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Advancing height growth models for the improved forest reproductive material of the main tree species in Latvia

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Abstract

The breeding of economically important forest tree species in the Baltic Sea region has contributed notably to the availability of quality wood for bioeconomy. Accordingly, the altered stand dynamics of improved trees should be identified and incorporated in growth models to accurately reflect these gains. Such advanced models can be used for assessment of different alternatives, e.g. strategies for increased carbon sequestration.

We tested and modified dynamic forms of the King-Prodan height growth function based on the remeasured National Forest Inventory plots in Latvia to predict the growth of improved Scots pine, Norway spruce and silver birch forest reproductive material (FRM) categories 'qualified' and 'tested' using height measurements from progenies of 371, 390, and 690 open-pollinated families, respectively. Both categories had steeper growth trajectories at young age compared to an unmodified function. Growth of category 'tested' for pine and birch exceeded that of category 'qualified' across the modelled age range, while trajectories mainly overlapped for spruce on lower site indices. The functions with FRM category-specific multipliers more accurately reflect the actual growth of improved stands, advancing planning of timely management activities like thinning. The single model with category-specific set of multipliers may be easy applicable in practice or incorporated in growth simulators without increased complexity for end-users. However, the predictions are limited to the sites with medium and high site indices, where improved planting stock is typically used.

Keywords: GADA approach, dynamic modelling, tree breeding, FRM categories

Introduction

Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* (L.) Karst.), and silver birch *(Betula pendula* Roth) are commercially the most important forest tree species in the eastern Baltic region, and breeding programmes for them have been ongoing since the middle of the 20th century. Currently, almost 100% of Scots pine, 75% of Norway spruce, and 37% of silver birch forest reproductive material (FRM) being produced are genetically improved – in categories 'qualified' and 'tested' in Latvia (Oficiālās statistikas portāls 2022). In the region, estimated genetic gains with respect to growth and production reach 10–35% over unimproved material depending on the trait and improvement level (Rosvall et al. 2002, Ruotsalainen 2014, Haapanen et al. 2016, Liziniewicz and Berlin 2019, Gailis et al. 2020). The use of genetically improved FRM has been evaluated to be financially profitable at final harvest (Ahtikoski 2000, Ahtikoski et al. 2012, Jansons et al. 2015, Zeltiņš et al. 2018), as well as during the first commercial thinning (Gailis et al. 2020) and when contributing to carbon sequestration (Ahtikoski et al. 2020).

Reliable long-term estimates of forest development are of great importance for planning management and evaluating alternative management options (Fahlvik and Nyström 2006, Ahtikoski et al. 2012). Growth and yield models are commonly used to describe and predict the growth of forests, yet usually based on extensive measurement of naturally developed and genetically unimproved stands (Gould et al. 2008). The substantial increase in production due to tree breeding suggests that existing growth models might be revised to incorporate genetic gains (Rehfeldt et al. 1991, Sabatia 2011, Egbäck et al. 2017).

Growth models for genetically improved material in the Baltic Sea region are still lacking. In Latvia, forest growth and yield tables have been used as a common practice to predict growth, yet calculations are commonly based on data from once surveyed sample plots, of which the majority were established in the 1960s and 70s (Matuzānis 1985). Since then increase in the forest growth have been observed not only due to genetic improvements, but largely explained by improved silvicultural practices and changes in environmental conditions like temperature, precipitation and increased nitrogen decomposition (Solberg et al. 2009, Kauppi et al. 2014, Henttonen et al. 2017, Etzold et al. 2020, Appiah Mensah et al. 2021). In the last decades, valuable data from the National Forest Inventory (NFI) have become available for building and calibrating new up-to-date growth functions (Donis et al. 2020). However, the establishment method for many forest stands is unclear, in most cases being the natural regeneration of unimproved material. Lack of accurate reflection of the growth of improved material in models may result in suboptimal forest management (Adams et al. 2006).

Appropriate growth models are becoming more important as the area planted with improved material is increasing, and the genetic gain resulting from improvement programmes also increases (Egbäck et al. 2017). Development of new functions for improved trees usually has limited applicability due to the lack of available repeated measurements up to the final harvest age (Joo et al. 2020). Hence, commonly used modifications of the existing models intended for unimproved trees are adjustment of site index (Buford and Burkhart 1987) or application of genetic multipliers (Carson et al. 1999, Kimberley et al. 2015). We chose the genetic multiplier approach to quantify height growth differences between improved and unimproved trees. Multipliers are commonly used to modify coefficients of an existing (reference) model built on empirical data from genetically unimproved trees, when limited data of improved material from progeny trials are available (Rehfeldt et al. 1991, Carson et al. 1999, Gould et al. 2008, Gould and Marshall 2010, Kimberley et al. 2015, Deng et al. 2020). Still, unlike the common approach to quantify genetic gains of different genetic entries, we introduced forest reproductive material category-specific multipliers for improved categories 'qualified' and 'tested' with the aim to apply them straightforward into practice.

Therefore, our aim was to test a dynamic generalized algebraic difference approach (GADA) form of the King-Prodan height growth functions (Krumland and Eng 2005) previously calibrated from the remeasured National Forest Inventory (NFI) plots in Latvia (representing mainly unimproved material) to better predict the growth of improved FRM categories 'qualified' and 'tested' with different levels of genetic improvement.

Materials and methods

The study comprised tree height data from the re-measured open pollinated progeny trials of Scots pine, Norway spruce and silver birch in Latvia (55°40'–58°05' N, 20°58'–28°14' E) (Figure 1). Age of the height measurements varied from 8 to 42 years, inventories being done two to four times per trial (Table 1).

The trials were established at the sites suitable for the species of interest. Scots pine sites could be characterized with relatively poor, sandy soil corresponding to the *Vacciniosa* forest type (Buss 1997). Norway spruce was planted in mesotrophic mineral soils with normal moisture regime (*Hylocomiosa* or *Oxalidosa* forest type). For silver birch, both trials were planted on silty dry soils in former agricultural land with mesotrophic conditions. Scots pine families were planted in 10- to 100-tree block plots in 5- to 8 replications using 1- to 2-year-old seedlings; initial spacing was 2 × 1 or 2 × 1.5 m. For Norway spruce, 3-year-old bare rooted seedlings were planted in 10 to 24 tree family block-plots with initial spacing varying from 1.5 × 3 m to 2.5 × 2.5 m. Silver birch trails had randomized block design of single tree plots in 10 to 93 replications with an initial spacing of 2 × 2.5 m. In total, progenies from 371, 390, and 690 families of Scots pine, Norway spruce and silver birch, respectively, were represented in the trials.

The mean annual temperature in Latvia ranges from +5.7°C in the more continental eastern part to +7.5…+7.9°C on the Baltic Sea coast. The mean monthly temperature ranges from –3.1°C in February to +17.8°C in July. The mean annual precipitation in Latvia is 685 mm, with July and August being the wettest months (76–77 mm) and April being the driest month (36 mm) (Klimata Portāls 2020).

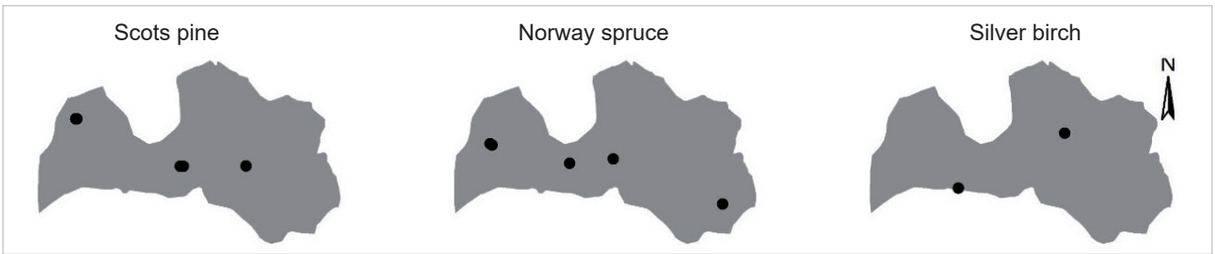

Figure 1. Locations of the progeny trials in Latvia with available tree height measurements for model testing and modifications

Table 1. Summary statistics of height measurement data from the progeny trials

Species	Trial	Age	Category: tested					Category: qualified				
			Mean (m)	*SD* (m)	Min (m)	Max (m)	N	Mean (m)	*SD* (m)	Min (m)	Max (m)	N
Scots pine	No 18	26	11.5	1.1	8.9	14	205	11.2	1.1	7.9	16	1023
		34	15.5	1.8	11	20	205	15.1	1.7	9.7	21	1023
	No 19	17	7.87	0.9	5.4	10	110	6.59	1	2.8	10	1071
		23	11.4	1.1	7.5	14	110	10.1	1.3	5.1	20	1071
	No 24	27	15.3	0.9	12	18	152	14.2	1.1	9.3	17	841
		42	23.6	1.7	17	27	152	22	2.2	14	27	841
	No 31	26	15.2	1	13	18	133	14.3	1.1	11	18	956
		39	21.2	1.7	16	24	133	20.1	1.9	14	25	956
	No 39	10	6.26	0.6	4.1	8.1	193	5.61	0.8	1.9	9.6	1409
		21	14.4	1.4	7	17	193	13.5	1.3	6.4	17	1409
	Zvirgzde	21	9.4	1.1	7	13	82	8.34	1.3	3.9	13	539
		28	13.9	1.6	10	18	82	12.5	2	6.6	18	539
Norway spruce	Andrupene	17	6.13	1.3	1.2	10	301	5	1.5	0.6	9.6	2845
		21	9.6	1.7	2.2	14	301	8.37	2	0.8	14	2845
	Jelgava	8	1.75	0.4	0.5	2.6	71	1.51	0.4	0.3	2.7	528
		9	2.37	0.6	0.6	3.6	101	2.01	0.6	0.5	3.6	754
		10	3.14	0.8	1	4.8	89	2.71	0.7	0.7	4.5	683
		12	4.88	0.9	2.6	6.6	69	4.16	0.9	1	6.4	521
	Kuldīga	12	3.07	1	0.7	5.2	266	2.23	0.9	0.3	5.4	2623
		13	3.52	1.1	0.8	5.7	379	2.63	1	0.4	6	3372
		14	4.07	1.2	1.2	6.5	379	3.07	1.1	0.5	6.8	3371
		15	4.71	1.2	1.7	7.5	265	3.62	1.2	0.8	7.3	2622
	Priedaine	17	8.57	1.7	2.3	12	194	7.23	2.1	1	13	1253
		26	13.2	2.5	3.4	18	194	11.8	3	2	18	1253
	Rembate	10	2.88	0.7	0.7	4.7	231	2.08	0.7	0.4	4.5	1889
		11	3.69	0.8	0.9	5.6	292	2.74	0.9	0.6	5.5	2931
		12	4.49	0.9	1.2	6.6	292	3.43	1.1	0.7	6.6	2931
		13	5.31	1	1.6	7.6	230	4.15	1.2	0.9	7.9	1888
Silver birch	Taurene	10	7.32	1.3	2.8	10	759	6.79	1.3	2.6	11	6940
		14	12.5	1.6	6.2	16	1263	11.6	1.7	4.5	16	10949
		22	20.1	1.5	11	23	500	18.6	2.1	11	23	4051
	Ukri	10	7.4	1.2	3.3	11	728	6.72	1.2	2.6	12	5801
		14	13.6	1.5	7.8	18	1555	12.6	1.7	4.2	17	10748
		22	20	1.4	13	23	823	19	1.7	11	23	4932

Note: *SD* – standard deviation, Min – minimum value, Max – maximum value, N – number of measured trees.

The modelling approach

As the category 'tested', 10% of families (standard selection intensity; Jansons et al. 2015) with the highest mean height were selected in each trial, while the other 90% of families were assigned category 'qualified' (Table 1). The GADA form of the King-Prodan equation was used (Krumland and Eng 2005):

$$H_2 = 1.3 + \frac{A_2^{b_1}}{b_2 + 100\, b_3 \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100 b_3 + A_1^{b_1}} + \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100 b_3 + A_1^{b_1}} A_2^{b_1}}, \quad (1)$$

where

H_1 is the height at the beginning of the forecast period, m;

H_2 is the height at the end of the forecast period, m;

A_1 is the breast height age at the beginning of the forecast period, years;

A_2 is the breast height age at the end of the forecast period, years; and

b_1, b_2, b_3 are empirical coefficients.

Difference between biological and breast height age assumed to be 4, 6, and 3 years for Scots pine, Norway spruce, and silver birch, respectively.

We used the empirical coefficients b_1, b_2 and b_3 of the height growth function previously approximated from the data of the National Forest Inventory (Table 2) as a part of Latvian State Forest Research Institute 'Silava' forest research long-term prognosis model AGM (Donis et al. 2018, 2020, Donis and Šņepsts 2019). The inclusion of the breeding effect in the equation was applied by introducing FRM as a fixed factor ('qualified' or 'tested'). Further, different combinations of the factor-specific genetic multipliers (g, g_1, g_2, g_3) were added and tested in front of the coefficients b_1, b_2 and b_3 (Supplementary 1) in the part of the reference GADA function that has been resolved from the

site-specific empirical coefficients $a_1 = b_1$, $a_2 = b_2 + b_3X$, and $a_3 = X$ in the base equation (Krumland and Eng 2005):

$$H = 1.3 + \frac{A^{a_1}}{a_2 + a_3 \cdot A^{a_1}}, \quad (2)$$

We did not adjust coefficients b_1, b_2 and b_3 in the solution of X_0 of unknown environmental conditions X:

$$X_0 = \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100b_3 + A_1^{b_1}}, \quad (3)$$

The theoretical variable X includes the number of unobserved environmental effects (Sharma et al. 2017, Cieszewski and Bailey 2000), hence assuming a similar impact on the two categories of FRM in the same trial.

Table 2. Reference height growth model coefficients b_1, b_2 and b_3 for the King-Prodan generalized algebraic difference approach form calibrated using National Forest Inventory data in Latvia (Donis et al. 2018)

Species	b_1	b_2	b_3
Scots pine	1.15697	–27.0403	16.4512
Norway spruce	1.28394	–47.3493	23.60081
Silver birch	1.257	–47.475	21.726

Data analysis

All data analysis was conducted in R, a software environment for statistical computing and graphics, v. 4.0.3 (R Core Team 2020).

For each studied tree species, modified functions with different combinations of included multipliers were tested (Supplementary 1) and the best-fit model was selected using Akaike's information criterion (*AIC*). The fitted models were evaluated using the adjusted coefficient of determination (R^2_{adj}), absolute mean residual (*AMRES*), and the root mean squared error (*RMSE*) (Montgomery et al. 2012). We did graphical analysis of trends in residuals plotted against predicted tree height and drawn height-age curves overlaid on the measured height data. For testing predictive accuracy of the final fitted models, we split the datasets (both 'qualified' and 'tested') into calibration (training) and validation data (70 and 30%, respectively). In addition, we used validation data also to test prediction accuracy of the unmodified reference model. The predictions were evaluated using R^2_{adj}, *AMRES*, and *RMSE*.

Results

The best fit was achieved when accounting for the breeding effect in the equation by introducing a category ('qualified' or 'tested') dependent genetic multiplier in front of the coefficients b_1, b_2 and b_3 in the part of the function that has been resolved from the empirical coefficients a_1 and a_2 of the base equation:

$$H_2 = 1.3 + \frac{A_2^{g_1 \cdot b_1}}{g_2 \cdot b_2 + g_3 \cdot 100\, b_3 \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100b_3 + A_1^{b_1}} + \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100b_3 + A_1^{b_1}} A_2^{g_1 \cdot b_1}}, \quad (4)$$

where g_1, g_2 and g_3 are the FRM category-specific genetic multipliers.

Final fitted functions for Scots pine and silver birch had all three multipliers (Supplementary 1, equation 8; Supplementary 2), while inclusion of multipliers g_2 and g_3 showed the best fit statistics for Norway spruce (Supplementary 1, equation 5; Supplementary 2).

For both FRM categories of all three species, the estimated genetic multipliers were statistically significant ($p < 0.01$). Overall, modified models fitted the calibration data with high accuracy ($R^2_{adj} \geq 0.918$), with Norway spruce having the smallest errors (*RMSE* = 0.717 m, *AMRES* = 0.44 m) (Table 3). We did not observe any trends in residuals over predicted height for Scots pine and silver birch, but there was a slight overestimation for higher trees and an underestimation for smaller trees for Norway spruce (Figure 2). The same tendencies were observed for the validation data. Still, prediction statistics of the modified functions ($R^2_{adj} = 0.908$, *RMSE* = 1.351 m, *AMRES* = 0.977 for Scots pine; $R^2_{adj} = 0.943$, *RMSE* = 0.738 m, *AMRES* = 0.445 m for Norway spruce; $R^2_{adj} = 0.922$, *RMSE* = 1.100 m, *AMRES* = 0.846 m for silver birch) indicated a good fit to the validation data (Table 3).

For comparison, a test of an unmodified (reference) model with validation data from progeny trials showed various results for different species. For Scots pine and Norway spruce, the prediction precision was slightly lower compared to the modified function yet good ($R^2_{adj} = 0.891...0.912$). On the contrary, the model for silver birch indicated substantially lower prediction power (*RMSE* = 2.222 m, *AMRES* = 1.935 m, $R^2_{adj} = 0.683$) with a distinct trend to underestimate tree height for smaller trees (Figure 2). Less pronounced yet similar tendency was indicated for Scots pine. For Norway spruce, the unmodified model tended to overestimate the height of larger trees (Figure 2).

The drawn height-age curves indicated differences in the height growth of improved and unimproved trees (Figure 3). In general, both improved FRM categories – 'qualified' and 'tested' – had curves above the reference model except for the highest site indices ($H_{100} \geq 33$ m) indicating overestimation when the genetic multipliers are not used. For Scots pine and silver birch, the curves of the category 'tested' were slightly above the ones for 'qualified' material, while both lines overlapped for spruce in lower site indices. The most distinct differences between improved and unimproved tree height growth were observed in silver birch, for which both measured height-age trajectories and projected curves had much steeper growth at young age compared to unmodified function based solely on NFI data (Figure 3). For all the studied species, the underlaying data coverage of height-age series for improved trees support drawn curves for rather the height site indices ($H_{100} > 21$ m) (Figure 3).

Table 3. Estimated forest reproductive material category-specific ('tested' and 'qualified') genetic multipliers g_1, g_2 and g_3 with standard errors (*SE*) and confidence intervals (*CI*) for the final best-fit models and their fit and prediction statistics

Genetic multiplier	Category	Scots pine			Norway spruce			Silver birch		
		Estimate (*SE*)	2.5% *CI*	97.5% *CI*	Estimate (*SE*)	2.5% *CI*	97.5% *CI*	Estimate (*SE*)	2.5% *CI*	97.5% *CI*
g_1	tested	1.011*** (0.014)	0.983	1.039				0.856*** (0.011)	0.835	0.878
	qualified	0.964*** (0.006)	0.953	0.975				0.814*** (0.004)	0.806	0.821
g_2	tested	0.860*** (0.059)	0.745	0.975	0.605*** (0.023)	0.560	0.650	0.275*** (0.009)	0.258	0.292
	qualified	0.682*** (0.018)	0.647	0.717	0.595*** (0.008)	0.579	0.610	0.285*** (0.003)	0.278	0.291
g_3	tested	0.870*** (0.058)	0.756	0.984	0.626*** (0.022)	0.582	0.669	0.282*** (0.009)	0.265	0.300
	qualified	0.693*** (0.018)	0.659	0.728	0.616*** (0.008)	0.601	0.631	0.290*** (0.003)	0.283	0.297
Fit statistics										
N		4308			19219			24535		
AIC		14399.5			41754.3			78007.2		
RMSE (m)		1.390			0.717			0.724		
AMRES (m)		0.950			0.441			0.833		
R^2_{adj}		0.918			0.951			0.926		
Prediction statistics										
N		2435			11022			10535		
RMSE (m)		1.351			0.738			1.100		
AMRES (m)		0.977			0.445			0.846		
R^2_{adj}		0.908			0.943			0.922		
Prediction statistics (unmodified model)										
N		2435			11022			10535		
RMSE (m)		1.467			0.920			2.222		
AMRES (m)		1.095			0.510			1.935		
R^2_{adj}		0.891			0.912			0.683		

Note: N – number of observations, *AIC* – Akaike information criterion, RMSE – root mean square error; *AMRES* – absolute mean residual, R^2_{adj} – adjusted coefficient of determination; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

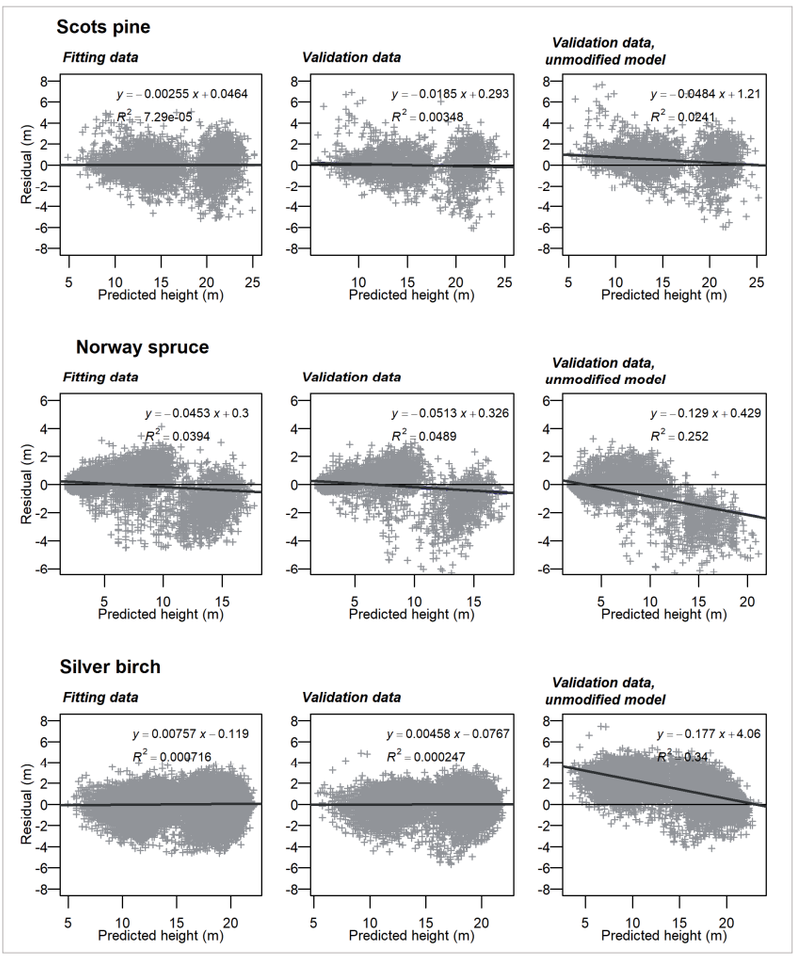

Figure 2. Residuals of fitting and validation data against the final best-fit models with multipliers (first two columns) and the unmodified reference model (third column) for Scots pine (upper three panels), Norway spruce (middle three panels) and silver birch (lower three panels)

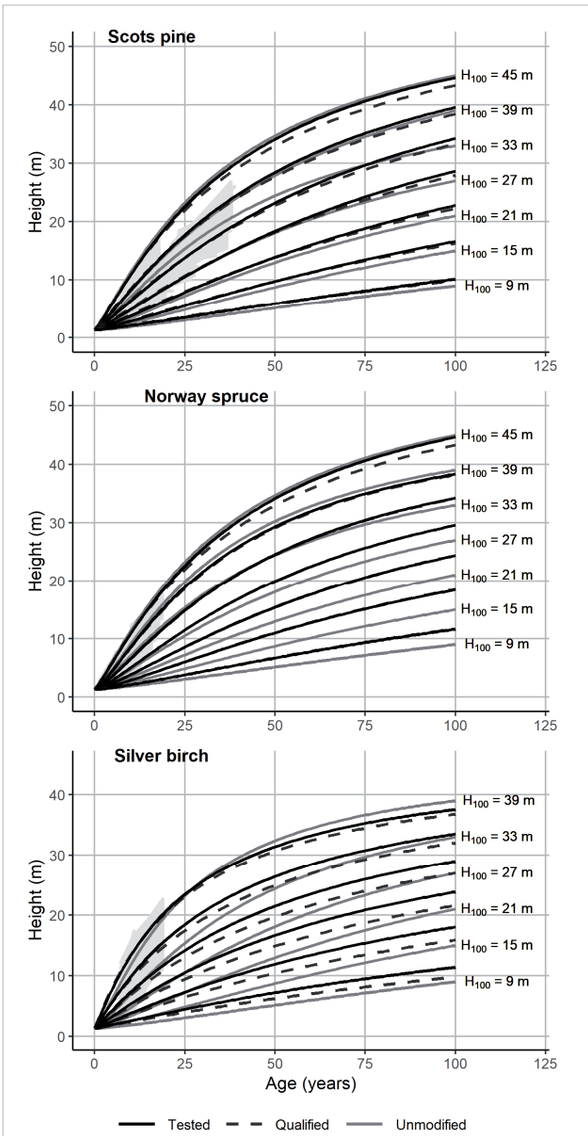

Figure 3. The final best-fit models with the genetic multipliers (black solid and dashed lines for improved categories 'tested' and 'qualified', respectively) vs. the unmodified model (dark grey solid lines) for Scots pine (upper panel), Norway spruce (middle panel) and silver birch (lower panel). Light grey colour in the background denote observed height-age series

Discussion

Considering available datasets with short time-series (up to four measurements) from the progeny trials with a limited age range (Table 1), we followed relatively simple yet effective genetic multiplier approach (Joo et al. 2020) to quantify breeding effect on height growth of Scots pine, Norway spruce and silver birch by adjusting parameters within the growth model (Haapanen et al. 2016). The approach allowed to specify general differences in the growth curves for genetically improved FRM categories 'tested' and 'qualified', while the dynamic GADA form itself provided invariance of various environmental effects like site quality (Cieszewski and Bailey 2000). The GADA functions with added the FRM category-specific multipliers predicted tree height growth with sufficient accuracy without any distinct trends in the residuals for Scots pine and silver birch, yet with negligible overestimation for higher and underestimation for smaller trees for Norway spruce (Figure 2). However, fit and prediction statistics showed statistically significant and biologically reasonable improvements of model accuracy for all three species with incorporation of the multipliers (Table 3; Figure 3) comparing to the unmodified functions with distinct residual bias (Table 3, Figure 2). Although the chosen reference models have shown sufficient precision when applied to NFI data consisting of measurements from mainly unimproved trees (Donis et al. 2018, Donis and Šņepsts 2019), the growth patterns of the improved FRM appeared to be different and were reflected in the modified growth equation curves to some extent (Figure 3).

The height-age curves of the improved trees differed from the predicted growth trajectories of the unmodified function depending on the species studied and site index (SI) (Figure 3). Both categories – 'qualified' and 'tested' – had growth trajectories above the reference curve based solely on NFI data, hence reasonably indicating better growth of improved planting stock. The selection of 10% of the tallest families was reflected in the curve of category 'tested', which was overall above the one for 'qualified' material, hence indicating a certain persistence of estimated gains over time. However, the projected height growth for the improved FRM was slightly lower for high SIs ($H_{100} \geq 33$ m) compared to the reference model. It could be explained by overestimations of the unmodified function for extremely fertile sites due to the lack of calibration data coverage from the NFI plots, while steep measured height trajectories from the progeny trials allowed for corrections with the incorporated multipliers. On the contrary, absence of progeny trial data from poor site conditions with potentially masked genetic differences (Carson et al. 1999) might have caused overlapping of Norway spruce curves for categories 'tested' and 'qualified', the former of which in other cases showed expected better growth compared to the latter (Figure 3). Therefore, we emphasize that model limitations must be considered to avoid inaccurate projections and it should be used for estimations on rather fertile sites, typically chosen to genetically improved planting FRM (Kimberley et al. 2015). Moreover, previous modelling studies have indicated bias for long-term predictions based on calibration data from short time – series (Sharma et al. 2017). In our study, the parametrisation of the genetic multipliers was based on data limited to rather young age – up to 42 years (Table 1), when the asymptote and, accordingly, the influence of genetics on it could not be determined (Sabatia and Burkhart 2013, Deng et al. 2020). However, the introduced genetic multipliers significantly improved the model accu-

racy for the young stands (Table 3), which is important for more efficient planning of early and mid-rotation silvicultural measures, such as first commercial thinning (Manso et al. 2022). Indeed, assuming that the first thinning should be done when the dominant height has reached ca. 15 m (Hynynen et al. 2010), timing of this measure might have been planned at least 5 years earlier for silver birch in fertile sites (for instance, when H_{100} = 33 m), which showed the largest differences among the studied species in growth rate at young age compared to the reference model (Figure 3). In contrast, the distinct underestimation of height observed during validation of the unmodified model for birch indicates delayed timing of planned activities, if the reference model is used for improved trees. In addition, the approach with one function for the particular species, but the FRM category-specific set of parameters could be a user-friendly tool in practice for forest owners and managers, who usually have information about the origin of planting stock. Incorporation of the modified functions into the forest growth simulators may result in advanced predictions, yet without added complexity to the end user.

Along with more precise management planning, Gwaze et al. (2002) suggested model parameters to better indicate altered growth patterns due to genetic improvements compared to separate measurements at specific age, hence serving as an exploratory tool in tree breeding practices. However, the determined differences in growth trajectories for the improved FRM might not be related solely to genetic effects, which could have interacted with other factors, such as site quality, climatic conditions, management activities etc. (Hamilton and Rehfeldt 1994, Costa e Silva et al. 2001, Kimberley et al. 2015, Egbäck 2016), resulting in enhanced growth rate and productivity (Deng et al. 2020). For instance, rapid early growth of improved silver birch could also be related to rather fertile former agricultural land, where the improved genotypes could better manifest themselves (Kimberley et al. 2015), yet the overall management (including planting density, weeding, etc.) and site quality of the studied progeny trials reflected traditional practices used for the specific species in production forestry. Furthermore, among other tree variables, we chose to model the height of improved planning stock due to its relative independence from such attributes of stands as density (Weiskittel et al. 2011) and serving as a sufficiently reliable proxy for areal production later in the rotation (Liziniewicz et al. 2018, Liziniewicz and Berlin 2019). However, we aimed to improve the accuracy of the practically applicable model rather than distinguish a clear genetic effect on the improved FRM category – specific model parameters, which have been reported to be vastly conflicting in earlier studies with a still vague biological basis (Deng et al. 2020). Still, we observed an altered growth rate and a potentially different upper asymptote for the best fitted models (Equation 4) with the category ('qualified' or 'tested') dependent genetic multipliers in front of coefficients b_1, b_2 and b_3 (Figure 3).

Conclusions

In conclusion, the tested growth functions with the best fitted FRM category-specific multipliers more accurately reflected the actual height growth of genetically improved Scots pine, Norway spruce and silver birch comparing to the unmodified reference function calibrated solely on data from the NFI. The modelling results indicate a faster growth rate of improved material at a younger age, especially for silver birch, suggesting a potentially altered management regime for young stands. A set of multipliers for each FRM category – 'tested' or 'qualified' – may be easy applicable in practice from the perspective of forest owners and managers, who usually have necessary information about origin of planting material used in forest regeneration. The advanced models for improved trees indicate potential to schedule such management activities as thinning more promptly, without eventual delay due to underestimation of growth. However, such predictions are limited to the sites with medium and high site indices, where improved planting stock is typically used.

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Supplementary material

Supplementary 1. Tested King-Prodan dynamic GADA models with category ('qualified' or 'tested') dependent genetic multipliers g, g_1, g_2 and g_3 in front of the coefficients b_1, b_2 and b_3 in the part of the function that has been resolved from the empirical coefficients a_1, a_2 and a_3 of base equation. The part of the function preceded by the category-specific multiplier is shown in red

Model I: all equation modified:

$$H_2 = 1.3 + g \cdot \frac{A_2^{b_1}}{b_2 + 100\, b_3 \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100 b_3 + A_1^{b_1}} + \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100 b_3 + A_1^{b_1}} A_2^{b_1}} \tag{1}$$

Model II: modified theoretical (unobserved) variable X:

$$H_2 = 1.3 + \frac{A_2^{b_1}}{b_2 + 100\, b_3 \cdot g \cdot \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100 b_3 + A_1^{b_1}} + g \cdot \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100 b_3 + A_1^{b_1}} A_2^{b_1}} \tag{2}$$

Model III: modified resolved a_1:

$$H_2 = 1.3 + \frac{A_2^{g_1 \cdot b_1}}{b_2 + 100\, b_3 \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100 b_3 + A_1^{b_1}} + \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100 b_3 + A_1^{b_1}} A_2^{g_1 \cdot b_1}} \tag{3}$$

Model IV: modified resolved a_2:

$$H_2 = 1.3 + \frac{A_2^{b_1}}{g_2 \cdot \left(b_2 + 100\, b_3 \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100 b_3 + A_1^{b_1}}\right) + \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100 b_3 + A_1^{b_1}} A_2^{b_1}} \tag{4}$$

Model V: modified b_2 and b_3 in resolved a_2:

$$H_2 = 1.3 + \frac{A_2^{b_1}}{g_2 \cdot b_2 + 100 \cdot g_3 \cdot b_3 \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100 b_3 + A_1^{b_1}} + \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100 b_3 + A_1^{b_1}} A_2^{b_1}} \tag{5}$$

Model VI: modified resolved a_3:

$$H_2 = 1.3 + \frac{A_2^{b_1}}{b_2 + 100\, b_3 \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100 b_3 + A_1^{b_1}} + g_3 \cdot \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100 b_3 + A_1^{b_1}} A_2^{b_1}} \tag{6}$$

Model VII: modified resolved a_1 and a_2:

$$H_2 = 1.3 + \frac{A_2^{g_1 \cdot b_1}}{g_2 \cdot \left(b_2 + 100\, b_3 \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100 b_3 + A_1^{b_1}}\right) + \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100 b_3 + A_1^{b_1}} A_2^{g_1 \cdot b_1}} \tag{7}$$

Model VIII: modified b_1, b_2, and b_3 in resolved a1 and a_2:

$$H_2 = 1.3 + \frac{A_2^{g_1 \cdot b_1}}{g_2 \cdot b_2 + 100 \cdot g_3 \cdot b_3 \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100 b_3 + A_1^{b_1}} + \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100 b_3 + A_1^{b_1}} A_2^{g_1 \cdot b_1}} \tag{8}$$

Model IX: modified resolved a_1 and a_3:

$$H_2 = 1.3 + \frac{A_2^{g_1 \cdot b_1}}{b_2 + 100\, b_3 \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100 b_3 + A_1^{b_1}} + g_3 \cdot \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100 b_3 + A_1^{b_1}} A_2^{g_1 \cdot b_1}} \tag{9}$$

Model X: modified resolved a_2 and a_3:

$$H_2 = 1.3 + \frac{A_2^{b_1}}{g_2 \cdot \left(b_2 + 100\, b_3 \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100 b_3 + A_1^{b_1}}\right) + g_3 \cdot \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100 b_3 + A_1^{b_1}} A_2^{b_1}} \tag{10}$$

Model XI: modified b_2 and b_3 in resolved a_2 and a_3:

$$H_2 = 1.3 + \frac{A_2^{b_1}}{g_2 \cdot b_2 + 100 \cdot g_3 \cdot b_3 \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100 b_3 + A_1^{b_1}} + g_3 \cdot \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100 b_3 + A_1^{b_1}} A_2^{b_1}} \tag{11}$$

Model XII: modified resolved a_1, a_2 and a_3:

$$H_2 = 1.3 + \frac{A_2^{g_1 \cdot b_1}}{g_2 \cdot \left(b_2 + 100\, b_3 \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100 b_3 + A_1^{b_1}}\right) + g_3 \cdot \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100 b_3 + A_1^{b_1}} A_2^{g_1 \cdot b_1}} \tag{12}$$

Model XIII: modified b_1, b_2, and b_3 in resolved a_1, a_2, and a_3:

$$H_2 = 1.3 + \frac{A_2^{g_1 \cdot b_1}}{g_2 \cdot b_2 + 100 \cdot g_3 \cdot b_3 \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100 b_3 + A_1^{b_1}} + g_4 \cdot \frac{\frac{A_1^{b_1}}{H_1 - 1.3} - b_2}{100 b_3 + A_1^{b_1}} A_2^{g_1 \cdot b_1}} \tag{13}$$

Supplementary 2. Fit statistics for tested King-Prodan dynamic GADA models with category ('qualified' or 'tested') dependent genetic multipliers (standard errors in brackets) in front of the coefficients b_1, b_2 and b_3 (model numbering as in Supplementary 1)

Genetic multiplier	Category	Model												
		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII
							Scots pine							
g	tested	1.030	0.997											
		(0.004)	(0.000)											
	qualified	1.029	0.997											
		(0.002)	(0.000)											
g_1	tested			1.011				1.019	1.011	1.018		0.828	1.019	0.241
				(0.001)				(0.015)	(0.014)	(0.005)		(0.029)	(0.032)	(0.126)
	qualified			1.011				0.970	0.964	1.035		0.781	0.970	0.476
				(0.001)				(0.006)	(0.006)	(0.002)		(0.012)	(0.013)	(0.041)
g_2	tested				0.957	0.823		1.030	0.860		0.953	0.839	1.030	0.041
					–0.005	(0.029)		(0.058)	(0.059)		(0.014)	(0.027)	(0.099)	(0.020)
	qualified				0.959	0.786		0.855	0.682		0.907	0.792	0.855	0.104
					–0.002	(0.012)		(0.019)	(0.018)		(0.006)	(0.011)	(0.032)	(0.016)
g_3	tested					0.833	0.913		0.870	1.057	1.010	0.952	1.000	0.053
						(0.027)	(0.011)		(0.058)	(0.040)	(0.032)	(0.034)	(0.068)	(0.018)
	qualified					0.799	0.923		0.693	1.211	1.132	1.070	1.000	0.116
						(0.011)	(0.005)		(0.018)	(0.017)	(0.014)	(0.015)	(0.033)	(0.017)
g_4	tested													–6.732
														(5.315)
	qualified													–1.777
														(0.463)
N		4308	4308	4308	4308	4308	4308	4308	4308	4308	4308	4308	4308	4308
AIC		14716.1	14789.8	14695.7	14674.2	14437.8	14834.5	14649.3	14399.5	14560.6	14591.6	14417.7	14653.3	14751.4
							Norway spruce							
g	tested	0.898	1.005											
		(0.003)	(0.000)											
	qualified	0.916	1.005											
		(0.001)	(0.000)											
g_1	tested			0.955				0.907	0.888	0.955		0.622	1.000	1.310
				(0.001)				(0.005)	(0.004)	(0.004)		(0.019)	(0.012)	(0.020)
	qualified			0.964				0.927	0.909	0.964		0.63	1.000	1.301
				(0.001)				(0.002)	(0.002)	(0.001)		(0.007)	(0.004)	(0.007)
g_2	tested				1.134	0.605		0.861	0.413		0.948	0.634	1.134	1.808
					(0.004)	(0.023)		(0.012)	(0.016)		(0.006)	(0.018)	(0.0270	(0.124)
	qualified				1.103	0.595		0.891	0.449		0.933	0.643	1.103	1.727
					(0.002)	(0.008)		(0.005)	(0.006)		(0.002)	(0.007)	(0.010)	(0.041)
g_3	tested					0.625	1.544		0.429	1.000	1.687	1.687	1.000	1.803
						(0.022)	(0.013)		(0.015)	(0.040)	(0.022)	(0.020)	(0.057)	(0.122)
	qualified					0.616	1.514		0.466	1.000	1.721	1.712	1.000	1.722
						(0.008)	(0.006)		(0.006)	(0.017)	(0.010)	(0.010)	(0.022)	(0.040)
g_4	tested													2.644
														(0.045)
	qualified													2.787
														(0.019)
N		19219	19219	19219	19219	19219	19219	19219	19219	19219	19219	19219	19219	19219
AIC		44285.8	44123.4	44287.1	45574.7	41754.3	40261.1	43758.9	41937.5	44291.1	39460	42984.3	45582.7	42473.1
							Silver birch							
g	tested	1.094	0.996											
		(0.002)	(0.000)											
	qualified	1.098	0.996											
		(0.001)	(0.000)											
g_1	tested			1.045				1.032	0.856	1.045		0.462	1.000	1.438
				(0.001)				(0.011)	(0.011)	(0.003)		(0.011)	(0.028)	(0.087)
	qualified			1.045				1.032	0.814	1.045		0.565	1.000	1.150
				(0.000)				(0.004)	(0.004)	(0.001)		(0.004)	(0.009)	(0.025)
g_2	tested				0.840	0.380		0.946	0.275		0.840	0.469	0.837	2.335
					(0.003)	(0.009)		(0.039)	(0.009)		(0.007)	(0.010)	(0.071)	(0.743)
	qualified				0.842	0.466		0.946	0.285		0.842	0.569	0.838	0.987
					(0.001)	(0.003)		(0.014)	(0.003)		(0.002)	(0.003)	(0.024)	(0.091)
g_3	tested					0.396	0.842		0.282	1.000	1.000	1.250	1.000	2.331
						(0.008)	(0.005)		(0.009)	(0.014)	(0.011)	(0.020)	(0.028)	(0.735)
	qualified					0.480	0.830		0.290	1.000	1.000	1.361	1.000	0.986
						(0.003)	(0.002)		(0.003)	(0.005)	(0.004)	(0.008)	(0.010)	(0.090)
g_4	tested													1.685
														(0.058)
	qualified													1.557
														(0.029)
N		24535	24535	24535	24535	24535	24535	24535	24535	24535	24535	24535	24535	24535
AIC		96556	98660.5	93642.9	91172.3	80446	103129.6	92890.8	78007.2	93646.9	91176.3	81938.3	91234.2	81882.9

Note: N – number of observations, *AIC* – Akaike information criterion.