www.ias.is
https://doi.org/10.16886/IAS.2022.01 ICEL. AGRIC. SCI. 35 (2022), 3-16

Individual-tree growth models for Sitka spruce (*Picea sitchensis*) in Iceland

Lárus Heiðarsson[1], Timo Pukkala[2] and Arnór Snorrason[1]
[1] *Icelandic Forest Research, Mógilsá, IS-116 Reykjavík, Iceland (lalli@skogur.is)*
[2] *University of Eastern Finland, P.O.Box 111, 80101 Joensuu, Finland (timo.pukkala@uef.fi)*

ABSTRACT
Sitka spruce (*Picea sitchensis*) is one of the main tree species used in forestry in Iceland, growing well in all parts of the country. In view of the importance of Sitka spruce in Iceland, there is need for a reliable growth model that will support multifunctional forest management and planning. This study developed growth models for Sitka spruce using data from permanent sample plots established by the Icelandic Forest Service between 1970 and 2020. The measurement interval on the plots varied from 3 to 16 years. To deal with irregular measurement intervals, an optimization approach was used to recover models for annual diameter increment and survival rate. The aim was to find parameters for diameter increment and survival models that would minimize the difference between the measured and simulated diameter distributions of the plots at the end of the measurement interval (when the simulation begins from the diameter distribution at the beginning of the interval). To enable the simulation of stand development, models for dominant height development and tree height were also developed.

Keywords: Diameter increment, height model, individual-tree model, site index model, stand dynamics

YFIRLIT
Jöfnur sem lýsa vexti sitkagrenis (Picea sitchensis) á Íslandi
Sitkagreni (*Picea sitchensis*) er ein af þeim trjátegundum sem mest hafa verið notaðar í Íslenskri skógrækt enda vex tegundin vel víða um land. Vegna mikilvægi tegundarinnar er þörf á að aðlaga jöfnur sem lýsa vexti hennar svo hægt sé að áætla lotulengd og hvaða umhirðuaðgerðir skila mestum arði til skógareiganda. Vaxtarjöfnur voru aðlagaðar fyrir sitkagreni með gögnum frá föstum mæliflötum sem Skógræktin stofnaði til á árunum 1970 til 2013. Tíðni endurmælinga á mæliflötunum var mismunandi eða frá 3 og upp í 16 ár. Vegna óreglulegrar tíðni endurmælinga þurfti að beita bestunar nálgun (optimization approach) til að endurskapa eins árs þvermálsvöxt og sjálfgrisjun skóga. Markmiðið var að finna fasta fyrir þvermáls- og sjálfgrisjunar jöfnurnar sem lágmarka munin á milli mældrar og útreiknaðar þvermálsdreifingar trjáa í enda mælingartímabilsins. Auk þvermáls- og sjálfgrisjunarjafna var aðlöguð yfirhæðarjafna sem lýsa frjósemi viðkomandi skógar og jafna sem lýsir hæðarvexti stakra trjáa.

INTRODUCTION
Sitka spruce (*Picea sitchensis* (Bong.) Carr.) is one of the main tree species used in forestry in Iceland, growing well in all parts of the country and covering an area of around 5,000 hectares (Snorrason 2014). No growth models exist for Sitka spruce in Iceland, and scientific knowledge regarding its growth, yield and management is scant. The main reason for this is the young age

of most Icelandic plantations. The oldest Sitka spruce forests were planted between 1940 and 1950. The size of these first plantations was usually smaller than one hectare. The small size of Icelandic plantations with a consequent edge effect and the small size of sample plots are common features of Icelandic tree growth data. Because of the young age of the forests, the longest measurement series is only 50 years and the oldest stands with permanent sample plots are less than 70 years old.

Forest growth models assist forest researchers and managers in many ways due to their ability to predict future yields in alternative management schedules. The importance of growth models is demonstrated by the large number and variability of models published and used (e.g., Hartig 1795, Wiedemann 1942, Clutter 1963, Newnham 1964, Pukkala 1987, Trasobares et al. 2004). The complexity of these approaches has varied from simple regression equations, expressing yield per hectare, to detailed equations that simulate the growth of single trees in a stand (Clutter et al. 1983).

Growth models can broadly be classified as stand-level or tree-level models. Stand-level models use stand variables (e.g. age, site index, basal area and number of trees per hectare) as predictors while at least some of the predictor variables in a tree-level model are individual tree characteristics (Clutter et al. 1983, Palahí et al. 2003, Weiskittel 2011). Stand-level models provide rather limited information about the forest stand, in some cases only stand volume (Vanclay 1994); they may also project the values of other stand variables such as basal area, mean diameter, height and number of trees per hectare (Mabvurira & Miina 2002). Tree-level models are further classified as distance-dependent (spatial) or distance-independent (non-spatial) models.

The first growth model for Iceland was developed by Heidarsson and Pukkala (2012) for Siberian larch. The model was a distance-independent individual-tree model. Distance-independent models do not use spatial information to express competition. Instead, they use predictors that describe stand density (for example, stand basal area) and thus express the overall competition in the stand (Vanclay 1994, Van Laar & Akca 1997).

Distance-dependent models include spatial competition indices as predictors. The competition index may differ from model to model, but it is usually a function of both the size and location of the subject tree in relation to the size and location of its competitors (Bella 1971, Ek & Monserud 1974, Pukkala 1988, 1989, Alegria & Tomé 2013). Distance-dependent models may provide more accurate information about individual tree growth than distance-independent models; however, they are more difficult to use because they require a map of the stand, which is often too costly in a routine forest management context (Munro 1974, Wimberly & Bare 1996). Moreover, distance-dependent models have sometimes shown little or no improvement over distance-independent models, especially in plantation forests (Munro 1974, Vanclay 1994, Dong et al. 2021).

When individual-tree information for a stand is available, tree-level models can be developed since they provide more detailed information on the stand structure and its dynamics than stand-level models (Mabvurira & Miina 2002, Palahí et al. 2003, Juma et al. 2014). The ideal data for the development of individual-tree models is repeated measurements of permanent sample plots, in which all trees have been numbered and measured at regular intervals for diameter and survival (Juma et al. 2014). However, this last requirement is not met in the permanent Sitka spruce sample plots in Iceland, where the measurement interval has varied between 3 and 16 years. The impact of irregular measurement intervals on modelling has received some attention in earlier research (Cao 2000, 2004, Nord-Larsen 2006, Crecente-Campo et al. 2010). Assuming a constant growth rate between measurements can lead to under- or over-estimation of tree growth when the growth dynamics are clearly nonlinear (Clutter 1963, McDill & Amateis 1992).

To deal with irregular measurement intervals in this research, an optimization approach originally suggested by Pukkala et al. (2011) and later used by de-Miguel et al. (2014), Juma et al.

(2014) and Jin et al. (2019) among others, was used to fit the diameter increment and survival models. This method seems to overcome some of the problems related to other methods and has been shown to produce similar models and model parameters to regression analysis (Pukkala et al. 2011).

The modelling approach used to fit diameter increment and survival models requires only the diameter distribution of plots at the beginning and end of the measurement interval. The method uses non-linear optimization to derive model parameters. Optimization seeks models than would minimize the difference between measured and simulated diameter distribution of the plot at the end of the measurement interval. The simulation begins from the measured diameter distribution at the beginning of the interval (Pukkala et al. 2011).

In view of the importance of Sitka spruce in Iceland, there is a need for a reliable system of growth models that would allow managers to predict harvests and future stand development in alternative treatment schedules, thus providing valuable support for silvicultural decision making. The plantations may also be aimed at carbon sequestration, in which knowledge of maximum stand volumes and long-term stand development is essential. Because of the young age of Sitka plantations in Iceland and considering that Sitka spruce can live 700–800 years and reach 80 m height (Savill 1991), it is not reasonable to postpone growth modelling until the data cover the whole life span of trees and stands. On fertile soils in coastal areas of western Norway, the yield of Sitka spruce will peak between the age of 70–115 years (Öyen 2005).

The aim of this study was to develop a system of models that allow managers to simulate the development of Icelandic Sitka spruce stands over a few decades. The system consists of site index and dominant height models and individual-tree models for diameter increment, tree height and tree survival.

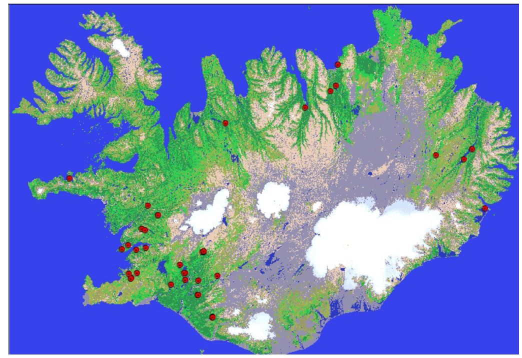

Figure 1. Geographical location of the study sites.

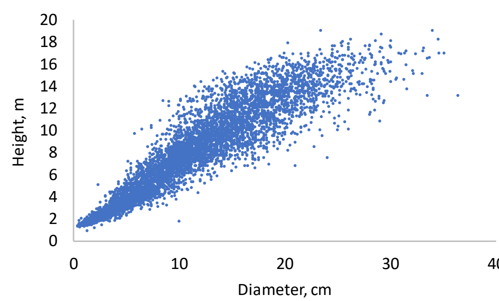

Figure 2. Observed height and diameter at breast height in the Sitka spruce plots.

MATERIALS

Two different datasets were used to develop the model: the dataset from permanent sample plots (PSP data) and data from the National Forest inventory (NFI data). The PSP data consists of measurements in 50 stands from seven locations, established in even-aged plantations (Figure 1). The NFI datasets were collected in 31 permanent sample plots from 27 locations (Figure 1). These 81 permanent sample plots were established in even-aged Sitka spruce stands by the Icelandic Forest Service between 1970 and 2013. They include a total of 197 measurement intervals. The stands are located in southern (37), western (29), northern (5) and eastern (13) Iceland and include both heavily thinned and unthinned sample plots. The plots cover a wide range of different site types and growth conditions. All the locations have an oceanic climate with annual precipitation of 700–1200 mm and a mean annual temperature of 3.2–4.5°C (1964–1990) (Vedurstofa Islands 2017). The mean

Table 1. Mean, standard deviation (SD) and range of the main characteristics in the empirical data of the study material. N: number of observations; Dbh: diameter at breast height; G: stand basal area; Age: stand age; Hdom: dominant height.

Variable	N	Mean	SD	Maximum	Minimum
Dbh (cm)	7276	9.46	7.17	36.4	0.0
Height	8432	5.92	4.62	19.0	0.28
G (m2ha-1)	197	18.25	15.89	79.38	0.0
Age (years)	197	36.6	15.7	63.0	6.0
Hdom (m)	197	8,65	5.1	18.0	0.38
Growth periods	197	5.48	1.62	16.0	3.0
Stems per hectare	197	2222	1414	5026	458

maximum daytime temperature in June, July and August was 12.9–13.6 ˚C during the period 1964–1990 (Vedurstofa Islands 2017). The range in elevation is between 60 and 180 m a.s.l.

The sample plots were either circular or rectangular. The plot size varied between 0.01 and 0.053 ha and the measurement interval was 3 to 16 years with an average of 5.5 years. There was mortality only among small trees in plots with a basal area up to 80 m^2/ha. On every measurement occasion, two measurements of diameter at breast height (1.3 m) at right angels were made using callipers, and the arithmetic mean of the two measurements was calculated. The total tree height was measured on standing trees using a height measuring pole or Vertex Laser VL5, and felled trees were measured on the ground using a tape measure. The measured heights and diameters of the trees are shown in Figure 2.

METHODS

Site index and dominant height modelling

The first equation required in the model set was the site index model, which was used to calculate the site index of the inventory plots. The index age was taken as 80 years, which has been previously used in Iceland (Heiðarsson & Pukkala 2012); site index is defined to be the dominant height of the stand at 80 years. Besides calculating site index, the site index model can be used to predict dominant height development. Based on experiences from previous studies in plantation forests (Palahí et al. 2004; Guzmán et al. 2012a, 2012b; Heiðarsson & Pukkala 2012, de-Miguel et al. 2013), the following equations were tested: Lundkvist & Korf (Korf 1939), Chapman and Richards (Richards 1959), McDill & Amateis (1992), and Schumacher (1939). Alternative models were compared based on the mean of squared errors and Akaike Information Criterion (AIC).

Of the tested models, the formula of McDill and Amateis was selected for predicting site index and dominant height development. When fitting the model, only the first and last measurement of each plot were used, which removed the need to include random plot factors:

$$H_{Last} = \frac{a_0}{1-\left(1-\frac{a_0}{H_{First}}\right)\times\left(\frac{T_{First}}{T_{Last}}\right)^{a_1}} + \varepsilon \qquad (1)$$

where H_{First} and T_{First} are, respectively, dominant height and stand age at the first measurement, and H_{Last} and T_{Last} are the same variables at the last measurement of the plot.

The model is used to calculate the site index as follows:

$$\hat{SI} = \frac{a_0}{1-\left(1-\frac{a_0}{H}\right)\times\left(\frac{T}{80}\right)^{a_1}} \qquad (2)$$

where $\hat{SI}$ is site index (dominant height at 80 years, m), H is dominant height (m) and T is stand age. When the model is used in simulations to calculate the dominant height for certain site index and age, H is replaced by SI, stand age T is replaced by 80 (index age), and 80 is replaced by stand age.

Tree height modelling

The model for individual-tree height was based on the model of Schumacher (1937). Two alternative models analysed by Mehtätalo et al. (2015), namely the models of Näslund (1937) and Curtis (1967) were also tested, but the model of Schumacher was selected based on the square root of the mean squared error (RMSE) and the Akaike Information Criterion. The models were fitted as mixed-effects models, by adding random plot factors to the fixed parameters. The best combination of random plot factors was found by comparing all possible combinations.

The parameters of the height curve were modelled as a function of stand characteristics, which allowed the diameter-height curve to change when the stand developed. Two versions of the height model were fitted. The first used dominant height as a predictor, in addition to diameter at breast height. Since this model is not suitable for simulations where the dominant height could decrease as a consequence of thinning from above, another model version was fitted where dominant height was replaced by site index and stand height. The two model versions were as follows:

Model 1

$$\hat{h} = 1.3 + [a_0 + (a_1 + a_{1k})H] \times exp\left[\frac{-\{(b_0 + b_{0k}) + (b_1 + b_{1k})H\}}{d}\right] \quad (3)$$

where a_0, a_1, b_0 and b_1 are fixed parameters and a_{1k}, b_{0k} and b_{1k} are random parameters for plot k.

Model 2

$$\hat{h} = 1.3 + [a_0 + (a_1 + a_{1k})T + (a_2 + a_{2k})SI] \times exp\left[\frac{-(b_0 + b_{0k})}{d}\right] \quad (4)$$

where a_0, a_1, a_2 and b_0 are fixed parameters and a_{1k}, a_{2k} and b_{0k} are random parameters for plot k.

Diameter increment and survival modelling

The diameter increment and survival data had the problem that the interval between measurements varied from 3 to 16 years. Since the linear growth rate or the constant survival rate during the whole interval cannot be assumed, the optimization approach originally suggested by Pukkala et al. (2011) and later used by de-Miguel et al. (2014), Juma et al. (2014) and Dong et al. (2021) was used to fit the diameter increment and survival models. The aim of the method is to find parameters for the diameter increment and survival models that minimize the difference between the measured and simulated diameter distributions of the plots at the end of the measurement interval, in cases when the simulation starts from the diameter distribution at the beginning of the interval. Diameter increment and survival were simulated in one-year time steps.

As the first step in modelling, predictors and model forms were selected based on previous literature, preliminary regression analyses and preliminary optimizations. The following model forms were selected:

$$\hat{i}_d = exp\left[a_0 + a_1 lnd + a_2 d + a_3\sqrt{G} + \frac{a_4 BAL}{ln(d+1)} + a_5 SI\right] \quad (5)$$

$$\hat{s} = \frac{1}{1 + exp\left[-\left(b_0 + b_1 lnd + b_2\sqrt{G} + b_3 BAL/ln(d+1)\right)\right]} \quad (6)$$

where $\hat{i}_d$ is diameter increment (cm/year), $\hat{s}$ is annual survival rate, d is diameter at breast height (cm), G is stand basal area (m^2/ha), BAL is basal area of trees larger than the subject tree (m^2/ha), SI is site index (m) and a_0,…, a_5, b_0,…, b_3 are regression coefficients. The subject tree is the tree for which the diameter increment or survival is predicted.

The minimized loss function was:

$$\underset{\theta}{argmin} \sum_{k=1}^{K}\left[\sum_{j=1}^{J_k} w_{jk} \sum_{i=1}^{I_j} v_G\left|G_{ijk}^{m} - G_{ijk}^{s}(\theta)\right|^{1.5} + v_F\left|F_{ijk}^{m} - F_{ijk}^{s}(\theta)\right|^{1.5}\right] \quad (7)$$

where Θ is the set of coefficients (parameters a_0,…a_5, b_0,…b_3 of Equations 5 and 6), K is the number of plots, J_k is the number of measurement intervals of plot k, I_j is the number of 3-cm diameter classes in measurement interval j of plot k, G_{ijk}^{m} and $G_{ijk}^{s}(\Theta)$ are, respectively, measured and simulated cumulative basal area (m^{2}ha^{-1}) of diameter class i at the end of measurement interval j of plot k, and F_{ijk}^{m} and $F_{ijk}^{s}(\Theta)$ are, respectively, the measured and simulated cumulative number of trees per hectare of diameter class i at the end of measurement interval j of plot k (see e.g. de-

Miguel et al. 2014 for details). The symbol w_{jk} is the weight of measurement interval *j* of plot *k*. The models were fitted with three alternative weighting schemes: (1) without weight (w_{jk} = 1 for all *j* and *k*), (2) using the area of plot *k* as the weight and (3) using the number of trees in plot *k* in the beginning on period *j* as the weight. Symbols v_G and v_F are the weights of the deviations of the basal area (in m^2ha^{-1}) and the number of trees per hectare. They also remove the effect of different units of basal area (*G*) and number of trees (*F*). They were as follows v_G = 1, v_F = 0.005.

The models were also fitted by adding a plot and measurement factor to both sub-models (diameter increment and survival probability). Since the 81 study plots had altogether 191 measurement intervals, the number of additional parameters in this model fitting was 382.

The optimization simultaneously produced the coefficients for the annual diameter increment model and the annual survival model. The method of Nelder and Mead (1965) was used in parameter optimization.

Since the optimization did not provide any statistics about the significance of the predictors, bootstrapping was used to assess the statistical significance of the regression coefficients. Fifty samples of 197 measurement intervals were selected using random sampling with replacement, and the same model fitting procedure as described above was performed with every sample (without plot and measurement factors, using number of trees as the weight).

RESULTS

Site index model

The parameters of the selected site index and dominant height model (Equation 1) were: a_0 (asymptote) 131.03, and a_1 1.3847. The RMSE of the model was 1.315 m. Figure 3 shows that the model depicts the dominant height development of the plots reasonably well. No signs of decreased dominant height growth rate with increasing age can be seen in the data or the model. The asymptote, i.e., the maximum possible dominant height, of the model is 131 m.

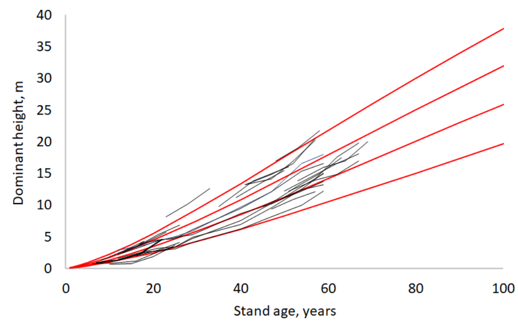

Figure 3. Dominant height development in site indices 15, 20, 25 and 30 m at 80 years according to the site index model (thick curves) and the measured dominant height development in some of the plots used as modelling data (thin black lines).

According to Harris (2022) Sitka spruce may live 700–800 years and reach a height of 60–90 m.

Height model

The parameters of the two versions of the individual-tree height model are shown in Tables 2 and 3. The RMSEs of the models were 0.752 m (Equation 3) and 0.765 m (Equation 4). Both models predict that the height curve of a stand rises when the stand develops and its dominant height or age becomes larger (Fig. 4)

Table 2. Parameters of the individual-tree height model where the predictors are diameter at breast height and dominant height (Equation 3).

Parameter	Value	t value
a_0	-1.1427	-4.2583
a_1	1.3357	55.8218
b_0	2.0137	5.4161
b_1	0.4334	13.8027
Random parameters	Standard deviation	
a_{1k}	0.7480	
b_{0k}	1.7725	
b_{1k}	0.1144	

Correlations: a_{1k}–b_{0k} 0.760; a_{1k}–b_{1k} -0.356; b_{0k}–b_{1k} -0.769

Table 3. Parameters of the individual-tree height model where the predictors are diameter at breast height, stand age and site index (Equation 4).

Parameter	Value	t value
a_0	-8.8135	18.2905
a_1	0.4229	16.3186
a_2	0.2849	31.2452
b_0	6.4704	28.3320
Random parameters	Standard deviation	
a_{1k}	0.0984	
a_{2k}	0.0548	
b_{0k}	1.6966	

Correlations: a_{1k}–a_{2k} -0.827; a_{1k}–b_{0k} 0.127; a_{2k}–b_{0k} 0.362

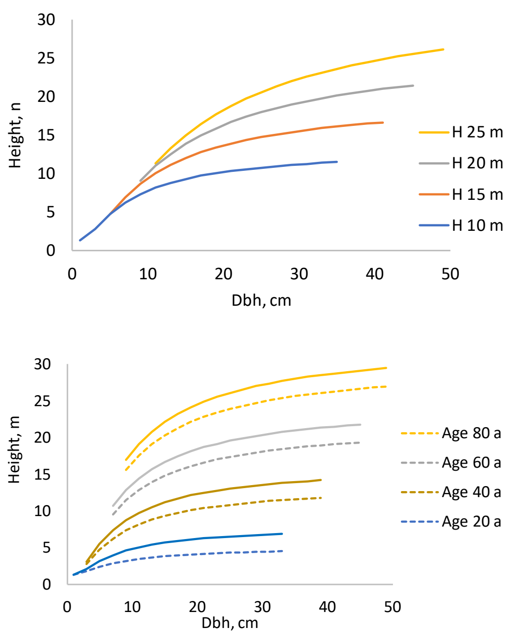

Figure 4. Relationship between diameter at breast height (Dbh) and tree height at different dominant heights (H) and stand ages according to the two versions of the height model (Top: Equation 3; Bottom: Equation 4). In the lower diagram, continuous lines show the tree height in site index of 25 m and dashed lines for site index of 15 m at 80 years.

Diameter increment and survival models

When the diameter increment and survival models were fitted using different weights in the loss function (w_k in Equation 7), or by adding plot and measurement factors to both models, the diameter increment models behaved slightly differently, as shown in Figure 5. The model versions where the plot area or the number of trees were used as the weight (w_k in Equation 7) were very close to each other. Since the loss functions of the fitting were not the same in different weighting schemes, the model versions cannot be compared based on the loss function value. Therefore, the models were compared by calculating the measured and predicted mean annual basal area increment (periodical increment divided by the length of the period) for each measurement interval of each plot. Then the square root of the area-weighted mean of the squared errors in annual basal area increment was calculated. According to this analysis, the

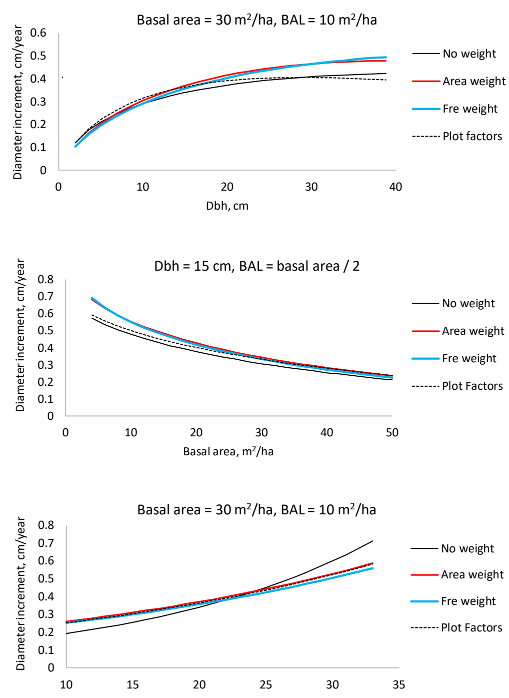

Figure 5. Dependence of diameter increment on diameter, stand basal area and site index according to four different versions of the diameter increment model (see text for explanation). "Fre weight" means that the number of trees within the plot was used as the weigh variable in the loss function (Equation 7).

use of number of trees as the weight resulted in the best model (area-weighted RMSE 0.444 $m^2ha^{-1}a^{-1}$) and a model fitted without any weight was the worst (RMSE 0.449 $m^2ha^{-1}a^{-1}$). Therefore, the model where the number of trees was used as the weight was selected for further analyses. The bias of the selected model, in terms of mean annual basal area increment, was -0.00086 $m^2ha^{-1}a^{-1}$ (0.064%). The model version that included additional plot and measurement factors was fitted using the number of trees as the weight.

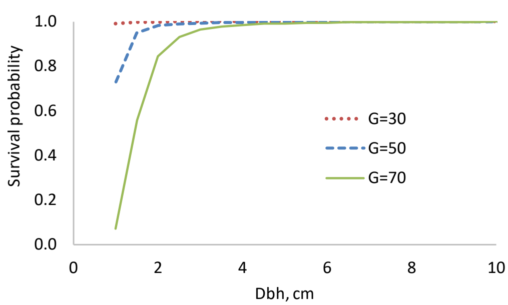

Figure 6. Dependence of one-year survival probability on diameter at breast height (Dbh) and stand basal area (G, m^2/ha) according to Equation 6.

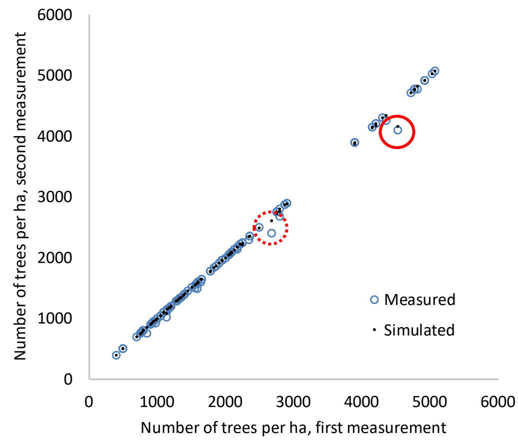

Figure 7. The measured and predicted number of trees per hectare in the beginning and at the end of the measurement interval (3–16 years). In most plots, there was no mortality between the two successive measurements. The two dots inside the circle drawn with the continuous red line show a case where the model successfully predicted the mortality. The dashed circle is a case in which the model failed to accurately predict mortality.

Table 4. Parameter estimates and bootstrap results for the optimization-based diameter increment and survival models. SD stands for standard deviation.

Predictor	Parameter	Parameter estimate[1]	Bootstrap results Min	Mean	Max	SD	SD/Mean
Diameter increment model							
Constant	a_0	-2.4548	-2.866	-2.419	-2.051	0.184	-13.110
ln(*d*)	a_1	0.6321	0.415	0.642	0.826	0.097	6.608
d	a_2	-0.0088	-0.040	-0.014	-0.006	0.007	-1.931
$\sqrt{G}$	a_3	-0.1895	-0.245	-0.163	-0.065	0.050	-3.281
BAL/ln(*d*+1)	a_4	-0.0353	-0.055	-0.036	-0.021	0.008	-4.438
SI	a_5	0.0505	0.027	0.046	0.076	0.010	4.630
Survival model							
Constant	b_0	14.3240	7.745	15.656	19.491	2.943	5.320
ln(*d*)	b_1	0.3552	-0.948	0.277	0.943	0.471	0.588
$\sqrt{G}$	b_2	-0.3392	-0.948	-0.424	-0.015	0.281	-1.506
BAL/ln(*d*+1)	b_3	-0.2424	-0.380	-0.205	-0.018	0.087	-2.359

[1] Number of trees within the plot was used as the weight variable in the loss function (Equation 7).

The survival model that was fitted simultaneously with the diameter increment model predicted mortality only among small trees with a very high stand basal area, which is in line with the data (Fig. 6). The model predicted significant mortality only in very few plots, which is also in line with the data (Fig. 6). Figure 7 shows that of the two cases in which there was significant mortality between the two measurements (i.e., more than one tree died), one case was predicted well (red circle drawn with continuous line in Fig. 7) and the other case was less successful (red circle drawn with dashed line).

The results of the bootstrapping (Table 4) indicated that the regression coefficients of the diameter increment model were significant whereas two of the coefficients of the survival model, particularly the coefficient for ln(d), had lower significance. However, the practical significance of this shortcoming is small, since the mortality rate of the Icelandic Sitka spruce plantations was very low and the model also predicted very low mortality except for heavily suppressed small trees.

The model set was used to simulate the development of plots 1 and 2 of the modelling dataset (Figs. 8 and 9) using the measured diameters of the trees at the age of 21 years as the starting point. Mortality was simulated by multiplying the frequencies of the trees by their predicted survival probability. In plot 1, the trees that were removed in light pre-commercial thinning in year 24 were removed also in the

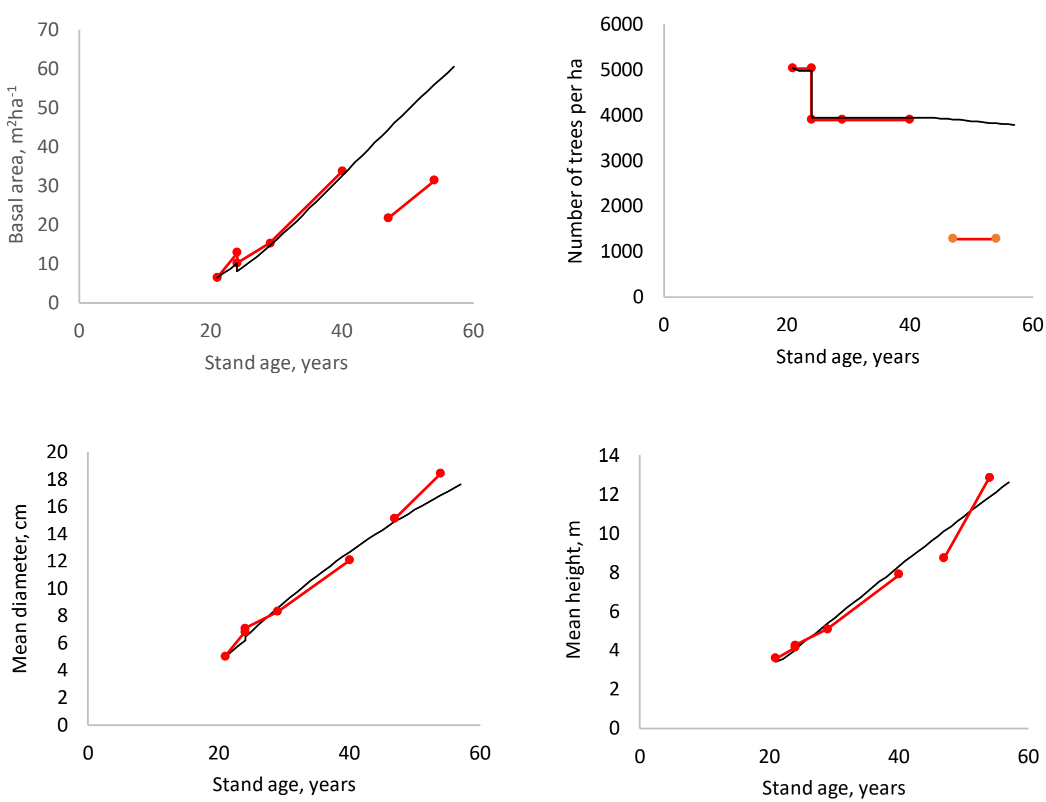

Figure 8. Development of plot 1 according to the measurements (red dots indicate measurements) and simulation (black line). The same trees that were removed in the light thinning at 24 years were also removed in the simulation. The thinning treatment between stand ages 40 and 47 was not simulated (the simulation is for non-thinned stand and the measurement at 47 and 57 years are for thinned stand).

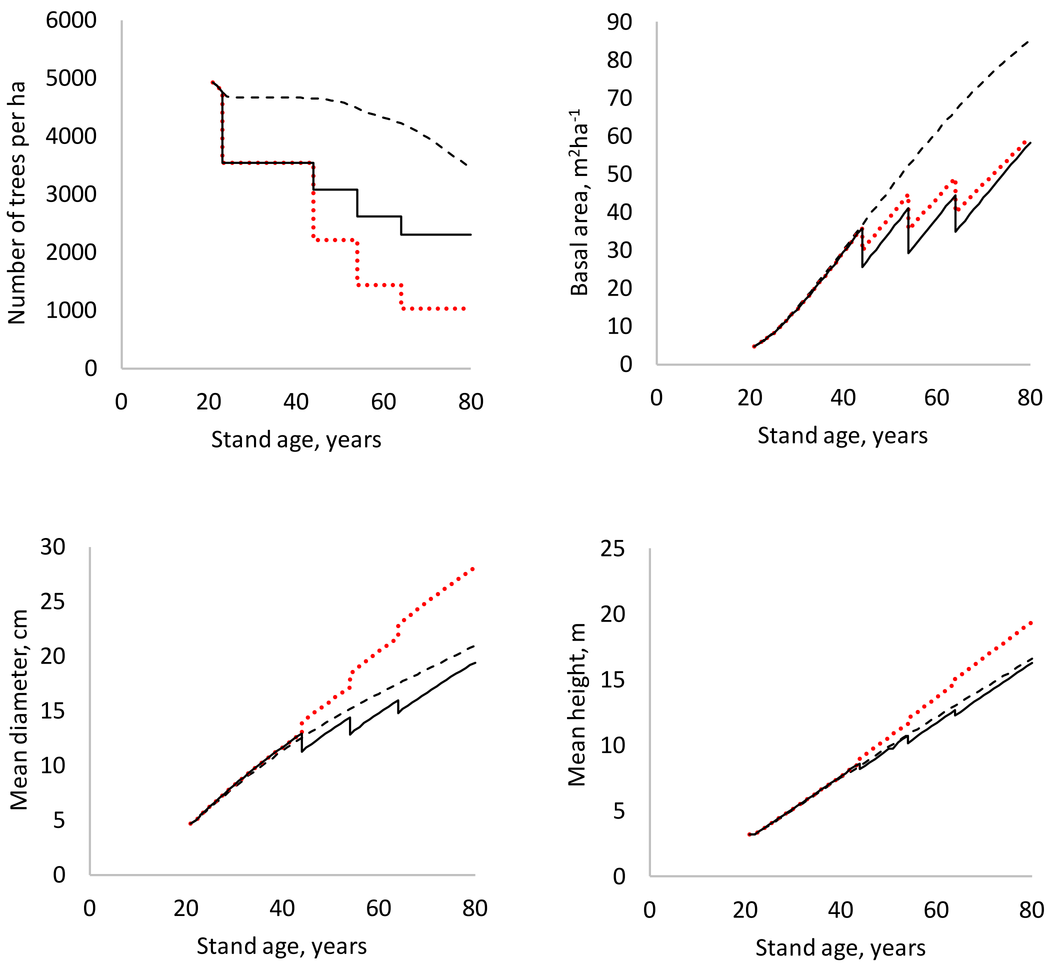

Figure 9. Simulated development of plot 2 without cuttings (black dashed line), and when the treatment schedule includes three thinnings from below (red dotted line) or three thinnings from above (black continuous line). In both thinning schedules, a pre-commercial thinning was simulated at 23 years, where the smallest trees were removed.

simulation. Plot 1 has been thinned also between 40 and 47 years but because it was not known which of the original trees were removed, the second thinning was not simulated. The simulated stand development was very close to the measured development until stand age 40 years, after which the plot was thinned (Fig. 8). When the simulation was continued beyond 40 years, without simulating the thinning treatment, the stand basal area reached 60.5 m^2ha^{-1} at 57 years. This is a logical basal area as there were a few plots in the dataset where the measured stand basal area exceeds 78 m^2ha^{-1} at stand ages ranging from 47 to 58 years (Table 1).

In plot 2, a pre-commercial thinning was simulated at 23 years where the smallest trees of the plot were removed. Then, the stand development was simulated until the stand age reached 80 years. The simulation was done: a) without any cuttings, b) with three thinnings from below and c) with three thinnings from above. The results (Fig. 9) do not reveal any anomalies in the simulated stand development. The simulations conducted for plots 1 and 2 (Figs. 8 and 9) suggest that the models may be used without problems to simulate the future development of Icelandic Sitka spruce stands until stand ages of about 80 to 100 years.

DISCUSSION

The article presents the first growth and yield models for Sitka spruce in Iceland. The models are distance-independent individual-tree models. The developed models include all the components required to simulate stand dynamics in the context of forest management planning. The model set of this study does not include a taper model, which would allow the prediction of the total and merchantable volumes for different definitions of industrial wood. Taper models for Icelandic Sitka spruce plantations should be developed in future studies. Before that, models developed in other countries (e.g., Fonweban et al. 2011) or models developed in Iceland for other conifers (Heiðarsson & Pukkala 2011) may be used.

According to the site index model, the dominant height growth rate starts to decrease after a stand age of 50 years. The model predicts that the dominant height of a stand with site index of 25 m would reach 31.5 m at 100 years and 45.9 m at 150 years. Although these predictions are not illogical (Savil 1991), other factors such as wind and snow may prevent Sitka spruce forests from reaching these heights in many parts of Iceland. Special attention was paid in this study to obtaining models that behave logically in extrapolations. Therefore, we are confident that the presented models can be used to analyse the growth and yield of Icelandic Sitka spruce in stands younger than 90 years old. However, since the modelling data set used in this study contained little data on mature stands, the models need to be updated as Sitka spruce plantations get older.

The weakest part of the model set is probably the survival model, but little mortality was measured on the sample plots, even at very high stand basal areas (Table 1). The model predicts density-related mortality, but mortality begins at very high stand density. A study from Alaska in natural mixed stands with Sitka spruce and Western hemlock showed much higher basal areas than this study, suggesting that Sitka spruce is able to grow and survive in very dense stands (Taylor 1934). In future growth studies, emphasis should also be given to collecting more data from unthinned stands and data from the northwest and southeast parts of the country, which were not included in the dataset of this study (Figure 1).

The method that was used to fit the diameter increment and survival models (Pukkala 2009) was able to deal with irregular measurement intervals. The method also works with datasets containing tree identification errors (de-Miquel et al. 2014), which means that tree numbering and labelling are not required. Previous studies have shown that with regular data (a constant measurement interval, no tree identification errors), the method produces very similar models to those obtained with regression analysis (Pukkala et al. 2011). When the measurement interval varies greatly, optimization has been reported to produce more logical models than obtained from regression analyses that assume a constant growth rate between two consecutive measurement occasions (Juma et al. 2014). When several models are fitted simultaneously, there is the possibility of having mutual errors that cancel out each other. For example, an overestimated diameter increment may be compensated for by overestimated mortality. However, the objective function used in the current study included the diameter distribution of both the stand basal area and number of trees, with the consequence that the possibility of this kind of error was small. If ingrowth models were estimated simultaneously with survival models, which is also possible (Pukkala 2009), the risk of mutual errors would be higher.

The developed growth models will be used in the forest management planning system at the Icelandic Forest Service. The planning system makes it possible to optimize the thinning schedules and rotation length to maximize the net present value, wood production, or carbon sequestration. The new models will be an important component of the management planning system used in Iceland because the stand structure and the amount of wood in Sitka spruce forests can now be better evaluated, and forest resources can be used more efficiently. Good knowledge about the yield and suitable rotation lengths of Sitka spruce plantations also provides investors with a better basis for making informed decisions.

REFERENCES

Alegria C & Tomé M 2013. A tree distance-dependent growth and yield model for naturally regenerated pure uneven-aged maritime pine stands in central inland of Portugal. Annals of Forest Science 70, 261–276.
DOI:10.1007/s13595-012-0262-8

Bella IE 1971. A new competition model for individual trees. Forest Science 17, 364-372.
https://doi.org/10.1093/forestscience/17.3.364.

Cao QV 2000. Prediction of annual diameter growth and survival for individual trees from periodic measurements. Forest Science 46, 127-131.

Cao QV 2004. Annual tree growth predictions from periodic measurements. In: Connor KF (ed) Proceedings of the 12th biennial southern silvicultural research conference, Gen. Tech. Rep. SRS-71, USDA, Forest Service, Southern Research Station, Asheville, NC, 212-215 pp.

Clutter JL 1963. Compatible growth and yield models for loblolly pine. Forest Science 9(3), 354–371.

Clutter JL, Fortson JC, Pienaar LV, Brister GJ & Bailey R 1983. Timber management: A quantitative approach. John Wiley & Sons, New York. 333 p.

Crecente-Campo F, Soares P, Tomé M & Diéguez-Aranda U 2010. Modelling annual individual-tree growth and mortality of Scots pine with data obtained at irregular measurement intervals and containing missing observations. Forest Ecology and Management 260, 1965–1974.
doi:10.1016/j.foreco.2010.08.044.

Curtis RO 1967. Height-diameter and height-diameter age equations for second-growth Douglas fir. Forest Science 13(4), 365–375.

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 Ecology and Management 291, 249-258.
http://dx.doi.org/10.1016/j.foreco.2012.11.026.

de-Miguel S, Pukkala T & Morales M 2014. Using optimization to solve tree misidentification and uneven measurement interval problems in individual-tree modelling of Balsa stand dynamics. Ecological Engineering 69, 232-236.
DOI: 10.1016/j.ecoleng.2014.04.008.

Dong L, Pukkala T, Li F & Jin X 2021. Developing distance-dependent growth models from irregularly measured sample plot data – a case for *Larix olgensis* in Northeast China. Forest Ecology and Management 486(7), 118965.
https://doi.org/10.1016/j.foreco.2021.118965.

Ek AR & Monserud RA 1974. A computer model for simulating the growth and reproduction of mixed species forests stands. Res. Rep. R2635, School of Natural Resources, University of Wisconsin, 13 p.

Fonweban J, Gardiner B, Mcdonald E & Auty D 2011. Taper functions for Scots pine (*Pinus sylvestris* L.) and Sitka spruce (*Picea sitchensis* (Bong.) Carr.) in Northern Britain. Forestry 84(1): 49-60.
https://doi.org/10.1093/forestry/cpq043.

Guzmán G, Morales M, Pukkala, T & de-Miguel S 2012a. A model for predicting the growth of *Eucalyptus globulus* seedling stands in Bolivia. Forest Systems 21(2), 202-209.
DOI: https://doi.org/10.5424/fs/2012212-02398.

Guzmán G, Pukkala T, Palahí M & de-Miquel S 2012b. Predicting the growth and yield of *Pinus radiata* in Bolivia. Annals of Forest Science 69: 335-343. DOI 10.1007/s13595-011-0162-3.

Harris AS 2022. Accessed 08.01.2022 at https://www.srs.fs.usda.gov/pubs/misc/ag_654/volume_1/picea/sitchensis.htm .

Hartig GL 1795. *Anweisung zu taxation der forsten oder zur bestimmung des Holzertrages der wälder* [Leiðbeiningar fyrir skógarúttekt til að ákveða viðarmagn skóga]. GieBen: Heyer Verlag. In German.

Heiðarsson L & Pukkala T 2011. Taper functions for lodgepole pine (*Pinus contorta*) and Siberian larch (*Larix sibirica*) in Iceland. Icelandic Agricultural Sciences 24: 3-11.

Heiðarsson L & Pukkala T 2012. Models for simulating the development of Siberian larch (*Larix sibirica* Ledeb.) plantations in Hallormsstaður Iceland. Icelandic Agricultural Sciences 25: 13-23.

Jin Xingji, Pukkala T, Li F & Dong L 2019. Developing growth models for tree plantations using inadequate data – a case for Korean pine in Northeast China. Silva fennica vol. 53, no 4. DOI:10.14214/sf.10217.

Juma R, Pukkala T, de-Miguel S & Muchiri M 2014. Evaluation of different approaches to individual tree growth and survival modelling using data collected at irregular intervals – a case for *Pinus patula* in Kenya. Forest Ecosystems 1:14 13 p. https://doi.org/10.1186/s40663-014-0014-3.

Korf V 1939. A mathematical definition of stand volume growth law. Lesnicka Prace 18, 337–339.

van Laar A & Akca A 1997. Forest mensuration. Cuvillier Verlag, Göttingen, Germany, 246 p. DOI https://doi.org/10.1007/978-1-4020-5991-9.

Mabvurira D & Miina J 2002. Individual-tree growth and mortality models for *Eucalyptus grandis* (Hill) Maiden plantations in Zimbabwe. Forest Ecology and Management 161, 231-245. DOI:10.1016/S0378-1127(01)00494-7.

McDill ME & Amateis RL 1992. Measuring forest site quality using the parameters of a dimensionally compatible height growth function. Forest Science 38(2), 409–429.

Mehtätalo L, de-Miguel S & Gregoire TG 2015. Modelling height-diameter curves for prediction. Can. J. For. Res. 45: 826-837 p. dx.doi.org/10.1139/cjfr-2015-0054.

Newnhan RM 1964. *The development of a stand model for Douglas-fir*. Vancover: Faculty of Forestry, University of British Columbia.

Munro D 1974. Forest growth models – a prognosis, in: Fries J. (Ed.), Growth models for tree and stand simulation, Proceedings of the IUFRO working party S4.01-4, 1974, 7–21 p.

Nelder JA, & Mead R 1965. A simple method for function minimization. The Computer Journal 7, 308-313. https://doi.org/10.1093/comjnl/7.4.308.

Nord-Larsen T 2006. Modeling individual-tree growth from data with highly irregular measurement intervals. Forest Science 52(2), 198-208. https://doi.org/10.1093/forestscience/52.5.609.

Näslund M 1937. Skogsförsöksanstaltens gallringsförsök i tallskog (Forest research intitute's thinning experiments in Scots pine forests). Meddelanden från statens skogsförsöksanstalt Häfte 29 (In Swedish).

Palahí M, Pukkala T, Miina J & Montero G 2003. Individual-tree growth and mortality models for Scots pine (*Pinus sylvestris* L.) in north-east Spain. *Ann. For. Sci.* 60 (2003) 1–10. DOI: 10.1051/forest: 2002068.

Palahí M, Tomé M, Pukkala T, Trasobares A, Montero G 2004. Site index model for *Pinus sylvestris* in north-east Spain. Forest Ecology and Management 187(1), 35–47. DOI:10.1016/S0378-1127(03)00312-8.

Pukkala T, Lähde E & Laiho O 2011. Using optimization for fitting individual-tree growth models for uneven-aged stands. European Journal of Forest Research 130(5), 829-839. DOI:10.1007/s10342-010-0475-z.

Pukkala T 1987. Simulation model for natural regeneration *Pinus sylvestris, Picea abies, Betula pendula and Betula pubescens*. Silva Fennica 21, 37–53. https://doi.org/10.14214/sf.a15462.

Pukkala T 1988. Studies on the effect of spatial distribution of trees on the diameter growth of Scots pine. Publications in Science No 13. University of Joensuu. https://doi.org/10.14214/sf.a15495.

Pukkala T 1989. Predicting diameter growth in an even-aged Scots pine stand with a spatial and non-spatial model. Silva Fennica 23, 101-116. https://doi.org/10.14214/sf.a15533.

Pukkala T 2009. Population-based methods in the optimization of stand management. Silva Fennica 43(2), 261-274. DOI: 10.14214/sf.211

Pukkala T, Lähde E & Laiho O 2011. Using optimization for fitting individual-tree growth models for uneven-aged stands. European Journal of Forest Research 130(5), 829-839. DOI:10.1007/s10342-010-0475-z.

Richards FJ 1959. A flexible growth function for empirical use. Journal of Experimental Botany 10, 290–300.

Savill, P. S. 1991. The Silviculture of Trees used in British Forestry. CAB International. Wallingford. 160 pp.

Schumacher FX 1939. A new growth curve and its application to timber yield studies. Journal of Forestry 37, 819−820.

Snorrason A 2014. *Information collected by the Icelandic NFI and reported in the JointForest Europe/UNECE/FAO Questionnaire on Pan-European Indicatiors for Sustainable Forest Mangement.* Geneva: UNECE/FAO Forestry and Timber Section.

Taylor RF 1934. Yield of second-growth Western hemlock – Sitka spruce stands in Southeastern Alaska. United States Department of Agriculture, Washington, DC. Technical bulletin No. 412.

Trasobares A, Tomé M & Miina J 2004. Growth and yield model for *Pinus halepensis* Mill. in Catalonia, north-east Spain. Forest Ecology and Management 203, 49–62. DOI:10.1016/j.foreco.2004.07.060.

Vanclay JK 1994. Modelling forest growth and yield: Applications to mixed tropical forests. CAB. International. 312 p.

Vedurstofa Íslands 2017. Accessed on 26.1.2017 at http://www.vedur.is/Medaltalstoflur-txt/Arsgildi.html.

Weiskittel AR, Hann DW, Kershaw Jr JA & Vanclay JK 2011. Forest growth and yield modeling. 1st Ed., John Wiley & Sons, 415 pp.

Widemann E 1942. Der gleichaltrige Fichten-Buchen-Mischbestand [Jafnaldra blandskógar af greni og beyki]. Mitteilungen aus Forstwirtschaft und Forstwissenschaft 13/1. In German.

Wimberly MC & Bare BB 1996. Distance-dependent and distance-independent models of Douglas-fir and western hemlock basal area growth following silvicultural treatment. Forest Ecology and Management 89, 1-11. https://doi.org/10.1016/S0378-1127(96)03870-4.

Øyen, BH 2005. Vekst og produksjon i bestand med sitkagran (*Picea sitchensis* Bong. Carr.) i Norge [Vöxtur og framleiðsla sitkagreniskóga (*Picea sitchensis* Bong. Carr.) í Noregi. Rapport fra skogforskningen 4/05: 1-46. In norwegian.

Manuscript received 7.12.2021
Accepted 15.3.2022