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RESEARCH ARTICLE

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# Evaluation of individual-tree growth models for *Picea abies* based on a case study of an uneven-sized stand in southern Sweden

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**ABSTRACT**

To develop recommendations for tree selection in Continuous Cover Forestry (CCF), access to valid tools for simulating growth at individual tree-level is necessary. To assist efforts to develop such tools, in this study, long-term observation data from two uneven-sized Norway spruce plots in southern Sweden are used to evaluate old and new individual-tree growth models (two established Swedish models, two new preliminary models and included as a reference, a Finnish model). The plots' historical management records and site conditions are the same, but their last thinning treatment differs. Observed diameter increment at tree-level is investigated in relation to treatment. Individual tree growth residuals of tested models are evaluated in relation to tree diameter, treatment, projection length and sensitivity to the predictor mean stand age. Furthermore, the relations between displayed residuals and basal area local competition are analysed. The analyses indicate that active thinning made annual diameter increment independent of tree diameter above a threshold level, while the absence of thinning supported a concave relationship. All tested models displayed a significant linear bias leading to overestimation of small trees' growth and increasing underestimations of larger trees' growth with tree diameter. All distance-independent models displayed residual trends related to local competition.

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Continuous Cover Forestry; single-tree growth models; selective cutting; uneven-aged; single-tree selection; growth prediction

## Introduction

Continuous Cover Forestry (CCF) is increasingly discussed as an alternative to conventional rotation forestry in boreal regions. CCF systems, according to Gadow (2001), are characterized by selective harvesting; the stand age is undefined and forest development does not follow a cyclic harvest-and-regeneration pattern. Trees are individually selected, with compromises between silvicultural, economic and conservation needs, often based on a combination of frame tree selection, crown thinnings and target diameter harvesting (Abetz and Klädtke 2002). Tree selection, furthermore, includes maintenance of some desired form of tree size diversity in the residual stand, in this study inclusively referred to as uneven-sized structure, to support regeneration and ingrowth (Meyer 1952; Pukkala et al. 2009), quality tending (Oliver et al. 1996; Seifert 1999) and large saw-logs yields (Hagner et al. 2001; O'Hara 1998; Pukkala et al. 2009).

To formulate optimal field recommendations for tree selection, access to valid tools for simulating growth at individual tree-level is necessary (Peng 2000; Weiskittel et al. 2011). Models applied for this purpose must be adapted to the management regime under study (Øyen et al. 2011; Vanclay 2012). Furthermore, dynamics that are of marginal importance in simulations of even-sized stands, e.g. spatial distribution of trees (Hyytiäinen and Haight 2012) and tree growth in relation to shading conditions (Tahvonen 2009), are important. Thus, individual growth prediction needs to consider the impact of local competitors.

Individual-tree models can be divided into distance-dependent and distance-independent models. Distance-dependent models use variables based on the coordinates of each tree, while distance-independent models assume an average spatial pattern of the involved trees (Munro 1974). In practice, distance-independent models, which account for local competition, typically use density estimates of total or sub-fractions of competitor basal area within concerned plots (e.g. Pukkala et al. 2013; Söderberg 1986). In uneven-sized Norway spruce stands, which usually are randomly distributed and aggregated from a spatial point of view (Hanewinkel 2004), additional tree selection criteria, complementary to tree size, are more likely to work better (Pukkala et al. 2015). In these circumstances, use of distance-dependent models enables development of selection criteria based on inter-tree distances.

Distance-dependent individual growth models, adapted to uneven-sized Norway spruce in Fennoscandia, have not been prioritized in research. Some distance-independent models for uneven-sized stands are available in Finland (Bianchi et al. 2020; Pukkala et al. 2013) and Norway (Øyen et al. 2011), however, valid predictions from these models, if used in the more southern parts of Sweden, cannot be expected.

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For Swedish conditions, the HEUREKA forest simulator is the most comprehensive tool available (Wikström et al. 2011). The central growth components are two statistical tree-list distance-independent models developed by Söderberg (1986) and Elfving (Elfving and Nyström 2010). Both models are calibrated on extensive data of national forest inventory plots, however, with limited attention to the issue of uneven-sized stand structures. The models incorporate variables in different ways that describe the social position of a tree within the defined plot. An obstacle for the application of these models to uneven-sized conditions is the required input of mean stand age. Stand age is an inappropriate parameter because of the wide ranges of individual tree ages in uneven-sized structures (Peng 2000; Vanclay 2012), due to both high diameter diversity and high age diversity within diameter classes (Tarasiuk and Zwieniecki 1990). The HEUREKA models have never been validated with uneven-sized data, and the statistical structure of the models could possibly make them sensitive to use outside of the stand structure types with which they were calibrated.

This study utilizes a unique data set of observed individual tree growth in southern Sweden for validation of available individual-tree growth models for Norway spruce. The data consists of tree measurements from two uneven-sized Norway spruce-dominated plots which have the same historical management record and site conditions but one of the plots was left untreated in the last selective cutting. This enables evaluation not only of model accuracy but also of how the thinning intensity in this case has affected tree growth of different diameter classes.

The thinning intensity is of particular importance in individual-tree selection since increased growing space is gained for trees of ever smaller size with increasing cutting intensity (Eyre and Zillgitt 1953). When the diameter at breast height (dbh) increment is not affected by smaller trees, it is an effect of one-way competition (Soares and Tomé 2003). In Sweden, individual tree growth is expected to be regulated mainly through one-way competition in the south, while two-way competition becomes increasingly important to further north (Lundqvist 1994). An optimum thinning level ensures that diameter increments of suppressed and sub-dominant trees are limited, to support quality tending, and less limited for dominant trees, which is beneficial for large saw-log yields (definitions of social classes from Hanisch and Kilz 1991).

The diameter increment of uneven-sized Norway spruce stands generally has a concave relationship with dbh, peaking between 20 and 30 cm dbh in Finnish boreal conditions (Pukkala et al. 2009) and around 35 cm dbh in Austrian stands (Monserud and Sterba 1996). Valkonen et al. (2017) studied diameter growth after diameter-limit cutting of uneven-sized Norway spruce stands in Finland. Their result indicated that thinning intensity at 45% level increased or at minimum maintained, diameter increment for diameter classes down to 7.5 dbh, 10–15 years after cutting. With an average of 60% thinning intensity, even classes down to 2.5 cm dbh displayed improved growth in the following 25 years. According to this, quality tending of small trees is possible to control in uneven-sized stand structures if appropriate levels of thinning intensity for the site conditions can be identified.

This study has two main aims:

1. to investigate how diameter increment in relation to tree size were affected by selective thinning in this case;
2. to evaluate the performance of available individual-tree growth models, adapted for southern Swedish forest conditions, when tested with this uneven-sized stand data

To address the first aim, the study evaluates the observed individual tree growth differences between the treated and the untreated plot and between size classes. To address the second aim, the performance of two Swedish individual tree growth models designated Söd (Söderberg 1986) and Elf (Elfving and Nyström 2010) and two recently proposed theoretically based models designated Loh (Lohmander 2017) and Ols (Olsson and Fagerberg 2019) are investigated. The Loh and Ols models are developed explicitly for uneven-sized Norway spruce stands but are still considered preliminary due to calibration with a limited data set. Additionally, a Finnish model designated Puk (Pukkala et al. 2013) is used as a reference in the initial analysis, although it is developed for more northern latitudes. The Puk model is included because it is the only one of the tested models that is comprehensively calibrated with uneven-sized data.

A general concern is whether the tested models are able to accurately predict the increased growth distributed to dominant trees in uneven-sized stands. Furthermore, prediction sensitivity to the measurement error of the predictor mean stand age (for tested models that rely on it) and prediction accuracy over time are evaluated. Finally, the relationships between tree-level measures of basal area local competition and individual basal area growth residuals are investigated in order to assess the models' responses to variation in local competition.

The following hypotheses are tested:

- Selective cutting, in this case, increased diameter increment for all diameter classes.
- Residual trends of individual basal area growth against tree diameter are positive linear for the tested distance-independent models (Elf, Söd, Loh and Puk).
- For models depending on the predictor basal area mean stand age (Elf and Söd), individual basal area growth prediction may be affected by measurement error.
- Mean individual basal area growth residuals are independent to projection length for the tested models (Elf, Söd, Loh and Ols).
- Basal area growth residuals of tested distance-independent models (Elf, Söd and Loh) are linearly correlated to measures of local basal area competition.

## Materials and methods

### Study site

The observational data is a unique data set for southern Sweden in terms of the length of the observation period in a stand with an unbroken record of selective cuttings. The

**Table 1.** Stand structure characteristics per plot at the time-point of initial revision.

| | *Thinned* | *Unthinned* |
|---|---|---|
| Time-point initial revision | 1988 | 1995 |
| Time since last thinning (yrs) | 6 | ~36 |
| Standing volume ($m^3$ $ha^{-1}$) | 190 | 412 |
| Basal area ($m^2$ $ha^{-1}$) | 20 | 38 |
| Stem density (no. $ha^{-1}$, dbh > 0) | 7400 | 3000 |
| Mean dbh (cm) | 14,9 | 18,5 |
| Proportion of Norway spruce (%)[a] | 72 | 68 |

[a] The proportion of Norway spruce is based on standing volume.

stand is situated on sandy-silty soil in Romperöd, Östra Göinge (Lat 56.2 °N), with a G30 site index, Blueberry field vegetation type and Mesic soil moisture type according to the Swedish classification system (Hägglund and Lundmark 1977). The altitude is 100 m, and inclination is 0–4̊ towards west. The stand's history is well documented. In 1920, it was subjected to a heavy selective cutting using a target diameter at breast height of 13 cm. Additional selective cuttings were conducted in 1945/46 and 1958/59, with approximately 80 $m^3$ $ha^{-1}$ of standing volume removed each time. During the following 20 years, only birch was thinned for firewood. All regrowth has been a result of natural regeneration. In 1980, two square demonstration plots (each 2500 $m^2$) were established next to each other in the center of the stand. The first plot (*Thinned*) was treated with selective cutting in 1982, with 37% of the standing volume removed. Thinning type ratio (mean volume of trees removed to mean volume of trees before thinning; Kerr and Haufe 2011) was 1.6. The second plot (*Unthinned*) was left untreated. Stand structure characteristics of the plots are presented in Table 1 and Figure 1. The revision periods are not identical for the two plots since plot *Thinned* was revised in 1988, 2002 and 2016, while plot *Unthinned* was revised in 1995 and 2014.

## *Data*

The data from the original revisions consist of both calipered and none-calipered trees (Table 2). The subset which was calipered (in this study termed *Only calipered*), represents the majority of the larger trees (Figure 1). This subset, *Only calipered*, is more thoroughly documented, compared to the remaining non-calipered trees, with tree-level information including identity number, tree height and diameter at breast height. The subset of non-calipered trees, which mainly consists of understory trees, contains at tree-level exclusively information on species and diameter class (5 and 2 cm classes in *Thinned* and *Unthinned*, respectively).

A tree-list including all trees with dbh ≥6 cm at initial revision was compiled for each plot, linking all individual tree observations between the revisions. Before this step, each non-calipered tree observed in the initial revisions was primarily assigned to the mean 1 cm diameter class of the wider diameter class to which it was originally assigned. Non-calipered observations in the first revision, which had no identity number, were manually paired with remaining unpaired tree identities in the last revision according to best-fit comparison. For this purpose, a fixed annual increment per diameter class was first assumed based on observations from the calipered trees.

In the *Thinned* plot, all trees were positioned with coordinates in the revision of 2016, using Postex equipment, which employs ultrasound distance measurement and triangulation techniques. Acquisition of coordinates of individual tree positions in this plot enabled testing of the distance-dependent growth model (Ols). To provide for a complete simulation, trees in *Thinned* recorded in the first revision that had died during the period and could not be linked to registered stumps were randomly positioned ($n = 43$).

Total mortality in *Thinned* during the observation period was 54 trees, and ingrowth was three trees (dbh ≥ 6 cm), while mortality in *Unthinned* was 135 trees and ingrowth was six trees (Table 2). Most trees that died in both plots had diameters less than 14 cm (first revision), 76% and 74% in *Thinned* and *Unthinned*, respectively. In *Thinned*, mortality accounted for 5% of stand basal area in the first revision period and 16% in the second period. In *Unthinned*, the corresponding value is 10% for the whole period.

Basal area mean stand age (BALD), defined as shown in equation (1), was calculated from measurements of trees in the dominating cutting class (D2; defined in Nilsson et al. 2020), according to recommendations for HEUREKA simulations (unpublished, Elfving B (2005) En grundytetillväxtfunktion för alla trädslag i hela landet. Swedish University of Agricultural Sciences), where $A$ is age and $x$ is basal area of tree $i$, both at breast height.

$$\mathrm{BALD} = \frac{\sum A_i x_i}{\sum x_i}. \tag{1}$$

BALD was estimated from a merged sample of trees from both plots ($n = 13$, *Picea abies* = 5, *Pinus sylvestris* = 8, 25 cm < dbh < 60 cm). Five test values of BALD, based on fixed percentage deviations from the estimated BALD ($\mathrm{BALD_B}$), were calculated per plot to enable an analysis of the simulation sensitivity of measurement error (Table 3).

Based on the original set of age sample trees from 1980, the relative BALD difference between the time before and after thinning was 2% ($n_1 = 12$, $n_2 = 6$). The corresponding difference, after thinning, between the two plots was 8% (*Thinned*, $n = 6$ and *Unthinned*, $n = 7$). These estimates indicate the possible scale of a measurement error for the $\mathrm{BALD_B}$ estimation. Individual tree age, a required predictor for Elf and Söd models, was calculated using HEUREKA with the age function for individual trees (Elfving 2003). This function includes BALD as a predictor variable.

## *The HEUREKA forest simulator*

Simulations with the Elf and Söd models were conducted in HEUREKA, application PlanWise. The HEUREKA simulator is described by Wikström et al. (2011) and Elfving and Nyström (2010). Simulations are performed based on one of the following three options: even-aged, uneven-aged, or unmanaged stands structures. To be classified as an uneven-aged stand, less than 80% of the stand volume

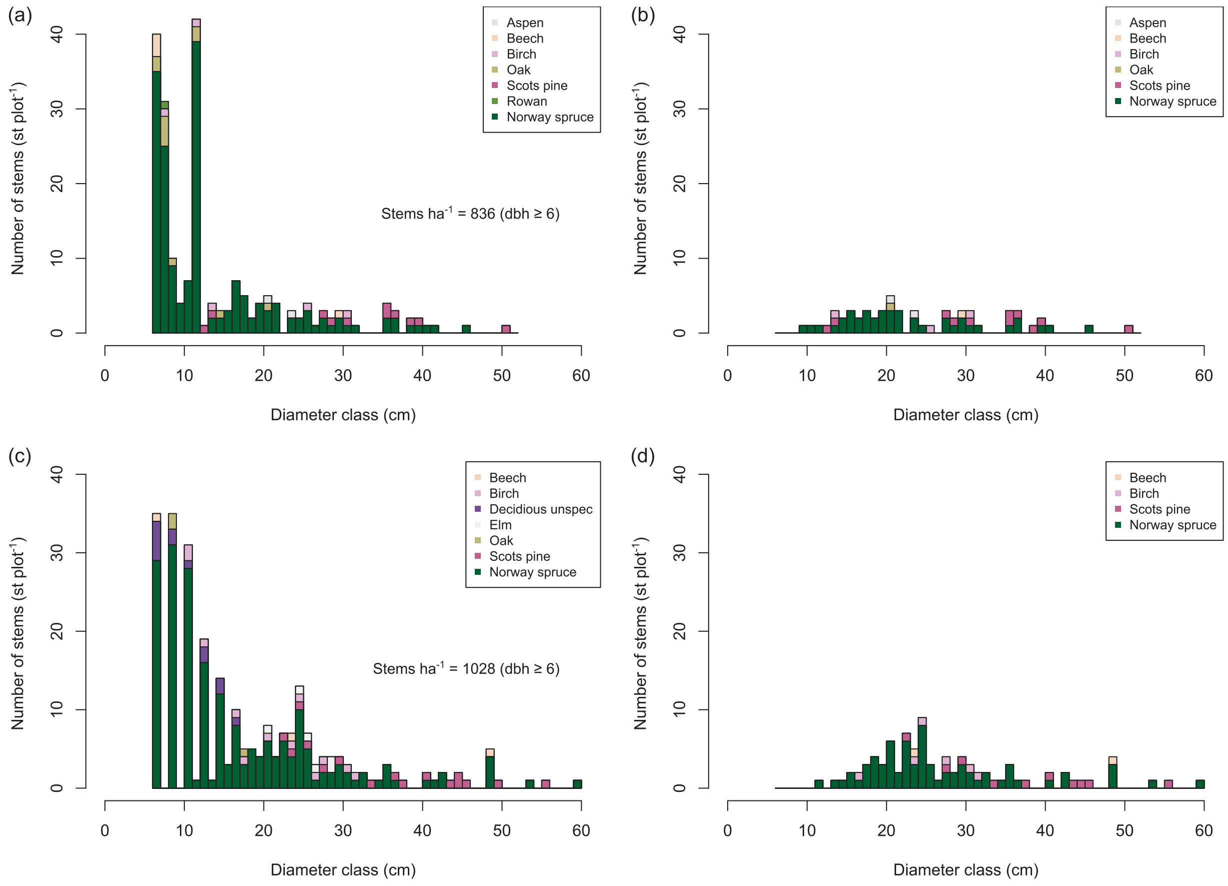

**Figure 1.** Diameter and species distributions per treatment and subset at initial revision point. (a) assumed distribution of plot *Thinned* with subset *All trees/all species*, (b) plot *Thinned* with subset *Only calipered/ all species*, (c) assumed distribution of plot *Unthinned* with subset *All trees/all species* and (d) plot *Unthinned* with subset *Only calipered/ all species*. The designation "assumed" indicates that trees which were not calipered are likely concentrated to some fewer diameter classes compared to the true distribution due to the procedure of assigning these trees to 1 cm classes. Example: In the *Thinned* plot, the diameter class 10–15 cm contained 47 spruce trees which were primarily assigned a dbh of 12 cm, but an individual tree could be adjusted to 15 cm dbh if it was considered likely from the matching data that this tree belonged to the upper end of the original class.

shall be present within a 20-year age-span (Elfving and Nyström 2010). Use of the uneven-aged option reduces the predictor variable of individual tree age by 10%. Single-tree models for ingrowth and mortality can be applied. Individual-tree growth predictions are generated either with a default configuration that combines tree- and stand-level growth models or with an alternative configuration that exclusively uses tree-level models. With the default setting, tree-level functions are used for distribution of growth to individual trees, and a stand-level function is used as a control function for total stand growth. A simulation requires an initial tree-list with species and diameter specified for all trees with dbh > 4 cm. Other minimum input variables are stand age, data about performed thinning, latitude, altitude, field vegetation type, soil moisture and site index according to site factors (Hägglund and Lundmark 1977). If tree positions are not available, coordinates are calculated by use of distribution functions.

**Table 2.** Numbers of living trees depending on subset and revision point. The term *All trees* refers to both calipered and non-calipered trees.

| | *Thinned* | | | *Unthinned* | |
|---|---|---|---|---|---|
| Subset | 1988 | 2002 | 2016 | 1995 | 2014 |
| All trees/all species | 209 | — | 155 | 257 | 122 |
| Only calipered/all species | 73 | 72 | 59 | 116 | 88 |
| Only calipered/only spruce | 54 | 53 | 41 | 83 | 70 |

## Tested models

The Söd model, described in Söderberg (1986), is a statistical individual-tree growth model that includes social position expressed as the dbh of the subject tree divided by the dbh of the largest tree within the measured plot (10 m radius). The dependent variable is the natural logarithm of 5-year basal area increment in cm$^2$. For Norway spruce in southern Sweden, there are up to 25 predictors for this growth model, covering characteristics describing subject tree, plot, climate, site, treatment and environment. Treatment is represented by one of three optional predictors: unthinned, thinned 0–5 years ago and thinned >5 years ago. There are six different functions for Norway spruce separated by three regions within Sweden and two age groups. The simulations reported here are based on the two functions for southern Sweden, which are calibrated with 3564 (>35yrs) and 2651 (<55yrs) subject trees, respectively.

The Elf model, described in Elfving and Nyström (2010), is a statistical individual-tree growth model that accounts for local competition through different combinations of

**Table 3.** Tested values of basal area mean stand age ($\mathrm{BALD}_{|x_i|}$) per plot. $\mathrm{BALD_B}$ is estimated basal area mean stand age. Percentages indicate deviation between tested basal area mean stand age and $\mathrm{BALD_B}$ values.

| Tested values of basal area mean stand age[a] | *Thinned* 1988[b] | *Unthinned* 1995 |
|---|---|---|
| $\mathrm{BALD}_{-40\%}$ | 62 | 66 |
| $\mathrm{BALD}_{-20\%}$ | 83 | 88 |
| $\mathrm{BALD_B}$ | 104 | 110 |
| $\mathrm{BALD}_{+20\%}$ | 125 | 132 |
| $\mathrm{BALD}_{+40\%}$ | 146 | 154 |

[a] Unit in years at dbh.

[b] During analysis, the initial year for the *Thinned* plot was changed from 1989 to 1988 to be consistent with how the revision times are indicated with calendar years. The BALD values for *Thinned* were never adjusted accordingly before simulation and thus are based on ages of trees in the calendar year 1989.

transformed variables based on (a) subject tree dbh; (b) basal area of larger trees within the plot; (c) proportion of the basal area within the plot which is not Norway spruce; (d) tree age; and (e) an indicator of the presence of old over-story trees. The dependent variable is the 5-year increase of squared diameter at breast height ($\mathrm{cm}^2$). Up to 20 predictors are used, covering the same spectra of characteristics as was presented above for the Söd model. Treatment is expressed with an additional predictor if the plot has been thinned within the last ten years. The model consists of one single function calibrated on 18500 inventory plots with a 10 m radius covering the whole of Sweden.

Three combinations of the HEUREKA models were simulated. The Elf model was tested only in the default configuration, designated Elf_s, since it was developed exclusively for use in combination with the stand function control. The Söderberg model was tested both with and without the stand-level function (Söd_s and Söd). The selected stand structure setting was uneven-aged.

The Loh model is an autonomous differential equation, in continuous time, with a closed-form solution (Lohmander 2017). It is based on the underlying assumptions that basal area increment is proportional to the sunlight projection area, essentially from the side of the tree, which in turn, is proportional to the square root of the tree basal area. The model is presented in equation (2), where $x$ is basal area at breast height ($\mathrm{cm}^2$), $t$ is time (yrs) with parameters $a = 0.5309$ and $b = 6.258\mathrm{E}^{-5}$ (Appendices, Table 6). Thus, Loh is an individual-tree growth model without adjustment to local competition.

$$\frac{dx}{dt} = ax^{0.5} - bx^{1.5}. \tag{2}$$

The general dynamic function, see (3), derived from equation (2) by Lohmander (2017), was used to simulate future basal area at time ($t$), where $c = \frac{b}{a} = 1.17869E^{-4}$.

$$x(t) = \frac{\left(\left(\frac{\sqrt{x_0}\sqrt{c}+1}{\sqrt{x_0}\sqrt{c}-1}\right)e^{(a\sqrt{c})t}+1\right)^2}{c\left(\left(\frac{\sqrt{x_0}\sqrt{c}+1}{\sqrt{x_0}\sqrt{c}-1}\right)e^{(a\sqrt{c})t}-1\right)^2}. \tag{3}$$

The Ols model is a distance-dependent model, in which two distance weighted size ratio functions are added to a discrete-time approximation of the Loh model (Olsson and Fagerberg 2019). Hence, the resulting model is a difference equation. The two additional parts, which account for local competition, represent (a) basal area of all competing trees and (b) basal area of all competing spruce trees. The model is presented in equation (4), where $x$ is basal area at breast height ($\mathrm{cm}^2$), $t$ is time (year), $i$ is the subject tree, $j$ represents the competitor tree, $AT$ is all competitor trees, $S$ is all spruce competitor trees and $x_{S,j}$ is basal area of the competitor tree $j$, if a spruce, otherwise 0. $R_{i,j}$ is the distance between tree $i$ and tree$j_,$ $a_1 = 72.55$, $b_1 = -84.67$, $c_{1,AT} = -83.73$, $c_{1,S} = -56.95$, $k_1 = 1.2106$, $k_2 = 0.1477$, $k_3 = 5.6670$ and $k_4 = 2$.

$$\begin{aligned}\frac{dx_i}{dt} &\approx \frac{\Delta x_i}{\Delta t}\\ &= a_1 x_i^{0.5} + b_1 x_i^{1.5}\\ &\quad + c_{1,AT}\left(\sum_{i\neq j}\left(\frac{x_j}{x_i}\right)^{k2} x_j e^{-\left(\frac{R_{i,j}}{k3}\right)^{k4}}\right)^{k1} x_i^{0.5}\\ &\quad + c_{1,S}\left(\sum_{i\neq j}\left(\frac{x_{S,j}}{x_i}\right)^{k2} x_{S,j} e^{-\left(\frac{R_{i,j}}{k3}\right)^{k4}}\right)^{k1} x_i^{0.5}.\end{aligned} \tag{4}$$

Both the Loh and Ols models were parameterized with trees from the Romperöd site. The training datasets (Loh, $n = 70$ and Ols, $n = 43$) overlap with the validation data of the *Thinned* plot as 30 of these training set trees are also represented in the subset *Only calipered/only spruce*. However, the projection time is different because the training sets rely on increment core estimations of annual ring widths between 2011 and 2016, unlike the 1988–2016 revision period on which the validation data is based. Due to the overlap, the residual patterns of outputs of the HEUREKA models and the two new models shall be compared with caution.

The reference model Puk is a distance-independent mixed-effects non-linear model (Pukkala et al. 2013), which calculates diameter growth in 5-year steps. The model is adapted to various stand structures, species compositions and forest sites, which provides for a high degree of flexibility. In total, 1816 plots (100–2400 $\mathrm{m}^2$) covering locations scattered throughout Finland were used for calibration. Site is described by temperature sum and the Finnish system for forest site type (Cajander 1949). Two-sided competition is described by stand basal area, and one-sided competition by the basal area of larger trees, divided into pines, spruces and hardwood species, respectively.

In the simulation with the Puk model, basal areas of larger trees were calculated as a sum of the respective plot. The site was Mesic (MT) and temperature sum 1442 day degrees above 5°C (Perttu and Morén 1994). All regression parameters were derived from Pukkala et al. (2013) without calibration to the local site. The authors recommend, with reference to de-Miguel et al. (2013), that mixed-effects models of this type are used with caution when applied in the absence of calibration data. Nevertheless, this model was judged to be the best available individual-tree growth model adapted for uneven-sized stands at this site.

## Simulation

The growth simulations of all tested models were performed with the subset *All trees/ all species* (Table 2 and Figure 1(a, c)). Input data at tree-level were species, dbh and for the *Thinned* plot tree position. Due to individual model structures, the HEUREKA models and the Puk model were simulated in five-year periods, while Loh and Ols models were simulated in one-year periods. Models with variables for local competition (all except the Loh model) were simulated in two separated runs per plot (*Thinned* 1988–2003, 2003–2016, *Unthinned* 1995–2005, 2005–2014), where all trees that had died between first and last revision were removed at one occasion at the end of the first run. Models simulated with five-year intervals were subsequently extrapolated or interpolated to the required revision year to conform to observational data revision time-points. Ingrowth was assumed to have a negligible effect on average tree growth due to the low levels observed. Ingrowth prediction was therefore excluded from the simulations.

## Data preparation

All growth statistics are based on basal area growth per individual tree (cm$^2$/yr), except for the section covering observed growth, which also includes evaluations of diameter increment per year (mm/yr). Non-calipered trees were excluded from the analyses after the completed simulation as the data of their initial diameters were less precise. The analyses were performed with the subset *Only calipered/only spruce* except for the analysis of BALD-measuring sensitivity, for which the subset *Only calipered/all species* were utilized to take into account that the estimated BALD$_B$-value was calculated with a sample that also included pine trees. All analyses are based on data for the entire revision period except the analysis of effects of projection time on prediction accuracy, for which the revision point of 2002 was added for the plot *Thinned*.

One outlier was removed from the *Unthinned* data set after simulation. Three observations from the *Unthinned* plot displayed negative diameter increments of 1 cm between the two revisions. These three observations were retained in the dataset since it was considered to be within the expected measurement random error.

Residuals (res) were calculated according to equation (5), where $y$ is observed value and $\hat{y}$ is estimated value (cm$^2$ year$^{-1}$).

$$res = y - \hat{y}. \quad (5)$$

Growth residual standard deviations were calculated for separate growth classes to identify possible variance trends. Trends were investigated both per individual model simulation and for all combinations of merged residual results of the individual models. Apart from the Puk model, which revealed a positive relationship for the higher growth classes, no systematic general trends were detected (Figure 2). Therefore, no transformation of the residuals was applied. The negative diameter increments observed for three trees in the *Unthinned* plot explain the diverging values of growth class 1.

## Statistics

Observed differences of tree-level growth between *Thinned* and *Unthinned*, depending on initial tree diameter, were investigated in three ways. In the first approach, mean values per integer diameter class were calculated per plot, each class represented by at least eight trees, adding trees from nearest neighbor classes if required. The second and third approaches used multiple linear regression with annual basal area growth (cm$^2$ yr$^{-1}$) and annual diameter increment (mm yr$^{-1}$), respectively, as response variables. The regression models were fitted per treatment, for the whole revision periods, with a second-order polynomial function; $y = \beta_0 + \beta_1\ d + \beta_2\ d^2$, where $\beta_0 = 0$ and $d$ is the initial diameter at first revision.

Individual basal area growth residual trends were analysed through simple linear regression with tree diameter at last revision as the predictor. Growth residual mean values were calculated per model and treatment. Growth residual means were also subdivided into 10 cm diameter classes in

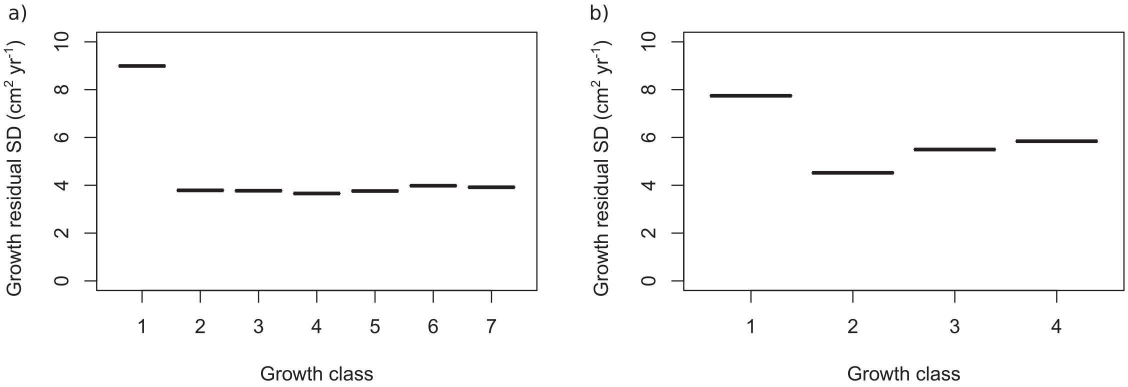

**Figure 2.** Basal area growth residual standard deviation per growth class. (a) including all model simulations except Puk model ($n = 485$, $22 < n/\text{class} < 135$), (b) including exclusively the results of the Puk model ($n = 111$, $9 < n/\text{class} < 49$). Class ranges with fixed growth intervals. Number of classes, and indirectly the interval size, were selected to have $n > 20$ observations per class, if possible, otherwise minimum 4 number of classes. Classes are ordinated in rising order starting with the lowest growth class (1). The calculations are based on simulations of both plots within the subset *Only calipered/ only spruce*. Only the Puk model displayed a different trend, hence the other models are presented in a fused diagram (a).

order to capture non-linear trends. For the projection length analysis in plot *Thinned*, growth residual means were calculated according to revision periods 0–14 and 15–28 yrs after initial revision, respectively. Relative predicted individual mean basal area growth (i.e. predicted mean growth divided with observed mean growth) was calculated per model and treatment.

The sensitivity of the BALD-measurement error ($|x_i|$) was investigated by analysing the difference in simulated mean growth ($\Delta_{\mathrm{BALD}_{|x_i|}j}$) between tested BALD estimations ($\mathrm{BALD}_{|x_i|}$) and the control estimation ($\mathrm{BALD}_\mathrm{B}$) for each (*j*) tested model. Simulated mean growth based on $\mathrm{BALD}_\mathrm{B}$ ($Mg_{BALD_{Bj}}$), per model (*j*), was used as the denominator to calculate the relative value of $\Delta_{BALD_{|x_i|}j}$ ($Rel\Delta_{BALD_{|x_i|}j}$, equation (6)).

$$Rel\Delta_{\mathrm{BALD}_{|x_i|}j} = \frac{\Delta_{\mathrm{BALD}_{|x_i|}j}}{Mg_{\mathrm{BALD}_{\mathrm{B}j}}}. \quad (6)$$

The threshold level of $|x_i|$ where $\Delta_{\mathrm{BALD}_{|x_i|}}$ is significant was approximated using the linear trends between the estimates of $\Delta_{BALD_{|x_i|}}$, when $|x_i| = 20$, and the zero reference $\Delta_{\mathrm{BALD}_\mathrm{B}}$ ($\Delta_{\mathrm{BALD}_\mathrm{B}} = 0$). The approximation relies on the assumption that the confidence intervals of the $\Delta_{\mathrm{BALD}_{|20\%|}}$-estimates are representative when $x_i \leq |20|$.

One-sample Student's *t*-test was generally applied to test the null hypothesis of estimates. In the analyses of BALD-measurement sensitivity and impact of projection length, statistical differences were calculated from simulations of the same sample. Consequently, the statistical significance was tested in these cases with the paired Student's *t*-test. Statistical differences between *Thinned* and *Unthinned* were evaluated using Welsh's *t*-test since the data sets of the two plots have different projection lengths (28 and 19 years, respectively) and different sample sizes. A two-tailed significance level of 0.05 was applied unless otherwise stated.

Simple linear regression analyses of the variables basal area growth residuals and measures of local basal area competition were performed with the Swedish models to investigate to what degree insufficient competition indices explain prediction errors. Four competition measures were tested: (1) basal area of all trees (*tot ba*); (2) basal area of larger trees (*ba l t*); (3) basal area of larger spruce trees (*ba l s*), and (4) basal area of all spruce trees (*ba a s*). The basal area was calculated within 6 m radius from the subject tree, using data from the 2016 revision of the plot *Thinned*. Statistics of regressions indicating greater significance than 0.05 are presented to provide evaluation data for possible correction functions for the analysed models.

## Results

### Observed individual tree growth

Trees in the plot *Thinned* had significantly larger diameter increment than trees in *Unthinned* when their initial dbh was either below 21 cm or above 32 cm (Figure 3). In *Thinned*, no clear maximum is visible, and all diameter classes above 16 cm show relatively constant diameter growth, with no clear decline for the largest tree classes. The results show that the selective thinning distributed increased diameter growth to all examined size classes except medium to slightly larger trees. Tendencies of growth suppression from larger trees, indicating a strong influence of one-way competition, started at around 15–16 cm and 24–27 cm dbh in *Thinned* and *Unthinned*, respectively.

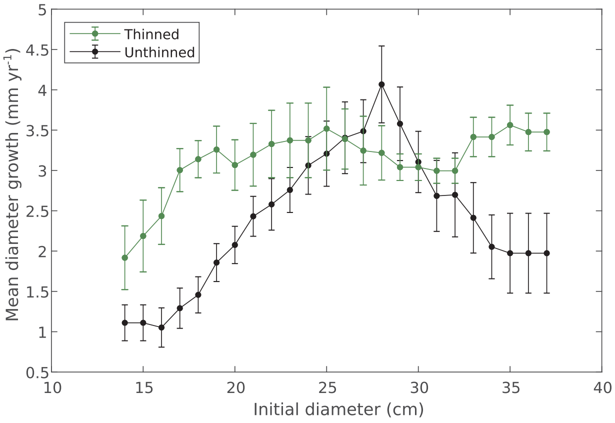

**Figure 3.** Mean diameter growth per initial breast height diameter. Error bars indicate standard error of mean values. Subset *Only calipered/only spruce*.

Scatterplots of observed individual tree growth, together with outputs of multiple linear models for individual basal area growth and diameter increment, are presented in Figure 4. and Appendices (Table 7). Fitted models suggest a later and higher diameter increment maximum in the *Thinned* plot. The effect on basal area growth, due to this difference in diameter increment, is visualized in Figure 4 (left).

In addition, mean individual basal area growth in plot *Thinned* was 3.8 cm$^2$/yr higher in the second revision period (21–34 years after thinning) compared to the first period (6–20 years after thinning).

### Prediction residual trends

In the analyses of the *Thinned* plot, all tested models display significant bias in the form of a positive linear slope of the relation between tree diameter and individual basal area growth residuals (*β*) (Table 4 and Figure 5(a)). However, the models of Puk and Söd_s display only weak significance for this trend (α = 0.1). The Heureka models generally overestimate small trees and predict increasing underestimations of larger trees with tree diameter. The transition point ($d_0$), where overestimation changes to underestimation ($\hat{y} = \beta d_0 + \alpha = 0$) is between 10 and 19 cm dbh for all three Heureka models. The new models express similar trends, with the Loh model generating the highest estimate (*β*) of all models. In contrast to simulations of the *Thinned* plot, treatment without thinning (*Unthinned*) shows no significant linear trends, except that the Puk model indicated a negative slope (Figure 5(b)).

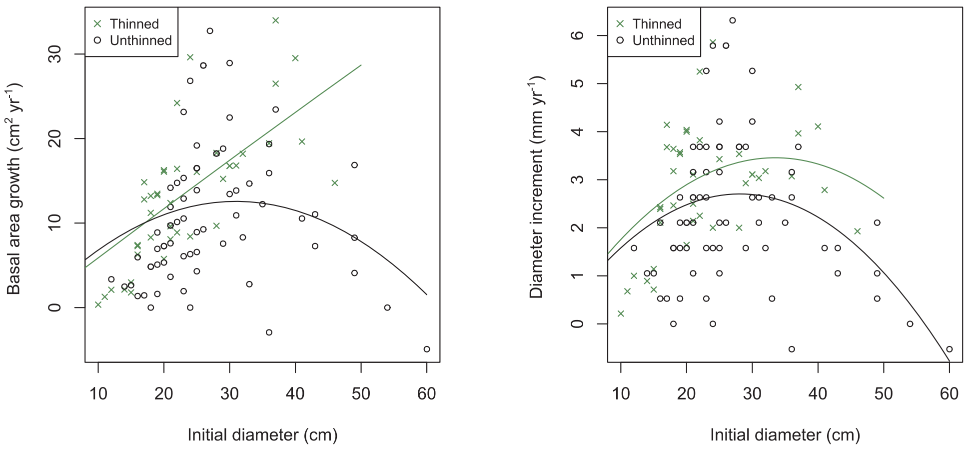

**Figure 4.** Norway spruce individual-tree growth observations in *Thinned* and *Unthinned* depending on initial dbh, presented with the response variable basal area growth per year (left) and diameter increment per year (right). The curves represent second-order with one predictor polynomial regression lines. Subset *Only calipered/only spruce*.

**Table 4.** Statistics of individual-tree basal area growth residuals ($cm^2\ yr^{-1}$) with estimates from fitted simple linear regression ($\alpha$, $\beta$) and mean values ($\bar{y}$) of *Thinned* and *Unthinned* plots, where predictor variable is observed diameter at the last revision. Subset *Only calipered/only spruce*. Two-way, one-sample Student´s *t*-test.

| | | *Thinned* | | | | | *Unthinned* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Model | Statistics | Estimate | s.e. | *p*-value | $R^2$ | *F*-value | Estimate | s.e. | *p*-value | $R^2$ | *F*-value |
| Elf_s | $\alpha$ | −7.3368 | 2.2047 | 0.002 | 0.471 | 34.7 | 4.1425 | 3.4514 | 0.234 | 0.003 | 0.2 |
| | $\beta$ | 0.3925 | 0.0666 | <0.001 | | | −0.0458 | 0.1046 | 0.663 | | |
| | $\bar{y}$ | 4.99 | 0.947 | <0.001 | | | 2.7 | 1 | 0.009 | | |
| Söd_s | $\alpha$ | −1.6478 | 2.6569 | 0.539 | 0.092 | 3.9 | 8.9156 | 3.8366 | 0.023 | 0.048 | 3.4 |
| | $\beta$ | 0.1594 | 0.0803 | 0.054 | | | −0.2156 | 0.1163 | 0.068 | | |
| | $\bar{y}$ | 3.36 | 0.871 | <0.001 | | | 2.11 | 1.137 | 0.068 | | |
| Söd | $\alpha$ | −2.26 | 2.5680 | 0.385 | 0.160 | 7.4 | 8.5051 | 3.8039 | 0.029 | 0.039 | 2.7 |
| | $\beta$ | 0.2118 | 0.0776 | 0.009 | | | −0.1906 | 0.1153 | 0.103 | | |
| | $\bar{y}$ | 4.39 | 0.876 | <0.001 | | | 2.49 | 1.122 | 0.030 | | |
| Loh | $\alpha$ | 11.0174 | 2.1820 | <0.001 | 0.490 | 37.5 | −1.8678 | 3.3702 | 0.581 | 0.000 | 0.0 |
| | $\beta$ | 0.4039 | 0.0659 | <0.001 | | | 0.0071 | 0.1022 | 0.945 | | |
| | $\bar{y}$ | 1.66 | 0.955 | 0.090 | | | −1.64 | 0.975 | 0.096 | | |
| Puk | $\alpha$ | −9.2381 | 2.4711 | <0.001 | 0.076 | 3.2 | 3.661 | 3.5103 | 0.3007 | 0.075 | 5.5 |
| | $\beta$ | 0.1334 | 0.0747 | 0.082 | | | −0.2503 | 0.1064 | 0.021 | | |
| | $\bar{y}$ | −5.0493 | 0.8032 | <0.001 | | | −4.238 | 1.0557 | <0.001 | | |
| Ols | $\alpha$ | −5.5311 | 2.4429 | 0.029 | 0.274 | 14.7 | | | | | |
| | $\beta$ | 0.2829 | 0.0738 | <0.001 | | | | | | | |
| | $\bar{y}$ | 3.35 | 0.8957 | <0.001 | | | | | | | |

When the growth residuals are analysed per diameter class, all model combinations tested on *Unthinned* also revealed the same linear trend of increasing underestimation as was identified for the *Thinned* plot, but only for tree sizes below 40 cm dbh, while larger trees tended to be overestimated (Figure 6).

All models, except the Loh model, significantly underestimate individual mean growth 6–34 years after thinning (*Thinned*), and furthermore, the models of Elf_s and Söd even underestimate growth 36–55 years after thinning (*Unthinned*). The three Heureka model combinations underestimate growth in *Thinned* most strongly with predictions of 63–75% of observed mean growth (Figure 7) and the Ols model also significantly underestimates growth (75%). In the *Unthinned* plot, Elf_s and Söd predicted 75% and 77% of observed mean growth, respectively. None of the Swedish models shows significant between-treatment differences in mean growth residuals.

The Puk model generally overestimates growth, suggesting that it is not well calibrated for the latitudes of this dataset. If the stand control function is excluded from the Söd_s model, the underestimation of mean growth significantly increases by 8% (*Thinned*) and 3% (*Unthinned*).

## *Sensitivity of the mean stand age variable*

The analysis of the measurement error of the BALD variable shows that the difference of simulated mean basal area growth ($\Delta_{BALD_{|x_i|}}$) of all tested combinations of models, treatments and $BALD_{|x_i|}$-estimations, are all significant (Figure 8 and Appendices, Table 8). The relative difference of simulated mean growth ($Rel\Delta_{BALD_{|x_i|}}$), when BALD-measurement error ($|x_i|$) is 20%, ranges from 10% to 23% for all tested models. Model Elf displays larger $Rel\Delta_{BALD_{|x_i|}}$ compared to Söd model, with a magnitude of 1–9 percentage units depending

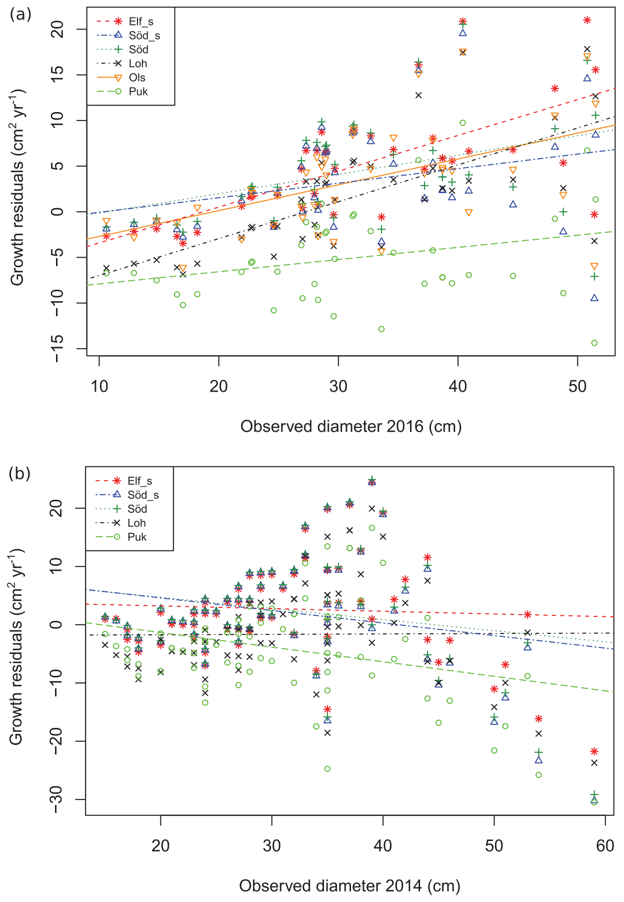

**Figure 5.** Individual basal area growth residuals for *Thinned* (a) and *Unthinned* (b), indicated per tree and model combination. Subset *Only calipered/only spruce*. The fitted lines are from simple linear regressions tested per model combination.

on the size of $|x_i|$. When the Söd model is used without default configuration, $Rel\Delta_{\text{BALD}_{|x_i|}}$ increase with 4–30 percentage units depending on the $|x_i|$-level. The point where the growth difference becomes significant is between 2% and 3% measurement error ($|x_i|$) ($M = 2.3$, $SD = 0.25$) for the analysed combinations ($n = 12$).

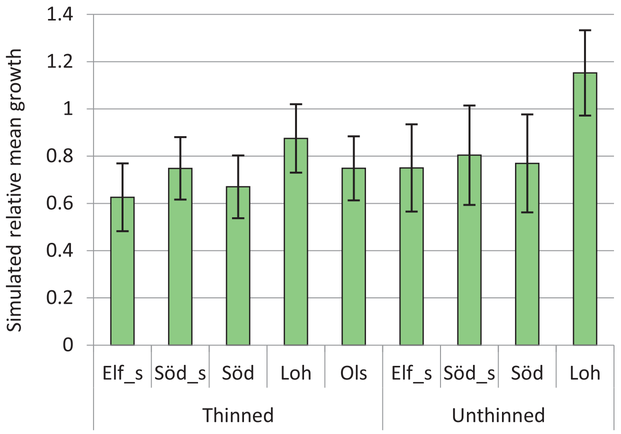

**Figure 7.** Simulated individual mean basal area growth divided by observed individual mean basal area growth, presented per treatment and model. Confidence intervals for the difference between the observed reference and the simulated relative mean (α = 0.05). Subset *Only calipered/only spruce*.

### *Influence of projection time*

In tests of the accuracy of simulations over time in plot *Thinned*, all of the models, except for Loh, significantly underestimate basal area growth during the first revision period (Figure 9). In the second revision period, all of the models significantly increased underestimation compared to the first revision period (Appendices, Table 9). The underestimations were larger for the HEUREKA models relative to the new models but more stable over time. The Loh model showed the smallest mean growth residual, irrespective of prediction period but also the largest relative increase between the periods.

### *Relationship between local competition and prediction residuals*

Significant linear trends were detected in outputs of all models except Ols (Table 5), showing that consideration of local competition (expressed in terms of basal area) could improve the performance of the concerned models. The models with the most scope for improvement by correction with a local competition variable are the Loh and Elf_s

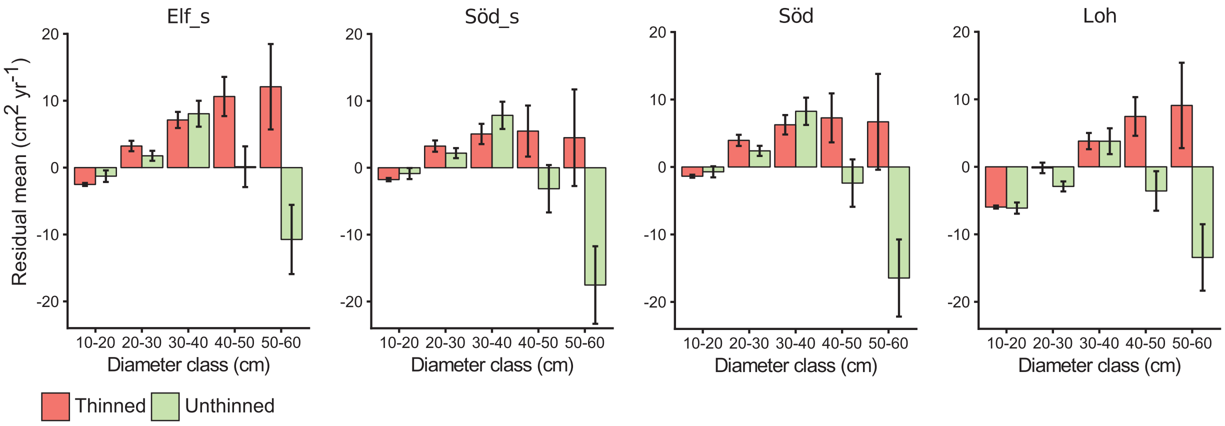

**Figure 6.** Individual basal area growth residual mean values presented per treatment, diameter class and model. Error bars depict standard error. The number of observations per diameter class for plot *Thinned* is (from smallest to largest class): 6, 16, 11, 5 and 3. Corresponding numbers for plot *Unthinned*: 8, 27, 24, 7 and 4. Diameters are from the end of the revision period. Subset *Only calipered/only spruce*.

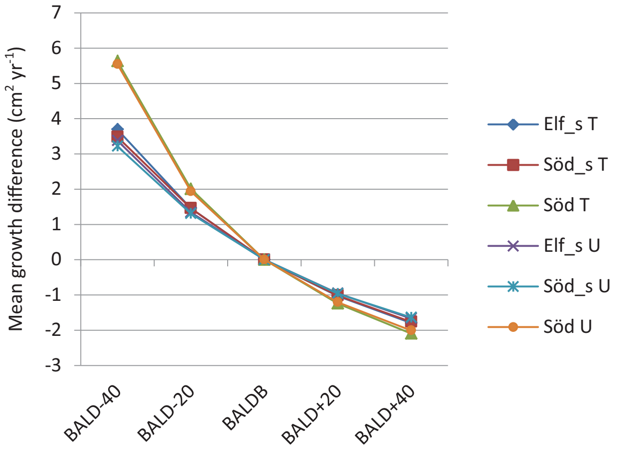

**Figure 8.** Individual tree predicted mean basal area growth differences ($\Delta_{BALD_{|x_i|}j}$) between the simulated value of each tested combination and corresponding $BALD_{Bj}$ zero reference value, per model combination (*j*), BALD estimation ($BALD_{|x_i|}$) and treatment (T = *Thinned*, U = *Unthinned*). Subset *Only calipered/all species*.

models. The competition variable with the highest coefficient of determination for both models is basal area of larger trees (*ba l t*, $R^2 = 0.27$, 0.26). The Loh model, which does not include any local competition parameter, also serves in this analysis as a reference to identify the most significant competition predictor for individual tree basal area growth. With that as starting point, *ba l t* is the most strongly related predictor to individual growth, followed by *tot ba*. All of the four models involved showed significant trends to *tot ba* and *ba a s*.

## Discussion

### Observed growth response

The hypothesis that the selective cutting treatment applied to the stand addressed in this study, increase diameter increment for all diameter classes, is rejected since diameter classes between 21 and 32 cm dbh did not display significant increases. It was mainly the codominant tree classes (Hanisch and Kilz 1991) that maintained diameter growth when local competition increased with time in the *Unthinned* plot. The independent and constant relationship between annual increment and diameter in the *Thinned* plot indicates that the thinning intensity was heavy enough to remove inhibitory one-way competition for many sub-dominant trees down to the threshold where the effect of this competition becomes more distinct, at approximately 16 cm dbh. This implies that thinning intensity could be used in tree selection as an active measure to control the dbh transition point for suppressed growth, which in turn is useful for roundwood quality tending. The results for the *Unthinned* plot are more consistent with the concave relationship often described in the literature (e.g. Wykoff 1990). Thus, the results suggest that increasing stand density due to longer periods without intervention, not only increases the dbh transition point for one-way competition but also decreases the upper dbh transition point where dominating trees no longer manage to maintain annual increment at the same level as their strongest competitors.

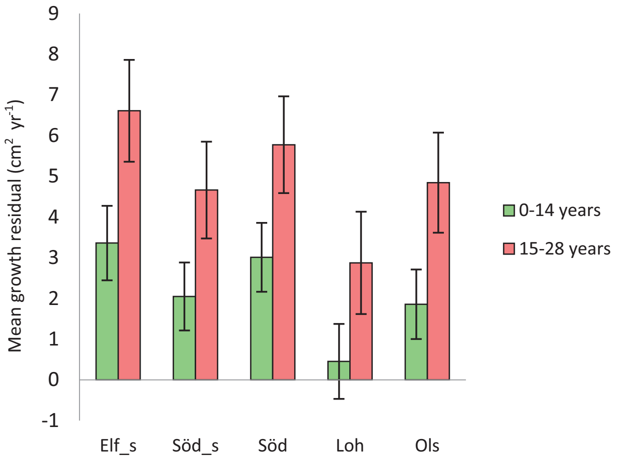

**Figure 9.** Individual tree mean basal area growth residuals per revision period. Error bars indicate standard error of mean values. Subset *Only calipered/only spruce*.

### Prediction accuracy

The hypothesis that the tested distance-independent models would show positive linear relationships between tree diameter and basal area growth residuals was only valid for the models of Elf_s, Söd and Loh for the thinned stand. Therefore, the results do not confirm a general connection between distance-independency and increasing growth bias with increasing tree size. However, since the linear trend shows prevalent in both treatments when the largest tree classes (>40 cm dbh) are excluded, it points to a worrying deficiency in the ability of the concerned models to capture the growth levels of the larger trees in uneven-sized stand structures. This indicated trend implies a risk of underestimation in management simulation analyses of individual tree selection in terms of productivity, and particularly profitability.

Regarding the levels of underestimation by the HEUREKA models, this is likely also an effect of incomplete adaptation to other variables apart from stand structure. Based on the study by Fahlvik et al. (2014), in which the same HEUREKA models were evaluated, the variables for site index, stand basal area and proportion of Norway spruce could all contribute to the underestimation shown in this study.

The hypothesis that mean basal area growth predictions of the HEUREKA models are significantly affected by measurement error of the predictor basal area mean stand age was validated for errors larger than 3%. Since the prediction accuracy is sensitive to this variable, which also is difficult to measure in practice in uneven-sized stands, the use of models depending on mean stand age entails a substantially increased risk of prediction errors. Accordingly, mean stand age is not used as a predictor in most of the CCF-oriented individual-tree models (e.g. Bianchi et al. 2020; Øyen et al. 2011; Pretzsch et al. 2002; Pukkala et al. 2009; Pukkala et al. 2013).

The hypothesis that basal area growth residuals of the tested models would not have temporal trends was not supported. However, the trends may have been amplified by the relatively high level of observed growth in the second period. Such late culmination of growth response after selective cutting is not the typical case for Scandinavian conditions

**Table 5.** Simple linear regression statistics with individual basal area growth residuals per model as the response variable (cm$^2$ yr$^{-1}$). The predictors of the local competition are *tot ba* = basal area of all trees, *ba l s* = basal area of larger spruce trees, *ba l t* = basal area of larger trees, *ba a s* = basal area of all spruce trees (m$^2$ ha$^{-1}$ within 6 m radius). Subset Only calipered/only spruce (df = 39). Functions with α < 0.05 are presented.

| Model | Predictor | Coefficients | Estimate | s.e. | *p*-value | R$^2$ | *F*-value |
|---|---|---|---|---|---|---|---|
| Elf_s | *tot ba* | $\alpha$ | 14.949 | 3.131 | <0.001 | 0.22 | 10.9 |
| | | $\beta$ | −0.462 | 0.140 | 0.002 | | |
| | *ba l s* | $\alpha$ | 8.001 | 1.286 | <0.001 | 0.20 | 9.9 |
| | | $\beta$ | −0.326 | 0.104 | 0.003 | | |
| | *ba l t* | $\alpha$ | 9.396 | 1.461 | <0.001 | 0.26 | 13.4 |
| | | $\beta$ | −0.334 | 0.091 | <0.001 | | |
| | *ba a s* | $\alpha$ | 11.165 | 2.303 | <0.001 | 0.18 | 8.4 |
| | | $\beta$ | −0.386 | 0.133 | 0.006 | | |
| Söd_s | *tot ba* | $\alpha$ | 9.749 | 3.080 | 0.003 | 0.11 | 4.7 |
| | | $\beta$ | −0.297 | 0.138 | 0.037 | | |
| | *ba a s* | $\alpha$ | 7.614 | 2.216 | 0.001 | 0.10 | 4.3 |
| | | $\beta$ | −0.266 | 0.128 | 0.045 | | |
| Söd | *tot ba* | $\alpha$ | 11.700 | 3.041 | <0.001 | 0.14 | 6.2 |
| | | $\beta$ | −0.339 | 0.136 | 0.017 | | |
| | *ba a s* | $\alpha$ | 9.195 | 2.196 | <0.001 | 0.13 | 5.6 |
| | | $\beta$ | −0.300 | 0.127 | 0.023 | | |
| Loh | *tot ba* | $\alpha$ | 11.786 | 3.150 | <0.001 | 0.22 | 11.2 |
| | | $\beta$ | −0.470 | 0.141 | 0.002 | | |
| | *ba l s* | $\alpha$ | 4.767 | 1.289 | <0.001 | 0.21 | 10.4 |
| | | $\beta$ | −0.335 | 0.104 | 0.003 | | |
| | *ba l t* | $\alpha$ | 6.218 | 1.461 | <0.001 | 0.27 | 14.3 |
| | | $\beta$ | −0.345 | 0.091 | <0.001 | | |
| | *ba a s* | $\alpha$ | 7.886 | 2.323 | 0.002 | 0.18 | 8.4 |
| | | $\beta$ | −0.389 | 0.134 | 0.006 | | |

(Ågren 2005; Øyen et al. 2011; Øyen and Nilsen 2004; Valkonen et al. 2017), and could possibly explain why the models fail to describe the growth development over time accurately.

The prediction accuracy of the Ols model was generally on par with the best distance-independent models, which corresponds to what can be expected according to previous research (e.g. Weiskittel et al. 2011; Wimberly and Bare 1996). The results give justification to the further development of a more validated distance-dependent model that can be used for simulation and optimization of individual tree selection. The simple validation analysis that caused calibration and validation sets to overlap is considered to have given sufficiently reliable results to be used for comparisons with the other tested models since the growth periods of the two sets represent separate stand development stages, i.e. 29–34 and 6–34 years after cutting, respectively. This is illustrated by the observed mean basal area growth difference of the 30 tree individuals that were included in both sets, which in the calibration period reached 79% of their growth in the validation period.

With regard to the Loh model, the analyses showed that despite its simplicity, it most often suffice in situations with average local competition and stand conditions. However, as expected and due to the absence of competition indices in the model structure, it becomes less reliable the further away from the average situation the prediction is performed.

### *Correction to account for basal area competition*

The hypothesis that basal area growth residuals are correlated to basal area local competition was found to be valid for all tested distance-independent models in this analysis. This implies that the tested models would benefit from adding linear correction functions for local competition if the models are to be applied in uneven-sized stands. However, scatterplots of the input data for the tested competition measures and model combinations reveal non-linear tendencies, suggesting that there are remaining possibilities for improvement by the use of suitable variable transformation. In summary, in uneven-sized application, there exists a reducible bias within the concerned models that can be addressed by including complementary predictors which incorporate impact from local competition, preferably in relation to subject tree social position (e.g. *ba l t).*

## Conclusions

The tested Swedish distance-independent growth models tended to increase underestimation with tree size when applied in uneven-sized conditions. This linear bias appears to be connected to the uneven-sized structure since it was detected in all tested combinations for the diameter classes below 40 cm dbh. Consequently, the trend is also connected to time since the last cutting as it diminishes with increasing numbers of older trees associated with dbh increment decline. In active management regimes, these mature trees are selected before they reach this declining state. Therefore, the bias is expected to be more pronounced in stands that are regularly treated with selective cutting. The analyses show that the prediction bias can partly be corrected by including more significant predictors for basal area local competition. However, mean stand age is not recommended as a predictor in tree growth models for uneven-sized stands, since it is both difficult to measure and sensitive to measurement errors.

## Acknowledgements

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## Disclosure statement

The authors declare that they have no conflict of interest(s).

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## Data availability statement

The data that support the findings of this study are openly available in the public repository Swedish National Data Service at https://doi.org/10.5878/wcbz-kq34, reference number 2020-52.

## References

Abetz P, Klädtke J. 2002. The target tree management system. Die Z-ntrollmethode. Forstwissenschaftliches Centralblatt. 121:73–82.

Ågren D. 2005. Tillväxtreaktion på kvarlämnade träd i Hagners "Naturkultur" försök [Growth response of retained trees in Hagneŕs "Liberich" experiments] [Master Thesis]. Department of Silviculture, Swedish University of Agricultural Sciences. p. 31.

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

Cajander AK. 1949. Forest types and their significance. Acta For Fenn. 56:1–71.

de-Miguel S, Guzmán G, Pukkala T. 2013. A comparison of fixed- and mixed-effects modeling in tree growth and yield prediction of an indigenous neotropical species (Centrolobium tomentosum) in a plantation system. Forest Ecol Manag. 291:249–258.

Elfving B. 2003. Ålderstilldelning till enskilda träd i skogliga tillväxtprognoser [Age allocation to individual trees in forest growth forecasts]. Department of Silviculture, Swedish University of Agricultural Sciences, Working Paper 182. p. 10.

Elfving B, Nyström K. 2010. Growth modelling in the Heureka system. Department of Forest Ecology and Management, Swedish University of Agricultural Sciences. p. 97. https://www.heurekaslu.se/w/images/9/93/Heureka_prognossystem_%28Elfving_rapportutkast%29.pdf

Eyre FH, Zillgitt WM. 1953. Partial cuttings in northern hardwoods of the Lake States: Twenty-year experimental results. Forest Service Lake States Forest Experiment Station Bromall PA, US Department of Agriculture. Technical Bulletin. 1076. p124.

Fahlvik N, Elfving B, Wikström P. 2014. Evaluation of growth functions used in the Swedish forest planning system Heureka. Silva Fenn. 48:1–17.

Gadow KV. 2001. Orientation and control in CCF systems. In: Gadow KV., Nagel J., Saborowski J, editor. Proceedings of the international IUFRO conference on continuous cover forestry. Assessment, analysis, scenarios. Göttingen: University of Göttingen; p. 211–217.

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

Hagner M, Lohmander P, Lundgren M. 2001. Computer-aided choice of trees for felling. Forest Ecol Manag. 151(1-3):151–161.

Hanewinkel M. 2004. Spatial patterns in mixed coniferous even-aged, uneven-aged and conversion stands. Eur J Forest Res. 123:139–155.

Hanisch B, Kilz E. 1991. Monitoring of forest damage: spruce and pine. London: Christopher Helm Pub Ltd.

Hyytiäinen K, Haight RG. 2012. Optimizing continuous cover forest management. In: von Gadow K., Pukkala T, editor. Continuous cover forestry. 2nd ed. New York: Springer; p. 195–227.

Kerr G, Haufe J. 2011. Thinning practice: a silvicultural guide. Forestry Commission, UK Government. p. 54. https://www.forestresearch.gov.uk/research/thinning-practice-a-silvicultural-guide/

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.

Lundqvist L. 1994. Growth and competition in partially cut sub-alpine Norway spruce forests in northern Sweden. Forest Ecol Manag. 65:115–122.

Meyer HA. 1952. Structure, growth, and drain in balanced uneven-aged forests. J For. 50:85–92.

Monserud RA, Sterba H. 1996. A basal area increment model for individual trees growing in even- and uneven-aged forest stands in Austria. Forest Ecol Manag. 80:57–80.

Munro DD. 1974. Forest growth models-a prognosis. In: J. Fries, editor. Growth models for tree and stand simulation. Stockholm: Department of Forest Yield Research; Royal College of Forestry; p. 7–21.

Nilsson P, Roberge C, Fridman J. 2020. Forest statistics 2020 - Official Statistics of Sweden. Department of Forest resource Management, Swedish University of Agricultural Sciences. Report 0280-0543. p. 158.

O'Hara KL. 1998. Silviculture for structural diversity: a new look at multi-aged systems. J For. 96:4–10.

Oliver CD, Larson BC, Oliver C. 1996. Forest stand dynamics. New York, NY: John Wiley & Sons Inc.

Olsson J-O, Fagerberg N. 2019. En avståndsberoende tillväxtmodell på trädnivå för gran:-en preliminär modell baserad på två skiktade bestånd i Götaland [A distance-dependent growth model at tree level for spruce: -a preliminary model based on two uneven-sized stands in Götaland]. Department of Forestry and Wood Technology, Linnaeus University, Report. p. 15. http://urn.kb.se/resolve?urn=urn:nbn:se:lnu:diva-80647

Øyen B, Nilsen P. 2004. Growth and recruitment after mountain forest selective cutting in irregular spruce forest. A case study in northern Norway. Silva Fenn. 38:383–392.

Øyen B-H, Nilsen P, Bøhler F, Andreassen K. 2011. Predicting individual tree and stand diameter increment responses of Norway spruce (Picea abies (L.) Karst.) after mountain forest selective cutting. Forestry Studies. 55:33–45.

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

Perttu K, Morén A-S. 1994. Regional temperature and radiation indices and their adjustment to horizontal and inclined forest land. Stud For Suec. 194:19.

Pretzsch H, Biber P, Ďurský J. 2002. The single tree-based stand simulator SILVA: construction, application and evaluation. Forest Ecol Manag. 162:3–21.

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

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

Pukkala T, Lähde E, Laiho O. 2015. Which trees should be removed in thinning treatments? For Ecosyst. 2:32.

Seifert T. 1999. Modelling wood quality of Norway spruce (Picea abies) depending on silvicultural treatment. In: Proceedings of the Third IUFRO; La Londe-Les-Maures. September 5-12. Topic 7:534-540.

Soares P, Tomé M. 2003. GLOBTREE: an individual tree growth model for eucalyptus globulus in Portugal. In: Amaro A., Reed D., Soares P., editors. Modelling forest systems. Wallingford: CAB International; p. 97–110.

Söderberg U. 1986. Functions for Forecasting Timber Yield: Increment and Form Height of Individual Trees of Native Tree Species in Sweden. [Dissertation]. Swedish University of Agricultural Sciences.

Tahvonen O. 2009. Optimal choice between even-and uneven-aged forestry. Nat Resour Model. 22:289–321.

Tarasiuk S, 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.

Valkonen S, Lappalainen S, Lähde E, Laiho O, Saksa T. 2017. Tree and stand recovery after heavy diameter-limit cutting in Norway spruce stands. Forest Ecol Manag. 389:68–75.

Vanclay JK. 2012. Modelling continuous cover forests. In: Pukkala T., von Gadow K., editors. Continuous cover forestry. 2nd ed. Dordrecht: Springer; p. 229–241.

Weiskittel AR, Hann DW, Kershaw Jr JA, Vanclay JK. 2011. Forest growth and yield modeling. West Sussex: John Wiley & Sons.

Wikström P, Edenius L, Elfving B, Eriksson LO, Lämås T, Sonesson J, Öhman K, Wallerman J, Waller C, Klintebäck F. 2011. The Heureka forestry decision support system: an overview. Mathematical and Computational Forestry & Natural Resource Sciences. 3:87–94.

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 WR. 1990. A basal area increment model for individual conifers in the northern Rocky Mountains. For Sci. 36:1077–1104.

## Appendices

**Table 6.** Multiple linear regression statistics from model fit of Loh ($\frac{dx}{dt} = ax^{0.5} - bx^{1.5}$, $x$ = basal area at breast height (cm$^2$), $t$ = time (yrs), $n = 70$). Basal area growth observational data of Norway spruce trees within ($n = 41$) and next to ($n = 29$) the plot *Thinned* at the Romperöd site recorded between 2011 and 2016. Residual M = −0.52, Residual SD = 6.59.

| Coefficients | Estimate | s.e. | *p*-value | R$^2$ | *F*-value | *p*-value |
|---|---|---|---|---|---|---|
| a | 0.5309 | 0.065 | <0.001 | 0.748 | 101.1 | <0.001 |
| b | $-6.258\text{E}^{-5}$ | <0.001 | 0.228 | | | |

**Table 7.** Multiple linear regression statistics of observed values from Thinned and Unthinned with basal area growth and diameter increment as response variables. Second-order polynomial regression (Intercept = 0) with initial diameter as predictor. Subset Only calipered/only spruce.

| Response[a] | Plot | Coefficients | Estimate | s.e. | *p*-value | R$^2$ | *F*-value | *p*-value |
|---|---|---|---|---|---|---|---|---|
| Growth | *Thinned* | $\beta_1$ | 0.5922 | 0.1180 | <0.001 | 0.874 | 134.8 | <0.001 |
| | | $\beta_2$ | −0.0004 | 0.0038 | 0.923 | | | |
| | *Unthinned* | $\beta_1$ | 0.8114 | 0.0925 | <0.001 | 0.703 | 80.3 | <0.001 |
| | | $\beta_2$ | −0.0131 | 0.0025 | <0.001 | | | |
| Diameter increment | *Thinned* | $\beta_1$ | 0.2065 | 0.0222 | <0.001 | 0.890 | 157.3 | <0.001 |
| | | $\beta_2$ | −0.0031 | 0.0007 | <0.001 | | | |
| | *Unthinned* | $\beta_1$ | 0.1923 | 0.0174 | <0.001 | 0.759 | 107.1 | <0.001 |
| | | $\beta_2$ | −0.0034 | 0.0005 | <0.001 | | | |

[a] Units in cm$^2$ yr$^{-1}$ for basal area growth and mm yr$^{-1}$ for diameter increment.

**Table 8.** Statistics of mean basal area growth residuals ($\bar{y}$) from simulations with different BALD estimations (BALD$_{|x_i|}$) per treatment and tested model combination (Subset = *Only calipered/all species)*. One-sample statistics of mean growth residuals (Two-way one-sample Student's *t*-test). Two-sample statistics of mean growth residual difference ($\bar{y}_i - \bar{y}_B$) with confidence intervals (CI) (Two-way, paired Student's *t*-test, df *Thinned* = 58, df *Unthinned* = 87, α = 0.05). Units in cm$^2$ yr$^{-1}$. Relative difference of simulated mean basal area growth ($Rel\Delta_{\text{BALD}_{|x_i|}}$) between estimations from BALD$_{|x_i|}$ and BALD$_\text{B}$, with simulated mean growth from BALD$_\text{B}$ as denominator, per treatment and model.

| | | One-sample statistics | | | Two-sample statistics | | | | |
|---|---|---|---|---|---|---|---|---|---|
| BALD | Treatment | Model | $\bar{y}$ | s.e. | $\bar{y}_i - \bar{y}_B$ | *t*-value | CI | | $Rel\Delta_{\text{BALD}_{\lvert x_i\rvert}}$ |
| BALD$_{+40\%}$ | *Thinned* | Elf_s | 7.28 | 0.961 | 1.80 | 15.6 | 1.57 | 2.03 | −0.22 |
| | | Söd_s | 6.52 | 0.869 | 1.77 | 15.5 | 1.54 | 1.99 | −0.18 |
| | | Söd | 7.87 | 0.896 | 2.09 | 15.6 | 1.83 | 2.36 | −0.23 |
| | *Unthinned* | Elf_s | 3.36 | 0.888 | 1.67 | 20.1 | 1.50 | 1.83 | −0.21 |
| | | Söd_s | 3.32 | 0.936 | 1.64 | 18.5 | 1.46 | 1.81 | −0.19 |
| | | Söd | 4.09 | 0.916 | 2.01 | 18.3 | 1.79 | 2.23 | −0.24 |
| BALD$_{+20\%}$ | *Thinned* | Elf_s | 6.52 | 0.937 | 1.03 | 15.8 | 0.90 | 1.16 | −0.12 |
| | | Söd_s | 5.78 | 0.864 | 1.02 | 15.7 | 0.89 | 1.15 | −0.10 |
| | | Söd | 7.02 | 0.884 | 1.24 | 15.9 | 1.09 | 1.40 | −0.14 |
| | *Unthinned* | Elf_s | 2.64 | 0.904 | 0.95 | 20.7 | 0.86 | 1.05 | −0.12 |
| | | Söd_s | 2.65 | 0.949 | 0.96 | 18.3 | 0.86 | 1.07 | −0.11 |
| | | Söd | 3.29 | 0.932 | 1.21 | 19.0 | 1.08 | 1.33 | −0.15 |
| BALD$_{-20\%}$ | *Thinned* | Elf_s | 4.03 | 0.883 | −1.46 | −16.3 | −1.64 | −1.28 | 0.17 |
| | | Söd_s | 3.30 | 0.867 | −1.46 | −16.3 | −1.63 | −1.28 | 0.15 |
| | | Söd | 3.77 | 0.866 | −2.01 | −15.8 | −2.26 | −1.75 | 0.22 |
| | *Unthinned* | Elf_s | 0.35 | 0.949 | −1.34 | −21.0 | −1.47 | −1.21 | 0.17 |
| | | Söd_s | 0.38 | 0.994 | −1.31 | −19.3 | −1.44 | −1.17 | 0.15 |
| | | Söd | 0.14 | 1.004 | −1.94 | −17.9 | −2.15 | −1.72 | 0.23 |
| BALD$_{-40\%}$ | *Thinned* | Elf_s | 1.80 | 0.849 | −3.69 | −16.6 | −4.13 | −3.24 | 0.44 |
| | | Söd_s | 1.28 | 0.899 | −3.48 | −17.1 | −3.89 | −3.07 | 0.35 |
| | | Söd | 0.15 | 0.913 | −5.63 | −17.0 | −6.29 | −4.97 | 0.63 |
| | *Unthinned* | Elf_s | −1.69 | 0.998 | −3.38 | −20.8 | −3.70 | −3.05 | 0.42 |
| | | Söd_s | −1.53 | 1.040 | −3.21 | −19.6 | −3.54 | −2.89 | 0.37 |
| | | Söd | −3.47 | 1.102 | −5.54 | −19.1 | −6.12 | −4.97 | 0.67 |
| BALD$_\text{B}$ | *Thinned* | Elf_s | 5.49 | 0.913 | 0 | | | | 0 |
| | | Söd_s | 4.76 | 0.863 | 0 | | | | 0 |
| | | Söd | 5.78 | 0.870 | 0 | | | | 0 |
| | *Unthinned* | Elf_s | 1.69 | 0.922 | 0 | | | | 0 |
| | | Söd_s | 1.68 | 0.970 | 0 | | | | 0 |
| | | Söd | 2.08 | 0.957 | 0 | | | | 0 |

**Table 9.** Statistics of mean growth residuals per revision period ($\bar{y}$). First period = 0–14 years after initial revision, Second period = 15–28 years after initial revision. Subset Only calipered/only spruce. One-sample statistics (df = 41). Two-sample statistics comparing second and first period (df = 40). Units in cm$^2$ yr$^{-1}$.

| | | One-sample statistics | | | Two-sample statistics | | |
|---|---|---|---|---|---|---|---|
| Model | Period | $\bar{y}$ | s.e. | *p*-value | $\bar{y}_2 - \bar{y}_1$ | *t*-value | *p*-value |
| Elf_s | First | 3.36 | 0.913 | <0.001 | 3.25 | 2.95 | 0.005 |
| | Second | 6.61 | 1.251 | <0.001 | | | |
| Söd_s | First | 2.05 | 0.835 | 0.019 | 2.61 | 2.40 | 0.021 |
| | Second | 4.66 | 1.189 | <0.001 | | | |
| Söd | First | 3.01 | 0.848 | 0.001 | 2.77 | 2.53 | 0.015 |
| | Second | 5.78 | 1.188 | <0.001 | | | |
| Loh | First | 0.45 | 0.921 | 0.627 | 2.42 | 2.20 | 0.034 |
| | Second | 2.87 | 1.258 | 0.028 | | | |
| Ols | First | 1.86 | 0.854 | 0.036 | 2.99 | 4.07 | <0.001 |
| | Second | 4.84 | 1.230 | <0.001 | | | |