in NE Lithuania. Bal For 17: 197-204.

Wagenmakers E.J, Farrell S, 2004. AIC model selection using Akaike weights. Psychonomic Bulletin & Review, 11, 192-196. http://dx.doi.org/10.3758/BF03206482

Weigelt A, Jolliffe P, 2003. Indices of plant competition. Ecol J 91: 707–720.http://dx.doi.org/10.1046/j.1365-2745.2003.00805.x

Wimberly MC, Bare BB, 1996. Distance-dependent and distance-independent models of Douglas-fir and western hemlock basal area growth following silvicultural treatment. For Ecol Manag 89: 1–11.

Wykoff WF, Crookston NL, Stage AR, 1982. User's guide to the Stand PrognosisModel. USDA Forest Service, Gen. Tech. Rep. INT-133.

Yearbook of Forest, 2013. Estonian environment information centre.Tartu [in Estonian].

Zhang C, Zhao X, Gao L, Gadow Kv, 2009. Gender, neighboring competition and habitat effects on the stem growth in dioecious Fraxinus mandshurica trees in a northern temperate forest. Annals of For Sci vc, 66(8): 812-819.

Zhao DH, Borders B, Wilson M, Rathbun SL, 2006. Modeling neighborhood effects on the growth and survival of individual trees in a natural temperate species-rich forest. Ecol Model 196: 90-102. http://dx.doi.org/10.1016/j.ecolmodel.2006.02.002