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Stand characteristic models for genetically improved and unimproved silver birch plantations in southern and central Finland

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ABSTRACT

The genetic gain from improved seedlings in silver birch (*Betula pendula*) plantations in Finland is receiving increasing attention, yet quantitative knowledge of their growth characteristics remains limited. This study developed stand characteristic models for silver birch plantations to predict growth differences between genetically improved and unimproved stands. Response variables were basal area-weighted mean height (HW, m), mean diameter (DW, cm), and stand basal area (G, m² ha⁻¹). Data comprised 2,183 plot observations from thinning, spacing, and breeding trials, and commercial forests across Finland (1,954 unimproved, 229 improved). Modelling employed a multivariate mixed-effects approach using seemingly unrelated regression with a random site intercept. Predictor variables included site index, stand age, number of trees, a dummy for former agricultural land, and thinning-related variables. The genetic improvement dummy variable was statistically significant in the DW and G models ($p < 0.0001$), reflecting superior stand yield. HW values in improved stands were higher than in unimproved stands, based on greater dominant height and site index for the improved stands as indicated by simulation results. Model fit statistics and simulations demonstrated logical predictive behaviour and reliability. The models can be used in forest decision-support systems for managing silver birch plantations, particularly those established with genetically improved material.

ARTICLE HISTORY

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KEYWORDS

Betula pendula Roth; genetic effect; multivariate linear mixed-effects models; seemingly unrelated regression; site index; thinning

HIGHLIGHTS

- Models for mean height, diameter, and stand basal area were developed for birch.
- Model performance differed between improved and unimproved birch stands.
- Improved stands showed superior stand characteristics and a higher site index.
- A genetic dummy variable explained superior mean diameter and stand basal area.
- Thinning simulations showed logical behaviour and reliability for practical use.

Introduction

Silver birch (*Betula pendula* Roth.) is a fast-growing, light-demanding pioneer broadleaf tree species that plays a key economic, ecological, and environmental role, particularly in northern Europe (Hynynen et al. 2010).

Increasing demand for birch pulpwood, plywood, and high-quality logs has made genetic improvement of forest reproductive material (FRM) an important tool for achieving sustainable and productive forest management (Jansson et al. 2017; Gömöry et al. 2021). In Finland, the planting of silver birch expanded from 5.4 to 12.5 million container-grown seedlings between 2020 and 2024, resulting in 2.3–5.5 thousand hectares of reforestation (Natural Resources Institute Finland 2025; Finnish Food Authority 2025a). The plant material was exclusively (97–100%) raised from genetically improved seed produced in greenhouse seed orchards (Natural Resources Institute Finland 2025). Consequently, there is growing demand for models that simulate the development of these improved silver birch plantations to support decision-makers and stakeholders.

Accurate growth and yield predictions of FRM are essential for quantifying the potential financial returns at final harvest from tree breeding programmes,

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comparing breeding strategies, assigning economic weights to selection criteria (Chang et al. 2019), and enhancing forest management profitability (Deng et al. 2020). Silver birch breeding has been conducted in Finland for several decades (Jansson et al. 2017; Haapanen 2024). Genetic gains from breeding are delivered to forestry through seed orchards, comprising grafts of selected plus trees planted in greenhouses. Currently, all silver birch plant material produced in nurseries originate from seed orchard seed (Finnish Food Authority 2025b).

Studies on the growth potential of genetically improved silver birch trees are few but increasing (Liziewicz et al. 2022; Zeltiņš et al. 2022, 2024; Haapanen 2024). Haapanen (2024) reported genetic gains for various economically important traits such as stem volume (from 1% to 31%) and the frequency of forks and ramicorn branches (on average, 16% and 7% reduction, respectively) from past Finnish silver birch seed orchards. A tendency of increasing genetic gains over time due to breeding progress was observed. All the studies on realised genetic gains and their economic value (Ahtikoski 2000; Jansons et al. 2011; Gailis et al. 2020) rely on early rotation performance of improved materials. Forest management revenue depends on harvest volumes over the entire rotation, necessitating a modelling approach to better understand performance throughout this period (Deng et al. 2020).

Genetic gain is traditionally incorporated into growth and yield models using one of three approaches: calculating specific genetic gain multipliers, adjusting the site index, or calibrating model parameters (Weiskittel et al. 2011; Burkhart and Tomé 2012; Deng et al. 2020). Theoretically, calibrating model parameters with empirical data from long-term trials provides broader adaptability and higher accuracy in stand models when sufficient data exist (Deng et al. 2020), while the other two methods are also widely used (Buford and Burkhart 1987; Knowe and Foster 1989; Sprinz et al. 1989; Gwaze et al. 2002; Xie and Yanchuk 2003; Sabatia and Burkhart 2013). Stand-level models incorporating calibration have demonstrated adequate accuracy and precision, particularly for managing plantation stands (Carson et al. 1999; Adams et al. 2006).

Stand models require relatively little information to simulate growth but generally provide insights into future stand conditions based on variables such as stand age, site index, and stand density for even-aged stands (Weiskittel et al. 2011; Burkhart and Tomé 2012). These models, focusing on key characteristics, are developed from commonly used independent

variables, making them accessible, easily applicable, and widely utilised (MacKinney and Chaiken 1939; Schumacher 1939; Bennett 1970; Knoebel et al. 1986; Fowler and Ffolliott 1994; Huuskonen and Miina 2007; Lauer and Kush 2011; Allen et al. 2020; Lee et al. 2023). Lee et al. (2024) developed models for silver birch plantations to predict mean diameter, mean height, and stand basal area, incorporating variables such as the number of trees, stand age, site index, thinning factors, and a dummy variable for former agricultural land. Nevertheless, this approach currently targets only unimproved silver birch plantations. These models can subsequently be integrated with diameter distribution models and individual tree height models (Lee et al. 2021).

Consequently, forest managers and researchers in Finland and Northern Europe still require reliable growth trajectories, practical reference guidelines, and decision-support tools for managing silver birch plantations under modern breeding and silvicultural practices. While previous growth and yield studies on silver birch in Finland focused exclusively on unimproved plantations (e.g. Lee et al. 2024), this study represents the first effort to develop comprehensive stand characteristic models that incorporate data from genetically improved stands. This research extends the foundation established by Lee et al. (2024) in several key respects. While Lee et al. (2024) provided baseline models restricted to unimproved plantations, the primary advancement of the present work lies in expanding the operational scope and coverage to genetically improved stands established with modern seed-orchard material.

Methodologically, this study advances stand yield modelling by integrating improved and unimproved stand data into a unified multivariate linear mixed-effects framework using seemingly unrelated regression. This approach simultaneously models basal area-weighted mean height, basal area-weighted mean diameter, and stand basal area, effectively capturing cross-equation error correlations and stand-level structural dependencies. Conceptually, this framework allows for the evaluation of how genetic gain manifests across multiple stand attributes within a single system.

The objective of this study is to develop multivariate stand characteristic models for genetically improved and unimproved silver birch plantations in southern and central Finland. Furthermore, the newly developed models were compared with those previously developed for unimproved silver birch plantations in Finland (Lee et al. 2024) to test their validity by examining observed data ranges

and applying the models across varying ranges of key predictor variables. Additionally, practical recommendations were provided for updating silvicultural guidelines.

Materials and methods

Data

The modelling data included genetically improved and unimproved silver birch trees on mineral soil sites from 124 forest stands in southern and central Finland. Lee et al. (2024) previously used the dataset of the unimproved stands and a subset of the improved stand data, providing a more comprehensive description of these data (Figure 1). Although our study originally focused on developing models for genetically improved stands, unimproved stands were also incorporated into the modelling dataset. This was necessary due to the limited measurements available for genetically improved material, which comprise short time spans, young ages, and single-time measurements. These constraints can result in model extrapolation over extended periods. The data from unimproved stands covering a broader temporal range, from early stages to final harvest, were included to enhance model robustness. The sites were classified as former agricultural land, OMT (i.e. relatively fertile, herb-rich heath sites, *Oxalis-Myrtillus* type), or MT (i.e. medium fertile, mesic heath sites, *Myrtillus* type) according to the Finnish forest site classification system (Cajander 1949; Tonteri et al. 1990).

Unimproved stands

The data for unimproved stands comprises two types of experiments: thinning and spacing experiments, mostly established between 1980 and 1990, and unimproved stands planted as control plots in tree breeding trials. Most data on unimproved stands originate from long-term thinning and spacing experiments. The initial measurements were taken when the biological stand age ranged from 11 to 32 years, followed by repeated remeasurements until the age of 39–53 years. Some plots exceeded the common final felling age, with the last measurements taken at 69 years. Plots containing naturally regenerated Norway spruce (*Picea abies* (L.) Karst.) in the understorey were retained in the dataset, as they represent the typical silver birch stands found in Finland.

Most thinning and spacing experiments were measured at five-year intervals. Except for the unthinned plots, the number and intensity of thinnings varied, with a maximum of one to four thinnings applied, including late heavy thinnings. The thinnings were carried out

using the thinning-from-below method, where suppressed and intermediate trees were removed, in addition to damaged trees. Tree diameter at breast height (DBH) was measured from all trees, as well as trees species and any tree damage were determined. Tree heights were measured on a sample of approximately 40 trees on each plot prior to the implementation of thinning treatments. The probability of sample trees being selected was proportional to its basal area at breast height; however, the sample trees were randomly located on the sample plots. The same sample trees were subjected to all subsequent measurements, and no additional sample trees were incorporated into the study following the thinning treatments (Niemistö and Huuskonen 2025). Further details on treatments and measurements are provided in Lee et al. (2024) and Niemistö and Huuskonen (2025).

Some of the unimproved stand data were also obtained from the control plots of the tree breeding trials. These sites were located on forest sites classified as OMT and MT, as well as on former agricultural lands. The following subsection provides detailed descriptions of the tree breeding trials, describing the plots of genetically improved trees (Table 1). Unlike the genetically improved stands in commercial forests, records of site preparation were either absent or indicated that no soil preparation had been carried out.

Genetically improved stands

A source of data representing 17 breeding trials was used to model the growth of genetically improved stands (Table 1; Supplementary Material, Section S1, Table S1). The breeding trials comprise progeny trials used in the tree breeding programme to determine the genetic values of plus trees based on the realised field performance of their offspring and planted stands aimed at demonstrating genetic gains achieved through breeding. Both types of trials include seedlots from natural stands as unimproved controls. All the progeny trials were established using a randomised complete block design, with the number of blocks varying from four to eight. Since some of the plot sizes in progeny trials are smaller than those in thinning and spacing experiments, data from all the plots smaller than 250 m² were pooled. Diameter at breast height (DBH), height, and mortality were measured for all trees. Most progeny trials had been thinned once or twice from below before measurement. Additional detailed information can be found in Lee et al. (2024).

Another source of data for genetically improved stands came from 66 commercial planted stands (Table 1) located in southern and central Finland covering at least 0.5 hectares each. The biological stand age

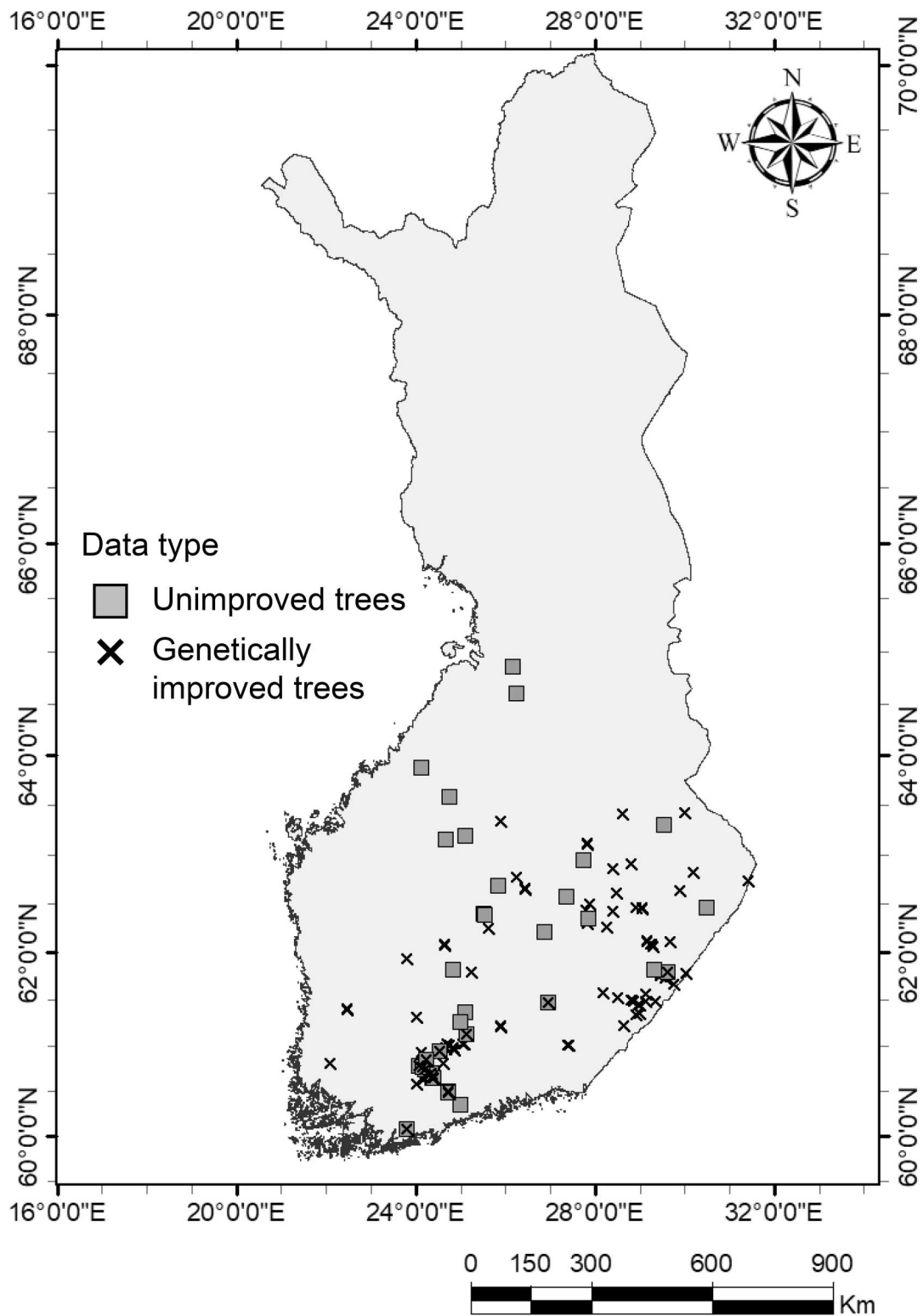


Figure 1. Locations of the silver birch experimental sites used for modelling of stand characteristics of unimproved (G0) and genetically improved (G1) trees.

ranged from 5 to 27.4 years, with decimal ages calculated based on measurements taken during the growing season. Depending on stand size, one to three circular plots of 300 m² (radius 9.77 m) were

randomly located and measured within each stand. The stands were established with materials from silver birch seed orchards established in the 2010s, thus representing the recent level of breeding progress (Finnish

Table 1. Characteristics and management of the silver birch plots in Southern and Central Finland.

Variable	Unimproved trees Thinning & spacing experiments and Progeny trials	Genetically improved trees	
		Breeding trials	Commercial stands
<i>Dataset structure</i>			
Number of forest stands	41	17	66
Number of experimental plots	271	70	140
Number of measurements by stand	1–9	1–3	1
Observation period by plot in year	25.0 ± 10.2 (0–42)	1.8 ± 4.4 (0–18)	–
Interval between measurements in year	5 ± 0.6 (4–11)	1.5 ± 2.2 (0–5)	–
Total number of plot-level observations	1954	89	140
<i>Management</i>			
Density ^a at the first measurement (trees ha ^{−1})	485–4467	818–2477	300–2200
Year of plot establishment	1977–2005	1987–2005	2024
Seed information	unimproved	improved	improved
Plot size (m ²)	490–4600	300–3310	300
Number of thinnings	0–4	0–2	0
Thinning intensity ^b (%)	36.4 ± 12.9 (1.8–66.3)	47.7 ± 18.4 (23.7–75.1)	–
Time after last thinning (year)	8.3 ± 7.7 (0–39)	8.8 ± 3.5 (0–12)	–
<i>Site characteristics</i>			
Latitude	N 60°5′–64°51′	N 60°5′–61°48′	N 60°35′– 63°26′
Longitude	E 23°47′–30°29′	E 23°47′–29°37′	E 22°4′–31°24′
Elevation above sea level (m)	40–204	40–150	50–198
Temperature sum above +5 °C (°C·days)	1070–1460	1287–1409	1091–1394
Site type ^c with no. of stands	Former agricultural land (Field) 26 Forest site (OMT) 4 Forest site (MT) 11	Former agricultural land (Field) 10 Forest site (OMT) 1 Forest site (MT) 6	Forest site (OMT) 32 Forest site (MT) 34
Site index ^d (SI, m)	27.0 ± 3.2 (18.6–33.0)	31.2 ± 3.1 (23.0–35.0)	30.6 ± 4.0 (23.0–35.0)

Note: Numeric values indicate either Mean ± SD (Min–Max) or Min–Max.

^aThe density is not always defined as initial planting density.

^bThinning intensity based on stand basal area.

^cOMT is *Oxalis-Myrtillus* (a herb-rich heath forest) site type and MT is *Myrtillus* (a mesic heath forest) site type (Cajander 1949).

^dSite index (m) with a base age of 50 years, with a maximum value of 33 m for unimproved stands and 35 m for genetically improved stands.

Food Authority 2025b). Although three types of seedling origins were present in the stands (planted, seed, and sprout), this study focused solely on planted trees from improved seedlings. Planted silver birches were distinguished by their faster growth compared to natural seed-origin silver birches and were located on mounds prepared for planting. Sprouts originated from stumps created in earlier stand management.

Diameter at breast height (DBH) was measured for every tree, while height was measured for every fifth tree within each plot. Missing tree height values were estimated at plot level using Näslund's height–diameter model (Näslund 1936) based on the sampled trees. Tree damage type, symptoms, and severity were recorded (Bianchi et al. 2026). At the plot level, if the proportion of damaged trees exceeded 0.75, the entire plot was excluded from analysis to prevent severe bias; consequently, seven observations were removed in advance from a total of 147 observations. The stands were established using standard soil preparation techniques, such as spot mounding. Precommercial thinning was applied in some stands (27 out of 140 observations); however, due to the limited sample size and lack of statistical significance in preliminary analysis, this variable was excluded from the modelling.

Stand characteristics and additional variables for modelling

The stand characteristics in this study were similar to those reported by Lee et al. (2024). A few stands, particularly those with unimproved trees, contained small, naturally regenerated Norway spruce trees in the understorey. These spruce trees were excluded from the stand characteristic calculations as they contributed minimally to stand basal area. The main stand variables were the number of trees (N, trees ha⁻¹), basal area-weighted mean height (HW, m), basal area-weighted mean diameter (DW, cm), stand basal area (G, m² ha⁻¹), dominant height (H00), and site index (SI) (Table 2). The biological stand age (AGE) is used in this study, defined as the time elapsed since seed germination, not plantation age or breast height age.

The H00 variable was defined as the mean height of the 100 thickest trees per hectare. The number of trees for H00 were selected proportionally based on plot size, and their mean height was calculated. The measured site index (SI) was directly calculated using Equation (1) based on the observed biological stand age and dominant height by applying the previously developed SI model for silver birch stands. However, when the SI is calculated for very young stands (e.g.

Table 2. Descriptive statistics of stand characteristics of the modelling dataset for silver birch plantations in southern and central Finland, based on the first and last measurements.

Stand characteristics	Unimproved trees		Genetically improved trees		
	Thinning & spacing experiments and progeny trials (n = 271)		Breeding trials (n = 70)		Commercial stands (n = 140)
	First	Last	First	Last	One-time measurement
<i>Time of measurements</i>					
Biological stand age (AGE, years)	20 ± 5 (11–32)	45 ± 11 (13–69)	18 ± 4 (11–24)	20 ± 5 (13–35)	14 ± 7 (5–27)
Stand density of silver birch (N, trees ha ⁻¹)	1745.3 ± 623.1 (485–4467)	755.1 ± 477.9 (171–3090)	1571.1 ± 529.7 (818–2477)	1547.6 ± 564.9 (439–2477)	1202 ± 387.5 (300–2200)
Dominant height (H00, m)	13.3 ± 3.4 (5.3–21.4)	25.3 ± 4.6 (10.9–33.0)	15.1 ± 3.8 (8.2–21.5)	16.2 ± 3.6 (9.9–25.1)	11.6 ± 5.5 (2.6–22.2)
Height, basal area-weighted mean (HW, m)	12.1 ± 3.3 (4.7–19.1)	24.0 ± 4.6 (9.1–32.0)	14.1 ± 3.8 (7.2–19.8)	15.1 ± 3.7 (9.1–24.3)	10.2 ± 4.8 (2.8–20.7)
Diameter, basal area-weighted mean (DW, cm)	10.8 ± 2.6 (4.6–15.8)	21.2 ± 4.6 (6.9–31.8)	11.9 ± 3.0 (6.4–17.8)	12.9 ± 3.3 (8.6–23.3)	8.6 ± 4.5 (1.4–18.9)
Stand basal area (G, m ² ha ⁻¹)	13.3 ± 5.0 (2.0–24.7)	20.5 ± 6.7 (6.2–39.9)	15.0 ± 6.2 (5.5–29.8)	16.6 ± 5.1 (9.6–29.8)	7.1 ± 5.7 (0.1–20.4)
Cumulative mortality at last measurement ^a (trees ha ⁻¹)	–	596.4 ± 556.6 (38–2536)	–	–	–

Notes: numeric values represent Mean ± SD (Min–Max).

n represents the number of plot-level observations from the first, last, or a single one-time measurement.

^aCumulative mortality was calculated as the difference in the number of remaining silver birch trees between the first and last measurements, provided the measurement period was over 20 years. This calculation was only performed on the unthinned plots.

less than 15 years old), the estimates can be unstable and prone to overestimation (Burkhart et al. 2018). To address this, the SI was capped at 35 m for genetically improved stands and 33 m for unimproved stands (Table 1). For plots with multiple observations from consecutive measurements, the SI values were averaged, and the mean was assigned as the plot's SI.

$$SI = H00 \times \left(\frac{1 - e^{-bAGE_0}}{1 - e^{-bAGE}} \right)^c \quad (1)$$

where H00 is the dominant height (m), defined as the average height of the 100 thickest trees per hectare. According to Lee et al. (2024), the model parameters b and c correspond to the values 0.0320 and 1.2239, respectively. AGE represents the biological stand age (years) and AGE₀ is the reference (base) age of 50 years.

Thinning effects were described using the *THIN* and *Talty* variables. *THIN* represents thinning intensity, calculated as the proportion of the stand basal area removed in each thinning, scaled from 0 to 1. *Talty* is defined as the number of years since the last thinning. *Talty*_{max25} was used, assigning values of 25 or less to *Talty* as their actual value, while greater values were fixed to 25. The *GDD5* variable is the long-term average of the annual effective temperature sum (degree-days above a threshold of +5 °C) for the period 1981–2010.

Modelling approach and statistical analysis

Models for basal area-weighted mean height (HW), basal area-weighted mean diameter (DW), and stand basal

area (G) were developed with data comprising a total of 2,183 plot-level observations from both genetically improved (229 observations) and unimproved (1,954 observations) experimental plots. During the modelling process, relationships among the response variables HW, DW, and G were considered using a multivariate modelling approach (Sullivan and Clutter 1972). Seemingly Unrelated Regression (SUR) was applied due to its efficiency in estimating and accounting for correlations between the models (Furnival and Wilson 1971; Borders and Bailey 1986). Furthermore, given the hierarchical nature of the data (i.e. the plots nested within the sites) and the repeated measurements, a multivariate mixed-effects model, or the SUR approach with random effects, was applied (Hall and Clutter 2004).

The data were restructured into a longitudinal format by replicating the independent variables for each dependent variable in the SUR approach of R statistical software (R Core Team 2019) (Supplementary Material, Section S5). A multiplicative model structure was assumed for each dependent variable (Equation 2), so HW, DW, and G were transformed to a logarithmic scale to linearise the model (Equation 3) (Siipilehto 2006). The logarithmic transformation addresses heteroscedasticity by homogenising the residual variance. Various data subsets were tested both separately and in aggregation, and the fit of the models and the parameter estimates examined. A dummy variable was used to represent genetically improved stands (*GeneticF*). Growing degree-days above 5°C (*GDD5*) and site types were also included in the model testing. Random effects and residual errors were assumed to have a

zero mean and multivariate normal distributions with parameterised site-level variance-covariance matrix D and residual covariance matrix R_i , as well as being correlated across the model equations (Supplementary Material, Section S4.1–S4.2). The Seemingly Unrelated Regression (SUR) system was estimated within a multivariate linear mixed-effects model framework using the `lme` function of the `nlme` package in R (R Core Team 2019; Pinheiro et al. 2023), rather than traditional OLS-based SUR packages (e.g. `systemfit`), to simultaneously account for cross-equation residual correlations and random site-level effects (Vonesh and Chinchilli 1997) (Supplementary Material, Sections S4.1–S4.2 and S5).

$$Y = e^{b_0} X_1^{b_1} \dots X_k^{b_k} e^{b_{k+1} X_{k+1} + \dots + b_n X_n + u_{\text{site}}} \varepsilon \quad (2)$$

$$\ln(Y) = b_0 + b_1 \ln(X_1) + \dots + b_k \ln(X_k) + b_{k+1} X_{k+1} + \dots + b_n X_n + u_{\text{site}} + \ln(\varepsilon) \quad (3)$$

where Y is the response variable (HW, DW, or G), e is Euler's number (≈ 2.71828), $\ln$ is the natural logarithm, $b_0 \dots b_n$ are model parameters, $X_1 \dots X_n$ are the predictor variables/terms, u_{site} is the site-level random effect for each respective equation (which are correlated across equations via matrix D , with standard deviations reported as $\text{std}(u_{\text{site}})$ in Table 3; see Supplementary Material, Section S4.1–S4.2), and $\ln(\varepsilon)$ is the residual error term. Specifically, $X_1 \dots X_k$ represent continuous predictors entering the model as power terms (log-log linearised as $\ln(X_i)$, e.g. $\ln(\text{SI})$, $\ln(\text{N})$), whereas $X_{k+1} \dots X_n$ represent non-logged predictors or functional transformations entering as exponential terms (log-linearised as linear, inverse, or binary dummy predictors, e.g. inverse age $1/(\text{AGE} + 1)$, $1/(\text{AGE} + 10)$, thinning variable terms, and binary indicator variables *Agric* and *GeneticF*). The specific predictor terms and parameter estimates for each model equation are presented in Table 3.

In the modelling stage, transformed variables (e.g. reciprocal, squared, square root, and natural logarithmic transformations of stand age, site index, and stand density) were tested to identify the most statistically significant and biologically logical predictors. In addition, a constant k varying from 0 to 20 was tested in the reciprocal form of AGE, $1/(\text{AGE} + k)$, to solve the curvilinearity and figure out most suitable predictor variables.

Simulation and model validity

All models developed in this study were examined and validated for statistical significance and goodness-of-fit using metrics such as AIC, BIC, and $-2 \log$ -likelihood. To evaluate model assumptions and verify unbiased

predictions in both transformed and original units, residuals (observed minus predicted values) were plotted against predicted and key predictor variables on both the logarithmic scale and the back-transformed arithmetic scale. Evaluating log-scale residuals verified model assumptions (homoscedasticity and residual normality), whereas arithmetic-scale residuals confirmed that no prediction bias was introduced during back-transformation.

To present 95% confidence intervals for the categories of the independent variables on the x-axis, residual plots with vertical lines were provided in the supplementary figures using the `whiskers()` function of the `lmfor` package (Mehtätalo and Kansanen 2022) (Supplementary Material, Section S2.1, Figures S1–S6). Overall accuracy was reported in terms of root mean square error (RMSE), mean absolute error (MAE), and mean absolute percentage error (MAPE) on both the logarithmic scale and the back-transformed arithmetic scale. Log-scale metrics provided scale-independent evaluations of model fit in the estimation space, whereas arithmetic-scale metrics reflected practical prediction accuracy in operational units. These error metrics were calculated for mixed-effects and fixed-effects predictions, as well as for the unimproved, improved, and entire datasets. RMSE% was expressed as a percentage by dividing RMSE by the observed mean of the stand characteristic in each model.

Predictions of HW, DW and G over stand age were used to illustrate the overall behaviour of the models on scatterplots of observations presented on a back-transformed arithmetic scale. During the back-transformation from the logarithmic scale, Baskerville's (1972) logarithmic bias correction factor – adding half of the residual variance ($s^2/2$) to the log-scale predictions prior to exponentiation – was applied to correct for inherent logarithmic underestimation (Baskerville 1972; Burkhart and Tomé 2012) (Supplementary Material, Section S3.4, Equations S12–S14). For practical applications, step-by-step local calibration procedures – demonstrating how field foresters can update out-of-sample stand predictions using empirical best linear unbiased prediction (EBLUP) under single or multiple local field measurements – are explicitly detailed in the Supplementary Material (Section S4.3).

Stand characteristics were predicted within the range of the modelling data to demonstrate model sensitivity. The dependent values were also predicted across discrete categories of key input variables in each panel (e.g. site index, SI, and stand density, N). Model simulations (Figures 4–6) were evaluated across continuous age trajectories and factorial grids of SI and N to represent expected stand development across the full operational spectrum of silver birch plantations, capturing

Table 3. Parameter estimates (Equation 3) and fit statistics of seemingly unrelated regression (SUR) models for basal area-weighted mean height (HW, m), basal area-weighted mean diameter (DW, cm), and stand basal area (G, m² ha⁻¹) in silver birch plantations.

		ln(HW) Estimate	S.E.	ln(DW) Estimate	S.E.	ln(G) Estimate	S.E.
Fixed effects	Intercept	0.6612	0.0794	2.1714	0.0917	-4.9889	0.1958
	ln(SI)	1.0943	0.0229	0.7788	0.0261	1.6091	0.0557
	1/(AGE+1)			-16.1182	0.1283	-32.8431	0.2723
	1/(AGE+10)	-44.2098	0.2064				
	ln(N)	-0.0333	0.0024	-0.2238	0.0027	0.4911	0.0057
	$THIN \times (\sqrt{Talty_{max25}} - 3.5)$			0.0757	0.0021	0.1370	0.0042
	<i>Agric</i>			0.1048	0.0314	0.2563	0.0666
	<i>GeneticF</i>			0.0411	0.0093	0.1009	0.0191
Random effects	std(<i>u</i> _{site})	0.0675		0.1654		0.3521	
	corr with DW	0.587					
	corr with G	0.590		0.992			
Residual	std(ϵ)	0.0516		0.0540		0.1161	
	corr with DW	0.574					
	corr with G	0.642		0.938			
Fit statistics	AIC	-21340.62					
	BIC	-21137.01					
	-2logLik	-21400.62					

Note: The total number of plot-level observations was 2,183, and the number of observations used in the SUR model fitting was 6,549, calculated by multiplying 2,183 by 3 for the dependent variables HW, DW, and G (Supplementary Material, Section S5). All fixed-effect parameters were highly significant ($P < 0.0001$) except for *Agric* ($P = 0.0009$ in DW model and $P = 0.0001$ in G model). The site-level random effects (*u*_{site}) across HW, DW, and G are fitted simultaneously within a Seemingly Unrelated Regression (SUR) framework and are correlated across equations; the reported correlation coefficients (corr) and standard deviations (std(*u*_{site})) define the off-diagonal covariances $Cov(u_i, u_j) = corr_{ij} \cdot \sigma_{u_{ij}} \cdot \sigma_{u_{ij}}$ of the 3×3 random-effects variance-covariance matrix *D* (Supplementary Material, Section S4.2). Residual errors standard deviation is denoted by std(ϵ), which are also correlated across equations. ln() is the natural logarithm. SI is the site index (m) at a base age of 50 years. *N* is the number of silver birch trees per hectare (trees ha⁻¹). AGE is the biological stand age (years). *Agric* is a dummy variable set to 1 if the site type is former agricultural land and to 0 if it is forest land. *THIN* is the proportion of thinning intensity based on stand basal area, scaled from 0 to 1. *Talty* is the time since the last thinning in years. *Talty*_{max25} is the time after the last thinning, with a maximum value of 25 years (equal to *Talty* if *Talty* < 25, or fixed to 25 if *Talty* ≥ 25). *GeneticF* is a dummy variable coded as 1 for genetically improved stands and 0 for unimproved stands. corr refers to correlation. std(ϵ) is the standard deviation of the residuals. AIC is the Akaike Information Criterion. BIC is the Bayesian Information Criterion. -2logLik is the value of -2 times the log-likelihood.

the full variation from lower-bound to upper-bound attainable yields. Within each panel, the predicted values of DW, HW, and G were calculated over stand age, distinguishing between unimproved and improved stands. To facilitate comparison with a previous study, predictions according to Lee et al. (2024) were also presented.

For the simulation of the developed stand models (e.g. Results, Section 3.3), the simulated site index (SI) was required for each genetic class, which in turn required the simulated dominant height (H00) as an input variable (Equation 1). The H00 values were first predicted using Equation (4) by applying a dummy variable for genetic effect, set to 1 for genetically improved materials and 0 for unimproved materials. From these predictions using Equation (4), the difference in H00 between the two genetic classes was 1.95 m at the base age of 50 years (Supplementary Material, Section S3.1, Figure S9). This site index difference was then applied in the simulations of stand characteristic models to illustrate the effect of genetic improvement, by adding 1.95 m from the site index of unimproved stands to that of genetically improved stands. Although the actual SI gap may vary depending on the genetic effect and site conditions, this difference was used for demonstration purposes. Note that, in this study, a

new H00 model was also tested using an extended dataset that included additional data from genetically improved commercial stands. However, the estimated parameters and model performance showed only negligible differences compared to those of Lee et al. (2024). Consequently, the original model was adopted, as shown in Equation (4), while the estimated parameters and fit statistics of the newly tested model are presented in the Supplementary Material, Section S2.3.

$$H00 = (a_0 + a_1 \times GeneticF)(1 - e^{-b \times AGE})^c \quad (4)$$

where H00 is the dominant height (m), defined as the average height of the 100 thickest trees per hectare. According to Lee et al. (2024), the model parameters a_0 , a_1 , b , and c correspond to the values 36.9164, 2.4096, 0.0320, and 1.2239, respectively. AGE represents the biological stand age (years), and *GeneticF* is the dummy variable for the genetic effect (1 for a genetically improved stand, 0 otherwise).

Finally, to evaluate the effect of thinning on the response variables, plots of unimproved stands were selected from long-term experiments according to the number of thinnings, one, two, or three. The models were compared with the observed data by using the measured values of the dependent variables as an

input to them. Additionally, the performance of the models was demonstrated for improved stands by applying the dummy variable of *GeneticF*. Supplementedly, when the site index model (Equation 1) cannot be applied due to unavailable dominant height – for example, in stands too young for dominant height estimation or newly established on bare land – but site index is still required for simulation, a supplementary site index equation was developed based on climatic and edaphic variables (degree days, site type) and genetic class (seed type) (Supplementary Material, Section S3.3, Table S3, and Figure S11).

Results

Model development applying genetic effect

The developed models demonstrated a statistically significant fit (Table 3). Most of the parameter estimates (AGE, SI, N, THIN with $Talty_{max25}$, and *GeneticF*) were highly significant ($P < 0.0001$), including the intercepts of the HW, DW, and G models, except for *Agric* in the DW and G models ($P = 0.0009$ and 0.0001 , respectively). The AGE variable in reciprocal form – with constants of 1 for DW and G models, and 10 for HW – showed the most logical development and solved curvilinearity. Consequently, predicted curves for DW, HW, and G exhibited more biologically reasonable and stable development (Figures 2 and 3), even compared between HW and H00 (Supplementary Material, Section S2.2 and Figure S7).

The *GeneticF* variable was highly significant in the DW and G models ($P < 0.0001$); however, it was only marginally significant in the HW model ($P = 0.0477$; not included in the final model or Table 3). This suggests that no additional genetic effect is required for HW beyond that accounted for by SI. Consequently, the *GeneticF* dummy variable was excluded from the HW model. Although the signs of all fixed-effect parameters aligned with those reported by Lee et al. (2024) for unimproved stands, their magnitudes were adjusted based on the consolidated dataset incorporating improved stands. The standard deviation of the random effects ($\text{std}(u_{\text{site}})$) increased across all models (HW, DW, and G) due to the inclusion of genetically improved stands. Furthermore, the correlations among random effects (u_{site}) were positive in all cases (Table 3).

The residual plots generally exhibited an unbiased, random pattern in relation to the predicted values and independent variables (Figure 2; Supplementary Material, Section S2.1, Figures S1–S6). For HW predictions, a minor curvilinear pattern was observed in raw residuals, with slight overestimation occurring when predicted HW exceeded 30 m (Figure 2). However,

across all height classes, no class mean residual deviated significantly from zero when evaluated with 95% confidence intervals (Figures S1 and S2) (Mehtätalo and Kansanen 2022). The slight deviation at extreme heights (>30 m) is attributable to data sparsity in older unimproved stands rather than structural model misspecification.

The random effects associated with the experimental sites (u_{site}) showed a slight offset for unimproved stands, indicating some overestimation in HW and underestimation in DW and G when relying solely on fixed effects (Figure 2). Due to site-specific management or trial characteristics not fully captured by the fixed terms, the random site effects (u_{site}) in the HW model for unimproved stands were slightly negative, while those in the DW and G models were predominantly positive. In contrast, the site-level random effects (u_{site}) for genetically improved stands remained centred around zero across all three models (Figure 2). Nevertheless, this minor offset in unimproved site random effects does not imply bias in practical forestry applications on new forest sites, as population-average predictions remain robust (Supplementary Material, Section S4). Supplementedly, when a fixed-effect dummy variable classifying specific thinning and spacing trial series (long-term, repeatedly remeasured unimproved stands; Table 1) was evaluated, the random effects (u_{site}) for unimproved stands showed no systematic offset. However, because this trial indicator added no meaningful explanatory value beyond general site labelling, it was omitted from the fixed effects to avoid potential overfitting.

Model performance and fit statistics

Data classified by the genetic effect dummy variable clearly demonstrated superior performance in height (HW), diameter (DW), and stand basal area (G) as stand age increased (Figure 3). The dataset included a full range of observations, encompassing both unthinned plots and those subjected to multiple thinnings. When the site index was adjusted for genetically improved stands (1.95 m taller than unimproved stands) based on simulated dominant height at base age 50 years (Equation 4), a clear difference was observed (Supplementary Material, Section S3.1, Figure S9). The site index lines of genetically improved stands distinctly reflected higher levels of stand characteristics in HW, DW, and G (Figure 3).

It should be noted that Figure 3 illustrates the predicted levels of stand characteristics while holding tree density constant at $700 \text{ trees ha}^{-1}$. Although this assumption may be unrealistic depending on the stage

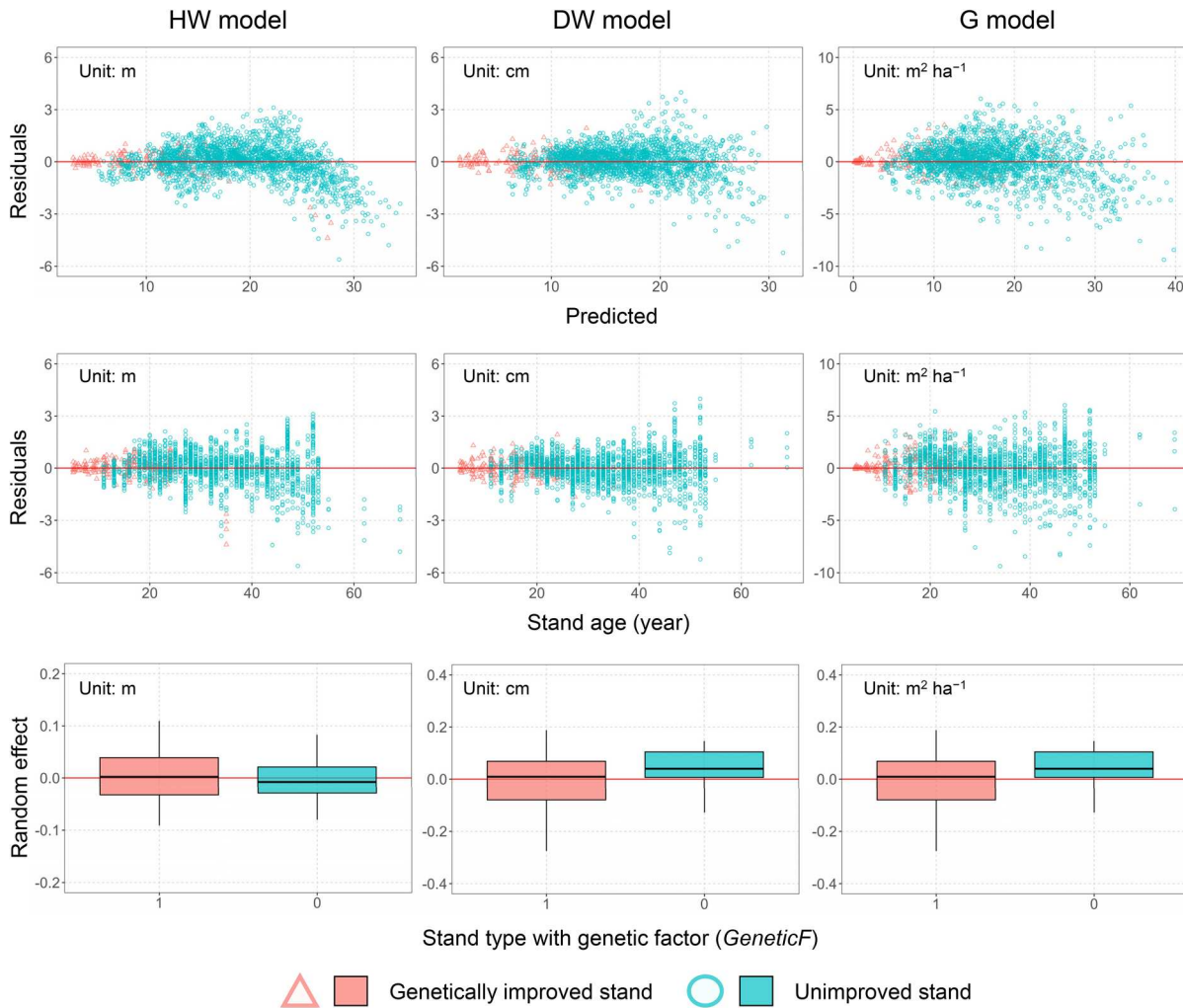


Figure 2. Residual (observed minus predicted) plots of model predictions based on mixed-effects parameters, plotted against predicted values and biological stand age on an arithmetic scale. Box-and-whisker plots show the distribution of random effects at the experimental site level, grouped by model type. HW: basal area-weighted mean height (m). DW: basal area-weighted mean diameter (cm). G: stand basal area per hectare ($\text{m}^2 \text{ha}^{-1}$). *GeneticF*: dummy variable; 1 for genetically improved stands, 0 for unimproved stands.

of stand development, it primarily serves to demonstrate the effects of site index and site type on the stand characteristics HW, DW, and G. Because the *Agric* dummy variable was not included in the HW model, the predictions for forest sites and former agricultural land were identical. Considering the site index ranges by genetic type (Table 1), the site index curves shown in Figure 3 are logically consistent, reflecting the differences between HW and H00. Furthermore, the comparison of HW and H00 model behaviour adequately reflected their development patterns, as illustrated in Figure S7. In the DW and G models, the data were well represented by most site index curves. Furthermore, predicted values for former agricultural land were consistently higher than those for forest sites (Figure 3). It is important to note that data points falling outside the range covered by the predominant site index curves

may be due to other stand characteristics; in this example, tree density was fixed at $700 \text{ trees ha}^{-1}$, which limits variation.

The error metrics of the mixed-effects models for both the unimproved and improved stands were comparable to those reported by Lee et al. (2024). However, the error metrics of fixed-effects were on average slightly higher in the present study, reflecting the inclusion of genetically improved and unimproved stands (Table 4). For example, the RMSE values on the arithmetic scale in this study, based on fixed effects, were 1.1959, 1.4935, and 3.2121 for HW, DW, and G, respectively. By comparison, the corresponding RMSEs reported by Lee et al. (2024) were lower: 1.0306 for HW, 1.1237 for DW, and 2.3306 for G. Similarly, the MAPE values in this study were 0.0496 for HW, 0.0782 for DW, and 0.1684 for G, which are higher than the

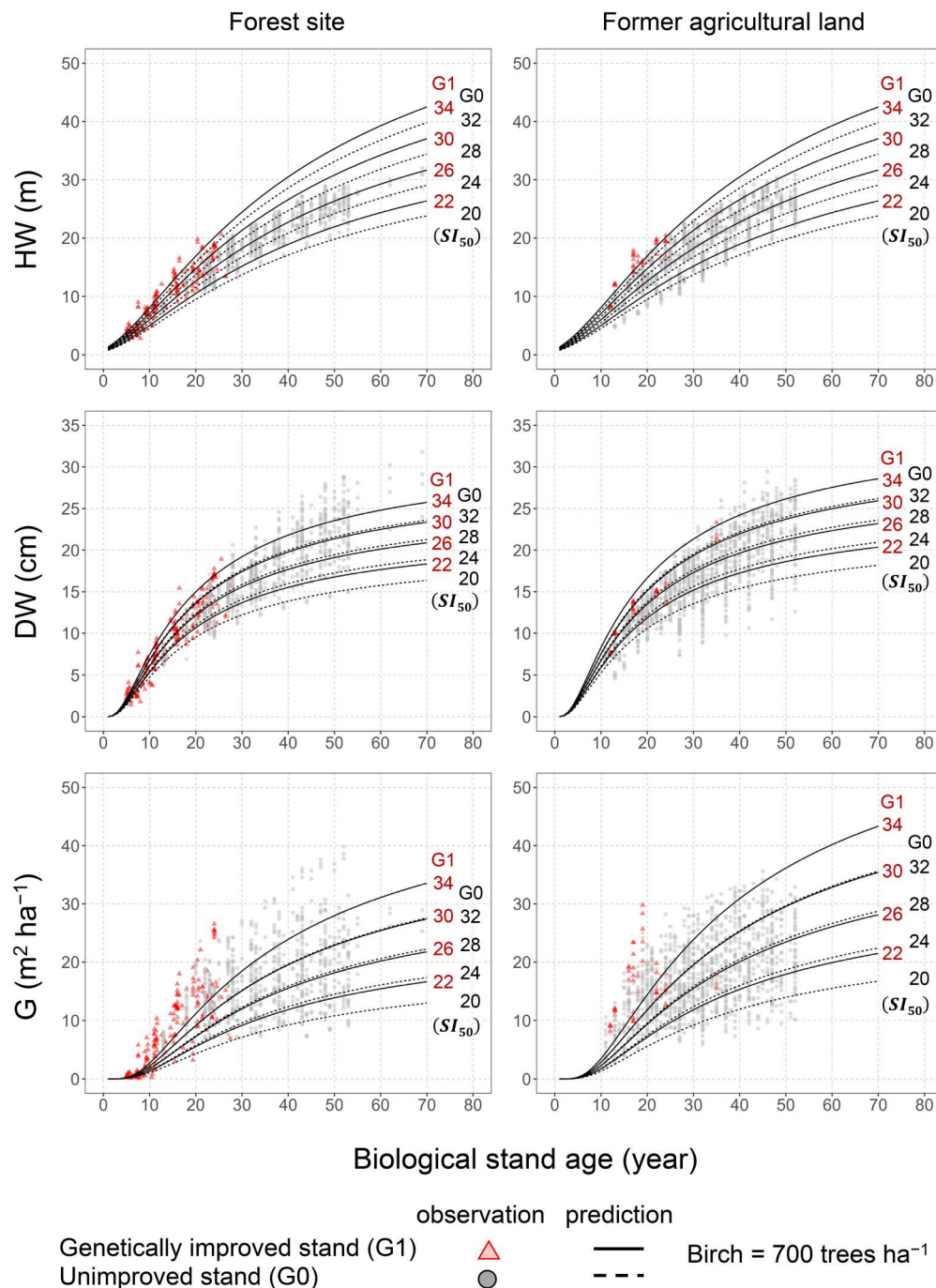


Figure 3. Scatterplots of observations by genetic background (unimproved vs. improved) with model curves for stand characteristics on forest sites and former agricultural land. Curves assume fixed stand density of 700 silver birch trees ha^{-1} and a 1.95 m site index difference (rounded to 2 m in figure panel values only) reflecting superior dominant height development predicted by Equation (4) at base age of 50 years. HW: basal area-weighted mean height (m); DW: basal area-weighted mean diameter (cm); G: stand basal area ($\text{m}^2 \text{ha}^{-1}$); SI: site index (m) at base age 50 years.

previously reported values of 0.0423, 0.0525, and 0.1069, respectively (Lee et al. 2024). The somewhat lower accuracy observed in this study is attributable to the broader range of genetic background included.

This effect was evident even when error metrics were calculated separately by genetic background. For the unimproved stands, the RMSE, MAE, and MAPE values

were worse than in the previous study (Lee et al. 2024) because the model was fitted to the entire dataset. Conversely, the RMSE and MAE were better for the genetically improved stands (Table 4). However, the generally smaller and younger stands in this group may have influenced these results, as the stand characteristics vary with maturity in terms of variation and consequently reduce

Table 4. Model accuracy metrics by tree type, including root mean square error (RMSE), mean absolute error (MAE), and mean absolute percentage error (MAPE) for basal area-weighted mean height (HW, m), basal area-weighted mean diameter (DW, cm), and stand basal area (G, m² ha⁻¹) in silver birch plantations.

Tree type	Effect	Model type	Logarithmic scale			Arithmetic scale		
			RMSE	MAE	MAPE	RMSE	MAE	MAPE
All	Mixed	HW	0.0505	0.0378	0.0140	0.9393	0.6712	0.0379
		DW	0.0528	0.0393	0.0160	0.8311	0.6044	0.0395
		G	0.1135	0.0832	0.0515	1.7157	1.2486	0.0852
	Fixed	HW	0.0640	0.0481	0.0180	1.1959	0.8685	0.0496
		DW	0.1041	0.0813	0.0335	1.4935	1.1907	0.0782
		G	0.2284	0.1810	0.1125	3.2121	2.5266	0.1684
Improved trees	Mixed	HW	0.0423	0.0317	0.0148	0.6199	0.3692	0.0317
		DW	0.0617	0.0467	0.0298	0.4998	0.3890	0.0468
		G	0.1361	0.1037	0.2174	1.0495	0.7751	0.1049
	Fixed	HW	0.0874	0.0635	0.0295	1.0177	0.7145	0.0623
		DW	0.1682	0.1189	0.0788	1.2700	0.9911	0.1223
		G	0.3578	0.2536	0.5220	2.6589	1.9074	0.2898
Unimproved trees	Mixed	HW	0.0514	0.0385	0.0139	0.9698	0.7066	0.0387
		DW	0.0516	0.0384	0.0144	0.8616	0.6297	0.0387
		G	0.1105	0.0808	0.0321	1.7775	1.3041	0.0829
	Fixed	HW	0.0607	0.0462	0.0166	1.2150	0.8866	0.0481
		DW	0.0938	0.0769	0.0282	1.5175	1.2141	0.0730
		G	0.2080	0.1725	0.0645	3.2708	2.5992	0.1542

accuracy. Nevertheless, the MAPE value was slightly higher for the genetically improved stands than for the unimproved ones. RMSE% on the arithmetic scale based on fixed effects for all tree types was 6.5%, 9.2%, and 18.6% for the HW, DW, and G models, respectively. For improved trees, RMSE% was 8.6%, 12.6%, and 25.9%, while for unimproved trees it was 6.3%, 8.8%, and 17.9%. The latter values are slightly higher than those reported by Lee et al. (2024), who found RMSE% values of 5.5%, 6.7%, and 13.0%, respectively.

Simulation and comparison

In simulation comparisons, how the predicted values were influenced by site index and tree density in each of the HW, DW, and G models was examined. The simulations incorporated both genetically improved and unimproved stands. Figures 4–6 show the main predictors – site index, tree density, and stand age – under unthinned conditions, as no thinning was applied during the simulations. Although such unthinned scenarios may be unrealistic, they demonstrate model behaviour. For the improved stands, a site index 1.95 m higher was applied in simulations based on the dominant height model with dummy variable of genetic effect *GeneticF* (Equation 4; Supplementary Material, Section S3.1). Additionally, when SI is required for simulation but the SI model (Equation 1) cannot be applied due to unavailable dominant height, a supplementary site index equation can be used to obtain different simulated values according to degree days, site type, and seed type at a broad scale (Supplementary Material, Section S3.3).

Firstly, the HW model predictions are shown over stand development by varying the site index and tree density (Figure 4). As the HW model predictions are influenced by stand age, site index, and the number of trees, the predicted developments illustrate all possible combinations of these variables. As expected, the predicted HW increases with increasing site index (Figure 4). Increasing stand density has a slight negative effect, although its magnitude is smaller compared to the effects of stand age and site index. For example, at a stand age of 50 years (AGE = 50) for genetically improved stands, HW ranges from 22.6 m to 34.0 m when the number of trees is (N) is 300 trees ha⁻¹, whereas at N = 900 trees ha⁻¹, it ranges from 21.7 m to 32.8 m (Figure 4). Compared with unimproved stands, the predicted HW for improved stands was higher, reflecting the site index effect derived from superior dominant height growth (Equation 4). The difference in HW between improved and unimproved stands was approximately 0.9 m at a site index of 20 m with N ranging from 300 to 900 trees ha⁻¹, and 1.2 m at a site index of 30 m at the same tree densities (Figure 4).

In the DW model, the basic pattern of predicted values was similar to that of the HW model. Specifically, DW predictions increased with stand age and site index but decreased with the number of trees, with both site index (SI) and tree density (N) having notable effects (Figure 5). Consistent with the positive parameter estimate for *Agric*, former agricultural land was associated with higher predicted DW values. Compared to unimproved stands, genetically improved stands yielded higher DW predictions. This increase was due not only

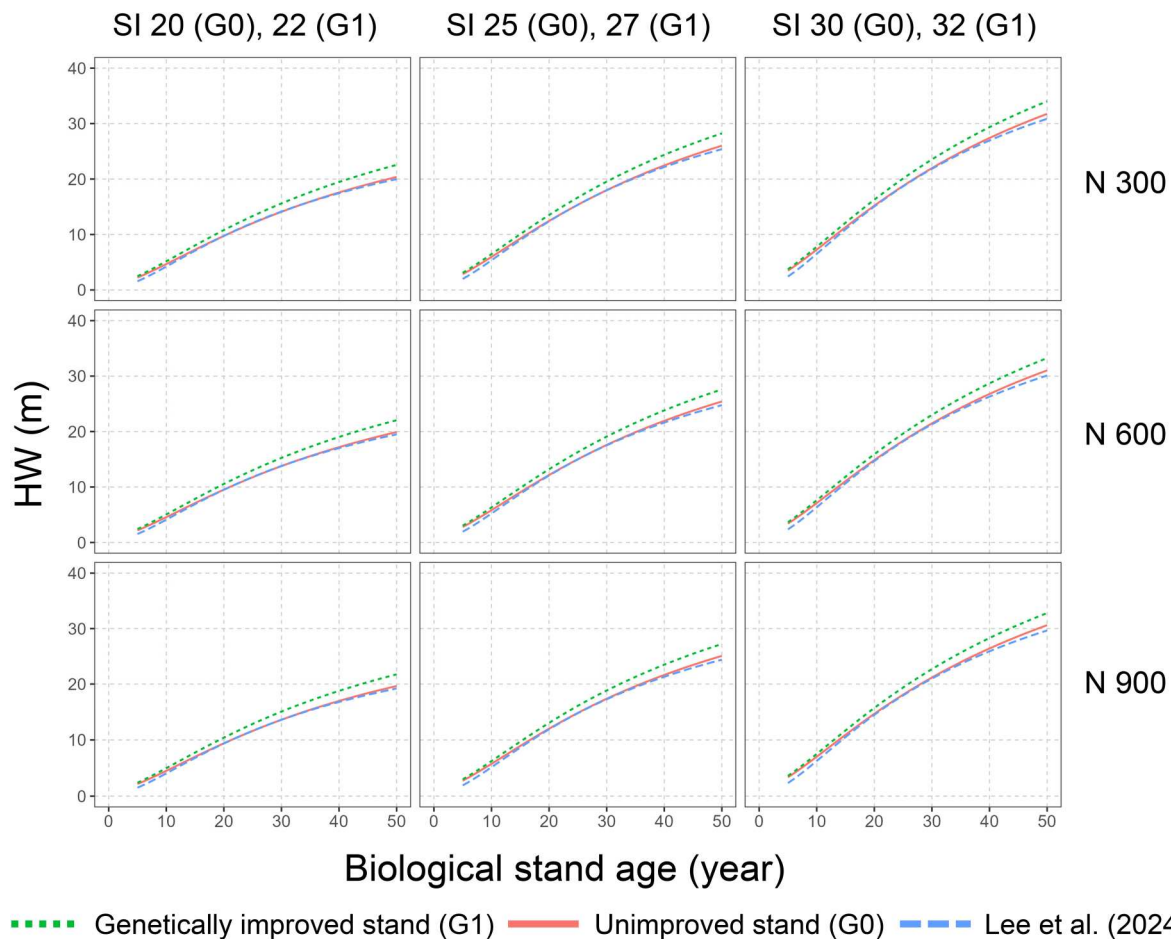


Figure 4. Simulation of basal area-weighted mean height (HW, m) plotted against biological stand age in silver birch plantations. The effects of site index (SI, m) and number of trees (N, trees ha⁻¹) are distinguished by different colours for genetically improved (G1) and unimproved (G0) stands, as well as the model from Lee et al. (2024). In the simulation, the site index for improved stands (G1) was set 1.95 m higher (rounded to 2 m in panel values only) than for unimproved stands (G0), reflecting superior dominant height development predicted by Equation (4) at base age of 50 years.

to the site index being 1.95 m higher, but also to the *GeneticF* dummy variable being incorporated in the DW model.

Accordingly, the simulated DW values for improved stands were consistently higher than those for unimproved stands in most scenarios. The difference between tree types generally ranged from 1.9 to 2.5 cm across all simulation combinations. For example, at SI 20 and AGE 50, the predicted DW values for improved and unimproved stands in former agricultural land were approximately 22.5 and 20.1 cm at N 300, and 17.6 and 15.7 cm at N 900, respectively. At SI 30, the predicted DW values were higher, with the improved stands again outperforming the unimproved ones. These values were about 30.1 and 27.6 cm at N 300, and 23.6 and 21.5 cm at N 900, respectively. The DW predictions for unimproved stands were comparable to those of Lee et al. (2024). Notably, the predictions were more similar in former agricultural land, while in forest sites, the previous

study's predicted DW values tended to be higher than those in the present study (Figure 5).

In the G model, stand basal area was predicted in a similar way to the DW model but it increased faster because stand basal area (G) is calculated as a function of diameter (DW) and tree density per unit area (Figure 6). The predicted range of G varied considerably with site index and number of trees. Due to the influence of tree density, the difference between improved and unimproved stands was greater than that observed in the DW model. The combined effects of a higher site index and the genetic advantage of improved stands resulted in substantially higher predicted G values compared to unimproved stands (Figure 6). For example, in stands of improved stands on former agricultural land, predicted G values were approximately 2.6 m² ha⁻¹ greater than that of unimproved stands at SI 20 and N 300, 3.9 m² ha⁻¹ greater at SI 30 and N 300, 4.5 m² ha⁻¹

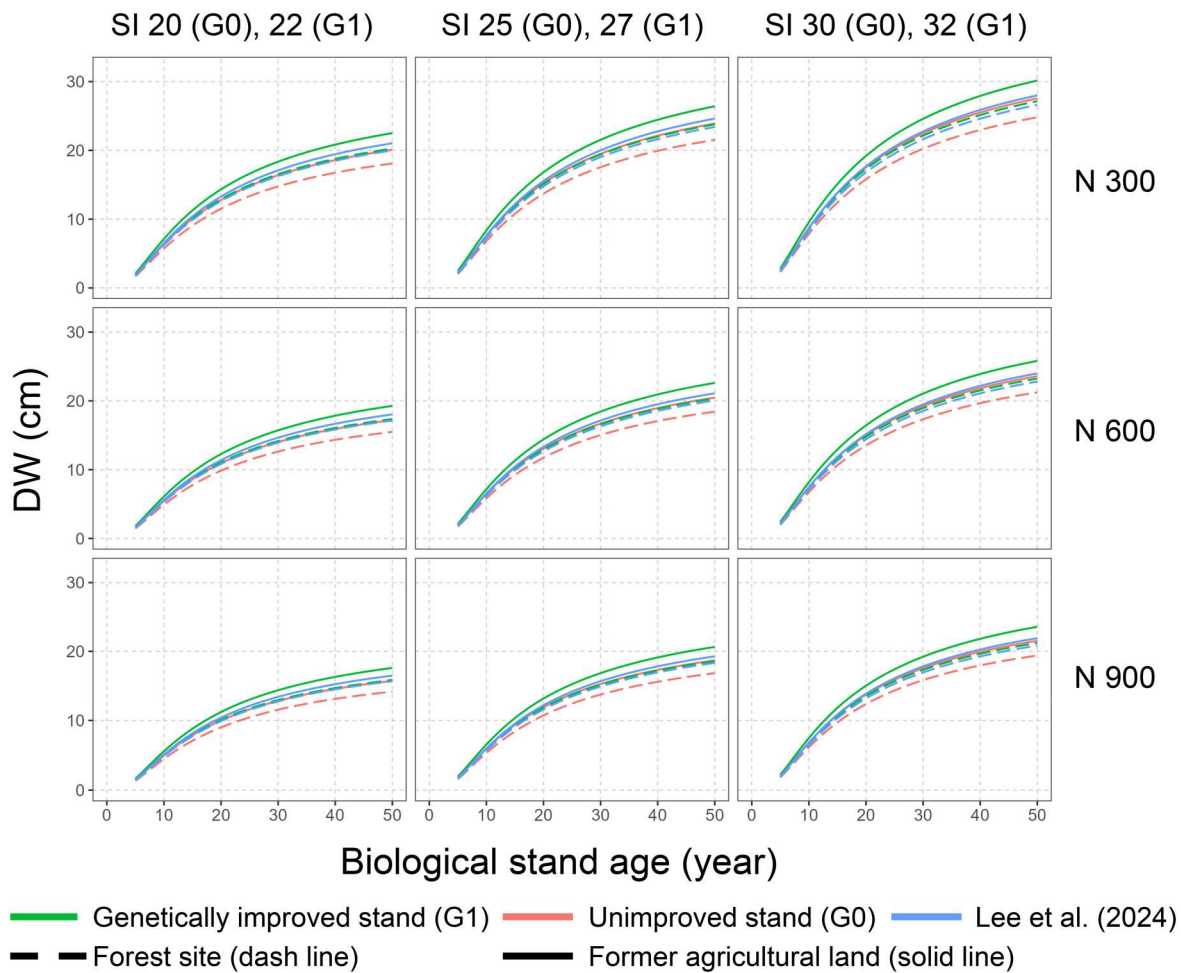


Figure 5. Simulation of basal area-weighted mean diameter (DW, cm) plotted against biological stand age in silver birch plantations. The effects of site index (SI, m) and number of trees (N, trees ha⁻¹) are distinguished by different colours for genetically improved (G1) stands (green line), unimproved (G0) stands (red line), and the model from Lee et al. (2024) (blue line). Additionally, the simulations are categorised by site type: forest (dashed line) and former agricultural land (solid line). In the simulation, the site index for improved stands (G1) was set 1.95 m higher (rounded to 2 m in panel values only) than for unimproved stands (G0), reflecting superior dominant height development predicted by Equation (4) at base age of 50 years.

greater at SI 20 and N 900, and 6.8 m² ha⁻¹ at SI 30 and N 900. A similar pattern was observed in both former agricultural land and forest sites, though the difference between improved and unimproved stands was slightly smaller in forest sites compared to former agricultural land.

When comparing unimproved stands in the present study with those in Lee et al. (2024), the predicted values in this study were consistently lower across all combinations of site index and tree density. This discrepancy was more pronounced in forest sites than on former agricultural land. The predicted G lines for unimproved stands were similar to those of Lee et al. (2024) on former agricultural land, but the lines in forest sites were noticeably lower than those of Lee et al. (2024). Nonetheless, the models developed here predicted higher values for former agricultural land than for forest sites based on the *Agric* dummy variable, and

consistently higher values for improved stands compared to unimproved ones, which is logical given the higher site index and the significant genetic effect represented by the *GeneticF* dummy variable (Figure 6).

Lastly, the model simulations were compared with empirical data from silver birch stands that were thinned one, two, or three times (Figure 7), presenting one randomly selected plot for each treatment. These examples illustrate that the stand characteristics (HW, DW, and G) varied depending on site conditions and treatment, ranging from higher to lower levels, demonstrating that the estimated parameters provided largely unbiased predictions. Across sites, the predicted HW, DW and G values exhibited similar behaviour. Some of the predicted DW and G lines tended to be lower than the observed values because the random effect (u_{site}) was rather positive for the unimproved stands, indicating a slight underprediction when random effects were

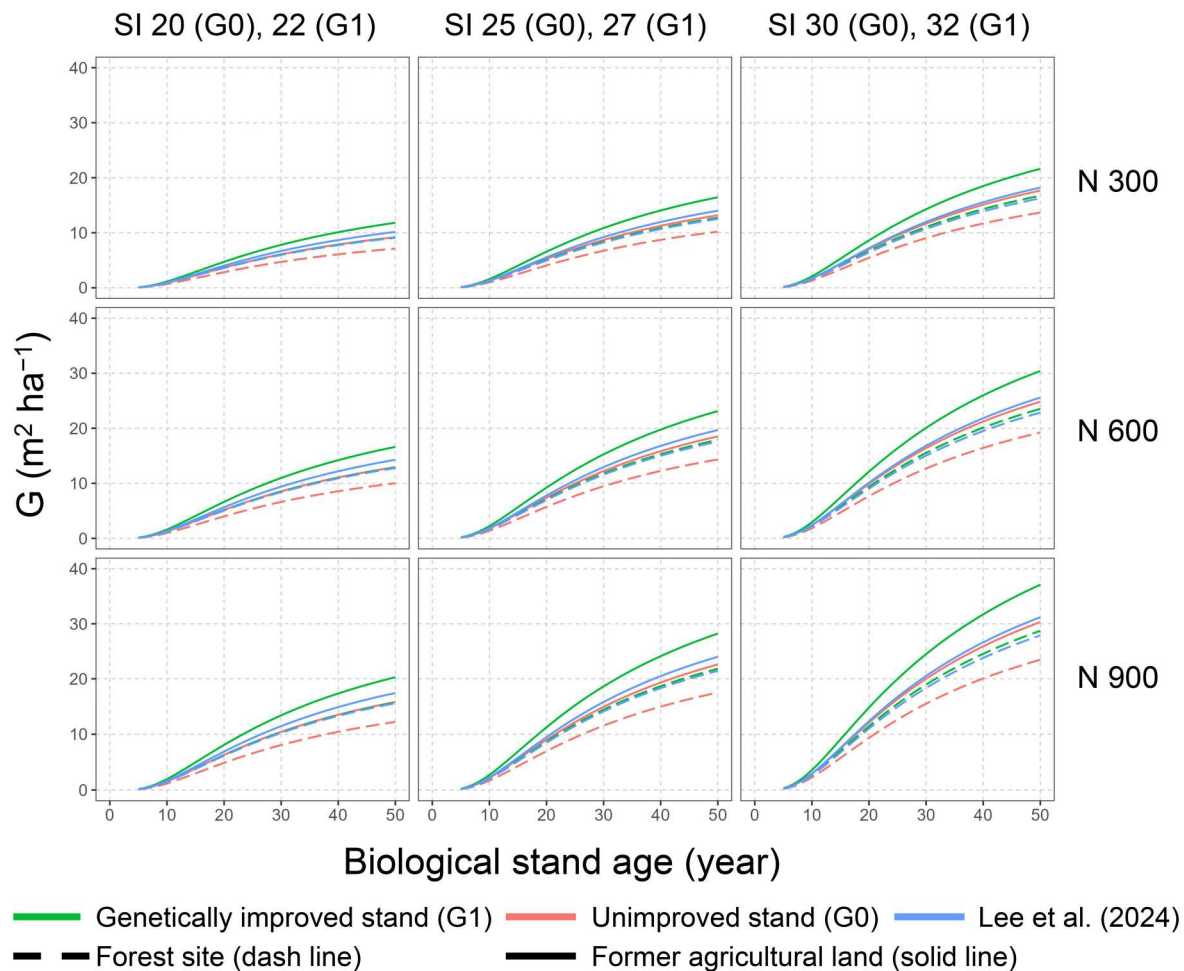


Figure 6. Simulation of stand basal area (G , $\text{m}^2 \text{ha}^{-1}$) plotted against biological stand age in silver birch plantations. The effects of site index (SI, m) and number of trees (N , trees ha^{-1}) are distinguished by different colours for genetically improved (G1) stands (green line), unimproved (G0) stands (red line), and the model from Lee et al. (2024) (blue line). Additionally, the simulations are categorised by site type: forest (dashed line) and former agricultural land (solid line). In the simulation, the site index for improved stands (G1) was set 1.95 m higher (rounded to 2 m in panel values only) than for unimproved stands (G0), reflecting superior dominant height development predicted by Equation (4) at base age of 50 years.

ignored (Figure 7). Still, this does not imply bias when applying the model to new sites in practice.

Furthermore, when comparing improved and unimproved stands, the model consistently predicted higher values for improved stands than for unimproved ones. This is in agreement with the simulation results shown in Figures 4–6, and is based on the parameter estimates presented in Table 3. Note that this single example does not represent the overall bias or accuracy. Depending on the experiment, the simulated line was higher or lower (Figure 7). In this thinning simulation, the magnitude of changes in stand characteristics (HW, DW, and G) was similar to those in the empirical data. Regardless of the number of thinnings or thinning intensity, our model simulations, particularly those incorporating the *GeneticF* dummy variable for unimproved stands, closely predicted and tracked the real observations

from long-term empirical experiments involving unimproved stands (Figure 7).

Discussion

Evaluation of the materials for modelling

Long rotation periods cause a long delay between the cultivation of improved FRM and the availability of mature stand measurements, making full rotation predictions of stand growth difficult (Sun et al. 2004; Jansson et al. 2017; Deng et al. 2020). Growth and yield models for genetically improved stands often rely on early-rotation growth data from test plantations (Deng et al. 2020). In this study, similar difficulties persisted due to insufficient data from older genetically improved stands (see Table 2, Figures 2 and 3).

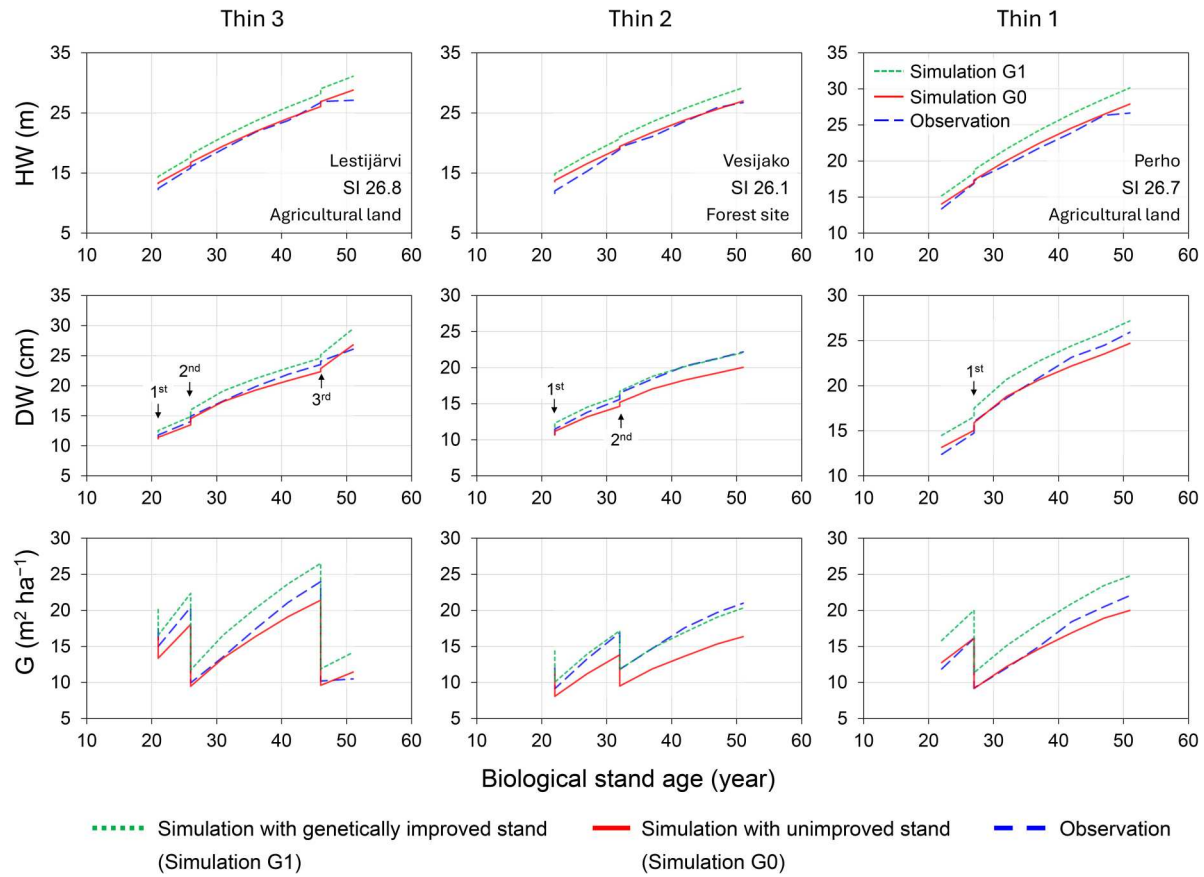


Figure 7. Comparison of model simulations with observations illustrating thinning cases applied one, two, or three times with varying thinning intensities. The observations are from long-term thinning experiments with unimproved stands (G0). Each example represents a plot from the corresponding experiment. Simulations with improved stands (G1) applied a site index (SI) 1.95 m higher than unimproved stands (G0) (rounded to 2 m in panel values only) to reflect superior dominant height development predicted by Equation (4) at base age of 50 years. HW: basal area-weighted mean height (m); DW: basal area-weighted mean diameter (cm); G: stand basal area ($\text{m}^2 \text{ha}^{-1}$); SI: site index (m) at a base age of 50 years.

Nevertheless, this study successfully developed stand models for height, diameter, and basal area of genetically improved silver birch by incorporating numerous recently measured plots, distinguishing it from Lee et al. (2024) who used a similar mixed-effects seemingly unrelated regression approach.

Repeated long-term measurements on genetically improved stands to assess thinning responses were lacking, but model behaviour from this study demonstrated logical model performance, reflecting genetic gains across variables including stand age, site index, tree density, and site type (Figures 3–7). Using an improved site index for improved stands combined with a genetic effect dummy variable, robust models suitable for simulation and prediction were developed. However, the current dataset lacks thinned stands and plantations over 25 years old since genetically improved plantations are still young, leaving no empirical data for older stands (Tables 1 and 2). Further research is needed to understand genetically improved stands' thinning

responses and long-term dynamics, as reliable growth and yield models require repeated, long-term data from permanent sample plots (Sun et al. 2004; Weiskittel et al. 2011). Including such data in future studies would improve model accuracy, precision, and validation (Deng et al. 2020).

Interpretation of the developed models

The parameter behaviour and values in the present models slightly differ from those reported by Lee et al. (2024), who used data solely from unimproved stands. Although additional data from genetically improved stands were incorporated in this study, model performance for unimproved stands remained comparable to that of Lee et al. (2024), indicating similar interpretability (Figures 4–7). Variables SI and *GeneticF* logically explained the growth of height, diameter, and basal area in improved stands (Table 3). However, in this study, *GeneticF* was not included in the HW model

because it was marginally significant ($P = 0.0477$; not included in the final model or Table 3), and model simulations comparing HW and H00 showed that including *GeneticF* did not improve the logic or feasibility (Supplementary Material, Section S2.2, Figure S7).

Similar to this study, previous research (Burkhart 1987; Knowe and Foster 1989; Sprinz et al. 1989; Gwaze et al. 2002; Xie and Yanchuk 2003; Sabatia and Burkhart 2013) analysed genetic gains on dominant height growth and site index using datasets where the asymptote has not been reached (Deng et al. 2020). However, increasing site index alone may not fully explain total yield, as site index captures height growth better than diameter growth (Weiskittel et al. 2011; Burkhart and Tomé 2012; Deng et al. 2020). This study introduced *GeneticF* as a significant variable in the DW and G models, positively reflecting faster growth of improved stands. Calibrating model parameters with long-term empirical data offers better adaptability than modifying site index alone, emphasising the value of sufficient long-term data for improved stands (Deng et al. 2020). Therefore, genetic gain is accounted for by both site index adjustment and the *GeneticF* dummy variable. When simulating genetically improved stands, site index should be set 1.95 m higher than for unimproved stands, and *GeneticF* set to 1.

Limitations and potential shortcomings in the current study

Although the stand characteristic models (height, diameter, and basal area) include genetically improved stands with statistical significance, several limitations must be acknowledged. Data on improved stands mostly consist of only one or two measurements without long-term repeated observations (Tables 1 and 2), a common challenge in modelling genetically improved stands (Talbert and Hyink 1988; Sun et al. 2004; Petrinovic et al. 2009; Gould and Marshall 2010; Weiskittel et al. 2011; Burkhart and Tomé 2012; Haapanen et al. 2016; Deng et al. 2020). Breeding trials typically have a limited scope and lack operational objectives, so simulations based on such data may not fully capture the effects of site quality, silviculture, and genetic improvements on the realised genetic gain (Talbert and Hyink 1988; Carson et al. 1999; Joo et al. 2020). Thinning response data for genetically improved stands were rarely available (Tables 1 and 2), which could impact model accuracy in predicting thinning effects. To ensure consistent growth representation throughout stand development (ages 10–50), long-term data from unimproved stands were retained due to their broad coverage. While thinning-related

variables were statistically significant, this inference is based solely on unimproved-tree data (Tables 3 and 4), requiring further validation with mature improved stands.

Another critical limitation arises from the age distribution of the genetically improved stand dataset, which consists primarily of young to middle-aged plantations (mostly under 30 years). Because these measurements precede the inflection point of full-rotation yield curves, parameterising growth models on young improved stand data combined with full-rotation unimproved stand data assumes that the early growth superiority of genetically improved stands persists throughout stand development (Figures 3–7). In reality, proportional genetic gains may diminish near rotation age as growth increments asymptote (Carson et al. 1999; Xie and Yanchuk 2003; Burkhart and Tomé 2012; Deng et al. 2020). While the absolute growth advantage of improved materials is unlikely to reverse suddenly after stand age 35–40, full-rotation trajectory projections (e.g. stand age 50) for improved stands should be interpreted as potential maximum trajectories until long-term empirical data from mature improved plantations become available to validate late-rotation growth convergence.

Regarding experimental setup, a potential source of bias arises from differences in plot design, including plot sizes and treatments, between unimproved and genetically improved stands. Plot sizes for unimproved trees typically ranged from 400 to 4600 m², whereas improved stands were measured in smaller plots ranging from 300 to 3310 m² in breeding trials and 300 m² in commercial forests. While some breeding trials pooled data to increase plot size for modelling purposes, inherent differences remain in experimental design – such as single-tree plots focusing on genetic traits rather than stand-level factors. Modelling based on small breeding trial plots may not fully capture genetic gains in yield over the full rotation period, since such designs often omit stand-level competition, silvicultural treatments, and site-related variables (Carson et al. 1999; Adams et al. 2006; Vergara et al. 2007; Kimberley et al. 2015; Deng et al. 2020). Large block-plot designs provide better prediction accuracy as they more closely represent operational stands and reduce potential competition effects from mixed genetics (Carson et al. 1999; Stoehr et al. 2010; Ye et al. 2010; Kimberley et al. 2015; Joo et al. 2020).

Hynynen and Ojansuu (2003) found that very small plots (averaging 116 m² and 10 trees) often produce unreliable predictions, whereas larger plots (around 331 m² and 37 trees) yield more reliable modelling results. Our study used plots of at least 300 m² –

including those from commercial forests – which aligns with recommendations by Hynynen and Ojansuu (2003), enhancing reliability. However, the limited number of improved stands and relatively small plot sizes, including fewer sample trees, may reduce precision and introduce bias, particularly in dominant height and basal area-weighted mean height (HW) measurements. Moreover, improved stands received more intensive soil preparation than unimproved ones, and such differences in plot size and silvicultural treatments may have influenced parameter estimates, contributing to observed biases or decreased model accuracy.

Applicability of the final models in practical forestry

The models developed for unimproved stands can be applied similarly to those of Lee et al. (2024) by setting the *GeneticF* dummy variable to 0 for unimproved stands. Still, the predicted DW and G lines of unimproved stands were evidently lower than those of Lee et al. (2024) in forest sites, although the parameter estimates for *Agric* were more significant in this study compared to Lee et al. (2024). These behaviours of the DW and G models in forest sites should be interpreted with caution, as most of the additional observations for forest sites in this study originated from genetically improved stands. Therefore, depending on site conditions and circumstances, the DW and G models developed by Lee et al. (2024) may be preferred over those presented here for unimproved stands in forest sites.

The primary advancement of this study pertains to genetically improved stands established with orchard-reproduced plant materials. When the models are applied with the *GeneticF* dummy set to 1, they specifically account for these stands. Regarding site index, if dominant height can be measured at a forest site, site index (SI) should be estimated using the site index model through the dominant height (Equation 1). If observed dominant height for genetically improved stands is unavailable for site index estimation, it may be assumed to be 1.95 m higher than that of unimproved stands based on Equation (4) (Supplementary Material, Section S3.1, Figure S9). When dominant height is unavailable and site index must be estimated at a broad level, the supplementary site index equation based on degree days and site type (Supplementary Material, Section S3.3) can be applied to both unimproved and genetically improved stands. This supplementary material (Section S3.3, Equation S5, Figure S11) is also useful for young stands (typically <20 years), where dominant height variation makes the standard site index model difficult to apply reliably.

The models' temporal and spatial applicability is suitable for southern and central Finland (see Figure 1), as these regions are covered by the modelling data in this study. Specifically, the most reliable application range extends to the recommended rotation age of 50 years and up to approximately 60 years, as indicated by the temporal range of our modelling data. Particular caution is warranted for HW predictions exceeding 30 m and ages above 50 years, as HW tends to be overestimated beyond 30 m in unimproved stands, with uncertainty remaining for genetically improved stands. Meanwhile, although basal area-weighted mean height (HW) exceeds dominant height (H00) in certain stands with extremely high site index and low density (Supplementary Material, Section S2.2 and Figure S7), this pattern is theoretically possible, particularly in small sample plots with low stand density at mature ages. While H00 is based on the 100 thickest trees ha⁻¹, HW incorporates all measured trees. Toward rotation end – when stem density is low – the thickest trees are not necessarily the tallest (Supplementary Material, Section S2.2 and Figure S7). This pattern was observed in several plots in our dataset and is thus supported both practically and theoretically, representing no practical limitation.

In practice, current silvicultural guidelines recommend thinning silver birch stands when dominant height reaches 13–15 m (TAPIO 2025). This study suggests that the first thinning could be carried out approximately two years earlier than the current recommendation, considering that genetically improved stands reach this target about one to two years sooner depending on site quality (Supplementary Material, Section S3). To facilitate operational implementation, explicit mathematical steps and numerical worked examples for EBLUP local calibration under various field sampling scenarios (e.g. when zero, one, or two stand variables are measured) are provided in Supplementary Material, Section S4.3. While empirical data confirm that improved stands reach first thinning and harvest thresholds 1–2 years earlier, projected yields for mature improved stands (>40 years) should be interpreted with caution, as parameter estimates reflect data prior to full growth deceleration. Overall, the current study can facilitate the updating of silvicultural guidelines in practical forestry.

Conclusion

This study successfully updated the stand characteristic models for both genetically improved and unimproved silver birch, employing a seemingly unrelated regression approach with mixed effects. The targeted stand

variables – basal area-weighted mean height (HW), basal area-weighted mean diameter (DW), and stand basal area (G) – were all well fitted, with highly significant independent variables. Importantly, including a sufficient number of plots from improved stands enabled the dummy variable for genetic effect to achieve statistical significance in the DW and G models. The models demonstrated logical behaviour across all predictor variables, and simulations illustrated credible stand development over stand age (AGE), site index (SI), number of trees (N), former agricultural land (*Agric*), thinning variables (*THIN* and *Talty_{max25}*), and the genetic effect (*GeneticF*). Comparisons between HW and dominant height (H00) further validated their reliability for field applications.

This study also identified a key difference between unimproved and improved stands in the development of HW, DW, and G. Genetically improved stands consistently outperformed unimproved stands across all stand characteristics. While simulations applied a 1.95 m higher site index for improved stands – based on a predicted, superior dominant height development of improved stands – more precise site index differences should be validated using observed dominant height data, as these may differentially affect stand development. By setting the *GeneticF* dummy variable, users can simulate and compare growth trajectories, thereby enhancing silvicultural planning. Insights derived from these simulations have practical implications for stand management in commercial forestry. Building on these achievements, future updates will be possible as more data become available, particularly long-term, repeated measurements from improved stands that include silvicultural practices such as thinning, enabling further refinement and validation of the models. Overall, the models developed in this study offer a robust tool for predicting growth and yield in practical forestry, especially supporting the effective utilisation of genetically improved silver birch plantations in southern and central Finland.

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Author contributions

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Data availability statement

The data are stored at Natural Resources Institute Finland (LUKE) and are not publicly available due to their ownership. The data in this study are available on reasonable request by contacting the authors.

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