Eesti Maaülikool
Estonian University of Life Sciences

COMPARATIVE GROWTH MODELLING OF GENETICALLY IMPROVED NORWAY SPRUCE, SCOTS PINE AND SILVER BIRCH FOREST STANDS

GENEETILISE SELEKTSIOONIGA PARENDATUD KUUSIKUTE, MÄNNIKUTE JA ARUKAASIKUTE KASVU VÕRDLEV MODELLEERIMINE

PAULS ZELTIŅŠ

A Thesis
for applying for the degree of Doctor of Philosophy
in Forestry

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filosoofiadoktori kraadi taotlemiseks
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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following papers; in the text references to them are given in Roman numerals. The papers are reproduced by the kind permission of the publishers.

I. **Zeltiņš, P.**, Kangur, A., Katrevičs, J., Jansons, Ā. 2022. Genetic parameters of diameter growth dynamics in Norway spruce clones. Forests, 13 (5), 679.

II. **Zeltiņš, P.**, Šņepsts, G., Donis, J., Rieksts-Riekstiņš, R., Kangur, A., Jansons, Ā. 2022. Advancing height growth models for the improved forest reproductive material of the main tree species in Latvia. Baltic Forestry, 28 (2), 682.

III. **Zeltiņš, P.,** Jansons, Ā., Baliuckas, V., Kangur, A. 2024. Height growth patterns of genetically improved Scots pine and silver birch. Forestry: An International Journal of Forest Research, 97 (3), 458–468.

IV. Matisons, R., **Zeltiņš, P.,** Kāpostiņš, R., Ozoliņš, K., Jansons, Ā. 2024. Productivity of local Norway spruce clones relates to weather sensitivity of height increment in the eastern Baltic region. Dendrochronologia, 85, 126187.

The contributions from the authors to the papers in alphabetical order are as follows:

	I	II	III	IV
Original idea	AK, ĀJ	AK, ĀJ, JD, **PZ**	**PZ**, ĀJ, AK	ĀJ, **PZ**, RM
Study design	AK, ĀJ, **PZ**	JD, AK, **PZ**	**PZ**, ĀJ, AK	ĀJ, **PZ**, RM
Data collection	JK	RR, GŠ	ĀJ, VB	RK, KO, **PZ**
Data analysis	**PZ**, JK	**PZ**, GŠ	**PZ**	RK, KO
Manuscript preperation	**PZ**, AK, ĀJ	**PZ**, GŠ, ĀJ, RR	**PZ**, ĀJ, VB, AK	ĀJ, KO, **PZ**, RM

AK – Ahto Kangur; ĀJ – Āris Jansons; GŠ – Guntars Šņepsts; JD – Jānis Donis; JK – Juris Katrevičs; KO – Kristaps Ozoliņš; **PZ – Pauls Zeltiņš**, RR – Raitis Rieksts-Riekstiņš; RM – Roberts Matisons; VB – Virgilijus Baliuckas.

ABBREVIATIONS

AAD	aggregated absolute value difference
AD	aggregated difference
AIC	Akaike's information criterion
AMRES	absolute mean residual
BIC	Bayesian information criterion
BLUP	best linear unbiased prediction
CV_g	genotypic coefficient of variation
DBH	diameter at breast height
FRM	forest reproductive material
GADA	Generalized Algebraic Difference Approach
GDP	gross domestic product
H^2	broad-sense heritability
HI	height increment
NFI	National Forest Inventory
R^2_{adj}	adjusted coefficient of determination
r_G	genotypic correlation coefficient
RMSD	root mean squared difference
RMSE	root mean squared error
SI	site index
SPEI	standardized precipitation evapotranspiration index

1. INTRODUCTION

Forests are a crucial natural resource in the Baltic Sea region, making the forestry sector a vital contributor to the bioeconomy (Hetemäki, 2020; Girdziušas et al., 2021). In the Baltic States, the forest sector's share of the gross domestic product (GDP) is between 2.4% and 4.0%, which is significantly higher than the European average of 0.72% (Olschewski et al., 2020). Additionally, the wood procurement and processing industry is one of the leading sectors in exports; in Estonia and Latvia, it accounts for around 20% of domestic exports (Official Statistics Portal, 2024; Statistics Estonia, 2024). With the rising demand for roundwood as a sustainable alternative to fossil raw materials, sustainable forest management has the potential to simultaneously increase timber production and enhance forest carbon sinks, thereby maximizing its contribution to the region's bioeconomy (Hetemäki, 2020). Norway spruce (*Picea abies* (L.) Karst.), Scots pine (*Pinus sylvestris* L.), and silver birch (*Betula pendula* Roth) are commercially the most important tree species in the region, and breeding programs for them have been ongoing since the middle of the 20th century. Today in Latvia 100% of Scots pine, ca. 80% of Norway spruce, and ca. 22% of silver birch seedlings produced are genetically improved (State Forest Service, 2024). The estimated potential genetic gain with respect to increased volume growth is 10–25%, depending on the selection intensity (Ruotsalainen, 2014).

The substantial increase in production due to tree breeding suggests that existing growth models need to be revised (Egbäck et al., 2017). Reliable long-term estimates about the development of the forest are of great importance to plan management and evaluate alternative management options (Fahlvik and Nyström, 2006; Ahtikoski et al., 2012). Growth and yield models are used to describe and predict the growth of forests. Nowadays the models are derived to answer the variable needs of end users and must be applicable on both stand and individual tree level. Growth models are usually based on extensive measurement of naturally developed and genetically unimproved stands (Gould and Marshall, 2008). However, documented increase in the growth of genetically improved nursery stock signals the necessity to analyse models' prediction capability. Accelerated height growth of genetically improved trees results in a clear change in the height curve. Information about the growth differences between stands originating from genetically improved and

unimproved material is required to incorporate genetic gain into the growth models (Rehfeldt et al., 1991; Sabatia, 2011).

Growth models derived solely from data relating to genetically improved material in the Baltic region are still lacking. In Latvia, forest growth and yield tables have been used as a common practice to predict forest growth. Model estimations are commonly based on data from onetime surveyed sample plots, of which the majority were established in the 1960s and 1970s (Matuzānis, 1985). Over the past decades, valuable data from the National Forest Inventory (NFI) have become available for building growth functions. However, the establishment method for many forest stands is unclear, and often natural regeneration of unimproved material is present. Keeping the functions intended for unimproved material may lead to biased growth predictions and may result in suboptimal forest management. Appropriate growth models are becoming more important as the area planted with improved material is increasing, and as the genetic gain resulting from improvement programs also increases (Egbäck et al., 2017).

This research builds upon extensive genetic field trials and aims to model the height growth of genetically improved trees as a reliable proxy for areal production, which can be incorporated into growth simulator systems (Burkhart and Tomé, 2012; Manso et al., 2021; Kuehne et al., 2022). The focus is on two categories of improved FRM: "tested" and "qualified". The "qualified" category represents first-generation seed orchard material with estimated genetic gains of 10–15% for growth compared to unimproved trees, while the "tested" category, representing 1.5-generation seed orchards, has predicted gains of 20–25% based on genetic field test findings (Ruotsalainen, 2014; Jansson et al., 2017).

This thesis is a synthesis of four research papers that examine the genetic effect on tree growth. Papers **II** and **III** study the effect of improved forest reproductive categories "qualified" and "tested" on tree height growth, adjusting existing height growth models (**II**) to account for the altered growth dynamics due to improvement, and building new height growth functions (**III**) intended for young stands originating from genetically improved planting stock. Papers **I** and **IV** focus on examining the clonal effect on Norway spruce growth up to the final harvest dimensions. Paper **I** estimates genetic parameters for Chapman-Richards function applied to characterize clonal diameter at breast height

(DBH) dynamics up to the age of 50 years. Enhancing models requires a deeper understanding of the biological basis of genetic gain and the interactions between genetic and non-genetic factors affecting this gain (Deng et al., 2020). Therefore, paper **IV** evaluates the long-term weather sensitivity and adaptive potential of height increment in 55-year-old Norway spruce clones, focusing on how different genotypes respond to weather fluctuations, particularly winter thermal regimes and summer moisture availability.

2. REVIEW OF THE LITERATURE

2.1. Genetic gains in tree breeding

Forest tree breeding in Europe began in the mid-twentieth century with the selection of plus trees, aiming to produce base material for seed production. Since then, the use of improved forest regeneration material has become a crucial component of forestry in the Baltic Sea region. Tree breeding programs aim to enhance the productivity and quality of wooden raw materials, as well as adaptability and forest health through selection, field testing, and controlled crossings (Ruotsalainen, 2014). In Latvia, for instance, a breeding program for economically important tree species (Scots pine, Norway spruce and silver birch) aims for systematic improvement to maximize investment returns and forest value (Jansons, 2008). Productivity selection considers tree height and diameter while maintaining wood density (Mullin et al., 2011), avoiding undesirable traits like double leaders or spike knots (Westin and Haapanen, 2013). As a result, forest value improves while environmental risks are reduced.

Currently, most improved materials in use are derived from first-generation phenotypic or tested seed orchards, estimated to result in yield gains of 10–25%, depending on the selection intensity (Ruotsalainen, 2014). Plus tree selection shows a 6% height improvement at stand closure (Danell, 1993). In Sweden and Finland, a 10% yield increase in first-generation seed orchards is reported (Andersson et al., 2007; Haapanen, 2020), while 10–25% and up to 35% gains are expected from second and third-generation Norway spruce orchards, respectively (Lindgren et al., 2008; Rosvall et al., 2011, 2002). The realized gains in southern Finland at ages 14–15 for Scots pine offspring from first-generation and 1.5-generation plus trees are 7.7% and 11.7% in height, 6.3% and 13.3% in diameter, and 11.5% and 23.9% in yield over unimproved stock, respectively. As a result of these gains, the rotation length is estimated to be reduced by 4 to 17 years (Haapanen et al., 2016). In Sweden, early height growth of Norway spruce seedlots has showed significant differences between improved and unimproved sources. The most advanced full-sib crossings of selected plus-trees were 36% and 30% taller than unimproved Swedish spruce at ages 5 and 8, respectively. Progeny from second-generation seed orchards were 25% and 21% taller than unimproved material at ages 5 and 8, respectively. A 20% difference between the best and worst tested

full-sib families indicated significant potential gains in new generations, confirming earlier genetic gain estimates for Norway spruce breeding programs (Liziniewicz and Berlin, 2019).

In Fennoscandia, silver birch breeding programs have significantly enhanced productivity and stem quality, achieving genetic gains of 5–30% (Hagqvist and Hahl, 1998; Rosvall et al., 2002; Jansson et al., 2017). In Finland, a recent study concluded that seed orchard material outperforms unimproved silver birch in studied growth and quality traits. Namely, the estimated gains in tree height, diameter at breast height (DBH), and stem volume ranged from 1.6% to 12.1%, 0.6% to 9.4%, and 1.0% to 31.1%, respectively (Haapanen, 2024). In Latvia, selecting the top 10% of silver birch families has been reported to result in genetic gains of 9.6–26.6% for tree height and DBH, and 25.3–61.6% for stem volume compared to the trial means (Gailis et al., 2020b). In Sweden, average gains of 22% and 16% for height and DBH, respectively, were observed over the worst-performing reference genotype. The corresponding gains at the age of 26 years were 20% and 51% for basal area and volume, respectively (Liziniewicz et al., 2022).

The economic impact of tree breeding programs is profound. In Sweden, the implementation of breeding programs and seed orchards for Norway spruce is projected to generate an annual income increase of approximately 177 million euros (Rosvall et al., 2011). In Latvia, the use of selected reproductive material for reforestation has shown to be more cost-effective than relying on natural regeneration, with financial benefits increasing with expanded planting and improved silvicultural practices (Jansons et al., 2015). A Finnish study indicates that forest regeneration with improved seed material not only increases maximum bare land value but also enhances sawing yields, providing financial benefits for both growers and sawmills (Ahtikoski et al., 2018).

Nevertheless, tree breeding contributes to the economy only when its results are applied in forest regeneration and afforestation. In recent years, the availability of improved forest reproductive material (FRM) in Latvia's forestry sector has increased, reflecting a shift towards higher-quality planting stock (State Forest Service, 2024). The volume of produced Scots pine planting material has been relatively stable, ranging between 20 and 30 million plants. However, the percentage distribution of FRM categories reveals a significant shift over time – by 2022, the

proportion of "qualified" material has decreased to about 25%, while "tested" material now dominates, accounting for approximately 75% of total production. The volume of unimproved material has consistently remained negligible across all types of forest ownership, including both state and private forests. Norway spruce production has fluctuated more in terms of volume, peaking at around 35 million units in some years, but the general trend remains somewhat stable. "Qualified" material has consistently been the dominant category, representing around 70% of total production by 2022. "Source-identified" unimproved material held a significant share early on, peaking in 2015, but has steadily declined as improved seeds from more frequent recent mast years became available, now making up about 10%. Meanwhile, "tested" material has seen an increase and now represents about 20% of total production. Silver birch shows a notable increase in production, from less than 2 million units in 2013 to around 5 million units by 2022. Initially, unimproved material made up the majority, but by 2022, its share has decreased to about 50%. "Tested" material has risen to around 30% in 2022, when seeds from new seed orchards became available. "Qualified" material has fluctuated but now represents around 20% of production (Figure 1).

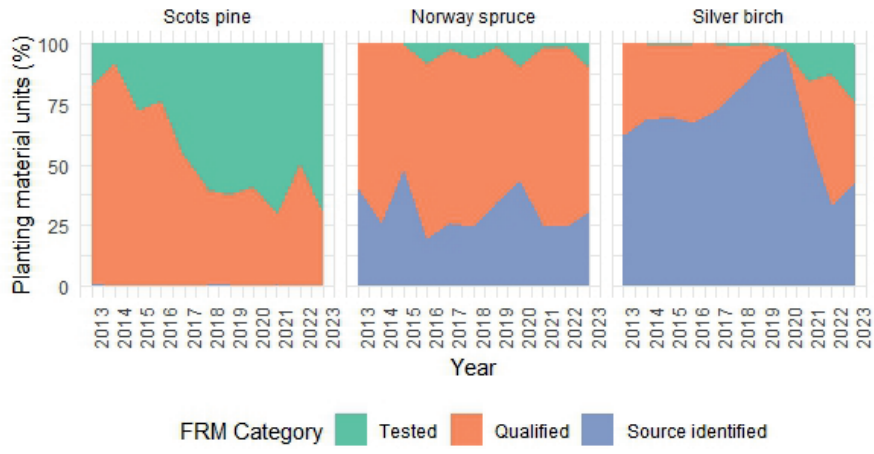

Figure 1. Proportion of planting material per forest reproductive material (FRM) category for Scots pine, Norway spruce and silver birch produced in Latvia in 2013–2023 (State Forest Service, 2024).

Looking forward, managed forests will be crucial sources of raw materials for a variety of products, including structural timber, pulp, paper and bioenergy. This is particularly significant as the demand for bio-based products rises within the bioeconomy (Hetemäki, 2020; Lutter et al., 2021). Sawn timber not only captures carbon but also substitutes for fossil-based materials, thereby contributing to climate change mitigation efforts (Brunet-Navarro et al., 2021; Jonsson et al., 2021). Consequently, forest tree breeding is set to play a crucial role in the bioeconomy by ensuring the production of large quantities of high-quality raw materials. This is expected to significantly enhance the long-term profitability of forestry and have a considerable economic impact (Ruotsalainen, 2014). The intensive development of vegetative propagation methods, which provide high genetic gain and material uniformity, and the advancement of genomic tools to increase the efficiency of selection processes, are both underway (Ruotsalainen, 2014; Egertsdotter, 2019; Gailis et al., 2021; Hazubska-Przybył et al., 2022). Predicted genetic gains using clonal deployment based on clonal mean selection generally yield the largest improvements, followed by specific full-sib family deployments and seedling deployments from open-pollinated selected parents or individuals. For instance, selecting the top 1% of replicated clones for vegetative propagation can result in genetic gains for DBH at the age of 12 years reaching 19.0%, which is a relative improvement of 48.4% over full-sib family deployment and 134.6% over half-sib family deployment at the same selection intensity (Chen et al., 2020). Some outstanding Scots pine plus tree crosses identified in mature progeny trials exhibit 50% faster growth than control seed lots and could be utilized in forestry through vegetative propagation if feasible for pine (Krakau et al., 2013).

2.2. Tree breeding for climate change adaptation

Improved FRM is characterized by its quality and suitability for specific planting conditions, promoting successful plantation establishment and ensuring that ecosystem services are restored promptly after harvesting (Thiffault et al., 2023). Moreover, tree breeding offers a proactive approach to help forests adapt to the rapidly changing climate. It has the potential to combine survival and resilience with desirable quality traits across a wide range of environmental conditions (Aarrestad et al., 2014). As the impacts of climate change intensify, forests face numerous challenges such as shifts in temperature, changing precipitation patterns, and increased vulnerability to pests and diseases (Lindner et al., 2010;

Seidl et al., 2017, 2023). By enhancing genetic resilience, matching planting material to potential future climates, and utilizing genetic diversity, breeding programs provide essential tools for ensuring the sustainability and health of future forests (Cavers and Cottrell, 2015).

Tree breeding programs focus on traits that help trees to adapt to climate extremes such as drought, heat, and changed dynamics of pests' outbreaks (Keskitalo et al., 2016). By selecting genotypes that show tolerance to these stresses, breeding efforts can improve overall resilience. For example, drought-tolerant trees are more likely to survive prolonged dry periods, which are expected to become more frequent with climate change. In maritime pine, a promising study has revealed that the lack of a trade-off between hydraulic conductivity and embolism resistance allows for enhanced productivity through increased hydraulic efficiency without compromising drought resistance (Song et al., 2023). Such adaptability ensures that selected genotypes can better withstand drier climates, supporting both growth and resilience. A recent study on Norway spruce clones in Eastern Latvia demonstrates that fast-growing genotypes can be selected without compromising wood density, which is crucial for both improving timber quality and enhancing drought resistance (Zeltiņš et al., 2024). Trees with lower wood density are more vulnerable to drought due to limited hydraulic conductivity during extreme summer drought events (Rosner et al., 2014). Genotypes with sufficient wood density reduce the risk of stem cracking due to prolonged summer droughts, which is particularly important for fast-growing plantations established on productive sites (Zeltiņš et al., 2018).

Breeding efforts also target disease and pest resistance, as warming temperatures and changing ecosystems can introduce new threats or exacerbate existing ones (Jansons et al., 2016). Breeding trees to resist pests or fungal diseases can ensure forests continue to thrive under these emerging pressures. For instance, observed significant genetic variation in resistance to needle cast damage in Scots pine, and selecting for increased growth could also reduce needle cast damage due to negative genotypic correlations between the two traits (Jansons et al., 2020, 2024). Incorporating resistance to natural infection by *Heterobasidion annosum* into the selection index for Scots pine proved to be an effective strategy for selecting more resistant families while still achieving satisfactory gains in growth traits (Rieksts-Riekstiņš et al., 2020). Moreover, the interaction between breeding effects and silvicultural practices, such

as reduced initial stand density and timely thinning and final cutting, is crucial for risk mitigation. This approach enhances stand stability, shortens the rotation period, and lowers susceptibility to risks like wind damage (Donis et al., 2020; Samariks et al., 2020), which may not be fully addressed through breeding alone.

2.3. Incorporation of genetic effects into growth models

Accelerating the growth of improved trees can alter height growth trajectories. With the use of genetically improved key tree species in forest management, accurate simulation and prediction of their growth under different conditions become essential. Therefore, integration of the above-described genetic gains into growth and yield models are important to enhance the accuracy of growth predictions, optimizing forest management practices (Kimberley et al., 2015). Understanding the growth dynamics differences between unimproved and improved forest reproductive material is crucial for incorporating the genetic effect into growth and yield models, which are originally designed for unimproved material (Rehfeldt et al., 1991; Sun et al., 2007; Sabatia, 2011). Growth models are usually based on large datasets from forests using unimproved reproductive material (Gould and Marshall, 2008), and incorporating genetic effects into these functions is not yet a common practice (Deng et al., 2020).

So far, most studies have focused on fast-growing conifer species (Buford and Burkhart, 1987; Rehfeldt et al., 1991; Hamilton and Rehfeldt, 1994; Carson et al., 1999; Adams et al., 2006; Gould and Marshall, 2008, 2010; Sabatia, 2011; Smith et al., 2014; Egbäck et al., 2015; Kimberley et al., 2015). Studies in southern Sweden have analysed the growth trajectories of improved Norway spruce and Scots pine (Egbäck, 2016). Three primary methods are used to incorporate genetic effects into growth and yield models for genetically improved stands: a) model parameter calibration, b) site index manipulation, and c) applying genetic gain multipliers (Deng et al., 2020).

Each method has its advantages and limitations. Developing new functions specifically for improved trees would be the most accurate method to reflect the effects of selection. However, this is hindered by the lack of long-term data up to the mature age from stands established with genetically improved planting material. This would require

extensive experiments across different growing conditions with periodic measurements throughout the forestry rotation cycle (Gould and Marshall, 2010). By the time data from long-term experiments becomes available, the currently selected genotypes might have been replaced by those from the next, more up-to-date breeding cycle (Hamilton and Rehfeldt, 1994). Due to these challenges, the other two more cost-effective and less time-consuming methods are usually applied.

The site index adjustment assumes that using selected material enhances site quality without impacting other stand dynamics linked to genetic improvements (Sabatia, 2011). The most common method for determining site index involves site index curves, which illustrate the relationship between tree height and age. This adjusts the site index to reflect genetic gains, modifying the height-age curve of the unimproved model system (Buford and Burkhart, 1987; Knowe and Foster, 1989; Sprinz et al., 1989; Danjon, 1995; Gwaze et al., 2002). This method presumes that genetic variation affects only the asymptotic height parameter (Sabatia and Burkhart, 2013). Site index adjustment has been used, for instance, for different seed sources and families of lodgepole pine (Nance and Wells, 1981; Buford and Burkhart, 1987). This method is effective if the growth patterns of improved genotypes are similar to those of unimproved seed lots on more fertile soils (Kimberley et al., 2015). For example, Lambeth (2000) observed a 3.9% increase in site index for selected *Pinus taeda* families. However, it is important to note that this assumes the site index remains constant over time, which may not always be accurate. Long-term growth predictions based on early height measurements can be unreliable and are valid only if the stand has not been excessively impacted by past events (Egbäck, 2016). Alternatively, functions can be developed to relate site quality to the geographic location, understory vegetation, or soil properties (Hagglund et al., 1977).

Genetic multipliers adjust the growth parameters of tree height or diameter to reflect the enhanced growth rates of improved trees compared to unimproved ones. The coefficient modifies the existing growth model coefficients to account for the selection effect (Rehfeldt et al., 1991; Hamilton and Rehfeldt, 1994; Carson et al., 1999; Gould and Marshall, 2008), without altering other aspects of the growth model (Gould and Marshall, 2010). Each coefficient is determined for a specific trait and correlates with its breeding value. Introducing such coefficients is the

most effective short-term solution, allowing the use of early measurement data from progeny tests (Gould and Marshall, 2008). However, similar to site index adjustments, these coefficients may not remain constant over time. Hamilton and Rehfeldt (1994) identified three different coefficients for *Pinus ponderosa* over a 19-year period, indicating variable growth superiority of selected material over time. Conversely, Carson et al. (1999) used constant coefficients for height and basal area in modelling the growth of various *Pinus radiata* genotypes, finding that a constant increase did not yield a constant percentage gain. Instead, their predictions showed a decrease in percentage gain from 15 to 40 years, though absolute differences between genotypes increased. In the Baltic Sea region, the development of improved Scots pine stands has been modelled by incorporating genetic gains in early-rotation height and diameter growth in the asymptote parameter of the Chapman–Richards growth function to compare different genetic improvement levels with unimproved seedlots (Haapanen et al., 2016; Ahtikoski et al., 2018).

Multiple methods can be combined to enhance accuracy. Adams et al. (2006) found that incorporating a coefficient along with site index adjustment for *P. taeda* reduced the error in yield predictions from 30% to 6% in a 17-year-old stand, compared to models using only site index adjustment. An alternative to the genetic effect coefficient is the time coefficient, which adjusts the stand age for different genotype groups (Egbäck, 2016). Smith et al. (2014) discovered that for open-pollinated families of *Pinus contorta*, the genetic multiplier was sufficiently accurate for most traits. However, the time coefficient was more effective for diameter and basal area, as it better accelerated or decelerated trait development in the model.

For modelling purposes, it is also important to consider that the relative performance of different genotypes can vary under different stand management regimes. Therefore, it is essential to evaluate whether genotypes that perform well under one management regime will show similar performance under alternative regimes. Studies on the incorporation of genetic effects in the growth models for *P. taeda* have indicated that the growth superiority of selected forest reproductive material is consistent across regions, stand densities, and ages, and the gains are found to be consistent also across different types of progeny tests (Carson, 2004). Trait differences become more pronounced in favourable environmental conditions (Kroon et al., 2011). For example,

Kimberley et al. (2015) found that the absolute increase in productivity indicators for selected *Pinus radiata* is greater in fertile growth conditions. However, the percentage genetic effect varies little between planting sites and regions, making it relatively easy to incorporate breeding effects into existing models.

2.4. Clonal differences in tree growth patterns

From the perspective of tree breeding, growth models allow to compare the differences in growth trajectories among different genotypes. Accurate model parameters capture growth patterns (Gwaze et al., 2002), as opposed to static trait measurements that only reflect the productivity of studied genotypes at a specific age and site (Skovsgaard and Vanclay, 2008). Predicting selection gains from early growth differences provides a practical alternative to traditional breeding methods and allows for predictions of older ages without direct measurements (Hamilton and Rehfeldt, 1994; Gwaze et al., 2002; Deng et al., 2020). Hence, models can guide the selection and evaluation of improved genetic material, for instance, a set of selected superior clones intended for intensive management, shortening breeding cycles and enhancing the efficiency of breeding programs (Wu, 1999; Deng et al., 2020).

Clonal propagation transfers and maintains genetic gains more efficiently contrasted with traditional propagation methods (Libby, 1982). Clonal forestry, which uses genetically identical ramets of clones, affects stand dynamics by reducing genetic variability, potentially resulting in more uniform stands, hence distinct and more predictable growth characteristics compared to stands established with seedlings (Sabatia, 2011; Wu, 2019). Vegetative propagation of clones serves as a valuable tool for both testing and deployment where feasible. Clonally replicated individuals facilitate efficient breeding and are the sole method for predicting the spatial plasticity of individual genotypes (Rosvall, 2019a). This technique enables the immediate use of tested genotypes in forest regeneration through clonal forestry, ensuring a continuous progression and transfer of genetic gains into practical forestry with only a potential five-year delay, unlike the typical 30-year delay of seed orchards (Rosvall, 2019a; Wu, 2019). Conversely, increased genetic uniformity through clonal selection may increase susceptibility to diseases, pests, and environmental shifts, potentially diminishing forest adaptability to climate change and raising concerns about long-term genetic diversity and ecosystem sustainability

(Zobel and Talbert, 1984; Burdon and Aimers-Halliday, 2003; Yanchuk and Allard, 2009; Wu, 2019). Nevertheless, employing a selection of 6 to 30 clones mitigates risks from both known and unknown pests in boreal forest tree species characterized by lengthy growth cycles, with marginal variations observed across these ranges (Yanchuk et al., 2006). Intensively managed plantations, when considered as a small component within the broader forest landscape, allows for utilization of selected superior genotype to produce high-quality planting material while preserving genetic diversity and providing a foundation for evolutionary processes (Ingvarsson and Dahlberg, 2019). In Sweden, it has been estimated that even under the most intensive management scenarios, 50% of the Norway spruce population will regenerate naturally (Rosvall, 2019b).

Norway spruce, chosen as a model species here, can be propagated easily from young plants, so that clonal replication can be an effective practice (Rosvall, 2019a). The species has shown substantial clonal differences in growth traits such as height, DBH, and volume (Zubizarreta-Gerendiain et al., 2007; Katrevičs et al., 2018; Liziniewicz and Berlin, 2019; Rosvall et al., 2019), suggesting implications for forest management and breeding programs. Selecting clones with rapid growth decreases rotation time, reduces establishment costs, and enhances financial returns (Pfister et al., 2007; Routa et al., 2019). Norway spruce, susceptible to a range of biotic and abiotic risks in a changing climate, could gain from shorter rotations, thereby reducing the risk of damage from factors such as wind, drought, root rot, and bark beetles (Arhipova et al., 2011; Donis et al., 2018; Zeltiņš et al., 2018; De Groot et al., 2019). Clonal propagation has demonstrated double the genetic gain in diameter growth compared to improved seedlings (Chen et al., 2020), highlighting its potential benefits under optimal conditions. Yet, the initial high investment required compared to traditional seedlings limits its widespread adoption (Ruotsalainen, 2014; Liziniewicz and Berlin, 2019). Nonetheless, vegetative propagation of spruce maintains a stable market share, supported by ongoing interest and production, particularly in countries like Sweden (Liziniewicz and Berlin, 2019).

As climate change impacts tree growth, clonal growth models can help predict how different clones will respond to changing conditions. This information is valuable for developing strategies to mitigate the effects of climate change and ensure the resilience of managed forests (Lindner et al., 2010). Therefore, developing clone-specific models also requires

a deeper understanding of the biological basis of the genetic effect and the interactions between genetic and non-genetic factors, for instance, climatic variables, affecting this gain (Deng et al., 2020). Understanding the variability and stability of climate-growth responses across genotypes is essential for adaptive management aimed at selecting productive and resilient trees (Lindner et al., 2014; O'Neill et al., 2014; Jansson et al., 2017; Forzieri et al., 2022). Analysing past growth rates across different environmental conditions provides valuable insights into growth sensitivity (Xu et al., 2017; Babst et al., 2018; Zhang et al., 2018). Measurements derived from growth rates help assess both the sensitivity and resilience of genotypes and enhance projection reliability (Lloret et al., 2011; Babst et al., 2018; Schwarz et al., 2020; Wilmking et al., 2020). Combining productivity and knowledge about climate-growth response, the cumulative effect of past conditions allows to assess the suitability of genotypes to changing conditions (Breed et al., 2018; Housset et al., 2018; Zhang et al., 2018; Harvey et al., 2020; Liepe et al., 2022). Therefore, understanding how historical climate conditions have influenced the growth patterns of Norway spruce clones would facilitate the development of growth models that integrate various climate variables. These models could then be used to predict growth under different future climate scenarios. For instance, factors such as total precipitation during the growing season and the range of average daily temperatures have played crucial roles in explaining changes in diameter growth and enhancing the accuracy of statistical forecasts for *Pinus resinosa* in Canada. Incorporating climate variables accounted for more than 99.5% of the variations in diameter growth (Sharma, 2021).

2.5. Research needs

As advancements in tree breeding progress, there is an increasing need to reassess the current growth models and their predictive capabilities for genetically improved material, as well as to develop new models that more accurately predict the growth trajectories of improved planting stock. Existing models, which are primarily based on unimproved genetic material, may not fully capture the growth patterns of genetically enhanced trees, which exhibiting accelerated growth rates (Egback, 2017). This indicates a gap in current modelling efforts and highlights the need for updated models that incorporate genetic gains from breeding programs. Incorporating such improvements into growth models is essential for commercially important species, including Scots pine, Norway spruce,

and silver birch, which are the focus of breeding programs. However, models used in the Baltic region, often based on data from the 1960s and 70s (e.g., Matuzānis, 1985), may no longer offer precise predictions due to the advancements achieved through genetic improvement (Rehfeldt et al., 1991; Sabatia, 2011). Documented differences in growth between improved and unimproved stands further underscore the importance of understanding how genetic improvements influence parameters in growth functions (Rehfeldt et al., 1991; Sabatia, 2011).

Moreover, research is needed to better understand the effects of clonal propagation on tree growth patterns, particularly in the context of changing climatic conditions. Clonal propagation of Norway spruce has demonstrated a potential for doubling the genetic gain in diameter growth compared to improved seedlings (Chen et al., 2020). However, the long-term genetic effects of clonal growth remain largely unexplored. Studying the growth trajectories of clonal plantations, especially those approaching the expected rotation age, could provide crucial insights into the unique genetic effects on growth and contribute to more precise growth predictions.

Additionally, the long-term relationship between clonal productivity and climate sensitivity remains under-studied for boreal tree species. As climate change progresses, understanding how clones respond to environmental stressors, such as drought and temperature extremes, is vital for the development of resilient breeding programs. The integration of climate variables with historical growth data, through retrospective analyses of growth increments, could offer valuable insights into the sensitivity and resilience of clonal genotypes, thereby improving our understanding of growth under changing environmental conditions (Babst et al., 2018; Zhang et al., 2018). Such research would contribute to forest management strategies aimed at enhancing the adaptability and resilience of clonal tree populations in planted forests.

3. AIMS OF THE STUDY

This thesis aims to analyse growth patterns for improved forest reproductive material of Scots pine, Norway spruce and silver birch and develop individual tree height growth models by a) incorporating genetic gains of different FRM categories into existing height growth models, and b) calibrating new model parameters based on height measurements from genetic field trials. A Norway spruce plantation that has reached the dimensions for final harvest served as a valuable case study, given the limited information on vegetatively propagated clone performance at such advanced ages. This plantation provided an opportunity to analyse clonal growth patterns and their varying sensitivity to meteorological conditions.

The specific aims of the doctoral thesis are:

1. To test a dynamic generalized algebraic difference approach (GADA) of the King-Prodan height growth functions previously calibrated from the remeasured National Forest Inventory (NFI) plots in Latvia to better predict the growth of improved FRM categories "qualified" and "tested" with different levels of genetic improvement (**II**);
2. To analyse the differences between the height growth patterns of different genetic improvement levels for the development of single tree height growth models to predict the height growth for improved Scots pine and silver birch in the Baltic region (**III**);
3. To determine the clone effect on the parameters of the Norway spruce diameter growth curve by applying a mixed-effect modelling approach (**I**);
4. To estimate the dynamics of the genetic parameters for diameter at breast height up to the target diameter dimensions (**I**);
5. To assess the sensitivity of the height increment of the local (Eastern Latvian) genotypes of Norway spruce to meteorological conditions growing near the advancing southern lowland limit (**IV**).

4. MATERIALS AND METHODS

4.1. Study area

The study was carried out in Latvia (**I–IV**) and Lithuania (**III**) (Figure 2), situated in the eastern European plain adjacent to the Baltic Sea, spanning approximately 55° to 58° N and 21° to 28° E. This region falls within the northern part of the temperate climate zone, characterized by a clear west-east gradient of continentality, transitioning from a milder maritime climate in the west to a more continental climate in the east (Laiviņš and Melecis, 2003; Galvonaitė et al., 2013). In Latvia, the average mean annual air temperature ranges from +5.7°C to +7.5°C, with an average of 6.4°C. Monthly temperatures fluctuate from -3.1°C in February to +17.8°C in July. Annual precipitation averages 685.6 mm, peaking at approximately 850 mm in coastal and upland areas, with the wettest months being July and August (75.7–76.8 mm) and the driest month being April (35.8 mm) (Latvian Environmental, Geology and Meteorology Centre, 2020). In Lithuania, the average annual temperature is 7.4°C, with July being the warmest month (18.3°C) and January the coldest (-2.9°C). Annual precipitation amounts to 695 mm, with July receiving the highest rainfall (84 mm) and April the lowest (37 mm) (Lithuanian Hydrometeorological Service, 2021).

4.2. Data collection

4.2.1. Progeny trials (II, III)

To update and construct height growth models (**II** and **III**), tree height data from re-measured progeny trials of Scots pine, Norway spruce, and silver birch were gathered (Figure 2). These progeny trials, established within forest tree breeding programs, serve as controlled experiments where the offspring of phenotypically selected trees (known as plus trees) are planted and their growth performance and quality characteristics are assessed comparatively. The dataset encompasses tree ages ranging from 8 to 42 years, with height-age series comprising two to seven height measurements for individual trees. The experimental design for the families included single-tree plots replicated in 10 to 93 replications and 10- to 100-tree block plots replicated in 3 to 8 replications. The

trials were established using 1- to 2-year-old seedlings for Scots pine and silver birch, while 3-year-old bare-rooted seedlings were used for Norway spruce, all planted at sites suitable for the respective species. Initial stand densities ranged from 1,600 to 5,000 trees per hectare for silver birch and Scots pine, respectively. The Scots pine trials were established in sites characterized by relatively poor, sandy soil typical of the *Vacciniosa* forest type. Norway spruce was planted in mesotrophic mineral soils with a normal moisture regime, corresponding to the *Hylocomiosa* or *Oxalidosa* forest type. In Latvia, silver birch trials were planted on silty dry soils in former agricultural lands with mesotrophic conditions, while in Lithuania, the birch trials were conducted on heavy-textured eutrophic soils of normal moisture, eutrophic drained histosols, and light-textured eutrophic gleyic soils with temporary over-moisture conditions.

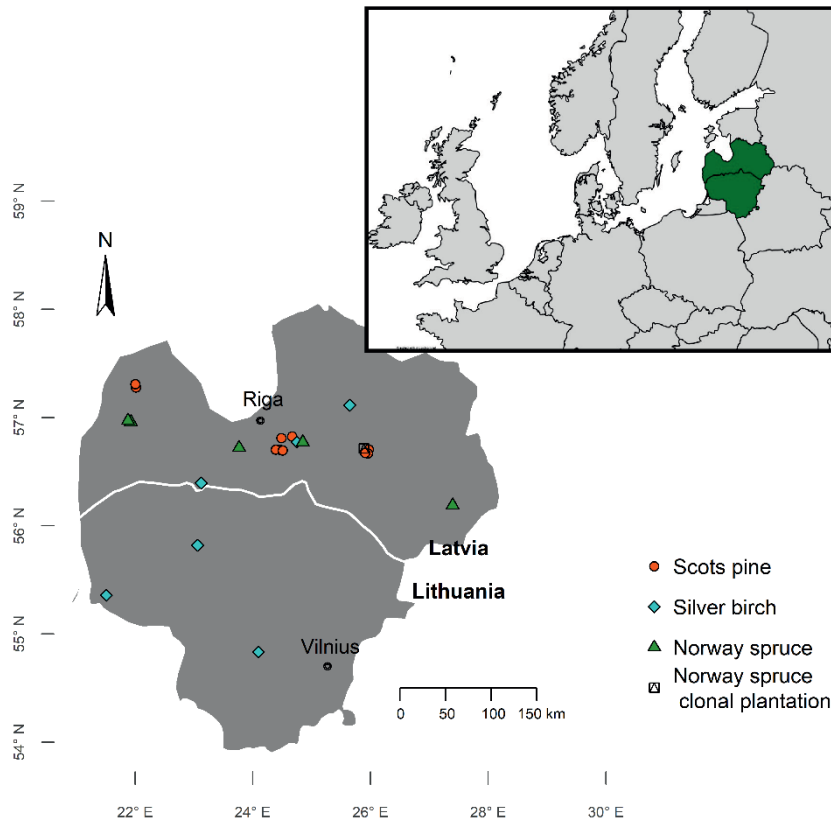

Figure 2. Locations of the studied progeny trials of Scots pine (**II** and **III**), Norway spruce (**II**) and silver birch (**II** and **III**), and Norway spruce clonal plantation (**I** and **IV**).

For modelling, the top 10% of families with the highest mean height in each trial were designated as the FRM category "tested", indicating the genetically superior material identified through comparative testing. The remaining 90% were classified as the FRM category "qualified", which reflects the genetic improvement typical of first-generation seed orchards using phenotypically selected individuals, with estimated genetic gains of 10–15%. In contrast, the tested material is anticipated to yield gains of 20–25% (Ruotsalainen, 2014; Jansson et al., 2017).

4.2.2. Clonal effect on Norway spruce growth (I, IV)

To investigate the clonal variation of growth patterns in Norway spruce (**I** and **IV**), data from a sparsely planted (400 trees per ha) clonal plantation of Norway spruce with minimized inter-tree competition were collected. The plantation, established in 1964, utilized vegetatively propagated two-year-old grafts sourced from local plus-trees located in the eastern part of Latvia (56°42′ N, 25°53′ E, 119 m above sea level) (Figure 2). The plantation was situated on flat terrain with mesotrophic soil, similar to the *Oxalidosa* site type. Initially, trees were spaced at 5 × 5 m intervals, and minimal management, limited to weed control during the first two years post-establishment, was implemented. 5-mm increment cores from 221 50-year-old trees were collected, representing 19 clones, with 7–19 ramets per clone. Only trees exhibiting straight growth with no visible crown asymmetry or stem defects were chosen for core sampling. Annual ring width data were acquired using high-frequency densitometry with a LignoStation, cross-dated, and verified using graphical inspection and COFECHA software (Holmes, 1983). The diameter at breast height (DBH) for each year was reconstructed (**I**) based on annual diameter increments and DBH measurements at the age of 50 years, resulting in time-series data for the DBH of each tree from the ages of 20 to 50 years.

To examine the link between a clone's productivity and how its height increment responds to weather conditions, we selected 10 trees (ramets) each from three clones with varying productivity levels (low, intermediate, and high, represented by clones No. 17, 13, and 18 respectively) based on prior inventory and radial growth analysis from **paper I**. An additional five trees from a highly productive clone (Clone No. 24), selected for its distinctive growth pattern, were also chosen. In autumn 2020, the trees were cut down, limbed, and segmented into 3–4-meter logs. At a sawmill, 50 mm thick planks, including the central pith and bark, were

sawn from the logs. The top segments were air dried. In the laboratory, the pith was exposed by milling away 2 mm layers of wood along the stem's entire length. For the upper segments, a belt grinder was used for this purpose. Height growth increments were measured to a precision of one millimetre along the stem's main axis. Any instances of missing tree tops were noted. To verify the dating of these growth increments, tree rings were counted at both ends of the planks, which were gradually ground down to enhance the visibility of the earlywood and latewood, aiding in accurate ring identification. If the dating was inconsistent at both ends, the planks were further cut into shorter sections for additional ring counting. Graphical and statistical crossdating within and across the clones using the COFECHA software was conducted.

4.3. Modelling approach (I, II, III)

The Generalized Algebraic Difference Approach (GADA) was employed to model the base-age-invariant individual tree height growth for each species separately (Cieszewski and Bailey, 2000; Cieszewski and Strub, 2007). Five different polymorphic dynamic site equations, previously derived from base equations (Table 1), were used to develop new functions (**III**). Additionally, the GADA form of the King-Prodan equation (Model M1 in Table 1, Krumland and Eng 2005), with coefficients approximated from NFI data (Donis et al., 2018; Donis and Šņepsts, 2019; Donis et al., 2020), was adjusted for the improved FRM categories (**II**). The GADA followed a general implicit form (Cieszewski and Bailey, 2000):

$$h_{ij} = f\left(h_{0ij}, t_{0ij}, t_{ij}, \boldsymbol{\beta}, \boldsymbol{\alpha_j}\right) + \varepsilon_{ij} \quad (1)$$

where h_{ij} is the observed height at age t_{ij} for tree i within the FRM category j, h_{0ij} is the height for tree i at a reference age t_{0ij}, $\boldsymbol{\beta}$ is the parameter vector affected by the fixed effect $\boldsymbol{\alpha}_j$ associated with the FRM category j, and ε_{ij} is the error term. For each species, all possible combinations of the fixed effect of the FRM category on the model coefficients b_1, b_2 and b_3 were tested:

$$h_{ij} = f\left(h_{0ij}, t_{0ij}, t_{ij}, \alpha_{j1} \cdot b_{1j}, \alpha_{j2} \cdot b_{2j}, \alpha_{j3} \cdot b_{3j},\right) + \varepsilon_{ij} \quad (2)$$

where α_1, α_2, and α_3 are fixed effects associated with the FRM category j that affects the corresponding parameters b_{1j}, b_{2j}, and b_{3j}. In developing new functions (**III**), the dummy variable approach was used to incorporate the fixed effect. Fixed effects for each "qualified" or "tested" level of the FRM category were separately estimated to determine group-specific impacts on the model parameters. These parameters were calculated using nonlinear least-square regression through the gnls function in the R package nlme (Pinheiro et al., 2021). To manage temporal autocorrelation from repeated measurements on each tree, a first-order autoregressive AR(1) error structure was utilized (Box et al., 1994). Variance functions (Pinheiro and Bates, 2000) were also applied to handle differing variances across FRM category levels within each trial. When adjusting the existing height growth model (**II**), various combinations of FRM category-specific genetic multipliers (g, g_1, g_2, g_3) were incorporated and tested against the coefficients b_1, b_2, and b_3.

The clone effect on the diameter–age relationship (**I**) was modelled as a random effect on the parameters of the Chapman–Richard base equation:

$$DBH_{iA} = [\beta_{10} + b_{1i}] \times \left(1 - e^{(-[\beta_{20}+b_{2i}]\times A)}\right)^{\beta_{30}+b_{3i}} + \varepsilon_{iA} \qquad (3)$$

where DBH_{iA} is the DBH for the *i*-th clone at age A, β_{10}, β_{20} and β_{30} are fixed effects, and b_{1i}, b_{2i} and b_{3i} are random effects on the asymptotic diameter, the rate, and the shape parameter, respectively, for the *i*-th clone, and ε_{iA} is a normally distributed zero-expectation random error. Errors' autocorrelations arising from ring width measurements on the same trees were handled using mixed first-order autoregressive and moving average structures (ARMA (1,1)). To compensate for differing variances across clones, variance functions were applied for each factor (clone). Equation (3) was fitted using nonlinear mixed-effects regression with the nlme package in R software.

Table 1. Tested base models and generalized algebraic difference models (GADA) fitted to height time series (**III**). a_1 a_2, and a_3 are parameters in the base model; b_1, b_2, and b_3 are parameters in the GADA models; h_0 and h are heights (m) at age t_0 and t_1 (years); X_0 is the solution for X with initial values of height (h_0) and age (t_0).

Design-ation	Base model	Site parameter	Solution for X	Dynamic equation	Reference
M1	King-Prodan $h = \frac{t^{a_1}}{a_2 + a_3 t^{a_1}}$	$a_2 = b_2 + b_3 X$ $a_3 = X$	$X_0 = \frac{\frac{t_0^{b_1}}{h_0 - b_2}}{b_3 + t_0^{b_1}}$	$h = \frac{t_1^{b_1}}{b_2 + b_3 X_0 + X_0 t_1^{b_1}}$	(Krumland and Eng, 2005)
M2	Hossfeld $h = \frac{a_1}{1 + a_2 t^{-a_3}}$	$a_1 = b_1 + X$ $a_2 = b_2 X$	$X_0 = \frac{h_0 - b_1}{1 - b_2 h_0 t_0^{-b_3}}$	$h = \frac{b_1 + X_0}{1 + b_2 X_0 t_1^{-b_3}}$	(Cieszewski, 2002)
M3	Hossfeld IV $h = \frac{a_2 t^{a_3}}{t^{a_3} + a_1}$	$a_1 = \frac{b_1}{X}$ $a_2 = b_2 + X$ $a_3 = b_3$	$X_0 = h_0 - b_1 + \sqrt{(h_0 - b_1)^2 + \frac{2h_0 \exp(b_2)}{t_0^{b_3}}}$	$h = h_0 \frac{t^{b_3}(t_0^{b_3} X_0 + \exp(b_2))}{t_0^{b_3}(t^{b_3} X_0 + \exp(b_2))}$	(Cieszewski, 2001)
M4	Chapman-Richards $h = a_1(1 - \exp(-a_2 t))^{a_3}$	$a_1 = \exp(x)$ $a_3 = b_2 + \frac{b_3}{X}$	$X_0 = \frac{1}{2}((lnh_0 - b_2 F_0) + \sqrt{(lnh_0 - b_2 F_0)^2 - 4b_3 F_0})$ $F_0 = \ln(1 - \exp(-b_1 t_0))$	$h = h_0 (\frac{1 - \exp(-b_1 t)}{1 - \exp(-b_1 t_0)})^{b_2 + \frac{b_3}{X_0}}$	(Cieszewski, 2004)
M5	Lundqvist $h = a \exp(-bt^{-c})$	$a = \exp(X)$ $b = b_1 + \frac{b_2}{X}$	$X_0 = \frac{1}{2}(b_1 t_0^{-c} + lnh_0 + F_0)$ $F_0 = \sqrt{(b_1 t_0^{-c} + lnh_0)^2 + 4b_2 t_0^{-c}}$	$h = \exp(X_0) \exp(-(b_1 + (\frac{b_2}{X_0}))t^{-c})$	(Cieszewski, 2004)

4.4. Genetic parameters (I)

In the clonal plantation (**I**) the genetic variance components for random model parameters and DBH were estimated using the following model:

$$y_{ij} = \mu + C_i + \varepsilon_{ij} \tag{4}$$

where y_{ij} is the observation on the *i*th tree from the *j*th clone, μ represents the overall mean, and C_i is the random clone effect. The broad-sense heritability (H^2) of DBH for each year was estimated as:

$$H^2 = \frac{\hat{\sigma}_G^2}{\hat{\sigma}_G^2 + \hat{\sigma}_\varepsilon^2} \tag{5}$$

where $\hat{\sigma}_G^2$ and $\hat{\sigma}_\varepsilon^2$ are the estimated variances of clone and residual, respectively.

The age–age genotypic correlations r_G of DBH were calculated as:

$$r_G = \frac{\widehat{Cov}_{(Gxy)}}{\sqrt{\hat{\sigma}_{(Gx)}^2 \times \hat{\sigma}_{(Gy)}^2}} \tag{6}$$

where $\hat{\sigma}_{(Gx)}^2$ and $\hat{\sigma}_{(Gy)}^2$ are the genotypic (clone) variances at two different ages and $\widehat{Cov}_{(Gxy)}$ is the estimated genotypic covariance between the two measurements, estimated from the multivariate model extending the univariate mixed model in Equation 4.

The genotypic coefficient of variation (CV_g) for random parameters in the final fitted model was calculated using:

$$CV_g = \sqrt{\hat{\sigma}_{b_x}^2} \cdot \frac{100}{\overline{\beta_x}} \tag{7}$$

where CV_g is the genotypic coefficient of variation, $\hat{\sigma}_{b_x}^2$ is the estimated variance for the random effect parameter x, and β_x is the fixed effect parameter x. The CV_g of DBH was calculated for each year. Standard errors were determined using Dickerson's approximation method (Dickerson, 1969).

The genetic gain realized at age 50 for each clone was calculated using the best linear unbiased predictions (BLUPs) from the final fitted model, expressed as a percentage of the average DBH for the trial.

4.5. Statistical analysis

4.5.1. Evaluation of fitted growth models (I, II, III)

The best-fit models were chosen based on the Likelihood Ratio Test, Akaike's information criterion (AIC), and Bayesian information criterion (BIC) (**I, II, III**). When constructing new functions (**III**), model performance was assessed using aggregated difference (*AD*), aggregated absolute value differences (*AAD*), and root mean squared difference (*RMSD*) (Salas et al., 2010). The model modifications (**II**) 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., 2021). The Likelihood Ratio Test determined the significance of fixed effects (**III**) and random factors by reductions for each random effect term (**I**). Graphical analysis of residuals plotted against predicted tree height was performed (**I, II, III**). Datasets were split into calibration and validation data (70% and 30%, respectively) to assess predictive accuracy (**II, III**). FRM category-specific height-age curves were inspected for different site qualities. Analyses were conducted using R, version 4.0.3 (R Core Team, 2020).

4.5.2. Clonal height increment reconstruction (IV)

Dendrochronological statistics, including first order autocorrelation, Gini coefficient, mean interseries correlation, expressed population signal, and signal-to-noise ratio, were computed to measure the environmental sensitivity of height increment (HI). To address the age trend in the measurement time series, detrending was performed using a flexible cubic spline with a wavelength of 30 years and a 50% frequency cut-off. Residual chronologies were calculated for each clone by averaging the spline-detrended and prewhitened time series. Bootstrapped Pearson correlation coefficients were then computed between the residual chronologies of HI and various meteorological variables within a defined climatic window from May of the year before terminal bud formation to August of the increment year. Gridded meteorological data (CRU TS4)

of meteorological variables (Harris et al., 2020), including monthly mean, mean minimum, and mean maximum temperatures, monthly precipitation sums, cloudiness (relative cloud cover), and standardized precipitation evapotranspiration indices (SPEI), were used.

To manage the complexity of meteorological influences on tree growth, multiple regression techniques were employed to pinpoint the meteorological drivers of HI. Generalized additive models were utilized, which permit the evaluation of nonlinear responses across environmental gradients (Wood, 2011). The spline-detrended and prewhitened time series of HI were selected as the response variable. A set of meteorological variables, chosen based on correlation analysis, biological realism, and model metrics like the AIC and R^2 values, were tested as fixed effects. Collinearity among the fixed effects was assessed by the variance inflation factor, and a model was fitted for each clone over the period of 1977–2020, excluding the first 13 years after establishment. However, the entire set of predictors was evaluated collectively and simultaneously across all four clones. Trees nested within the year of formation were included as random effects in the model, and a first-order autocorrelation term was incorporated to address residual ageing effects. The models were fitted using the restricted maximum likelihood approach, based on a calibration data subset which comprised 80% of the crossdated time series. To prevent overfitting, regression spline with shrinkage and smoothing parameters were estimated using the generalized cross-validation method (Wood, 2011). Anticipating responses with up to three inflection points (bell-shaped), the basis dimension for the smoothing spline was limited to four, ensuring alignment with biological realism and reducing the risk of overfitting. Diagnostic plots were utilized to verify compliance with statistical assumptions. Additionally, cross-validation of the refined models using the verification data subset (20% of crossdated time series) was conducted to confirm the absence of overfitting.

The tolerance analysis was employed to assess the resilience components of HI to environmental extremes. This analysis utilized the crossdated time series of trees without standardization or prewhitening. Time series of resistance, recovery, resilience, and relative resilience were calculated, considering four-year pre- and post-disturbance periods, along with a recovery period of up to 10 years. Clonal differences in resilience components were evaluated by selecting years with growth anomalies according to the framework proposed by Schwarz et al. (2020).

Pointer year indices were computed for each clone based on the relative growth change. Thresholds of 40% for improvement and 30% for reduction in increment were utilized to identify event years. A pointer year was deemed significant if at least 50% of trees exhibited consistent positive or negative growth changes. To link pointer years with meteorological extremes, rolling 30-year interval z-scores were calculated for meteorological variables, where conditions with a z-score of 2.0 or higher were considered extreme. The identified pointer years were cross-referenced with weather anomalies using the online almanac of the Latvian Environment Geology and Meteorology Centre.

Linear mixed effects models were employed to assess clonal differences in tolerance components during identified significant pointer years involving at least two clones. Resilience components in negative pointer years, which provide insights into weather anomalies, were analysed as separate response variables. The model included clone as the sole fixed effect and accounted for dataset dependencies and causality differences of pointer years by incorporating the year and tree as random effects. Models were fitted using the restricted maximum likelihood approach, and the significance of the fixed effect was evaluated using Wald's $\chi 2$ test. Estimated marginal means of clones were compared using Tukey's test. Data analysis was conducted in R v. 4.2.1, utilizing the libraries "mgcv" (Wood, 2011), "lme4" (Bates et al., 2015), "dplR" (Bunn, 2008), "treeclim" (Zang and Biondi, 2015), and "pointRes" (van der Maaten-Theunissen et al., 2021).

5. RESULTS

5.1. Optimizing tree height predictions via genetic multipliers (II)

The best fit was achieved by incorporating the breeding effect into the equation using category-specific genetic multipliers ("qualified" or "tested") in front of the coefficients b_1, b_2, and b_3 within the function derived from the empirical coefficients a_1 and a_2 of the base equation (Table 1). The final models for Scots pine and silver birch included all three multipliers, while for Norway spruce, the best fit included g_2 and g_3. These genetic multipliers were statistically significant ($p < 0.01$) for all species and categories.

The modified models showed high accuracy ($R^2_{adj} = 0.918$), with Norway spruce showing the smallest errors (*RMSE* = 0.717 m, *AMRES* = 0.44 m). No trends in residuals were observed for Scots pine and silver birch, though Norway spruce showed slight overestimations for taller trees. Validation data showed good fit statistics ($R^2_{adj} = 0.908–0.943$) for the predictions of modified models.

Unmodified (reference) model validation showed varied results: good prediction precision for Scots pine and Norway spruce (R^2_{adj} =0.891–0.912), but lower for silver birch (*RMSE* = 2.222 m, *AMRES* = 1.935 m, $R^2_{adj} = 0.683$), with a trend to underestimate the heights of smaller trees. Scots pine showed a less pronounced similar tendency, while Norway spruce overestimated the heights of larger trees. Height-age curves indicated that improved FRM categories generally had higher growth curves than the reference model, especially for silver birch, with steeper growth at young age compared to the unmodified function based on NFI data (Figure 3). Data coverage supports drawn curves for higher site indices ($H_{100} > 21$ m) for all species.

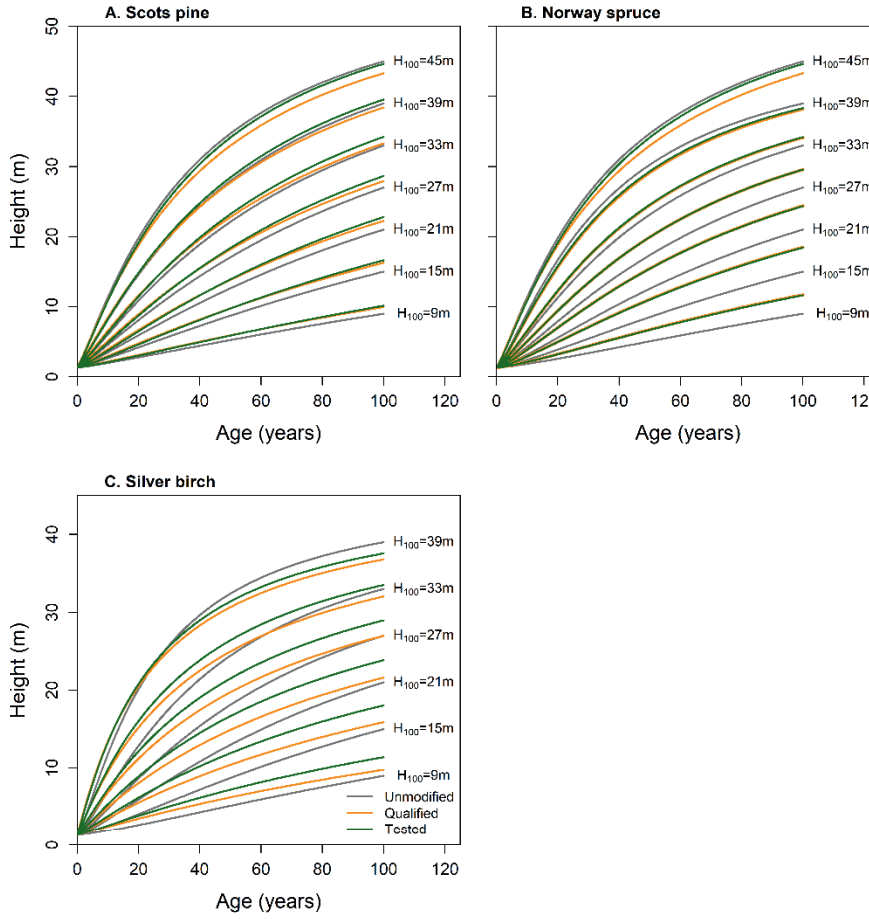

Figure 3. Final best-fit models with genetic multipliers (green and orange lines for improved categories "tested" and "qualified", respectively) vs. unmodified model (grey lines) for Scots pine (A), Norway spruce (B) and silver birch (C) (**II**).

5.2. Development of new height growth models for improved trees (III)

The study (**III**) successfully developed dynamic height growth models for Scots pine and silver birch, incorporating genetic improvement levels categorized as "qualified" and "tested" (Figure 4). These models were calibrated using extensive height-age data from progeny trials in Latvia and Lithuania (Figure 2). For Scots pine, the dynamic model derived from the Chapman–Richards base equation with FRM category-specific parameters b_1 and b_2 showed the best fit. For silver birch, the King–Prodan base equation was most suitable, having all FRM category-

specific parameters b_1, b_2 and b_3. The models demonstrated high accuracy in predicting height growth, with *AAD* of 0.695 meters for Scots pine and 1.023 meters for silver birch, and corresponding relative values 6.7% and 7.3%. The residuals for predicted height were scattered around zero for both species, with no distinct trends, though there was a slight increase in variance with the height for Scots pine. The model slightly underestimated the height of the tallest Scots pine trees (around 23 m) and somewhat underestimated the growth of silver birch trees in the 7–12 m range.

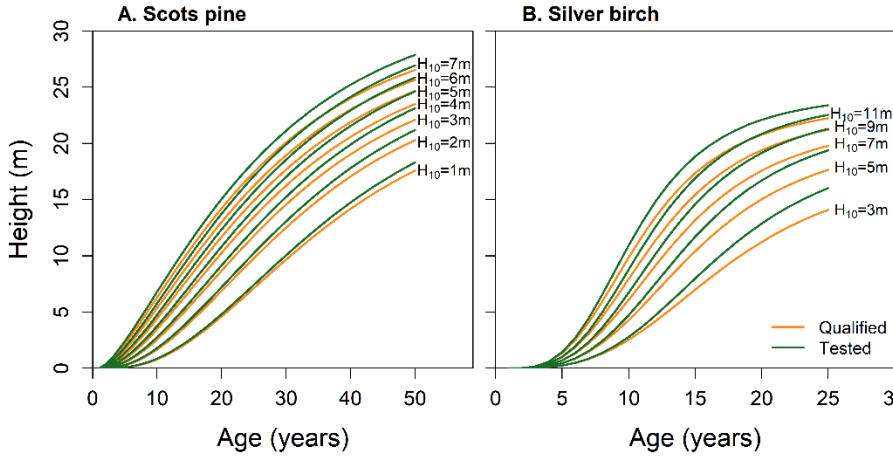

Figure 4. Height growth curves of the final best-fit models (green and orange lines for the improved categories "tested" and "qualified'", respectively) for Scots pine (A) and silver birch (B) (**III**).

The height growth of the "tested" category was generally superior, with 7.5% higher growth for Scots pine and 10.8% for silver birch at the base age of 10 years, compared to the "qualified" category. This superiority was consistent and even increased with age for both species (Figure 4). The study confirmed that the genetic gains observed in early growth stages persisted through mid-rotation. These growth advantages were consistently observed across various site qualities, with the models producing reliable height predictions as evidenced by low *AD* and *RMSD* values. The "tested" material's superior performance highlights the significant impact of genetic improvements on tree growth.

The model fitting showed small differences between the tested equations, but both selected models were precise enough to predict height growth accurately for high-quality sites. The results are significant for improving forest management planning and can aid in the timing of commercial thinnings, particularly for young stands up to the age of 40 years for Scots pine and 20 years for silver birch.

5.3. Genetic influence on diameter growth dynamics in Norway spruce clones (I)

5.3.1. Growth pattern analysis

The study utilized a Chapman–Richards growth model with three random parameters: asymptote (b_{1i}), rate (b_{2i}), and shape (b_{3i}). This model showed the lowest AIC value (-189.152), indicating the best fit compared to other models. The inclusion of random rate and shape parameters significantly improved the model's fit compared to using only the random asymptote parameter ($p < 0.01$). The residuals of the final model were symmetrically distributed around zero and adhered to normality assumptions ($p = 0.154$). The model effectively represented the dataset, with a mean bias of -0.57 cm and a root mean square error of 3.61 cm. The analysis demonstrated significant genetic variation among clones, affecting the DBH and the growth rate and shape parameters (Figure 5).

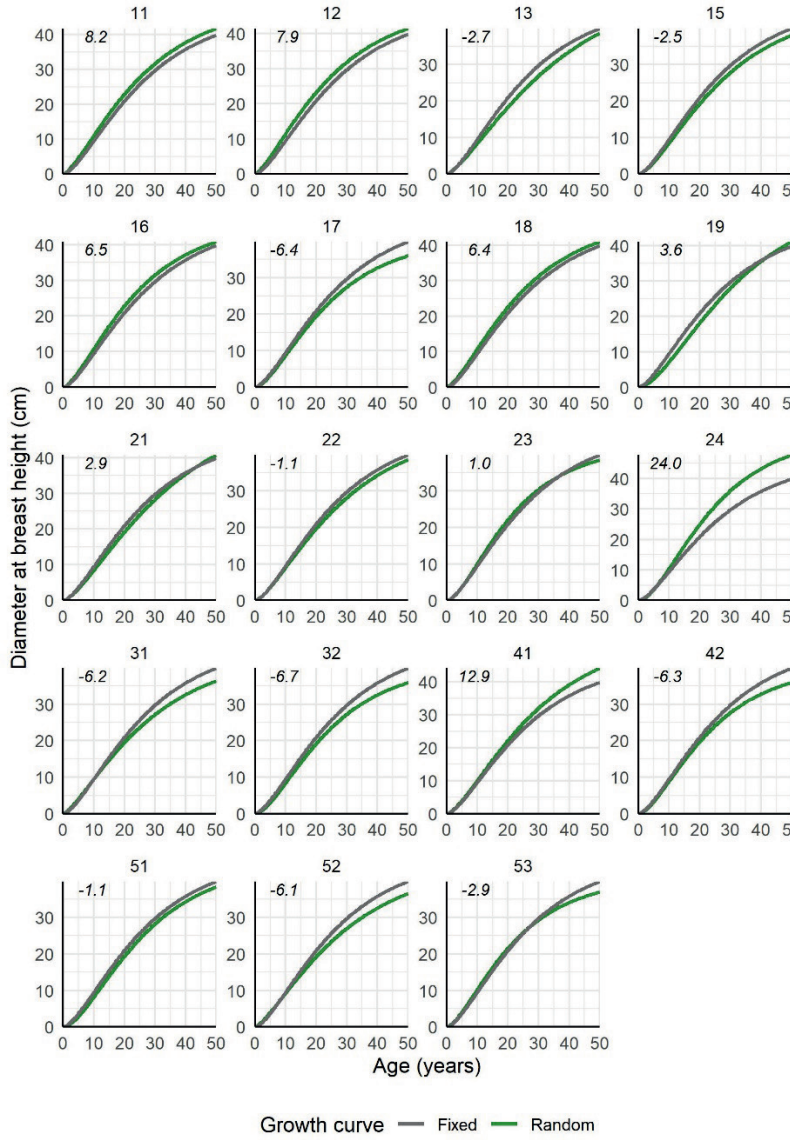

Figure 5. Predicted trajectories of DBH growth curves for population mean (fixed), and each individual clone (random) and its realised genetic gain (numbers in italics, %) at the final harvest age of 50 years (45 years of breast height age) with the final fitted model clone (**I**).

5.3.2. Genetic parameter dynamics

The study tracked the broad-sense heritability (H^2) and genotypic coefficient of variation (CV_g) for DBH over time in a clonal plantation. H^2 for DBH increased from 0.19 at age 20 to 0.35 at age 40, then slightly decreased to 0.32 at age 50. Conversely, CV_g was the highest at the age of 20 years (12.9%) and decreased to 7.8% by age 45, remaining stable thereafter. For tree height at age 50, H^2 was 0.41 and CV_g was 5.6%.

The study also estimated the CV_g for the growth model parameters: 11.0% for β_1, 17.1% for β_2, and 11.9% for β_3. Clonal effects on asymptotic DBH showed greater variance (σ^2_{b1} = 26.69 cm) compared to within-clone error variance ($\sigma^2\varepsilon$ = 23.05 cm). Predicted DBH growth curves varied significantly among clones, with realized genetic gains ranging from -6.3% to +24.0% around the trial mean at the final harvest age (50 years) (Figure 5).

Age–age genotypic correlations (r_G) were generally very strong (>0.80), although slightly weaker for older trees (>0.76). Correlations between similar ages increased with age; for example, the correlation between DBH at ages 45 and 50 was perfectly 1.00, while the correlation between ages 20 and 15 was 0.97.

5.4. Clonal height growth patterns of Norway spruce in relation to weather (IV)

The study (**IV**) analysed the height increment (HI) from 1977 to 2020 of selected Norway spruce clones in the plantation studied in the **paper III**, focusing on their weather sensitivity and resilience. The clones exhibited significant sensitivity to various meteorological variables, particularly temperature and precipitation (Figure 3 in **IV**). Differences in sensitivity were observed among clones, with more productive clones showing distinct responses compared to less productive ones. Fast-growing and superior clones showed higher sensitivity to specific weather conditions, such as high cloudiness in June and significant temperature thresholds in May and April.

Several "significant" pointer years, indicative of abrupt changes in growth, were identified. Positive pointer years, such as 1979, were linked to cool and moist summers, while negative pointer years, like 1996 and

2000, were associated with temperature anomalies and dry conditions. The resilience components, including resistance, recovery, and relative resilience, varied among clones. Fast-growing and superior clones exhibited lower recovery and relative resilience but higher resistance compared to other clones.

Significant clonal differences were found in the type and magnitude of weather-growth responses, suggesting varying degrees of phenotypical plasticity among the clones (Figure 3 in **IV**). The observed non-linear responses (Figure 4 in **IV**) indicated that the clones were approaching the limits of their climatic adaptation, highlighting the importance of local climatic gradients on growth sensitivity. The study highlighted that meteorological extremes have a substantial impact on the growth increments of Norway spruce. The clones demonstrated varied resilience to these extremes, reflecting their genetic and phenotypic differences.

6. DISCUSSION

6.1. Development of height growth models for improved trees

In this study, the aim was to deepen the understanding of the height growth dynamics of genetically improved forest reproductive material, focusing specifically on Scots pine, Norway spruce and silver birch in the Baltic region. Drawing from the methodologies outlined in Carson et al. (1999) and Kimberley et al. (2015), a genetic multiplier approach was integrated with established GADA growth models to capture the genetic improvement factor. This enabled to discern significant differences in growth trajectories between the FRM categories "tested" and "qualified", while mitigating confounding effects arising from variations in site quality (Cieszewski and Bailey, 2000). The utilization of the GADA function, augmented with FRM category-specific multipliers, emerged as a tool for predicting tree height with notable accuracy, as supported by the findings of Sharma et al. (2011, 2017) and Kimberley et al. (2015). The study underscored the efficacy of this approach in differentiating growth patterns among species, despite challenges such as short time-series data and the need for robust statistical fitting, as addressed by Cieszewski and Strub (2007).

An important facet of the study **II** was the development of user-friendly models that integrate FRM category-specific parameters into forest growth simulations. By simplifying the complexities associated with genetic improvements, the approach aligns with the practical needs of forest owners and managers, as advocated by Manso et al. (2022). This ensures that the benefits of genetic enhancements can be readily incorporated into management planning without imposing undue complexity on end-users.

New functions were calibrated (**III**) based on a larger data set from progeny trials to predict the height growth of improved Scots pine and silver birch. Despite being considered the most accurate approach (Weiskittel et al., 2011; Sabatia and Burkhart, 2013), the use of model parameter calibration is usually limited due to the costly and time-consuming nature of repeated measurements of improved trees (Sabatia and Burkhart, 2013; Joo et al., 2020; Manso et al., 2022). Nevertheless, progeny trials encompassing current breeding populations (Baumanis et

al., 2014; Gailis et al., 2020b) were used as study material, enabling the development of models for actual young improved stands up to 40 years for Scots pine and 20 years for silver birch. The parameter sets calibrated for each category improved prediction accuracy by determining the genetic control of the curves (Gwaze et al., 2002). This approach, with the same functional form but FRM category-specific parameterization, similar to the application of FRM category-specific genetic multipliers (**II**), is easily applicable in practice and communicable across different users (Manso et al., 2021).

The criterion of biologically realistic trajectories (Nunes et al., 2011) was satisfied by all tested equations for the age range covered. While the modified (**II**) and newly calibrated (**III**) models demonstrated sufficient performance in capturing early to mid-rotation growth dynamics, extrapolating beyond the covered age ranges remains a point of caution. As highlighted by Sabatia and Burkhart (2013) and Manso et al. (2022), the reliability of long-term predictions depends on the availability of comprehensive data spanning the entire rotation period. Thus, future efforts should prioritize expanding data coverage to refine models for full rotation applications.

However, planning of management in young production stands up to half of the rotation cycle, including the first commercial thinnings, can be improved by the newly calibrated models. For highly productive sites, thinning silver birch is recommended around the twelfth growing season when trees reach about 15 meters (Hynynen et al., 2010), whereas for Scots pine, thinning is typically expected between 25–30 years (Niemistö et al., 2018; Donis et al., 2020). Early commercial thinning for silver birch can be economically viable as early as 14 years, yielding a 9.4% internal rate of return (Gailis et al., 2020a). Accurate growth predictions for young stands are crucial for maximizing profitability.

6.2. Clonal growth of Norway spruce

The study **I** used the Chapman–Richards equation to analyse the clonal effect of Norway spruce on DBH over time, revealing that all three model parameters – asymptote, growth rate, and shape – were significantly affected by clone. The variance within and among clones was significant for all model parameters, indicating the potential for genetic improvement in DBH growth patterns (Schielzeth and Nakagawa, 2013; Harrison et

al., 2018; Oddi et al., 2019). The variation in DBH among the clones was greater than that within them (Table 1 in **I**), indicating the great importance of random-effect variance, namely, clonal differences for the selection. The coefficients of variation for the model parameters ranged from 11.0% to 17.1%, suggesting potential for rapid radial growth improvement. The growth trajectories of clones indicate stable rankings over time, with significant genotypic variance in growth parameters (CV_g ≥ 11.0%), comparable to variance found in other conifers (Chen et al., 2014; Hiraoka et al., 2019).

Heritability and the genetic coefficient of variation for DBH changed over time, stabilizing after 40–45 years, likely due to canopy closure and increased competition (Hiraoka et al., 2019). The findings align with other studies on Norway spruce and Scots pine, indicating that both H^2 and CV_g are dynamic and influenced by age and competition (Hannrup et al., 2004; Wahid et al., 2012; Chen et al., 2014; Hong et al., 2015;).

The results of this study (**IV**) highlight the significant clone-specific influence of environmental factors on height increment in the selected subset of Norway spruce clones, emphasizing genotypic plasticity and individual growth variations. These findings are consistent with previous studies reporting genotype-dependent responses to environmental variation (Cavin and Jump, 2017; Klisz et al., 2019). The height growth of spruce was highly weather-sensitive, a response heighlighted by common environmental forcing and consistent with earlier observations of weather-driven growth patterns (Salminen and Jalkanen, 2005; Mäkinen et al., 2018). Notably, the lower autocorrelation of HI observed here suggested inter-annual variation and potential compensation for weather effects over a longer formation period, a phenomenon that has also been described in tree-ring and xylogenesis studies (Cuny et al., 2019; Matisons et al., 2021). Clone-specific weather-growth responses found in this study showed uneven phenotypic plasticity and local adaptation, supporting the adaptability of local populations to environmental changes (Forzieri et al., 2022; Liepe et al., 2022). More productive clones showed higher resistance to environmental fluctuations but lower resilience. Sensitivity-productivity relationships indicate that more productive clones are less sensitive to adverse weather (Housset et al., 2018; Liepe et al., 2022).

For the studied Norway spruce clones, the thermal regime during dormancy and summer moisture availability significantly impacted

HI, suggesting lower drought sensitivity compared to that observed for radial increment in earlier studies (Matisons et al., 2021). In this study, temperature in March of the prior year was a key driver of HI, likely due to cold damage proportional to productivity (Pearce, 2001; Beck et al., 2004). The significant effects of July and September precipitation likely result from intensifying summer droughts and extended growing seasons, consistent with broader climatic trends (Forzieri et al., 2022; Meier et al., 2022). Overall, HI measurements appear to provide valuable complementary information for evaluating productivity and adaptation of spruce clones under changing climatic conditions, in line with earlier conclusions (Sharma et al., 2011; Socha et al., 2021).

6.3. Comparing growth patterns of various forest reproductive material

From a tree breeder's perspective, the developed models enable comparisons of height growth dynamics between FRM categories with different genetic improvement levels. The height-age curves of improved trees differed significantly from the predicted growth trajectories of the unmodified function (**II**), with variations depending on species and site index (SI). Both FRM categories "qualified" and "tested" showed growth trajectories above the reference curve based solely on NFI data, indicating better growth of improved planting stock (Figure 3). At the age of 10 years (a typical time for the first inventory in the progeny trials), the height of the "tested" category was, on average, 7.5% and 10.8% higher for Scots pine and silver birch, respectively, compared to the "qualified" material, with differences increasing over time (Figure 4), as indicated by the developed model (**III**). This suggests that the early superiority of tested material persists at least until mid-rotation, dismissing concerns about diminishing gains from tree breeding programs over time (Hamilton and Rehfeldt, 1994). Additionally, an increase in height growth was observed with a better site index for Scots pine (**III**), with trait differences becoming more pronounced in suitable environmental conditions (Kroon et al., 2011). Kimberley et al. (2015) concluded that the selected *Pinus radiata* show greater absolute productivity increases in fertile conditions, though percentage gains vary little across sites. Thus, the selection effect can be easily incorporated into models.

However, considering available data sets, comprehensive height growth comparison of different FRM (unimproved, improved seed orchard material and vegetatively propagated clonal material) could be done for Norway spruce. Applying the GADA function with genetic multipliers (**II**) to a) the average height growth performance of the studied FRM categories "qualified" and "tested" in the progeny trials (**III**), b) the mean height growth in the clonal plantation and for the best performing clone No. 24 (**IV**, both considered "tested" FRM in the model), and c) NFI inventory data (National Forest Inventory, n.d.) for unimproved spruce growth on fertile sites *Hylocomiosa* and *Oxalidosa* (modelled as a reference with unmodified models as in paper **II**), average growth trajectories could be plotted (Figure 5). The plotted synthesis of curves shows that genetic improvement substantially influences height growth, with successive levels – from unimproved reference material to FRM categories "qualified" and "tested", clonal mean, and superior clone No. 24 – showing increasingly greater height increases compared to the reference. At 50 years of age, the unimproved material reached a height of 19 m. In comparison, the FRM category "qualified" achieves 22.7 m, marking a 19% improvement over the reference. Further advancement is evident with the tested FRM, reaching 24.8 meters, which is a 2.1 m increase over the category "qualified" and a 30% improvement compared to the unimproved material. The modelled gains for FRM categories "qualified" and "tested" are generally slightly higher than reported from the early inventories (Liziniewicz and Berlin, 2019). Clone No. 24 reaches 26.6 m at 50 years, surpassing the mean plantation height by 1.8 m, equating to a 7.5% increase. Although clonal mean gains are comparable to that of open-pollinated progenies with the FRM category "tested", the superior clone is 7.5 m taller than the unimproved reference material, reflecting a 40% improvement. The exceptional performance of the selected clone No. 24 underscores the significant potential of clonal selection in enhancing tree growth, exceeding gains from traditional improvement methods (Wu, 2019; Chen et al., 2020).

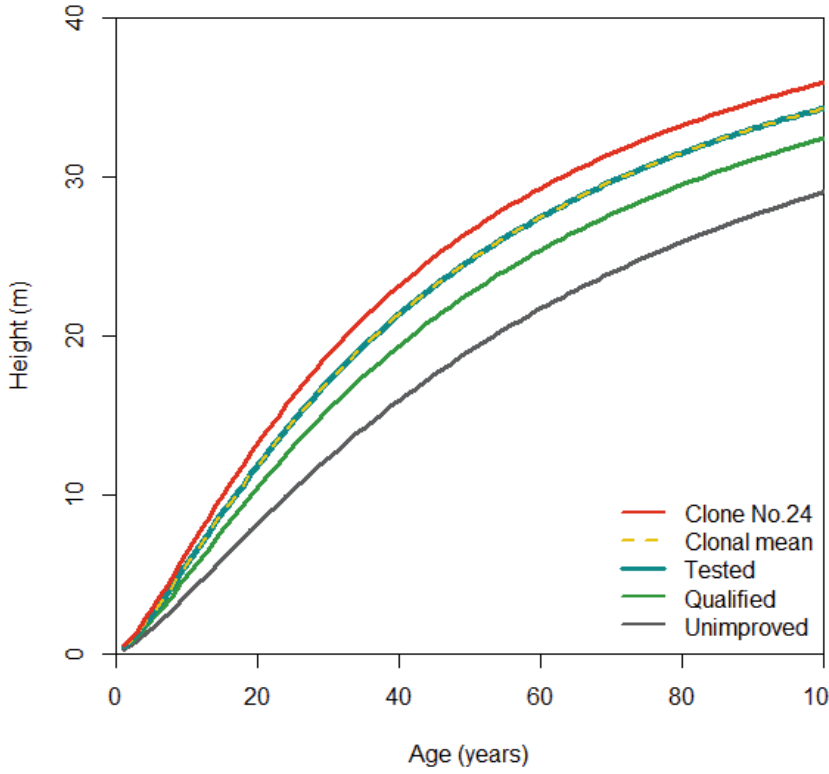

Figure 5. Synthesis of modelling height growth for different genetic improvement levels of Norway spruce. Average height growth curves of unimproved material (NFI data), progeny of open-pollinated families representing FRM categories "qualified" and "tested", studied clonal plantation Druvēni, and the superior clone No. 24.

7. 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 on former agricultural land, suggesting a potentially altered management regime for young stands. 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. 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 the necessary information about the origin of planting material used in forest regeneration. However, such predictions are limited to the sites with medium and high site fertility, where improved planting stock is typically used (**II**).

The polymorphic dynamic derivatives of the Chapman–Richards and King–Prodan base equations provided the best fit and high accuracy for describing the individual tree height growth of genetically improved Scots pine and silver birch, respectively. Different growth patterns were observed between the FRM categories of "qualified" and "tested", reflected in category-specific sets of estimated model parameters for both species. The observed growth curves indicated that the superiority in height growth for the "tested" category at an early age remains at least until mid-rotation, suggesting a long-term nature of genetic gains. For silver birch, the differences between both FRM categories appeared consistent over the represented site quality range, while for Scots pine, they tended to increase with better site quality, suggesting a more effective manifestation of the tree breeding effect on appropriate sites. The model is recommended for use in young stands up to 40 years for Scots pine and 20 years for silver birch on suitable sites. This modelling approach provides more precise information for guiding silvicultural activities, such as the timing of first commercial thinnings, and contributes to more accurate regional-level biomass estimations, essential for evidence-based policy-making in regions where improved planting stock has a substantial share in forest regeneration. (**III**).

Different growth patterns among the studied Norway spruce clones were found. The substantial genetic variation in the growth rate, shape and asymptote of the Chapman–Richards function suggests a potential for more precise selection using predictions for not only final dimensions, but also desirable patterns of growth trajectories. Based on this information, clone-specific genetic modifiers should be tested using dynamic base-age-invariant functions for future growth predictions in practical forestry in order to improve the prediction accuracy for genetic entries with various genetic gains (**I**).

The long-term variability in height increment indicated the weather sensitivity of primary growth in selected Norway spruce clones, suggesting responsiveness to changing climate. Weather conditions affected clones differently, indicating sensitivity-productivity relationships with the potential to maintain the productivity and sustainability of spruce forests in the eastern Baltic region. Since height increment formation is a two-year process, weather conditions showed direct and carry-over effects, indicating complex climatic controls. Despite the drought sensitivity of Norway spruce, height increment showed the strongest positive relationships with temperature during the dormancy period, while summer conditions had secondary effects. More productive clones were less sensitive to adverse weather, highlighting height increment measurements as valuable complementary information for selecting productive and resistant Norway spruce clones under changing climatic conditions (**IV**).

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SUMMARY IN ESTONIAN

GENEETILISE SELEKTSIOONIGA PARENDATUD KUUSIKUTE, MÄNNIKUTE JA ARUKAASIKUTE KASVU VÕRDLEV MODELLEERIMINE

Sissejuhatus

Metsasektor on Läänemere piirkonna biomajanduses olulisel kohal, moodustades Balti riikide SKT-s 2,4–4,0%, mis ületab tunduvalt Euroopa keskmist (0,72%)(Olschewski *et al.*, 2020). Puidu varumine ja töötlemine annavad Eesti ja Läti ekspordimahtudest ligikaudu 20% (Official Statistics Portal, 2024; Statistics Estonia, 2024). Puit on fossiilsete toorainete jätkusuutlik alternatiiv, seetõttu on kestliku majandamise eesmärk kasvava nõudluse tingimustes suurendada puidu tootmist ja tõhustada süsiniku sidumist (Hetemäki, 2020). Piirkonna peamiste majandatavate puuliikide – hariliku kuuse (*Picea abies* (L.) Karst.), hariliku männi (*Pinus sylvestris* L.) ja arukase (*Betula pendula* Roth) – aretusprogrammid kestavad alates eelmise sajandi keskpaigast. Lätis on hariliku männi, hariliku kuuse ja arukase geneetilise selektsiooniga parendatud istutusmaterjali osakaal vastavalt 100, 80 ja 22% (State Forest Service, 2024), mis kasvuperioodi kohta moodustab varasemaga võrreldes kõrgema puistu ja 10–25% suurema tagavara (Ruotsalainen, 2014).

Puude parema kasvu saavutamine geneetilise selektsiooni ulatusliku rakendamise abil tingib kasvumudelite uuendamise, kuna need põhinevad selektsioonist puutumata puistute kasvuandmetel (Gould & Marshall, 2008). Läti puistute kasvumudelid tuginevad 1960.–1970. aastatel tehtud proovitükkide mõõtmistele (Matuzānis, 1985) ning on geneetilise selektsiooniga parendatud puistute kasvu prognoosimisel ebatäpsed, mis võib viia valede majandamisotsusteni. Parendatud istutusmaterjaliga uuendatud metsade kasvu prognoosimiseks tuleb selektsiooni mõju arvesse võtta ja kasvumudelid vastavalt kalibreerida (Egbäck *et al.*, 2017).

Doktoritöö põhineb ulatuslikel välikatsetel varasemalt rajatud geneetiliselt parendatud kultiveerimismaterjaliga puistutes ning keskendutakse kaht tüüpi geneetiliselt parendatud metsauuendusmaterjalile, mida uurimuses

nimetatakse vastavalt „kvalifitseeritud" ja „katsetatud" materjaliks. Kvalifitseeritud materjali puhul on tegemist esimese põlvkonna metsataime seemlatest pärineva istutusmaterjaliga, mille kasvutõus on 10–15%. Katsetatud materjal pärineb 1,5 põlvkonna seemlast, mille kasvutõus on 20–25% (Ruotsalainen, 2014; Jansson *et al.*, 2017). Väitekirjas täpsustatakse neljas artiklis avaldatud tulemuste põhjal geneetilise selektsiooniga parendatud istutusmaterjaliga puistute kasvu prognoosimist. **II** ja **III** artiklis uuritakse selektsiooniga parendatud puistute kõrguskasvu, kohandatakse mudeleid geneetilise selektsiooni kasu arvestamiseks ja koostatakse parendatud puistute kõrguskasvu hindamiseks uued kõrguskasvu mudelid. **I** ja **IV** artiklis analüüsitakse hariliku kuuse liigisisest kasvuvarieerumist kogu rotatsiooniperioodi jooksul. **I** artiklis käsitletakse Chapman-Richardsi funktsiooni abil ka hariliku kuuse kloonide rinnasläbimõõdu suurenemist ning **IV** artiklis analüüsitakse 55-aastaste kuusekloonide rinnasläbimõõdu ja kõrguskasvu seost kliimatunnustega.

Uurimistöö eesmärk oli analüüsida hariliku männi, hariliku kuuse ja arukase parendatud metsauuendusmaterjali kasvu, et a) hinnata ja võrrelda kvalifitseeritud ja katsetatud geneetiliselt parendatud metsauuendusmaterjali vastavat geneetilist kasu sisaldavaid puistu kõrgusmudeleid olemasolevate puistu kõrguse kasvumudelitega ja b) kalibreerida olemasolevate kasvumudelite parameetreid ja koostada uusi mudeleid, mis põhinevad parendatud uuendusmaterjaliga puistute välikatsete kõrguste mõõtmisandmetel, ning lisada mudelitesse geneetiline kasu. Geneetilise valikuga parendatud hariliku kuuse kultuurpuistu, mis on jõudnud uuendusraieks sobivasse vanusesse, oli väga väärtuslik katsematerjal arvestades väheseid ja geograafilise päritolu hindamiseks piiratud andmeid vegetatiivselt paljundatud eri vanuses kloonide kasvu kohta. Sellise katsekultuuri andmerida võimaldas analüüsida kloonide kasvu varieeruvust ja sõltumist kliimatunnustest.

Doktoritöö eesmärgid:

1. analüüsida üldistatud algebraliste diferentsmudelite (*generalized algebraic difference approach*, GADA) rakendatavust geneetiliselt parendatud metsauuendusmaterjalist puistute kasvu prognoosimiseks, kasutades selleks kvalifitseeritud ja katsetatud materjali, ning võrrelda GADA mudeleid Läti riikliku statistilise

metsainventuuri kordusmõõtmiste andmete alusel kalibreeritud King-Prodan puistu kõrguskasvu mudelitega (**II**);

2. analüüsida geneetiliselt parendatud metsauuendusmaterjalist kasvavate puistute kõrguse kasvumustrite erinevusi üksikpuude kasvumudelite väljatöötamiseks, et ennustada geneetiliselt parendatud uuendusmaterjalist kasvavate hariliku männi ja arukase puistute kõrguskasvu Balti regioonis (**III**);

3. hinnata hariliku kuuse erinevate kloonide kasvuerisuste mõju rinnasläbimõõdu kasvukõvera mudeli parameetritele, kasutades selleks segamõjudega modelleerimist (**I**);

4. analüüsida geneetiliste tunnuste varieeruvuse mõju rinnasläbimõõdu muutumise dünaamikale kuni puistu raiet lubava läbimõõdu saavutamiseni (**I**);

5. hinnata hariliku kuuse kohalike (Ida-Läti) genotüüpide kõrguskasvu mõjutavaid peamisi ilmastikutingimusi (**IV**).

Materjal ja metoodika

Uurimus viidi läbi Lätis ja Leedus Ida-Euroopa tasandikul Läänemere-äärsetes piirkondades, koordinaatidega 55° kuni 58° N ja 21° kuni 28° E. Sellele piirkonnale on omane lääne-idasuunaline parasvöötme kliima, mis läheb leebemast merelisest kliimast läänes üle rohkem mandrilisele idas (Laiviņš & Melecis, 2003; Galvonaitė *et al.*, 2013). Lätis on aasta keskmine õhutemperatuur +6,4 °C, jäädes vahemikku -3,1 °C veebruaris kuni +17,8 °C juulis. Aastane keskmine sademete hulk on umbes 685,6 mm, kusjuures vihmasemad kuud on juuli ja august ning kõige kuivem on aprill. Leedus on sarnane ilmastik: aasta keskmine temperatuur on +7,4 °C ja keskmine sademete hulk 695 mm, mis on suurim juulis ja väikseim aprillis (Latvian Environmental, Geology & Meteorology Centre, 2020; Lithuanian Hydrometeorological Service, 2021).

Puistu kõrguse kasvumudelite uuendamiseks ja uute koostamiseks koguti üksikpuude kõrguste andmeid hariliku männi, hariliku kuuse ja arukase järglaskatse katsealadelt, mis on rajatud metsapuude parendusprogrammide raames (**II, III**). Neid järglaskatsete katseseeriaid

võib vaadelda kui kontrollitud katseid, mille käigus istutati fenotüübiliselt valitud puude e plusspuude järglased, et võrdlevalt hinnata nende kasvu ja puidu kvaliteeti. Mõõtmisandmed saadi 8–42-aastastelt puudelt, kõrguse-vanuse seeriad sisaldasid kahte kuni seitset mõõtmist fenotüübi kohta. Katseplaanid varieerusid: oli 10–93 kordusega üksikpuude katseid, 10–100 puuga proovitükkidega katsealasid ning 3–8 kordusega fenotüüpe. Katseseeriate rajamisel kasutati hariliku männi ja arukase istutusmaterjalina 1–2-aastaseid seemikuid ning hariliku kuuse katsetes 3-aastaseid paljasjuurseid seemikuid. Kasvukohad valiti vastavalt iga liigi sobivusele. Algtihedused varieerusid olenevalt rajatava kultuuri liigist ja kasvukoha omadustest vahemikus 1600–5000 puud hektari kohta. Mõlemas riigis rajati hariliku männi järglaskatsed peamiselt mustika ja pohla metsakasvukohatüübile iseloomulikele liivastele muldadele, hariliku kuuse puhul naadi või jänesekapsa kasvukohatüübile vastavatele parasniisketele mineraalmuldadele ning arukase katseseeriad erinevatele mullatüüpidele.

Puude kõrguste baasvanusest sõltumatute kasvumudelite väljatöötamiseks kasutati GADA arvutusmudeleid (Cieszewski & Bailey, 2000; Cieszewski & Strub, 2007). Uute mudelite loomiseks tuletati olemasolevatest baasvõrranditest viis dünaamilist kasvumudelit (**III**). King-Prodani mudeli GADA kuju kohandati parendatud metsauuendusmaterjali (*forest reproductive material*, FRM) jaoks – 10% katsetest klassifitseeriti kvalifitseeritud materjaliks perekondadest, mis esindasid geneetiliselt paremat materjali ja olid parimate kasvunäitajatega. Ülejäänud 90% materjali iseloomustasid esimese põlvkonna seemlatest pärit tüüpilised geneetilised parendused ning liigitus katsetatud materjali kategooriasse (Ruotsalainen, 2014; Jansson *et al.*, 2017).

Lisaks järglaskatsetele analüüsiti erinevate hariliku kuuse kloonide kasvu, kasutades selleks 1964. aastal rajatud hõreda seaduga istutatud pookekultuuri andmeid (**I, IV**). Selle katsekultuuri rajamisel kasutati kaheaastaseid kohalike plusspuude poogendeid, mis istutati algtihedusega 400 puud hektari kohta. Kasvutrende hinnati puursüdamike abil, mis pärinesid 221 puult ja esindasid 19 perekonda (**I**). Aastarõngaste laiused mõõdeti kõrgsagedusliku densitomeetria abil ning rinnasläbimõõt rekonstrueeriti iga puu jaoks eraldi, kusjuures puude vanus varieerus vahemikus 20–50 aastat. Kloonide rinnasläbimõõdu kasvu varieerumise analüüsimiseks kasutati Chapmani-Richardi baasvõrrandit mittelineaarse segaregressiooniga (**I**). Mudelis arvestati korduvate mõõtmiste korral

olulist juhuslikkust ja kattuvate kasvukohtade autokorrelatsiooni. Geneetilisi parameetreid, nagu laiatähenduslikku pärilikkust (H^2), genotüübilisi korrelatsioone ja geneetilist kasu hinnati mudeli variatsioonikomponentide põhjal.

Sobivaimate mudelite valimiseks kasutati tõenäosussuhte testi, Akaike kriteeriumi (AIC) ja Bayes'i kriteeriumi (BIC) (**I, II, III**). Uute funktsioonide konstrueerimiseks (**III**) hinnati mudeli toimivust agregeeritud erinevuste (AD), agregeeritud absoluutväärtuse erinevuste (*average absolute differenc,* AAD) ja ruutkeskmiste erinevuse (RMSD) abil (Salas *et al.*, 2010). Mudeli muutusi (**II**) hinnati kohandatud determinatsioonikordaja (R^2_{adj}), absoluutse keskmise jäägi (AMRES) ja keskmise ruutvea (*root mean square error*, RMSE) abil (Montgomery *et al.*, 2021). Samuti kasutati tõenäosussuhte testi, et juhusliku mõju vähendamise kaudu määrata fikseeritud mõju ja juhuslike tegurite olulisus. Viidi läbi jääkide graafiline analüüs võrreldes tegelikke puude kõrguseid prognoositud puukõrgustega (**I, II, III**). Prognoositava täpsuse hindamiseks jagati andmed kalibreerimis- ja valideerimiskogumiteks (vastavalt 70% ja 30%) (**II, III**).

Kõrguse kasvuseeriate analüüsil rakendati dendrokronoloogilist statistilist andmeanalüüsi, mille käigus arvutati esimese astme autokorrelatsioon ja Gini kordaja, et hinnata kõrguse juurdekasvu (HI) tundlikkust keskkonnategurite suhtes (**IV**). Detrendimiseks kasutati libisevat kuupkeskmist (30 aasta vaatlusaken), ning koostati iga klooni kasvule vastavad jääkkronoloogiad. Nende jääkkronoloogiate ja meteoroloogiliste muutujate vahel arvutati Pearsoni *bootstrap*-korrelatsioonikordajad, kasutades ilmastiku ja juurdekasvude andmeid mõõteaasta maist augustini. Juurdekasvu mõjurite tuvastamiseks kasutati üldistatud aditiivseid mudeleid, kusjuures püsimõjud valiti välja korrelatsioonianalüüsi ja AIC-i kriteeriumi alusel. Mudelid kohandati ajavahemikule 1977–2020, jättes välja esimesed 13 aastat alates katseala rajamisest.

Taluvusanalüüsiga hinnati puude juurdekasvu äärmuslikes keskkonnatingimustes, arvestades puude vastupanuvõimet, taastumist ja säilenõtkust kindlaksmääratud ajavahemike jooksul ja standardiseerimata aegridade alusel. Oluliste kasvumuutuste põhjal arvutati näitaastate indeksid, kusjuures künniseks määrati juurdekasvu suurenemise puhul 40% ja vähenemise korral 30%. Lineaarsete segamõjude mudelitega

hinnati kloonikultuuri erinevusi oluliste näitaastate jooksul, mille hulka arvati juhuslike mõjudena aasta ja puu. Andmeanalüüs tehti tarkvaraprogrammi R versioonidega 4.0.3 ja 4.2.1.

Tulemused ja järeldused

Prognoositava kõrguskasvu optimeerimine geneetiliste kordajate abil (**II**)

Uurimuses lisati kõigi kolme liigi kõrguskasvu mudelitesse geneetilised kordajad ning see suurendas geneetiliselt parendatud materjali prognooside täpsust oluliselt. Hariliku kuuse jaoks saadi geneetiliste kordajate lisamisega suurimat prognoositavat täpsust võimaldav mudel, mille R^2_{adj} oli 0,91 ja RMSE 0,71 meetrit. Parendatud metsauuendusmaterjali puhul võimaldavad uuendatud mudelid kõrguskasvu täpselt prognoosida, eriti viljakatel aladel, kus geneetilised eelised on parendamata materjaliga võrreldes kõige suuremad. Ka männi ja arukase muudetud mudelite prognoosimistäpsus oli seni kasutatutega võrreldes märkimisväärselt parem, ning see võimaldab metsamajanduslike otsuste tegemisel lähtuda senisest täpsematest kasvuprognoosidest (**II**).

Parendatud metsauuendusmaterjali jaoks uute kõrguskasvumudelite väljatöötamine (**III**)

Männi ja kuuse jaoks töötati uued kõrguskasvumudelid välja järglaskatsete mõõteandmeid kasutades. Männi parendatud uuendusmaterjali jaoks oli Chapman-Richardsi võrrandist tuletatud mudel suure ennustustäpsusega (AAD = 0,695 m). Arukase parendatud uuendusmaterjali puhul prognoosis King-Prodani võrrandil põhinev mudel suuremat kasvu kuni puude 20. kasvuaastani täpselt (AAD = 1,023 m). Katsetatud materjali kõrguskasv oli üldiselt parem, kusjuures männi kasv oli 10 aasta vanuselt 7,5% ja arukase kasv 10,8% suurem kui kvalifitseeritud materjalil. See paremus oli mõlema liigi puhul järjepidev ja isegi suurenes vanusega, mis näitab, et metsauuendusmaterjali geneetiline parendamine toetab kõrguskasvu pikaajaliselt. Katsetatud materjali parematest tulemustest järeldub, et geneetiline parendus mõjutab puude kasvu oluliselt. Need tulemused on väärtuslikud metsamajandamise prognooside täpsustamisel, eelkõige kuni 40-aastaste männikute ja kuni 20 aastaste arukaasikute valgustusraiete planeerimisel (**III**).

Geneetilise aretustöö mõju hariliku kuuse kloonide diameetrikasvu dünaamikale (**I**)

Genotüüp mõjutab kuuse kloonide diameetrikasvu suurel määral, järelikult kujundab klonaalne aretustöö kasvutunnuseid – kloonide rinnasdiameetri erinevused olid märkimisväärsed, kusjuures parimatel kloonidel oli kasv kuni 24% suurem kui populatsiooni keskmisel. Rinnasdiameetri pärilikkuse hinnang suurenes 20. kasvuaasta 0,19-lt 40. kasvuaastaks 0,35-ni, mis näitab, et geneetika mõjutab puude kasvu järjepidevalt. Välja töötatud mudel kajastas selgelt geneetilise aretustöö mõju kloonidele, näidates, et kõrge tootlikkusega kloonide valimine võib parandada puistu kogutootlikkust. Kasvutrendide võrdlemise tulemustest järeldub, et kloonide valimine toetab kuusekultuuride kasvu optimeerimist (**I**).

Ilmastiku mõju kuusekloonide kõrguskasvule (**IV**)

Hariliku kuuse kloonid osutusid kliimatingimuste suhtes tundlikuks, sealjuures mõjutas kasvuaasta juurdekasvu temperatuuri ja sademete varieerumine. Kiiresti kasvavad kloonid reageerisid kasvuperioodi alguses temperatuurimuutustele ja sademete hulgale väga tundlikult, samas näitas vastupidavuse analüüs, et need kloonid taastusid ka paremini. Kasvuandmete põhjal tuvastatud näitaastad tõid esile positiivse kasvureaktsiooni jahedatel ja niisketel suvedel ning kasvu vähenemise soojadel ja kuivadel perioodidel. Need tulemused rõhutavad geneetilise selektsiooni rolli puude kliimakindluse suurendamisel ning näitavad, et on oluline valida sellised kloonid, mis suudavad kasvada ka äärmuslikult varieeruvate ilmastikuolude tingimustes. See käsitlus annab väärtuslikke teadmisi kliimaga kohaneva metsanduse tarbeks, sest aitab majandatavates kuusepuistutes leevendada kliimariske (**IV**).

Kokkuvõte

Geneetiliselt parendatud männi, kuuse ja arukase kõrguskasvu kajastasid parendatud metsauuendusmaterjali kategooriapõhiste kordajatega varustatud kasvumudelid täpsemini kui üksnes statistilise metsainventuuri andmetel põhinevad modifitseerimata võrdlusmudelid. Modelleerimise tulemused näitavad, et parendatud metsamaterjali kasvutempo on nooremas eas kiirem, eriti arukase puhul endisel põllumajandusmaal, mis osutab noorte puistute majandamisviisi muutmisvajadusele. Täiustatud

mudelid võimaldavad õigeaegselt planeerida harvendustöid ilma kasvu alahindamisest tingitud viivitusteta. Mõlema, nii katsetatud kui ka kvalifitseeritud parendatud istutusmaterjali kordajate kogumit saavad metsaomanikud ja -majandajad praktikas rakendada, sest nad reeglina teavad uuendamisel kasutatava istutusmaterjali päritolu. Need prognoosid sobivad siiski eelkõige keskmise ja kõrge viljakusega kasvukohtade jaoks, kus tavaliselt kasutatakse parendatud istutusmaterjali (**II**).

Chapman-Richardsi ja King-Prodani baasvõrrandite polümorfsed dünaamilised tuletised sobisid geneetiliselt parendatud männi ja arukase kõrguskasvu vastavalt kirjeldamiseks kõige paremini. Kvalifitseeritud ja katsetatud materjali erinevad kasvumustrid kajastusid mõlema liigi puhul konkreetsetes hinnangulistes mudeliparameetrites. Kasvukõverad näitasid, et kõrguskasvus on eelis katsetatud materjalil kuni raieringi keskpaigani, mis näitab geneetilise selektsiooni pikaajalist mõju. Arukase puhul olid kasvukõrguse erinevused kvalifitseeritud ja katsetatud istutusmaterjali vahel püsivad sõltuvalt kasvukoha kvaliteedist. Männi puhul suurenesid erinevused vastavalt kasvukoha viljakuse paranemisele, mis viitab aretuse tõhusamale mõjule sobivates kasvukohtades. Mudelit soovitatakse kasutada kuni 40-aastaste männinoorendike ja 20-aastaste arukaasikute puhul sobivates kasvukohtades, sest mudel annab konkreetsemaid suuniseid metsamajandustöödeks, näiteks esmaste valgustusraiete planeerimiseks. Mudel sobib kasutamiseks täpsete piirkondlike biomassihinnangute koostamisel, mis on olulised tõenduspõhiste poliitiliste otsuste tegemisel (**III**).

Uuritud kuusekloonidel täheldati erinevaid kasvumustreid, mis viitab geneetilisele varieeruvusele kasvukiiruses, Chapman-Richardsi funktsiooni kujus ja asümptoodis. See võimaldab täppisselektsiooni, mis põhineb raievanuses puu mõõtmete ja kasvutendentside prognoosimisel. Kasvuprognooside tegemisel tuleks baasvanusel põhinevates muutumatutes funktsioonides katsetada kloonipõhiseid geneetilisi täiendusi, et parandada prognooside täpsust geneetiliselt parendatud istutusmaterjali kasutamisel (**I**).

Pikaajaline varieeruvus kõrguse juurdekasvus näitab valitud kuusekloonide tundlikkust ilmastiku suhtes ja nende reaktsiooni kliimamuutustele. Ilmastikutingimused mõjutasid kloone erinevalt, seega võib tundlikkuse ja tootlikkuse vaheliste seoste arvestamine toetada Läänemere idaosa kuusemetsade tootlikkust ja plastilisust muutlikele kliimatingimustele.

Kuna kõrguskasvu kujunemine kestab kaks aastat, ilmnesid ilmastikutingimuste otsesed ja kaudsed mõjud. Puude puhkeperioodi ajal oli kõrguskasv temperatuuriga tugevas positiivses seoses, samas oli suvistel ilmastikutingimustel sekundaarne mõju. Tootlikumad kloonid olid vähem tundlikud ebasoodsate ilmastikutingimuste suhtes, mistõttu on kõrguskasv oluline tunnus vastupidavamate kuusekloonide valimisel muutuvates ilmastikutingimustes (**IV**).

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I

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Article

Genetic Parameters of Diameter Growth Dynamics in Norway Spruce Clones

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Abstract: The breeding of Norway spruce in northern Europe has substantially contributed to the production of high-quality wood. The vegetative propagation of robust elite clones could help to sustain the provision of high-quality timber in the face of changing climates. For the adequate evaluation of genetic gains, the altered tree growth dynamics of the clones need to be understood, yet essential information about the long-term growth dynamics of improvedboreal trees is still lacking. We examined a 50-year-old clonal plantation in Latvia to distinguish the clonal effects on diameter growth function parameters and estimate the genetic parameters. A mixed-effect modelling approach was used, in which the clones were applied as random effects on the parameters of the Chapman–Richard equation. All model parameters showed significant variance in the genotypic coefficients of variation CV_g which ranged between 11.0 and 17.1%, with the highest being for the growth rate. The heritability (H^2) of the diameter at breast height (DBH) reached 0.35 at the age of 40, while CV_g decreased from 12.9% to 7.8% between the ages of 20 and 45. Age–age genotypic correlations were positive and were strong or very strong (>0.76). The realised genetic gain varied from −6.3 to +24.0% around the trial mean. A substantial improvement in DBH was indicated when elite clones were selected for vegetative propagation based not only on early measurements, but also considering the genetic variance in the model parameters.

Keywords: clonal selection; genetic variance; growth modelling; Norway spruce; realised genetic gain

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1. Introduction

In the Baltic Sea region, the planting of forests has a substantial economic impact [1]. The breeding of Norway spruce (*Picea abies* (L.) Karst.) has taken place since the middle of the 20th century due to the financial importance of coniferous trees [2]. The profitability of long-term investment in genetic selection has been proven by increased productivity, quality and resistance to the risks of a changing environment, which has resulted in an improved monetary value [1–5]. The growing demand for wood-based biomass continues to maintain the significance of tree breeding in the future [1]. In addition, the financial performance of genetically improved material has been enhanced by the inclusion of carbon pricing [4], which indicates the additional benefits of breeding in terms of carbon sequestration.

When appropriately managed (e.g., in a sparsely planted plantation), Norway spruce can rapidly reach its target diameter [6], thereby shortening rotation time, reducing establishment costs and increasing financial outcomes [7,8]. In turn, a reduced rotation time can mitigate the risk of biotic and abiotic damage, such as that from wind, drought, root rot, bark beetle attacks, etc., which are commonly acknowledged threats for successful Norway spruce management in a changing climate [9–13].

Tree breeding has been estimated to advance production by 10–35% compared to unimproved material [14]. Substantial variations in genetic gains exist among the different improvement levels, including the combination of additive and non-additive genetic

variance in clonal selection [15], which can increase the genetic gain for conifers by 5–20% compared to that from familial selection [16]. A recent study in Sweden showed a double genetic gain in diameter at breast height (DBH) for clonal deployment compared to improved seedlings [17]. The clonal propagation of Norway spruce is justified by a substantial growth improvement [1], the immediate transfer of genetic gains to new plantations, the flexibility to quickly adapt nursery production to various environmental conditions and management objectives [18] and its profitability [19]. Overall, considerable knowledge has been obtained from clone testing, which can be implemented in the practical management of clonal plantations [20]. Despite this, the relatively high initial investment that is required compared to more common types of reproductive materials (seedlings) restricts the wider deployment of vegetative propagation [1,19], even though it has a stable market share (for example, in Sweden, circa 1 million rooted cuttings are produced annually) and the interest of buyers is growing [19].

The substantial variation in genetic gains for growth has resulted in altered stand dynamics for improved planting stocks [21,22]. Growth and yield modelling is commonly used for the long-term estimation of forest development and the evaluation of alternative management options [23–25], although it is usually based on data from unimproved stands [26]. To avoid biased predictions, differences in the growth dynamics of different genetic entries must be understood to allow for the adequate inclusion of genetic gains in the growth functions [21,22,27]. Genetic improvement can affect height and diameter growth differently [28], and so the commonly applied site index adjustment alone [29–32] may not accurately account for the altered dynamics of the DBH, which is also an important component in reliable predictions of forest yield [33–37].

Overall, little is known about the long-term genetic effects of cloning on Norway spruce diameter growth. To ensure an efficient breeding cycle, the genetic gains are usually estimated from young field trials and the optimal selection time for Norway spruce is the age of 10–16 years [38]. This is justified by sufficiently high correlations between the early measurements and the resulting production at the end of the rotation [39], although the realised yield can be higher than was expected based on the early height [19]. Therefore, an exceptionally widely planted (5×5 m) clonal Norway spruce plantation at rotation age with presumably delayed inter-tree competition could provide insights into the diameter growth differences among the various genetic entries, which could indicate distinct clonal effects on the growth function parameters. The origin of the study material (vegetative propagation) was expected to demonstrate a large proportion of the genetic variations [17,40], with clones representing the highest level of genetic uniformity [41]. Although the utilisation of vegetatively propagated Norway spruce is still not a common practice in commercial forestry, this trial was expected to provide essential information about genetic effects up to rotation age, which is currently lacking, in order to obtain more precise predictions of diameter growth [18].

Thus, the aim of this study was (i) to determine the clone effect on the parameters of the Norway spruce diameter growth curve by applying a mixed-effect modelling approach and (ii) to estimate the dynamics of the genetic parameters for diameter at breast height up to the final harvest dimensions. We hypothesised that all model parameters would have significant genetic variance.

2. Materials and Methods

2.1. Study Site and Material

The study was carried out in a Norway spruce clonal plantation, which is located on fertile mineral soil under mesotrophic conditions in eastern Latvia (56°42′ N, 25°53′ E) at 119 m above sea level. The plantation is comparable to the *Oxalidosa* forest type [42]. The site index was 36.0 m. The mean annual temperature in the study area was circa +6.0 °C, with the mean monthly temperature ranging from −6.4 °C in February to +17.1 °C in July. The mean annual precipitation was circa 700 mm [43].

The plantation was established in 1964 using vegetatively propagated (grafted) planting material from 20 selected fast-growing plus trees of local origin, at a spacing of 5 × 5 m (400 trees ha^{-1}). The rootstock material comprised seedlings of local origin. In total, 421 trees were planted in randomly distributed single-tree plots (11–31 replications (ramets) per clone). Weed control was carried out in the planting year and the first year after planting. No thinning was conducted prior to the sampling. No measurements had been performed before during the trial.

Both DBH and height were measured for all mature trees (i.e., 50 years old or more) in the plantation. The plantation growth and yield data for trees at the age of 50 years were published previously by Katrevičs et al. [6].

Cores from pith-to-bark at breast (1.3 m) height were collected at 5-mm increments from 221 50-year-old trees, which represented 19 of initially planted 20 clones (7–19 ramets per clone). Only straight trees with no visible crown asymmetry or other stem defects, such as visible root rot, double tops or severe browsing damage, were selected for core sampling. Annual ring width data were obtained using high-frequency densitometry with a LignoStation [44]. These were cross-dated and verified by graphical inspection and using the COFECHA software [45].

The tree ring data allowed for the study of the age–diameter relationship at an annual resolution [46]. The DBH for each year was reconstructed using annual diameter increments, which were based on the measurements that were taken at the age of 50 years. For the diameter reconstruction, the tree stems were assumed to be circular so that the DBH could be calculated from the incremental cores. As a result, time-series data for the DBH of each tree were obtained for the ages of 20–50 years (Figure 1).

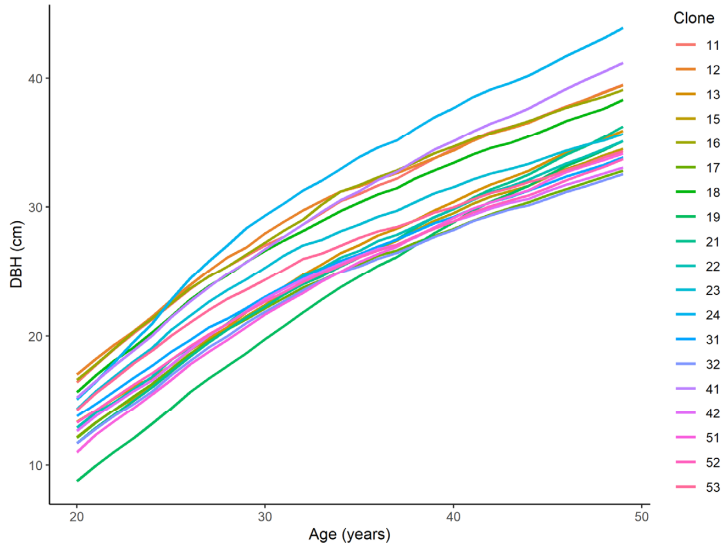

Figure 1. The mean diameter growth trajectories of the 19 Norway spruce clones that were analysed in this study.

2.2. Modelling Approach

The clone effect on the parameters of the diameter–age relationship was investigated by applying the Chapman–Richard base equation:

$$DBH_{iA} = \beta_1\left(1 - e^{(-\beta_2 A)}\right)^{\beta_3} + \varepsilon_{iA} \quad (1)$$

where DBH_{iA} is the DBH for the i-th clone at age A, β_1 is the asymptotic diameter parameter, β_2 is the rate parameter, β_3 is the shape parameter and ε_{iA} is a normally distributed zero-expectation random error due to the DBH that was observed at age A [47]. We followed the approach of using models that had been previously fitted successfully by other researchers [48]. The preliminary analyses and previous studies have suggested that the Chapman–Richard function is a biologically reasonable selection for modelling tree growth curves [34,46,49,50].

The clone effect on the diameter–age relationship was modelled as random effects on the parameters in Equation (1) using the function:

$$DBH_{iA} = [\beta_{10} + b_{1i}] \times \left(1 - e^{(-[\beta_{20}+b_{2i}]\times A)}\right)^{\beta_{30}+b_{3i}} + \varepsilon_{iA} \quad (2)$$

where DBH_{iA} and ε_{iA} are as defined as for Equation (1), β_{10}, β_{20} and β_{30} are fixed effect parameters and b_{1i}, b_{2i} and b_{3i} are random effect parameters for the i-th clone ($b_{1i} \sim N\left(0, \sigma^2_{b_1}\right)$, $b_{2i} \sim N\left(0, \sigma^2_{b_2}\right)$ and $b_{3i} \sim N\left(0, \sigma^2_{b_3}\right)$ with no correlation among these parameters). Heteroscedasticity in the error term ε_{iA} was not detected. The autocorrelations of the errors that were due to ring width measurements on the same trees were modelled by mixed first-order autoregressive and moving average structures (ARMA (1,1)). To remove the effects of the various variances in the different clones, we modelled different variances for each factor (clone) using the variance function [51].

Equation (2) was fitted using nonlinear mixed-effect regression with the nlme package in R software [52]. The effects of the clone on the model parameters were investigated using a common approach: eliminating the random effect parameters from the model one by one by using random effects for all parameters initially. Different combinations of parameters were tested and the best model was selected using the likelihood ratio test, Akaike's information criterion (AIC) and the Bayesian information criterion (BIC). The fitted model was evaluated using mean bias and root mean squared error [53]. The significance of random factors in the final fitted model was evaluated by applying likelihood ratio tests of model reductions for each random effect term, which were provided by the rand function in the lmerTest package [54]. The normality of the final fitted model residuals was tested by applying the Jarque–Bera test.

2.3. Genetic Parameters

To estimate the variance components, the following model was used:

$$y_{ij} = \mu + C_i + \varepsilon_{ij} \quad (3)$$

where y_{ij} is the observation of the ith tree from the jth clone, μ is the overall mean, C_i is the random effect of the cloning and ε_{ij} is the random error. To evaluate the dynamics of the genetic parameters, (i) the broad-sense heritability (H^2) of DBH for each year and (ii) the age–age genotypic correlations of DBH among the years were estimated as follows:

$$H^2 = \frac{\hat{\sigma}^2_G}{\hat{\sigma}^2_G + \hat{\sigma}^2_\varepsilon} \quad (4)$$

where $\hat{\sigma}^2_G$ and $\hat{\sigma}^2_\varepsilon$ are the estimated variance components of clone and residual, respectively, and:

$$r_G = \frac{\widehat{Cov}_{(Gxy)}}{\sqrt{\hat{\sigma}^2_{(Gx)} \times \hat{\sigma}^2_{(Gy)}}} \quad (5)$$

where $\hat{\sigma}^2_{(Gx)}$ and $\hat{\sigma}^2_{(Gy)}$ are the genotypic (clone) variances at two different ages and $\widehat{Cov}_{(Gxy)}$ is the estimated genotypic covariance between the two measurements.

For the final fitted model, we adapted a formula for calculating the genotypic coefficient of variation (CV_g) [55] in order to describe the extent of genetic variability among the clones for any random effect parameter:

$$CV_g = \sqrt{\hat{\sigma}^2_{b_x}} \cdot \frac{100}{\hat{\beta}_x} \quad (6)$$

where CV_g is the genotypic coefficient of variation, $\hat{\sigma}^2_{b_x}$ is the estimated variance for the random effect parameter x and β_x is the fixed effect parameter x. The CV_g of DBH was calculated for each year. For comparison, the H^2 and CV_g of tree height at the age of 50 years was estimated.

The realised genetic gain at the age of 50 years (final harvest age) was estimated for each clone using the best linear unbiased predictions (BLUPs) from the final fitted model as a percentage of the trial mean DBH.

3. Results

3.1. The Growth Model

The model form with all three random parameters (random asymptote (b_{1i}), random rate (b_{2i}) and random shape (b_{3i})) had the lowest value of the AIC statistic (−189.152) (Table 1). Overall, the model fit was significantly improved by addition of the random rate and/or shape into the model that already contained the random effect parameter b_{1i} compared to the anamorphic random asymptote equation ($p < 0.01$).

Table 1. Parameter estimates (fixed effect parameters: β_{10}, β_{20} and β_{30}; estimated variance components: $\sigma^2_{b_1}$, σ^2_{b2}, $\sigma^2_{b_3}$, σ^2_ε) and model statistics (AIC, Akaike's information criterion; BIC, Bayesian information criterion; logLik, log likelihood test) of the Chapman–Richard base equation when applying different combinations of random asymptotes (β_1), random rates (β_2) and random shapes (β_3), which were fitted to diameter at breast height from the 19 clones that were used in the study.

Random Parameter in Model	Parameter Estimates									
	β_{10}	β_{20}	β_{30}	$\sigma^2_{b_1}$	σ^2_{b2}	$\sigma^2_{b_3}$	σ^2_ε	AIC	BIC	logLik
β_1	46.403	0.0466	1.610	16.417	n/a	n/a	24.253	−73.140	96.806	61.57
β_1, β_2	46.630	0.0472	1.640	25.116	3.53×10^{-5}	n/a	23.509	−184.040	−0.498	119.02
β_1, β_3	46.262	0.0471	1.650	15.141	n/a	0.0436	23.0467	−153.329	30.213	103.66
$\beta_1, \beta_2, \beta_3$	46.991	0.0467	1.624	26.686	6.37×10^{-5}	0.0371	21.678	−189.152	14.783	124.58

The residuals of the final model were distributed symmetrically around zero with an approximately even variance and did not violate the assumption of normality ($p = 0.154$). The model provided a good representation of the dataset (Figure 2). The distribution of the random effects did not indicate any noticeable violations of the assumption of normality. For the final fitted model, the mean bias was −0.57 cm with a root mean square error of 3.61 cm.

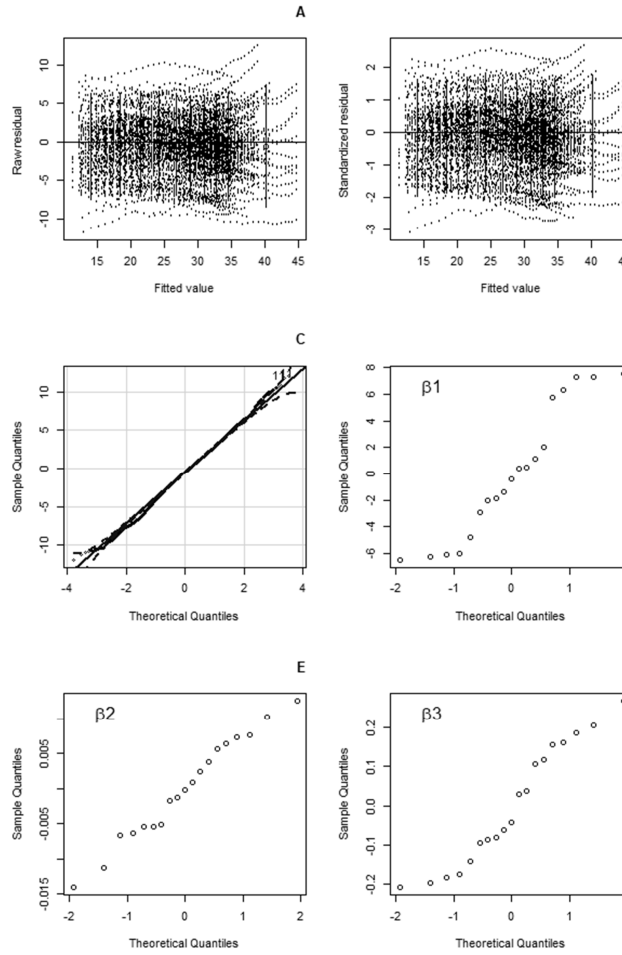

Figure 2. Statistics of the final fitted Chapman–Richard mixed model that was applied to investigate the clone effect of the diameter–age relationship on the parameters: (**A**,**B**) plots of raw (**A**) and standardised (**B**) residuals for the final equation. The whiskers denote the 95% confidence intervals of the residuals for the classified fitted values. (**C**) Quantile–quantile plot of the final fitted model. (**D**–**F**) Normal plots of the estimated random effects of the asymptotic diameter parameter β_1 (**D**), the rate parameter β_2 (**E**) and the shape parameter β_3 (**F**) for the final fitted model.

From the data that were used in this study, genetic variety (clone) significantly ($p \leq 0.05$) affected the asymptotic DBH and the rate and shape parameters of the Chapman–Richards diameter–age model. Thus, there was a significant polymorphism among the diameter–age trajectories of the different clones.

3.2. Dynamics of Genetic Parameters

The estimated broad-sense heritability (H^2) ± standard error (SE) for DBH increased from 0.19 ± 0.087 at the age of 20 years to 0.35 ± 0.131 at the age of 40 years (Figure 3). Afterwards, H^2 gradually decreased and was 0.32 ± 0.123 at the age of 50 years. On the contrary, the genotypic coefficient of variation (CV_g) was the highest at the age of 20 years (12.9%) and decreased to 7.8% at the age of 45 years, after which it remained stable for the following 5 years. The H^2 and CV_g for tree height at the age of 50 years was 0.41 ± 0.088 and 5.6%, respectively.

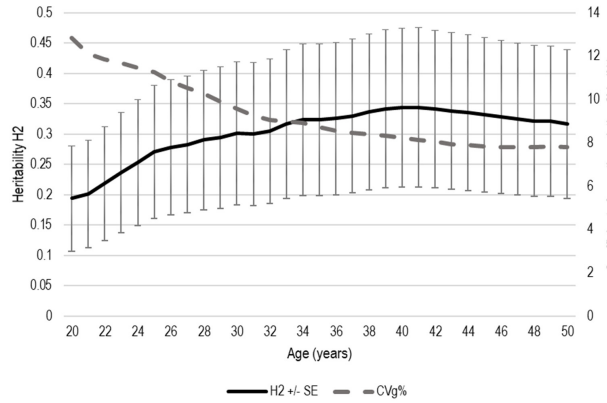

Figure 3. Dynamics of the estimated broad-sense heritability (H^2) and genotypic coefficient of variation (CV_g) during the studied period (age 20–50 years) of Norway spruce clones. The whiskers denote the standard error for H^2.

The estimated CV_g for the DBH growth model parameters β_1, β_2 and β_3 were 11.0, 17.1 and 11.9%, respectively. Overall, variance in the asymptotic DBH due to the clonal effects was slightly greater ($\sigma^2_{b_1}$ = 26.69 cm) than the within-group (within-clone) error variance (σ^2_{ε} = 23.05 cm) (Table 1). The realised genetic gains of the clones at the final harvest age varied from −6.3 to +24.0% around the trial mean (Figure 4).

The estimated age–age genotypic correlations (r_G) were positive and mainly very strong (>0.80), although they were slightly weaker, yet still strong (>0.76), for the older trees (age 20–22 versus age 46–50 years). There was a trend of slightly stronger correlations between similar ages with increasing age. For instance, DBH between age 45 and 50 was 100% genetically correlated, while r_G between ages 20 and 15 was 0.97.

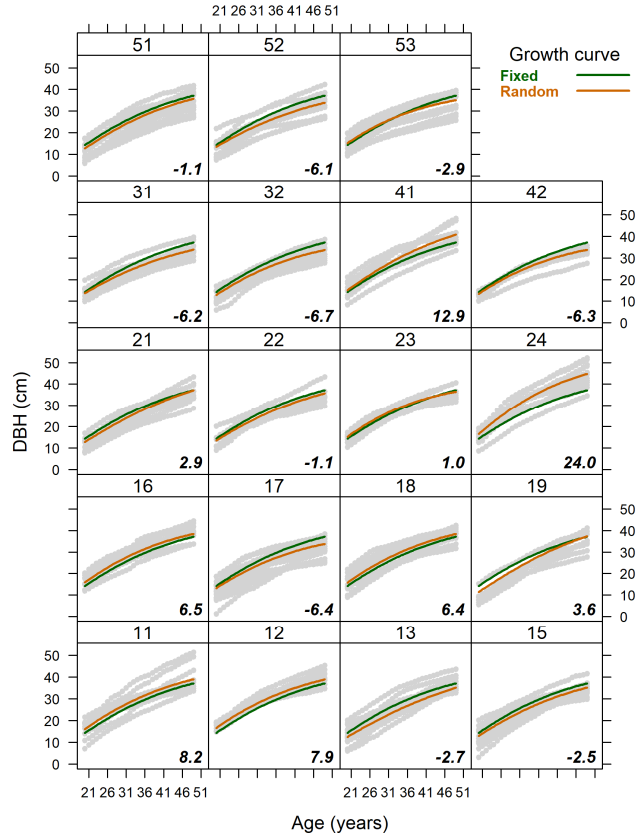

Figure 4. Predicted trajectories of DBH growth curves for population mean (fixed), each individual clone (random) and its realised genetic gain (numbers in bold and italic, %) at the final harvest age of 50 years (45 years of breast height age) using the final fitted model. Grey dots represent the sample data for each clone.

4. Discussion

Growth curve fitting is a common procedure that is used to understand general biological growth trends [56] and incorporating factors that affect this curve can improve the accuracy of the function under different conditions [33,57]. These factors include any silvicultural treatment over time [58], among which clonal effects are perceived. In our study, the Chapman–Richards equation, with its sigmoid form, inflection point and asymptote, fitted the data well (Figure 2) and the function parameters were meaningful for the analysis of the response of DBH to clonal effects over time [58,59].

Applying a mixed model, we estimated the population mean response that was common to the entire clonal plantation as fixed effect parameters [34], while random effect parameters that varied around the fixed mean [60] represented the specific responses of the clone grouping variable (Table 1, Figure 4). The possibility of estimating the variance within and among the clones for the random effect parameters [51,61] was an important advantage in terms of analysing the growth modelling results from a tree breeding perspective, since this field of study widely utilises genetically determined variations in traits of interest (in our case, the model parameters) to estimate quantitative genetic parameters and breeding values [55].

Our final model fitting results showed that all three model parameters (asymptote, growth rate and shape) were significantly affected by clone. There are not many previous studies on this issue, but those that do exist have mainly explored the tree height growth response to genetic effects. For loblolly pine (*Pinus taeda* L.), Sabatia and Burkhart [62] found that clone significantly affected the asymptotic height and shape parameters of the Chapman–Richards height–age model, while Knowe and Foster [63] concluded that half-sib families had an effect on the asymptote and rate. Half-sib genetic varieties and provenance have been reported to only affect the asymptote of the Korf function [29,64]. In contrast, Sprinz et al. [65] only reported the effects of half-sib families on the shape parameter. In Chinese fir (*Cunninghamia lanceolata* (Lamb.) Hook.), height growth trajectories in stands with different provenances only differed in the asymptote [66]. A strong genetic influence on the asymptote has also been reported for Konishii fir (*Cunninghamia konishii* Hay.) using an application of the Weibull-based function of DBH [67].

4.1. Dynamics of Clone-Specific Diameter Growth and Its Genetic Parameters over Time

Although variance component analyses are of primary interest in quantitative genetic studies, the random effect variances in the model parameters have been rarely reported or interpreted within ecological modelling [68]. Our results of the random effects showed significant variances in all three model parameters that were determined by the genetic effects. The overall magnitude of variation in DBH among the clones was greater than that within the clones (Table 1), which indicated the great importance of random effect variance, i.e., clonal differences, for selection [61,68,69]. Moreover, the genotypic coefficients of variation for the model parameters (asymptote, growth rate and shape) ranged between 11.0 and 17.1%, which exceeded the variation in DBH at the time of final felling (7.8%) and suggested the potential for genetic improvement in the asymptotic DBH, as well as a more rapid radial growth trajectory. For DBH growth function of Konishii fir, provenance and family have been reported to account for 26% of the variation in the asymptote, but only 4% in both the rate and shape [67]. For the loblolly pine height curve, the coefficients of variation among the clones in the asymptote and shape of the Chapman–Richards function have been estimated to be 4.2 and 2.8%, respectively [70].

By comparison, the CV_g for DBH in trials involving 19-year-old Norway spruce clones has been reported to vary between 13.6 and 15.9% [71]. Still, our results showed that CV_g and H^2 were not constant and changed over time. The estimated H^2 increased from 0.19 at the age of 20 years to a peak of 0.35 at the age of 40 years. A similar trend has been observed for the narrow-sense heritability h^2 of DBH in open- pollinated progenies of Norway spruce in southern Sweden, for which h^2 stabilised at circa 0.22 at the cambial age of 10 years after increasing from close to zero near the pith [72]. For Scots pine full-sib families in Sweden, a trend of increasing h^2 has been observed for wood quality traits and cumulative ring width, for which this parameter increased from very low to 0.25 at the age of 20 years [73]. Hannrup et al. [71] reported a H^2 of 0.34–0.50 for 19-year-old Norway spruce clones, while a low H^2 (< 0.14) was estimated for juvenile white spruce (*Picea glauca* (Moench) Voss) somatic clones 4 years after outplanting [74].

In contrast to H^2, CV_g decreased by almost half from 12.9% at the age of 20 years to 7.8% at the age of 45, after which it remained stable (Figure 3). Similar to descendent trend that was observed for CV_g in our study, spruce clones in series of experiments in northern

Germany demonstrated a steady decrease in genetic variance in height from circa 20% at the age of 3 years to a plateau of 7% after the age of 8 years [75]. Joint site data from Sweden showed that the coefficient of additive genotypic variation CV_a for DBH in Norway spruce decreased from 15.45% to 11.91% at the ages of 12 and 21 years, respectively [76]. The estimated CV_a showed a marked decline with age for both H and DBH (from 25–33% to 7–14%) in Silver fir (*Abies alba* Mill.) up to the ages of 10–15, after which they became stable [77].

In our study, H^2 and CV_g stabilised after the age of 40–45 years (Figure 3), which was likely due to reaching the moment of canopy closure and the intensification of inter-tree competition [78] as diameter increment is considered to be the trait that is most (first) affected by competition [79]. Canopy closure depends on the initial planting density and the increment of the trees. The onset of inter-tree competition in loblolly pine has been estimated to be after 5 years in the most densely planted plots (1.2 × 1.2 m) and after 8.6 years in the most sparsely planted plots (3.7 × 3.7 m) [80]. The latter age corresponds to circa 35% of the rotation age for managed *P. taeda* [81], which indicates a longer period of competition-free early growth for the wider spacing. Although canopy closure in Norway spruce progeny plots in northern Europe with conventional spacing is typically observed at the age of 10–20 years [79], the low planting density (5 × 5 m) in the study site could have delayed it substantially [82,83].

Nevertheless, we acknowledge that the exceptionally sparsely planted trial is an unusual competitive environment for plantations. Some of the commonly known risks for fast growing sparely planted Norway spruce include reduced wood density and stronger branching, which reduce timber quality [71,72,84]. Still, despite the unfavourable negative phenotypic correlations between fast growth and wood quality traits, selection for both may be possible at a clonal level [12,85]. Our study site also differed from common Norway spruce plantations in terms of its reproductive material (vegetatively propagated grafted clones), which is not commonly used as planting stock. Liziniewicz et al. [39] concluded that growth differences among different genetic varieties can be assumed to be independent of plant type, although they compared seedlings to rooted cuttings. The rootstock × scion effect has been reported as being inessential to the growth of loblolly pine, which is contrary to the genetic and site impacts [86]. The fast growth of the studied plantation indicated no potentially negative effects of cyclophysis [87–90], which has occasionally been detected in clonal trials [91]. However, we stress that our interest was in fitting the model as an analytical tool to investigate the differences in the response curve trajectories of different clones of the same propagation type with a wide range of realised genetic gains for DBH (Figure 4). Still, the clones characterise a local population and thus, had to be generalised with caution.

4.2. Age–Age Genotypic Correlations

The growth pattern of each individual tree is shaped by a combination of both its genetics and environment [92]. Still, the DBHs of individual trees are unlikely to be affected by competition at a genetic level over time from the indirect additive effect of neighbouring trees [79], which was indicated by the strong to very strong positive genotypic age–age correlations that were observed in this study ($r_g > 0.76$).

Somewhat stronger r_G at older ages have also been reported previously for various conifer tree species, which could be associated with the cumulative nature of the growth traits [93,94]. Our results corresponded well to earlier studies of growth traits in progeny trials, which showed very strong genotypic relations among similar ages, with a slight decline as the age differences increased [72,75,77,78,94].

Overall, the strong age–age correlations and clone-specific DBH growth trajectories, which were mostly without pronounced rank shifts during the studied period (Figure 1), justify the early selection for DBH. We observed that the clone-specific DBH growth curves are primarily relatively parallel to the population mean curve (Figure 4) and that there were no trends of superior clones, in terms of asymptotic DBH, having a more rapid growth rate.

Nevertheless, all DBH growth curve parameters showed substantial genotypic variance ($CVg \geq 11.0\%$, Table 1) and separate clones (e.g., clone numbers 19, 24, 53) had obviously different growth shapes and rates (Figures 1 and 5), which were likely associated with the different genetically determined growth responses of certain clones to climatic factors [95].

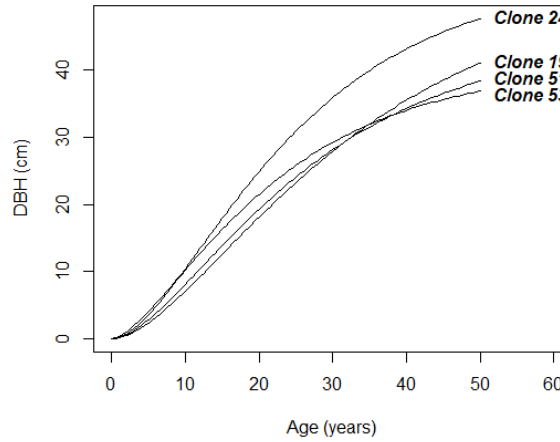

Figure 5. Growth curves of the selected clones (19, 24, 51, 53) with markedly different DBH growth trajectories.

Thus, we argue that the selection of superior clones using early measurements of DBH could be combined and improved with information about the genetic variations in growth curve parameters when such data (e.g., increment cores) become available from long-term trials. In particular, intensive tree breeding that applies vegetative propagation would benefit from the knowledge of genotype-specific growth trajectories when a set of only a few superior clones is selected. Precise growth functions can improve the effectiveness of tree breeding, which supports the early selection of superior genetic entries using more reliable information on their expected future performance and the subsequent economic outcome of their selection [62,63]. Even small differences in the predicted growth traits can have a substantial impact on the ranking of clones [63]. The knowledge of genetic variances in function parameters can be utilised to develop and test more practically desirable and dynamic base–age–invariant functions [96] by incorporating genetic effects as modifiers for the model parameters [97], which is just as important in practical applications in forestry.

5. Conclusions

We found different growth patterns among the studied Norway spruce clones. There were significant differences between clones in terms of all three of the parameters of the Chapman–Richards function: asymptote, rate and shape. All diameter growth curve parameters demonstrated genotypic variations between the clones that were sufficient for selection with a wide range of realised genetic gains in DBH (up to +24%) that had the potential for genetic improvement. The studied clones possessed considerable heritability ($H^2 = 0.32$) and a significant genotypic coefficient of variation ($CV_g = 7.8\%$), which tended to stabilise at the age of 40–45 years. Although the mainly very strong age–age genotypic correlations would justify selection for DBH at earlier age, we suggest that growth curve parameters are just as important for tree breeding in terms of the selection of elite clones,

once the data from long-term clonal tests are available. The substantial genetic variation in growth rate, shape and asymptote suggests the potential for more precise selection using predictions for not only final dimensions, but also desirable patterns of growth trajectories. Based on this information, clone-specific genetic modifiers should be tested using dynamic base–age–invariant functions for future growth predictions in practical forestry in order to improve the prediction accuracy for genetic entries with various genetic gains.

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II

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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).

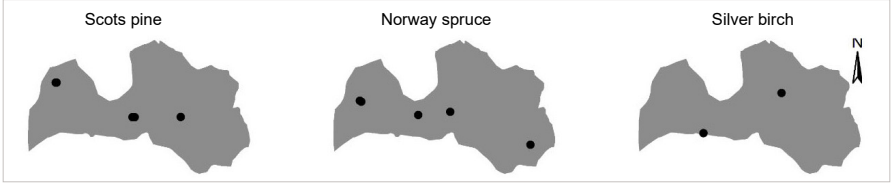

Figure 1. Locations of the progeny trials in Latvia with available tree height measurements for model testing and modifications

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; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

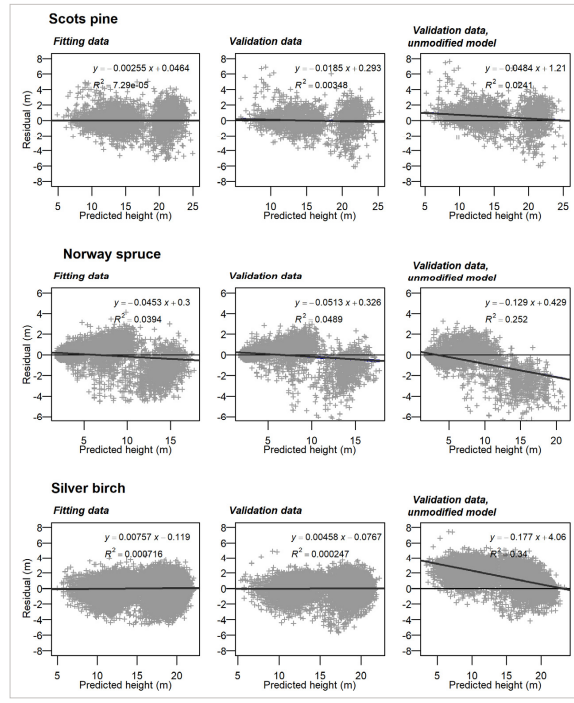

Figure 2. Residuals of fitting and validation data against the final best-fit models with multipliers (first two columns) and the unmodified reference model (third column) for Scots pine (upper three panels), Norway spruce (middle three panels) and silver birch (lower three panels)

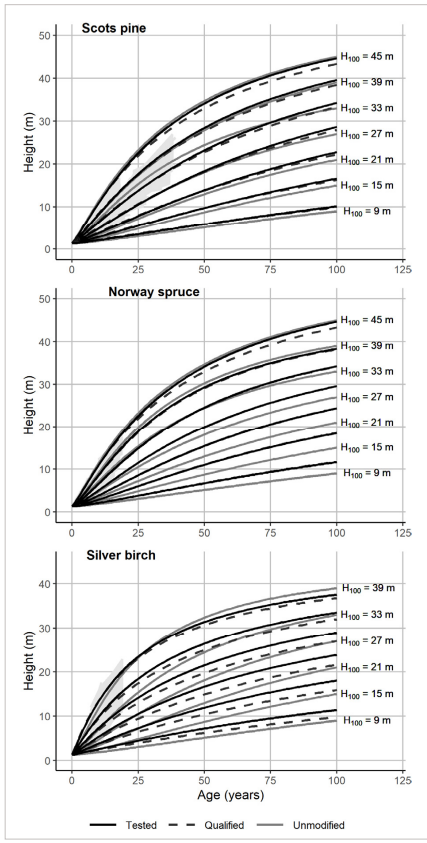

Figure 3. The final best-fit models with the genetic multipliers (black solid and dashed lines for improved categories 'tested' and 'qualified', respectively) vs. the unmodified model (dark grey solid lines) for Scots pine (upper panel), Norway spruce (middle panel) and silver birch (lower panel). Light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

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

Model II: modified theoretical (unobserved) variable X:

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

Model III: modified resolved a_1:

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

Model IV: modified resolved a_2:

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

Model V: modified b_2 and b_3 in resolved a_2:

$$H_2 = 1.3 + \frac{A_2^{b_1}}{g_2 \cdot b_2 + 100 \cdot g_3 \cdot b_3 \frac{A_1^{b_1}}{100b_3 + A_1^{b_1}} + \frac{A_1^{b_1}}{100b_3 + A_1^{b_1}} A_2^{b_1}} \quad (5)$$

Model VI: modified resolved a_3:

$$H_2 = 1.3 + \frac{A_2^{b_1}}{b_2 + 100\, b_3 \frac{A_1^{b_1}}{100b_3 + A_1^{b_1}} + g_3 \cdot \frac{A_1^{b_1}}{100b_3 + A_1^{b_1}} A_2^{b_1}} \quad (6)$$

Model VII: modified resolved a_1 and a_2:

$$H_2 = 1.3 + \frac{A_2^{g_1 \cdot b_1}}{g_2 \cdot (b_2 + 100\, b_3 \frac{A_1^{b_1}}{100b_3 + A_1^{b_1}}) + \frac{A_1^{b_1}}{100b_3 + A_1^{b_1}} A_2^{g_1 \cdot b_1}} \quad (7)$$

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

$$H_2 = 1.3 + \frac{A_2^{g_1 \cdot b_1}}{g_2 \cdot b_2 + 100 \cdot g_3 \cdot b_3 \frac{A_1^{b_1}}{100b_3 + A_1^{b_1}} + \frac{A_1^{b_1}}{100b_3 + A_1^{b_1}} A_2^{g_1 \cdot b_1}} \quad (8)$$

Model IX: modified resolved a_1 and a_3:

$$H_2 = 1.3 + \frac{A_2^{g_1 \cdot b_1}}{b_2 + 100\, b_3 \frac{A_1^{b_1}}{100b_3 + A_1^{b_1}} + g_3 \cdot \frac{A_1^{b_1}}{100b_3 + A_1^{b_1}} A_2^{g_1 \cdot b_1}} \quad (9)$$

Model X: modified resolved a_2 and a_3:

$$H_2 = 1.3 + \frac{A_2^{b_1}}{g_2 \cdot (b_2 + 100\, b_3 \frac{A_1^{b_1}}{100b_3 + A_1^{b_1}}) + g_3 \cdot \frac{A_1^{b_1}}{100b_3 + A_1^{b_1}} A_2^{b_1}} \quad (10)$$

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

$$H_2 = 1.3 + \frac{A_2^{b_1}}{g_2 \cdot b_2 + 100 \cdot g_3 \cdot b_3 \frac{A_1^{b_1}}{100b_3 + A_1^{b_1}} + g_3 \cdot \frac{A_1^{b_1}}{100b_3 + A_1^{b_1}} A_2^{b_1}} \quad (11)$$

Model XII: modified resolved a_1, a_2 and a_3:

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

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

$$H_2 = 1.3 + \frac{A_2^{g_1 \cdot b_1}}{g_2 \cdot b_2 + 100 \cdot g_3 \cdot b_3 \frac{A_1^{b_1}}{100b_3 + A_1^{b_1}} + g_4 \cdot \frac{A_1^{b_1}}{100b_3 + A_1^{b_1}} A_2^{g_1 \cdot b_1}} \quad (13)$$

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 (0.004)	0.997 (0.000)											
	qualified	1.029 (0.002)	0.997 (0.000)											
g_1	tested			1.011 (0.001)				1.019 (0.015)	1.011 (0.014)	1.018 (0.005)		0.828 (0.029)	1.019 (0.032)	0.241 (0.126)
	qualified			1.011 (0.001)				0.970 (0.006)	0.964 (0.006)	1.035 (0.002)		0.781 (0.012)	0.970 (0.013)	0.476 (0.041)
g_2	tested				0.957 –0.005	0.823 (0.029)		1.030 (0.058)	0.860 (0.059)		0.953 (0.014)	0.839 (0.027)	1.030 (0.099)	0.041 (0.020)
	qualified				0.959 –0.002	0.786 (0.012)		0.855 (0.019)	0.682 (0.018)		0.907 (0.006)	0.792 (0.011)	0.855 (0.032)	0.104 (0.016)
g_3	tested					0.833 (0.027)	0.913 (0.011)		0.870 (0.058)	1.057 (0.040)	1.010 (0.032)	0.952 (0.034)	1.000 (0.068)	0.053 (0.018)
	qualified					0.799 (0.011)	0.923 (0.005)		0.693 (0.018)	1.211 (0.017)	1.132 (0.014)	1.070 (0.015)	1.000 (0.033)	0.116 (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 (0.003)	1.005 (0.000)											
	qualified	0.916 (0.001)	1.005 (0.000)											
g_1	tested			0.955 (0.001)				0.907 (0.005)	0.888 (0.004)	0.955 (0.004)		0.622 (0.019)	1.000 (0.012)	1.310 (0.020)
	qualified			0.964 (0.001)				0.927 (0.002)	0.909 (0.002)	0.964 (0.001)		0.63 (0.007)	1.000 (0.004)	1.301 (0.007)
g_2	tested				1.134 (0.004)	0.605 (0.023)		0.861 (0.012)	0.413 (0.016)		0.948 (0.006)	0.634 (0.018)	1.134 (0.0270	1.808 (0.124)
	qualified				1.103 (0.002)	0.595 (0.008)		0.891 (0.005)	0.449 (0.006)		0.933 (0.002)	0.643 (0.007)	1.103 (0.010)	1.727 (0.041)
g_3	tested					0.625 (0.022)	1.544 (0.013)		0.429 (0.015)	1.000 (0.040)	1.687 (0.022)	1.687 (0.020)	1.000 (0.057)	1.803 (0.122)
	qualified					0.616 (0.008)	1.514 (0.006)		0.466 (0.006)	1.000 (0.017)	1.721 (0.010)	1.712 (0.010)	1.000 (0.022)	1.722 (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 (0.002)	0.996 (0.000)											
	qualified	1.098 (0.001)	0.996 (0.000)											
g_1	tested			1.045 (0.001)				1.032 (0.011)	0.856 (0.011)	1.045 (0.003)		0.462 (0.011)	1.000 (0.028)	1.438 (0.087)
	qualified			1.045 (0.000)				1.032 (0.004)	0.814 (0.004)	1.045 (0.001)		0.565 (0.004)	1.000 (0.009)	1.150 (0.025)
g_2	tested				0.840 (0.003)	0.380 (0.009)		0.946 (0.039)	0.275 (0.009)		0.840 (0.007)	0.469 (0.010)	0.837 (0.071)	2.335 (0.743)
	qualified				0.842 (0.001)	0.466 (0.003)		0.946 (0.014)	0.285 (0.003)		0.842 (0.002)	0.569 (0.003)	0.838 (0.024)	0.987 (0.091)
g_3	tested					0.396 (0.008)	0.842 (0.005)		0.282 (0.009)	1.000 (0.014)	1.000 (0.011)	1.250 (0.020)	1.000 (0.028)	2.331 (0.735)
	qualified					0.480 (0.003)	0.830 (0.002)		0.290 (0.003)	1.000 (0.005)	1.000 (0.004)	1.361 (0.008)	1.000 (0.010)	0.986 (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.

III

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Original Article

Height growth patterns of genetically improved Scots pine and silver birch

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Abstract

The breeding of forest tree species in the Baltic region has notably contributed to wood production for the bioeconomy. Growth modelling is used for long-term estimates of forest development. However, usually based on data from unimproved stands, they may underestimate the growth of improved trees. Accordingly, it is important to identify and integrate the altered stand dynamics associated with improved planting stock into existing growth models to accurately capture the resulting gains or, alternatively, develop new functions specifically designed for improved trees. We used the generalized algebraic difference approach to model and analyze height growth patterns of Scots pine and silver birch with different genetic improvement levels (improved forest reproductive material categories 'qualified' and 'tested'). Modelling was based on 14 260 and 55 926 height–age series from open-pollinated progeny trials in Latvia and Lithuania with an age range of 3–46 and 5–22 years for pine and birch, respectively. Dynamic generalized algebraic difference approach forms of commonly applied height growth functions with forest reproductive material-category-specific sets of coefficients were tested. The dynamic form of the Chapman–Richards and King–Prodan equations had the best fit for Scots pine and silver birch, respectively. The expected height growth of the category 'tested' was slightly better than the one for 'qualified', with more distinct differences in silver birch. The model with forest reproductive material-category-specific coefficients reflected the actual growth of improved trees; however, such application is limited to sites with medium and high site indices, where improved planting stock is typically used. We recommend the model for young stands up to the age of 20 and 40 years for pine and birch, respectively, considering the empirical data cover on which the functions are based. A unified dynamic height model with the same functional form but category-specific parameterization for different improvement levels allows a practical applicability and effective communication amongst diverse users, thereby promoting the utilization of the model amongst forest owners and managers who possess information regarding the origin of planting stock.

Keywords: GADA approach; dynamic modelling; genetic improvement

Introduction

Forests are a major natural resource in the Baltic region, and the forestry sector is a vital contributor to the bioeconomy on a pan-European scale along with the forestry sectors of the Nordic countries (Hetemäki 2020; Klauss 2020; Girdziušas *et al.* 2021). The forest sector is a significant contributor to the gross domestic product (GDP), providing employment in timber harvesting, processing, and transport. Forest products are also major exporting goods of the region, providing a valuable source of income. Namely, the GDP share of the forest sector in the Baltic States reaches 2.4%–4.0%, which is several times higher than the European average (0.72%) (Olschewski *et al.* 2020). Given the growing demand for roundwood as an alternative to fossil raw materials, sustainable management of forests aims to simultaneously increase timber production and forest carbon sinks (Hetemäki 2020) to maximize its potential in the region's bioeconomy.

In the Baltic region, Scots pine (*Pinus sylvestris* L.) is a dominant coniferous tree species with high economic importance for the sawn softwood market, whilst silver birch (*Betula pendula* Roth) is a dominating broadleaved species serving as raw material for plywood industry (Klauss 2020; Girdziušas *et al.* 2021). Considering the commercial importance of these species, breeding programmes have been conducted since the middle of the 20th century aiming to improve growth, quality, and resistance to biotic and abiotic risks (Jansons *et al.* 2006; Krakau *et al.* 2013; Gailis *et al.* 2020b). Regional tree breeding programmes are estimated to achieve 10%–30% of genetic gains in growth, resulting in profitability from increased production of high-quality timber (Jansons *et al.* 2011; Ruotsalainen 2014; Jansson *et al.* 2017; Gailis *et al.* 2020a). In 2021, 99.5% of the 23.9 million and 37% of the 5.4 million nursery seedlings of Scots pine and silver birch, respectively, in Latvia (LV) were grown from improved seed orchards' seeds (State Forest Service 2022). Considering the substantial share of improved seeds (for both sawing and planting) in Scots pine regeneration, as well as purposeful afforestation of marginal agricultural land over the last decades with improved birch seedlings aiming for high-quality plywood (Liepins and Rieksts-Riekstins 2013), the estimated noteworthy gains in growth need to be better reflected in forest management planning.

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Growth and yield models are common tools to predict forest development, plan silvicultural activities, or evaluate different management scenarios (Ahtikoski *et al.* 2012). However, existing growth models for the Baltic region are usually based on empirical data from unimproved trees collected several decades ago (Gould *et al.* 2008; Kuehne *et al.* 2022). Hence, concerns about incorrect predictions for improved material have been raised, which highlights a need to incorporate and reflect the enhanced growth of improved trees in growth models (Rehfeldt *et al.* 1991; Egbäck *et al.* 2017; Deng *et al.* 2020). Such growth models, which are calibrated or modified to account for altered dynamics for improved nursery stock, in the Baltic region are still lacking.

Given the available data from extensive genetic field trials of the main coniferous and broadleaved tree species Scots pine and silver birch, respectively, in the Baltic region, we aim to model height growth of genetically improved trees as a reliable proxy for areal production (Burkhart *et al.* 2012; Manso *et al.* 2021; Kuehne *et al.* 2022) with further potential to be implemented in growth simulator systems. We model the growth of the two categories of improved forest reproductive material (FRM)—'tested' and 'qualified', assigned to phenotypically selected material with or without determined superiority by comparative testing, respectively (Gömöry *et al.* 2021). The category 'qualified' represents first-generation seed orchard material with estimated genetic gains of 10%–15% for growth compared to unimproved trees, whilst predicted gains reach ∼20%–25% for the best genetically superior material (corresponding to 1.5-generation seed orchards) based on genetic field test findings (category 'tested') (Ruotsalainen 2014; Jansson *et al.* 2017). Therefore, the main objective of the study was to develop dynamic single tree height models for improved Scots pine and silver birch in the Baltic region to predict height growth and analyze differences in height growth patterns of different genetic improvement levels.

Methods

Study material

The study was carried out in the Baltic region—including data from LV and Lithuania (LT)—situated on the eastern European plain next to the Baltic Sea between ca. 55° and 58°N and 21° and 28°E (Fig. 1). Both are typical lowland countries with plains and low hilly elevations, with the highest peaks reaching 311.6 and 293.8 m above sea level in LV and LT, respectively. The region is located in the northern part of the temperate climate zone, with a distinct western–eastern gradient of continentality from a milder sea climate in the west to a more continental inland climate in the east (Laiviņš and Melecis 2003; Galvonaitė *et al.* 2013). The average mean annual air temperature in LV is 6.4°C ranging from +5.7°C to +7.5°C (from the inland to the coastal regions). The mean monthly temperature varies from −3.1°C to +17.8°C in February and July, respectively. The mean annual precipitation is 685.6 mm, reaching ca. 850 mm in coastal and upland regions. July and August are the wettest months (75.7–76.8 mm), whilst April is the driest (35.8 mm) (Latvian Environment, Geology and Meteorology Centre 2020). In LT, the average annual temperature is 7.4°C. The warmest month is July (18.3°C), whilst the coldest is January (−2.9°C). The average annual precipitation sum is 695 mm, the most of which falls in July (84 mm) and the least in April (37 mm) (Lithuanian Hydrometeorological Service 2021).

The study comprises tree height data from 11 remeasured progeny trials of Scots pine and silver birch (Fig. 1). Such trials are controlled experiments in tree breeding, where the offspring of phenotypically selected trees (plus trees) are planted and observed to comparatively evaluate their growth and characteristics, aiding in the selection of superior trees (genotypes) for further breeding and seed production. In total, 14 260 and 55 926 height–age series were used for pine and birch, respectively (Fig. 2). The available data covers ages from 8 to 42 years with height–age series consisting of two to seven height measurements for a single tree (Supplementary Tables S1 and S2). In total, the trials comprised progenies from 638 and 1048 families (an offspring from each plus tree forms a separate family) of Scots pine and silver birch, respectively (Supplementary Table S3). Experimental design for the families comprised single-tree plots in 10–93 replications (silver birch trials Taurene and Ukri) and 10–100-tree block plots in three to eight replications. The trials were established using 1–2-year-old seedlings at sites suitable for the particular species, with initial planting densities typically used in practice (from 2 × 1 to 2.5 × 2.5 m for Scots pine and silver birch, respectively). Scots pine was planted on relatively poor, sandy soil corresponding to the *Vacciniosa* forest type (Buss 1997). Silver birch trials in Latvia were planted on silty dry soils in former agricultural lands with mesotrophic conditions. In Lithuania, the birch trials were characterized by heavy-textured eutrophic soils of normal moisture (Šiauliu), eutrophic drained histosols (Dubravos), and light-textured eutrophic gleyic soils with temporarily over moisture (Šilutės).

For the modelling purposes, 10% of families (standard selection intensity in tree breeding) with the highest mean height were assigned as the FRM category 'tested' in each trial, representing the best genetically superior material demonstrated by comparative testing, whilst the other 90% of families were assigned as the category 'qualified'. The latter genetic improvement level characterizes first-generation seed orchards with phenotypically selected individuals and estimated genetic gains of 10%–15%, but the tested material is predicted to provide gains of 20%–25% (Ruotsalainen 2014; Jansson *et al.* 2017). In the present study, the functions for each of the species are built specifically for the improved trees and are not compared to unimproved FRM due to the lack of control plots with basic local seed sources without phenotypic selection.

Modelling approach

We used the generalized algebraic difference approach (GADA) to model base-age-invariant individual tree height growth for each species separately (Cieszewski and Bailey 2000; Cieszewski and Strub 2007). We consider five different polymorphic dynamic site equations previously derived from base equations to model height growth (Table 1).

The GADA models after solving the base equation for unobservable theoretical site variable X (Cieszewski and Bailey 2000) has the following general implicit form:

$$h_{ij} = f\left(h_{0ij}, t_{0ij}, t_{ij}, \boldsymbol{\beta}, \boldsymbol{\alpha_j}\right) + \varepsilon_{ij} \quad (1)$$

where h_{ij} is the observed height at age t_{ij} for tree i within FRM category j, h_{0ij} is the height for tree i at a reference age t_{0ij}, $\boldsymbol{\beta}$ is the parameter vector affected by the fixed effect $\boldsymbol{\alpha_j}$ associated with FRM category j, and ε_{ij} is the error term representing unobserved factors and random noise. For each species, we estimated the model parameters by applying all possible combinations of the fixed effect of the FRM category on the model coefficients b_1, b_2, and b_3 (Supplementary Table S4):

$$h_{ij} = f\left(h_{0ij}, t_{0ij}, t_{ij}, \alpha_{j1} \cdot b_{1j}, \alpha_{j2} \cdot b_{2j}, \alpha_{j3} \cdot b_{3j},\right) + \varepsilon_{ij} \quad (2)$$

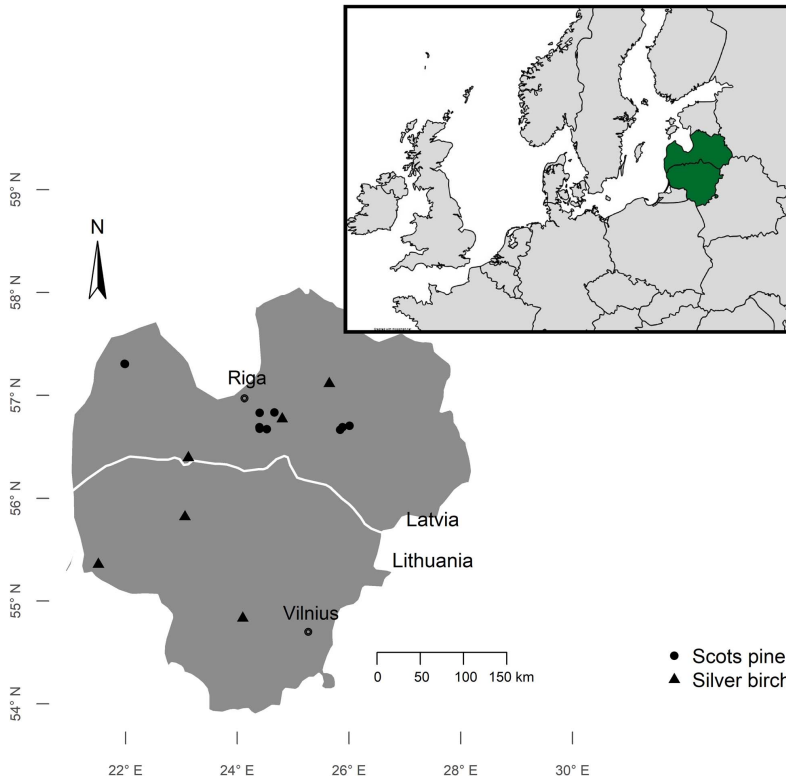

Figure 1. Location of progeny trials in Latvia and Lithuania (denoted with black dots and triangles) with available tree height measurements for model calibration and validation.

where α_1, α_2, and α_3 are fixed effects associated with FRM category j that affects the corresponding parameters b_{1j}, b_{2j}, and b_{3j}. The chosen nonlinear-fixed-effects (NFE) approach demonstrates the desirable characteristics associated with logical behaviour of growth models (Cieszewski and Strub 2018).

In the model specification, the fixed effect was incorporated using the dummy variable approach. Separate fixed effects were estimated for each level ('qualified' or 'tested') of the FRM category, allowing the estimation of group-specific effects on the corresponding model parameters. The model parameters were estimated with nonlinear least-square regression using the function gnls of the R package nlme (Pinheiro *et al.* 2021). Due to multiple measurements from each tree, we applied a first-order autoregressive AR (1) error structure to account for temporal autocorrelation (Supplementary Fig. S1) (Box *et al.* 1994). We modelled different variances for different FRM category levels within each trial using a variance function (Pinheiro and Bates 2000).

Statistical analysis

We tested five different GADA functions with all possible ($n = 7$) combinations of forest reproductive material category ('qualified' and 'tested') specific coefficients b_1, b_2, and b_3 (in total, 35 functions for each Scots pine and silver birch, Supplementary Table S4). The best-fit model for each species was selected using the likelihood ratio test, Akaike's information criterion (AIC), and Bayesian information criterion (BIC) (Supplementary Table S4). The fitted models were evaluated using the aggregated difference (AD, similar to mean residual), aggregated absolute value differences (AAD), and the root mean squared difference (RMSD) (Salas-Eljatib *et al.* 2010):

$$\mathrm{AD} = \frac{\sum_{i=1}^{n} (y_i - \hat{y}_i)}{n} \tag{3}$$

$$\mathrm{AAD} = \frac{\sum_{i=1}^{n} |y_i - \hat{y}_i|}{n} \tag{4}$$

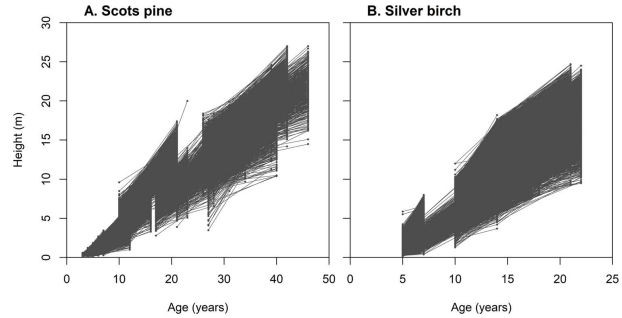

Figure 2. Height–age series from progeny trials of Scots pine (a, $n = 14\,260$) and silver birch (b, $n = 55\,926$).

Table 1. Tested generalized algebraic difference models (GADA) fitted to height time series and their corresponding base models with the solutions. a_1, a_2, and a_3 are parameters in the base model; b_1, b_2, and b_3 are parameters in the GADA models; h_0 and h are heights (m) at age t_0 and t_1 (years); X_0 is the solution for X with initial values of height (h_0) and age (t_0).

Designation	Base model	Site parameter	Solution for X	Dynamic equation	Reference
M1	King–Prodan $h = \frac{t^{a_1}}{a_2+a_3 t^{a_1}}$	$a_2 = b_2 + b_3 X$ $a_3 = X$	$X_0 = \frac{\frac{t_0^{b_1}}{h_0} - b_2}{b_3 + t_0^{b_1}}$	$h = \frac{t_1^{b_1}}{b_2 + b_3 X_0 + X_0 t_1^{b_1}}$	Krumland and Eng (2005)
M2	Hossfeld $h = \frac{a_1}{1+a_2 t^{-a_3}}$	$a_1 = b_1 + X$ $a_2 = b_2 X$	$X_0 = \frac{h_0 - b_1}{1 - b_2 h_0 t_0^{-b_3}}$	$h = \frac{b_1 + X_0}{1 + b_2 X_0 t_1^{-b_3}}$	Cieszewski (2002)
M3	Hossfeld IV $h = \frac{a_2 t^{a_3}}{t^{a_3} + a_1}$	$a_1 = \frac{b_1}{X}$ $a_2 = b_2 + X$ $a_3 = b_3$	$X_0 = h_0 - b_1 + \sqrt{(h_0 - b_1)^2 + \frac{2h_0 \exp(b_2)}{t_0^{b_3}}}$	$h = h_0 \frac{t^{b_3}\left(t_0^{b_3} X_0 + \exp(b_2)\right)}{t_0^{b_3}\left(t^{b_3} X_0 + \exp(b_2)\right)}$	Cieszewski (2001)
M4	Chapman–Richards $h = a_1\left(1 - \exp(-a_2 t)\right)^{a_3}$	$a_1 = \exp(x)$ $a_3 = b_2 + \frac{b_3}{X}$	$X_0 = \frac{1}{2}\left((\ln h_0 - b_2 F_0) + \sqrt{(\ln h_0 - b_2 F_0)^2 - 4 b_3 F_0}\right)$ $F_0 = \ln\left(1 - \exp(-b_1 t_0)\right)$	$h = h_0 \left(\frac{1-\exp(-b_1 t)}{1-\exp(-b_1 t_0)}\right)^{b_2 + \frac{b_3}{X_0}}$	Cieszewski (2004)
M5	Lundqvist $h = a\ \exp\left(-bt^{-c}\right)$	$a = \exp(X)$ $b = b_1 + \frac{b_2}{X}$	$X_0 = \frac{1}{2}\left(b_1 t_0^{-c} + \ln h_0 + F_0\right)$ $F_0 = \sqrt{\left(b_1 t_0^{-c} + \ln h_0\right)^2 + 4 b_2 t_0^{-c}}$	$h = \exp(X_0) \exp\left(-\left(b_1 + \left(\frac{b_2}{X_0}\right)\right) t^{-c}\right)$	Cieszewski (2004)

$$\mathrm{RMSD} = \sqrt{\frac{\sum_{i=1}^{n} |y_i - \hat{y}_i|}{n}} \quad (5)$$

where n is the number of observations and y_i, $\overline{y}_i$, and $\hat{y}_i$ are the observed, average, and predicted height values, respectively. We did a graphical analysis of trends in residuals plotted against predicted tree height and drawn height–age curves overlaid on the measured height data. For testing the predictive accuracy of the final fitted models, we split the datasets into calibration and validation data (70% and 30%, respectively). The prediction statistics included mean prediction error (MPE; calculated similarly to AD), ADD, and RMSD. The likelihood ratio test was used to test the significance of the fixed effect. For graphical inspection of model growth curves for different site quality (height classes) plotted against observed height series, we selected a reference age of 10 years, which is a common time when evaluations of progeny trials are done. Average realized genetic gains in height (%) of category 'tested' over 'qualified' was estimated at this reference age and used when plotting category-specific curves. All modelling and data analysis were conducted in R, v 4.0.3 (R Core Team 2020).

Results

All tested models showed good fit statistics with statistically significant coefficients ($P < .001$) and rather small differences between them for both species, except for an insignificant parameter b_2 in the GADA form of the Hossfeld equation for silver birch regardless of the category-specific combinations (Supplementary Table S4). For Scots pine, the GADA model derived from the Chapman–Richards base equation with FRM category-specific parameters b_1 and b_2 showed the smallest AIC, BIC, and highest log likelihood and was therefore chosen for further analyses. For silver birch, the GADA form derived from the King–Prodan base equation with all FRM category-specific parameters b_1, b_2, and b_3 exhibited the most favourable fit statistics (Table 2 and Supplementary Table S4).

The final selected models fitted the data with high accuracy—AAD was 0.695 and 1.023 m for Scots pine and silver birch, respectively, with corresponding relative values of 6.7% and 7.3%. The AD and RMSD were higher for silver birch (AD = 0.221 m, RMSD = 1.346 m) than for Scots pine (AD = 0.041 m, RMSD = 1.079 m). Relative values AD_r were small (0.4%–1.6%), yet

Table 2. Estimated coefficients with standard errors (SE) and confidence intervals (CI) of the final best-fit models for Scots pine and silver birch, and their fit and prediction statistics [N—number of observations; $_r$ (%) = denotes respective relative error]

		Scots pine			Silver birch		
	Category	**Estimate (SE)**	**2.5% CI**	**97.5% CI**	**Estimate (SE)**	**2.5% CI**	**97.5% CI**
b_1	Tested	0.047*** (0.001)	0.045	0.049	3.157*** (0.021)	3.115	3.199
	Qualified	0.048*** (0.000)	0.047	0.049	3.017*** (0.007)	3.002	3.032
b_2	Tested	−21.209*** (1.390)	−23.935	−18.484	−1474.788*** (243.673)	−1952.393	−997.182
	Qualified	−21.514*** (1.410)	−24.277	−18.751	−831.973*** (37.543)	−905.557	−758.388
b_3	Tested	78.910*** (4.690)	69.716	88.104	37 960.938*** (5777.893)	26 636.124	49 285.751
	Qualified				21 082.885*** (848.442)	19 419.917	22 745.853
Fit statistics							
n		9988			39 135		
AIC		17 555.7			143 393.2		
RMSD (m)		1.079			1.346		
$RMSD_r$ (%)		10.363			9.590		
AD (m)		0.041			0.221		
AD_r (%)		0.394			1.573		
AAD (m)		0.695			1.023		
AAD_r (%)		6.678			7.288		
Prediction statistics							
n		4272			16 791		
RMSD (m)		1.185			1.360		
$RMSD_r$ (%)		11.245			9.697		
MPE (m)		0.044			0.221		
MPE_r (%)		0.421			1.576		
AAD (m)		0.742			1.030		
AAD_r (%)		7.041			7.342		

*$P < .05$. **$P < .01$. ***$P < .001$.

$RMSD_r$ was ca. 10% for both species (Table 2). The distribution of the residuals over predicted height were scattered around zero without distinct trends for both species, yet slight increase in variance with increasing height for Scots pine (Fig. 3). A slight underestimation was observed for the highest trees (around ca. 23 m) of Scots pine, whilst the model for silver birch somewhat underestimated the growth of trees of ca. 7–12-m height.

Predictions statistics also indicated sufficient fit of both models (AAD = 0.742 m, AAD_r = 7.0%, RMSD = 1.185 m, $RMSD_r$ = 11.3%, MPE = 0.044 m, MPE_r = 0.4% for Scots pine; AAD = 1.030 m, AAD_r = 7.3%, RMSD = 1.360 m, $RMSD_r$ = 9.7%, MPE = 0.221 m, MPE_r = 1.6% for silver birch) to the validation datasets (Table 2) with similar slight tendencies of underestimation for model fitting dataset described above (Fig. 3).

When comparing the growth curves of the two species studied, silver birch showed faster early height growth than Scots pine. The most productive birch reached a height of 23 m after 22 years, whilst the same height for the fastest-growing Scots pine took ~35 years with a flatter growth trajectory (Fig. 4). Within the range of available data, we observed more distinct differences in growth patterns for different height classes for silver birch compared to Scots pine That is, with higher productivity, the increase in birch height growth was more rapid compared to trees growing in poorer site conditions, whilst the height curves for different height classes of Scots pine were more parallel.

The graphical inspection of the height growth curves confirmed the statistically estimated differences in model parameters for the distinct FRM categories ‘qualified’ and ‘tested’ (Table 2, Fig. 4). For both species, differences between the FRM categories tended to somewhat increase with the age. At the base age of 10 years, the height of the category ‘tested’ was on average 7.5% and 10.8% higher for Scots pine and silver birch, respectively, comparing to the ‘qualified’ material. Still, growth patterns for different categories varied between the species. For Scots pine, differences in category-specific growth indices appeared to increase with increasing site productivity, whilst being rather similar for birch in different site indices.

Discussion

We built dynamic models for height growth of genetically improved trees of Scots pine and silver birch in the Baltic region. These species have undergone considerable productivity and quality gains due to a relatively long breeding history. The use of the base age invariant polymorphic GADA model form (Cieszewski and Bailey 2000) in combination with FRM category-specific coefficients allowed a successful modelling of tree height growth, considering genetic improvements, across different site qualities, even with rather short time series data (Cieszewski and Strub 2007; Sharma *et al.* 2011, 2017; Kimberley *et al.* 2015). For the

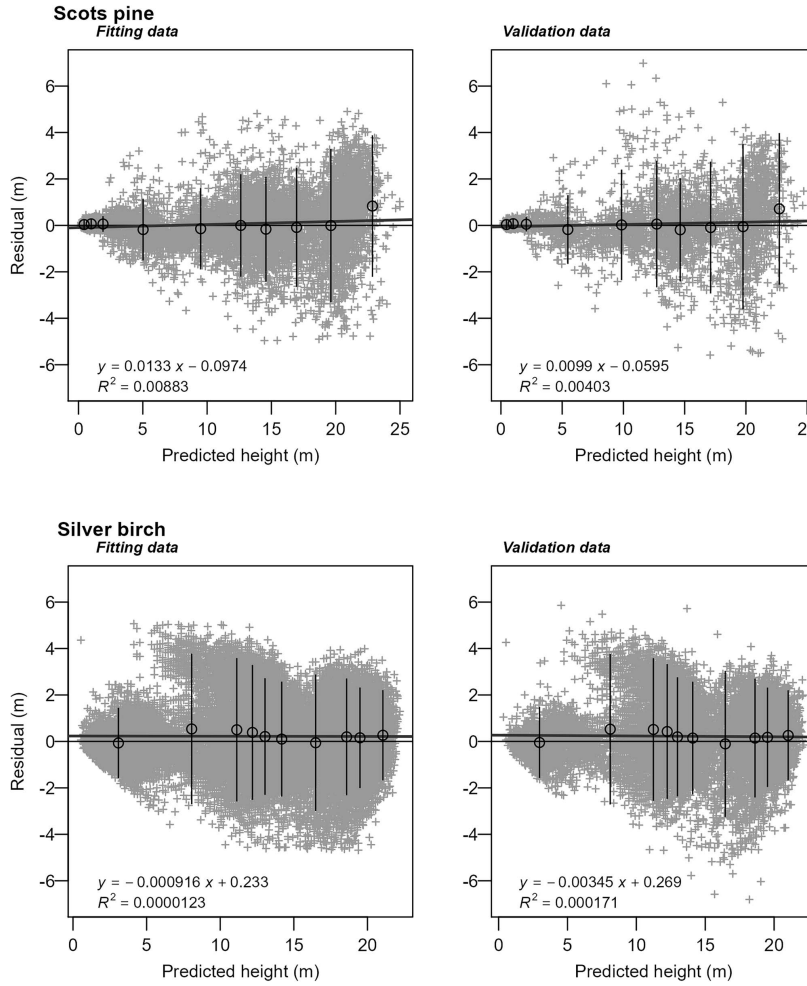

Figure 3. Residuals of fitting (first column) and validation (second column) data against final best-fit models for Scots pine (upper panels) and silver birch (lower panels) with trendline, its regression equation, and *R*-square value. Grey crosses denote the residuals; black circles with vertical lines show the means of the residuals in 10 classes with a 95% confidence interval of the class mean.

studied datasets of improved progenies, GADA models derived from the Chapman–Richards (for Scots pine) and King–Prodan (for silver birch) base equations showed the best statistical fit (Supplementary Table S4, Table 2, Fig. 4). The AR(1) error structure successfully accounted for temporal autocorrelation in final fit models for both species (Supplementary Fig. S1). Although residuals for silver birch model showed homogenous variance, applied variance structure did not fully remove heteroscedasticity in the final fit function for Scots pine leaving a slight trend of increasing variance for higher trees (Fig. 3). Still, overall

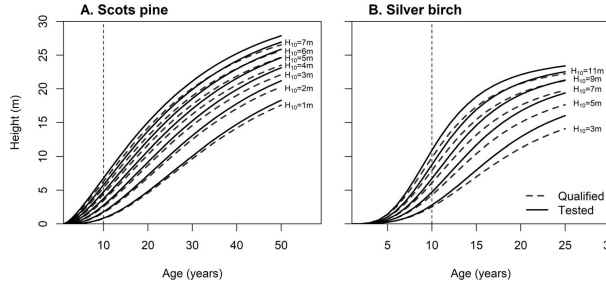

Figure 4. Expected height growth of the final best-fit models (solid black and dark grey dashed lines for the improved forest reproductive material categories 'tested' and 'qualified', respectively) for Scots pine (a) and silver birch (b). The growth curves represent different height classes at the base age of 10 years.

good model fit statistics suggest that the presence of such heteroscedasticity would not undermine the validity of the nonlinear model (Louangrath 2013).

Nevertheless, all tested equations equally satisfied the criterion of biologically realistic trajectories (Nunes *et al.* 2011) for the covered age range. Historically, both final fitted types of base height–age equations have been recognized and frequently used (Zeide 1993). Furthermore, the dynamic derivatives have been commonly reported to have good fit for height, dominant height, or diameter predictions (Nunes *et al.* 2011; Sharma *et al.* 2011, 2017, 2019; Kahriman *et al.* 2018; Manso *et al.* 2021).

We calibrated completely new functions based on empirical data from progeny trials intended to predict height growth of improved Scots pine and silver birch. Although considered to be the best and most accurate approach (Weiskittel *et al.* 2011; Sabatia and Burkhart 2013), calibration of the model parameters has been commonly reported to have limited use due to the lack of costly and time-consuming repeated measurements of improved trees (Sabatia and Burkhart 2013; Joo *et al.* 2020; Manso *et al.* 2022). Thus, relatively simple modifications of existing models originally intended for unimproved trees—adjustment of site index (e.g. Nance and Wells 1981; Buford and Burkhart 1987) and application of genetic multipliers (e.g. Carson *et al.* 1999; Kimberley *et al.* 2015; Ahtikoski *et al.* 2020)—are methods traditionally chosen over developing new models. The authors emphasize that progeny trials for boreal tree species are typically measured at an early age (~10–15 years), which means that the growth patterns of mature improved trees cannot be fully assessed. Mature tested material with known growth patterns may already be surpassed by more productive and recently selected genotypes (Burkhart *et al.* 2012; Haapanen *et al.* 2016; Egbäck *et al.* 2017; Deng *et al.* 2020). However, our study material derived from progeny trials encompassed current breeding populations (Baumanis *et al.* 2014; Gailis *et al.* 2020b), enabling the development of models specifically tailored for young improved stands up to 40 years of age for Scots pine and 20 years for silver birch. We acknowledge that projections for the full rotation time of ca. 80 and 50 years for Scots pine and silver birch, respectively, would still be extrapolation outside fitting data coverage and thus should be used with caution.

Chapman–Richards GADA models are generally recognized to be robust to extrapolation (Manso *et al.* 2021), and graphical inspection of Scots pine height growth curves tended to confirm this, showing continuous gradual increase in height outside the data coverage tending to reach realistic asymptotes ~30 m for the highest height classes (Fig. 4a). Meanwhile, the King–Prodan GADA model for silver birch showed a tendency for too-fast growth cessation above the upper age limits of tree data used for model fitting (>22 years), therefore quickly reaching an unreasonably low asymptote at older ages (Fig. 4b). Such trend was irrespective of the type of base equation for the GADA derivatives tested. We explain it with characteristics and temporal limits of the underlying data that determine the sigmoid form of the curve (Salas-Eljatib *et al.* 2021): potentially, the delayed point of the inflection and rapid growth afterwards during the second phase seem to determine a rather fast decrease of the growth rate in the third phase (Fig. 4b). We already noticed a too-long phase of slow growth before the point of inflection during preliminary modelling and analysis of data from solely Latvian trials due to the lack of early height measurements (the first inventory was done at the age of 10 years, Supplementary Table S1). The inclusion of younger height measurement data from Lithuania (age ≥5 years, Supplementary Table S1) appeared to correct the growth trajectories to be more biologically reasonable during the first 10 years, whilst lack of measurements after the age of 22 years still appears to lead to a premature start for the phase of decreased growth rate. Still, the residual analysis did not indicate any trend of underestimating the growth of the highest trees at the upper age limits of the data (Fig. 3), which could be expected when extrapolated to older ages.

The newly calibrated models for improved trees with enhanced growth trajectories can sufficiently improve planning of management in young production stands up to around half of the rotation cycle including first commercial thinnings (Manso *et al.* 2022). For silver birch, thinning may need to be done as early as around the 12th growing season on high-productivity sites, where the improved trees have reached a height of ca. 15 m (Fig. 4) (Hynynen *et al.* 2010), whilst the corresponding age for pine could be expected ~25–30 years (Niemistö *et al.* 2018; Donis *et al.* 2020). The first commercial thinning at the age of 14 years is reported to be already profitable with an internal rate of return reaching 9.4% for the best improved silver birch genetic entries (Gailis *et al.* 2020a), which highlights the need for reasonable growth predictions already in young stands.

In addition to being the first attempt to build height growth model for improved FRM in the Baltic region, a major objective of this study was to dynamically incorporate FRM categories into the

models to more accurately predict the growth of improved trees categorized as 'qualified' and 'tested'. Consequently, separate sets of parameters were successfully calibrated for each of the two categories (Table 2) and appeared to improve prediction accuracy for both species by determining genetic control of the curves (Gwaze *et al.* 2002). Such approach with the same functional form, but FRM category-specific parameterization could be easily applicable in practice and communicable across different users, as similarly suggested by Manso *et al.* (2021) for a common dynamic top height model for various species in Great Britain. For forest owners and managers, who usually have information about the origin of planting stock, such approach may encourage the use of the model in practice.

From the perspective of tree breeders, the developed models allow to compare the differences in height growth dynamics between FRM categories with different genetic improvement levels. Gwaze *et al.* (2002) emphasize the importance of model parameters in accurately capturing growth patterns in improved stands, as opposed to static height measurements that only reflect the productivity of studied genotypes at a specific age and site (Skovsgaard and Vanclay 2008). We observed varying height growth patterns across different improvement levels (Table 2, Fig. 4). In our study, the height of the category 'tested' was on average 7.5% and 10.8% higher for Scots pine and silver birch, respectively, comparing to the 'qualified' material at the selected base age of 10 years, but the differences tended to increase with age (Fig. 4). Our results indicate that the superiority of the tested material over the qualified one, observed at a young age, remains at least until the mid-rotation, dismissing concerns of diminishing gains from tree-breeding programmes over time (Hamilton and Rehfeldt 1994). The most distinct differences in growth patterns were observed for silver birch, reflecting the three category-specific coefficients b_1, b_2, and b_3, whilst genetic control was observed for b_1 and b_2 in Scots pine (Table 2). Although the coefficients derived from the base equations do not have straightforward biological meaning, the observed variable genetic gains and drawn height growth curves indicated FRM category-affected asymptote, shape, and rate (Deng *et al.* 2020). Nevertheless, the strength of the genotype by site interaction determines whether improvement (subsequently, also growth patterns) is consistent across various environments. It is hence of high importance for matching relatively expensive improved planting stock to appropriate sites for the best performance (Bourdon 1977; Kimberley *et al.* 2015). In our study, we observed that the category-specific differences tended to vary to some extent based on site quality. For Scots pine (Fig. 4a), an increase in differences between categories was observed with site quality. However, for silver birch (Fig. 4b), the dominance of the 'tested' category remained relatively consistent across the represented site types. The latter result coincides with earlier extensive research of the silver birch breeding population in Latvia, which found a negligible genotype by environment effect on tree growth over different trials and ages (Gailis *et al.* 2020b). However, the source of data for model calibration in this study was genetic field trials, which might represent limited growth conditions, as compared to, e.g. datasets from national forest inventories (Sharma *et al.* 2011). In addition to constraints of use up to the mid-rotation, this limits the application of the model to relatively high-quality sites. We find this to be acceptable, since genetically improved material is typically planted on sites with suitable properties for the particular species. Although earlier studies stress that such factors as higher planting density and different management of genetic field trials may alter tree growth compared to typical productive forest stands (Carson *et al.* 1999; Deng *et al.* 2020; Joo *et al.* 2020), the studied progeny trials were established with initial densities commonly used in practical forestry and maintained to be similar to conventional even-aged productive forest stands. The fitting and prediction statistics confirmed that both models are sufficiently precise (Table 2) to predict height growth for rather high-quality sites represented by the experimental data.

Considering tree height as a reasonable proxy for areal production (Skovsgaard and Vanclay 2008; Liziniewicz *et al.* 2018; Liziniewicz and Berlin 2019; Manso *et al.* 2021; Kuehne *et al.* 2022) and considering the persistent gains of improvement for the studied age range, the developed models of this study can contribute to more accurate growth and yield predictions, when incorporated into forest growth simulators. The intended regional scale use for genetically improved FRM of Scots pine and silver birch may further serve as a tool to evaluate contributions of tree breeding and forest management as such to biomass production and carbon sequestration, hence reducing risks of under- or overestimations resulting from more global functions or empirical models calibrated for other regions (Landsberg 2003; Liepiņš *et al.* 2018; Socha *et al.* 2021). This is of high importance, for instance, in developing justified carbon policies and regional reference levels for greenhouse gas emissions (Lazdiņš *et al.* 2020).

Conclusion

The polymorphic dynamic derivatives of the Chapman–Richards and King–Prodan base equations had the best fit and high accuracy to describe the individual tree height growth of genetically improved Scots pine and silver birch, respectively. We found different growth patterns between the FRM categories 'qualified' and 'tested', reflected in category-specific sets of estimated model parameters for both species. The observed growth curves showed that superiority in height growth for category 'tested' at early age remains at least until mid-rotation, indicating a long-term nature of genetic gains. The differences between both FRM categories appeared to be consistent over the represented site quality range for silver birch, whilst they tended to increase with better site quality for Scots pine, thereby suggesting tree breeding effect to manifest itself more effectively on appropriate sites. We acknowledge the limitations for model application due to the empirical data coverage used for model fitting and hence suggest to use it for young stands up to the age of 40 and 20 years for Scots pine and silver birch, respectively, on sites suitable for the particular species. Still, this modelling approach can provide more precise information for guiding silvicultural activities, such as the timing of first commercial thinnings, and contribute to more precise regional-level biomass estimations, which are essential for evidence-based policy-making in any country or region, where improved planting stock has a substantial share in forest regeneration.

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Supplementary data

Supplementary data are available at *FORESJ Journal* online.

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Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

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Productivity of local Norway spruce clones relates to weather sensitivity of height increment in the eastern Baltic region

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ABSTRACT

In the eastern Baltic region, Norway spruce (*Picea* abies) is predicted to decrease in abundance, resulting in substantial economic consequences. Such predictions have been based on distribution, as well as the sensitivity of growth, largely neglecting the adaptive potential of local populations. Under such circumstances, information on growth sensitivity and its genetic control, as well as productivity-sensitivity relationships is necessary to evaluate the adaptability of populations. Radial increment, which is highly sensitive to local conditions has been mainly used for weather-growth analysis, while height increment, which is a better proxy of productivity due to lower dependence on local density, has been neglected due to laborious gathering of data. Long-term weather sensitivity of annual height increment to weather fluctuations and anomalies (extremes) was estimated by the time series decomposition and multiple regression techniques. Clones of plus-trees from a local population differing by productivity at the age of 55 years growing in an experimental plantation in Latvia were studied. Meteorological conditions prevailingly had carry-over effects on height increment. Thermal regime in winter was the primary driver of height increment with moisture availability in summer showing secondary effects, presuming a positive effect of warming on growth. Abrupt changes in annual increment were related to the co-occurrence of a few weather anomalies, suggesting robustness of height growth. Height increment showed explicit sensitivity-productivity relationships with more productive genotypes being more tolerant and resistant to weather fluctuations. Considering that narrow spatial scale and climatic gradient were analysed, linear and nonlinear responses to weather conditions were estimated implying local adaptation and varying phenotypic plasticity of the genotypes, thus suggesting the persistence of adaptive potential of the local non-marginal population.

1. Introduction

Climatic changes are marginalizing growing conditions of forest tree populations (Isaac-Renton et al., 2018; Montwe et al., 2018), particularly near the distribution limits (Klisz et al., 2019; Cavin and Jump, 2017). Accordingly, shifts in species range (Buras and Menzel, 2019) with notable economic consequences are expected (Knoke et al., 2021). Still, the populations of widespread species differ by phenotypic plasticity and local adaptation, hence susceptibility to rapid environmental changes (Liepe et al., 2022; Cavin and Jump, 2017; Chen et al., 2012). This suggests the persistence of the adaptive potential of local genotypes, particularly if enhanced by adaptive management (Liepe et al., 2022; Zeltiņš et al., 2019; Jansson et al., 2017; Keenan, 2015; O'Neill et al., 2014; Lindgren, 1993).

The effects of climatic changes on forests vary locally and regionally (Forzieri et al., 2022; Harvey et al., 2020; Kapeller et al., 2017; Reyer et al., 2017), adding uncertainties regarding the sustainability of local tree populations (Liepe et al., 2022; Dyderski et al., 2018; Tei et al., 2017). The effects of phenotypic plasticity are particular near the distribution margins of species/populations, determining utilization of local conditions and hence competitiveness and survival (Zeltiņš et al., 2019; Oboite and Comeau, 2019; Trujillo-Moya et al., 2018; Lindgren, 1993). Accordingly, comprehensive information on the variability and stationarity of climate-growth responses of genotypes is crucial for adaptive management (Forzieri et al., 2022; Jansson et al., 2017; O'Neill et al., 2014; Lindner et al., 2014).

Retrospective analysis of increment across the ecological gradients is a powerful tool providing comprehensive information on growth sensitivity (Babst et al., 2018; Zhang et al., 2018; Xu et al., 2017). Derivatives of increment measurements allow a comprehensive assessment

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of sensitivity and resilience of growth (Schwarz et al., 2020; Babst et al., 2018; Lloret et al., 2011; Cook, 1987), which affect the adaptability of genotypes, thus aiding the reliability of projections (Wilmking et al., 2020; Babst et al., 2018). Information on growth sensitivity is complementary to the productivity estimates, which are based on the dimension of trees, hence the cumulative product of past conditions (Breed et al., 2018; Zhang et al., 2018), particularly when assessing ecological plasticity and adaptability of genotypes (Liepe et al., 2022; Harvey et al., 2020; Housset et al., 2018). Tree ring width is a common proxy of increment, though it is strongly affected by local conditions (Sharma et al., 2017; Xu et al., 2017; Cook, 1987).

Variation of height increment (HI), which is a more straightforward proxy of productivity due to lower sensitivity to local density (Socha et al., 2021; Sharma et al., 2011; Skovsgaard and Vanclay, 2008), has received less attention due to laborious gathering of data (Jansons et al., 2015b; Metslaid et al., 2011; Salminen and Jalkanen, 2005). Under the temperate climate, formation of HI is a two-year process, which depends on the number of growth initials formed at the end of the previous growing period, and their extension (Nezval et al., 2021; Mäkinen et al., 2018; Lanner, 1976). Thus, the time window, when environmental conditions affect HI, appears longer compared to radial increment, presuming higher complexity of environmental controls (Oboite and Comeau, 2019; Jansons et al., 2015b, 2013; Salminen and Jalkanen, 2005). Nevertheless, environmental information archived in HI can be complementary to that from tree-ring width (Nezval et al., 2021; Mäkinen et al., 2018; Lanner et al., 1976).

In Northern Europe, Norway spruce (*Picea abies* H. Karst.) is an economically important, yet weather-sensitive species (Matisons et al., 2021; Klisz et al., 2019; Trujillo-Moya et al., 2018; Mäkinen et al., 2001), hence adaptive management is implemented to increase its sustainability (Zeltiņš et al., 2019; Jansson et al., 2017; Jansons et al., 2015a; Baliuckas et al., 2004; Lindgren, 1993). Still, due to phenotypic plasticity of populations in terms of environmental sensitivity (Liepe et al., 2022; Matisons et al., 2021; Trujillo-Moya et al., 2018), the future projections regarding growth of Norway spruce appear divergent, particularly near the southern lowland distribution limit in the Eastern Baltic region (Knoke et al., 2021; Buras and Menzel, 2019; Reyer et al., 2017; 2014). The abundance of the species has been predicted to decrease due to intensifying disturbances related to water shortage and, particularly, biotic agents (Dyderski et al., 2018; Seidl and Rammer, 2017; Reyer et al., 2017). This is supported by the loss of genetic differences in responses to weather extremes on the distribution margin (Klisz et al., 2019; Kapeller et al., 2017) and intensifying drought sensitivity (Bosela et al., 2021; Matisons et al., 2021; Mäkinen et al., 2018; 2001).

Despite the pessimistic projections of distribution, the productivity of Norway spruce in the Eastern Baltic is predicted to locally increase due to ameliorated growing conditions (Reyer et al., 2017; 2014), implying resistance to the reduction in abundance, as indicated by increased height growth (Liepe et al., 2022). Still, the changes in productivity bear local specifics due to site conditions (Dyderski et al., 2018; Keenan et al., 2015; Lindner et al., 2014), as well as disturbance regimes (Knoke et al., 2021; Seidl and Rammer, 2017; Reyer et al., 2017). The resistance of spruce to climatic changes is also supported by the phenotypic plasticity of populations (Liepe et al., 2022; Trujillo-Moya et al., 2018) and adaptive management (e.g., national breeding programmes) (Jansson et al., 2017; Jansons et al., 2015a; Baliuckas et al., 2004). Hence, local populations might still have adaptive potential against environmental changes in the region (Liepe et al., 2022, Zeltiņš et al., 2019; Baliuckas et al., 2004). Under such conditions, the susceptibility of Norway spruce to disturbance might be mitigated by adaptive management, e.g., shorter rotation (Zeltiņš et al., 2022; Knoke et al., 2021; Kapeller et al., 2017; Seidl and Rammer, 2017). Nevertheless, the climatic changes are intensifying climatic clines, testing the adaptability of genotypes on the distribution margin (Harvey et al., 2020; Liepe et al., 2022; Klisz et al., 2019), as well as that of core populations (Isaac-Renton et al., 2018; Montwe et al., 2018; Cavin and Jump, 2017).

The aim of the study was to assess the sensitivity of HI of local genotypes of Norway spruce to meteorological conditions growing near the advancing southern lowland limit. We hypothesised that the more productive genotypes were less sensitive to meteorological fluctuations and showed higher resilience of HI. Considering the extension of the local climatic gradient, we also presumed the presence of nonlinear meteorological conditions to have a nonlinear effect on increment (Wilmking et al., 2020; Klisz et al., 2019).

2. Material and methods

2.1. Plantation, sampling, and measurements

A clonal plantation of Norway spruce established in 1964 by vegetatively propagated two-year-old grafts of local plus-trees from the eastern part of Latvia (56°42′ N, 25°53′ E, 119 m a.s.l.), was studied. The rootstocks were propagated in a nursery from a homogenized (shuffled) seed stock obtained from local open-pollinated trees growing in a stand. The plantation was situated on a flat topography with mesotrophic (former agricultural) soil comparable to the *Oxalidosa* site type (Bušs, 1997) with an approximate site index of 36. The climate of the site was moist continental (Kottek et al., 2006) with some coastal features determined by the dominant westerlies and proximity of the Baltic Sea (Supplementary material, Fig. S1). The annual mean temperature and precipitation sum (± standard deviation) were 6.4±0.8 °C and 686 ±85 mm, respectively. January and July were the coldest and warmest months (mean monthly temperature of −4.2±2.7 and 17.9±1.6 °C, respectively). During the active vegetation season (May–September) mean temperature was 14.9±0.9 °C and the precipitation sum was 346 ±66 mm, which comprised approximately half of the annual.

Initially, 427 trees representing 20 clones were planted in 11–31 randomly distributed single-tree replications. The initial spacing of the plantation was 5 × 5 m (400 trees ha^{-1}). No other management except weed control during the first two years after the establishment has been implemented. According to a trial inventory in 2014 (at the age of 50 years), 293 (ca. 69%) of the initially planted trees had survived reaching a mean (± standard deviation) stem diameter at the breast height of 36.5 ±5.9 cm and height of 24.3±4.9 m (Katrevičs et al., 2018). The clonal mean stem diameter and tree height ranged from 31.9±5.6–43.9 ±5.4 cm and from 20.9±6.6–28.1±1.1 m, respectively, indicating pronounced differences in productivity.

To assess the relationships between the productivity of a clone and the sensitivity of its HI to meteorological conditions, three clones with low, intermediate, and high productivity (clones No. 17, 13, and 18, respectively) were selected for sampling based on the inventory data. Considering the stem diameter reconstruction of the plantation (Zeltiņš et al., 2022), additionally a clone with superior productivity (Clone No. 24) and a distinctive growth pattern was selected. The number of sample trees for this clone was lower to preserve the genotype *in situ*. Sample trees representing the stem diameter distribution of the clones, yet avoiding leaning, double-top, visually unhealthy, and damaged trees were chosen during the stratified selection based on the inventory and radial growth reconstruction (homogeneous growth pattern; Zeltiņš et al., 2022). The details of sampled trees are shown in Table 1.

The selected sample trees were felled in the autumn of 2020. During the felling, attempts were made to preserve the integrity of the stems. The felled trees were limbed and cut into 3–4 m long logs for the convenience of transportation. In a sawmill, 50 mm thick mid-planks containing the pith were cut from the logs maintaining the bark. The top segments were air dried. In a laboratory, the pith of the planks was uncovered by a gradual milling of wood (with a step of 2 mm) along the entire axis of the stem segments. For the top segments, the pith was uncovered by gradual grinding with a belt grinding machine. Height increment was measured as the distance between the borders of

Table 1
Dimensions of the sampled trees of clones of local Norway spruce plus-trees differing by productivity in a 55 years old clonal trial in Latvia and their relation to the trial means.

Clone No.	Field performance	Number of trees	Mean stem diameter (± standard deviation), cm	Mean tree height (± standard deviation), m	Relative stem diameter (to trial mean)	Relative tree height (to trial mean)
17	Slow-growing	10	31.7±4.7	22.4±1.6	86.8%	89.1%
13	Intermediate	10	37.0±2.9	26.0±0.8	101.3%	103.5%
18	Fast-growing	10	38.2±3.4	25.4±1.4	104.6%	101.3%
24	Superior	5	44.4±4.9	27.9±0.8	121.6%	111.1%
Plantation mean		293	36.5±5.5	25.1±2.3	-	-

subsequent HIs along the main axis of the stem with an accuracy of one mm. The occurrence of lost tops was recorded. To ensure the correct dating of the measured HI, tree rings were counted at both basal (terminal) plates of the planks (segments). These plates were progressively grinded to increase the contrast between the earlywood and latewood, thus ensuring correct recognition of tree rings. In case of inconsistent dating at both ends, the planks were cut into shorter segments and tree-rings were counted on the additional sections.

2.2. Data analysis

To warrant correct dating of HI, and to verify the quality of the measurement, graphical and statistical crossdating using COFECHA program (Holmes, 1983) was performed within and between the clones. Dendrochronological statistics, such as first order autocorrelation, gini coefficient, mean interseries correlation, expressed population signal, and signal-to-noise ratio were calculated as the measures of environmental sensitivity of HI. Considering that the measurement time series contained an age trend (Jansons et al., 2015b; Salminen and Jalkanen, 2005), these calculations were based on time series detrended by a flexible cubic spline with a wavelength of 30 years and 50% frequency cut-off, thus highlighting the inter-annual variation.

To assess the correlation between HI and meteorological variables, a residual chronology was calculated for each clone by averaging (by the biweight robust mean; Bunn, 2008) the spline-detrended and prewhitened (first order autoregressive model) time series. Bootstrapped (nonparametric percentile interval bootstrap, 1000 iterations; Zang and Biondi, 2015) Pearson correlation coefficients were calculated between the residual chronologies of HI and meteorological variables: monthly mean, mean minimum, and mean maximum temperatures, monthly precipitation sums, cloudiness (relative cloud cover), and standardized precipitation evapotranspiration indices (SPEI; Vicente-Serrano et al., 2010). Considering that formation of HI is a two-year process (Lanner, 1976) and that meteorological conditions can have carry-over effects on increment (Matisons et al., 2021; Jansons et al., 2015b), meteorological variables were arranged into the climatic window from May in the year before the formations of terminal bud (bprev.) to August in the year of the increment (shoot elongation). Gridded meteorological data (CRU TS4) were acquired from the online repository provided by the climatic research unit of the University of East Anglia (Harris et al., 2020) for the grid point closest to the studied trial (< 25 km).

To account for the complexity of meteorological control over tree growth in the eastern Baltic region (Matisons et al., 2021; Harvey et al., 2020), multiple regression techniques were applied to identify the set of meteorological drivers of HI (Wilmking et al., 2020). Considering the location of the studied population in the southern part of the specie's lowland range and the anticipated extension of local climatic gradients (Buras and Menzel, 2019; Klisz et al., 2019; Lloyd et al., 2013), generalized additive models, which allow assessment of nonlinear (plastic) response splines, were used (Wood, 2011). Such models are sufficient for the assessment of realistic and stationary ecological responses across environmental gradients (Matisons et al., 2021; Wilmking et al., 2020; Cavin and Jump, 2017; Lloyd et al., 2013). The spline-detrended and prewhitened time series of HI of trees, which represent annual relative additional increment, were used as the response variable.

An arbitrary set of meteorological variables, selected considering the correlation analysis, compliance to the biological realism, and model metrics such as Akaike information criterion and R^2 values, was tested as the fixed effects. The fixed effects were checked for collinearity by the variance inflation factor. A model was fit for each clone for the common period of 1977–2020 (omitting the first 13 years after establishment), yet the set of predictors was tested as a complex, simultaneously for all four clones. The refined set of fixed effects had to maximize the total amount of variance explained while showing significant effects for at least one clone. Considering the intrinsic dependencies and standardization of the data, tree nested within year of formation were included in the model as the random effects. The first order autocorrelation term was included in the models to account for residual ageing effects.

The models were fit by the restricted maximum likelihood approach based on the calibration data subset, which consisted of 80% of the crossdated time series (20% of the series were randomly selected for verification). Regression spline with shrinkage was used for smoothing. To reduce the possibility of overfitting, which can occur for spline responses, smoothing parameters were estimated according to the generalized cross-validation procedure, which penalizes excessive flexibility of responses (Wood, 2011). Considering that the responses with up to three inflection points (bell shaped) were expected, the basis dimension for the smoothing spline was restricted to four, thus ensuring compliance with biological realism and minimizing the possibility of overfitting. The models were checked for compliance with statistical assumptions by the diagnostic plots. Cross-validation of the refined models based on the verification data subset was performed to ensure the lack of overfit.

The tolerance analysis was used to evaluate the resilience components of HI to environmental extremes (van der Maaten-Theunissen et al., 2021; Schwarz et al., 2020; Lloret et al., 2011). The analysis was based on the crossdated time series of trees without standardization nor prewhitening. Time series of resistance, recovery, resilience and relative resilience were calculated considering four-year pre- and post-disturbance periods and a recovery period of up to 10 years (Schwarz et al., 2020). To assess the clonal differences in resilience components, years with growth anomalies were selected according to the framework proposed by Schwarz et al. (2020).

For each clone, pointer year indices were calculated based on the relative growth change (Jetschke et al., 2019). Considering that trees were growing under mesotrophic conditions and their growth was not suppressed, the relative threshold of changes of 40% and 30% was used for improvements and reduction of increment for identification of event years, respectively. A pointer year was considered "significant" if ≥ 50% of trees showed consistent (positive or negative) event year. To relate pointer years with meteorological extremes, rolling 30-year interval z-scores were calculated for meteorological variables; conditions with a z-score ≥ 2.0 were considered "extremes". Additionally, the identified pointer years were checked for weather anomalies based on the online almanac of the Latvia Environment Geology and Meteorology Centre (https://klimats.meteo.lv).

Linear mixed effects models (Bates et al., 2015) were used to estimate the clonal differences in tolerance components in the identified pointer years "significant" for at least two clones. Resilience components in negative pointer years, which are informative regarding weather

anomalies (Schwarz et al., 2020), as the response variables were analysed separately. Clone was included as the sole fixed effect. To account for the dependencies in the dataset, as well as the differences in causality of the pointer years, year and tree were included in the model as random effects. Models were fitted by the restricted maximum likelihood approach. The significance of the fixed effect was estimated using the type II Wald's χ^2 test. Estimated marginal means of clones were compared by Tukey's test. Data analysis was conducted in R v. 4.2.1 (R Core Team, 2022) using the libraries "mgcv" (Wood, 2011), "lme4" (Bates et al., 2015), "dplR" (Bunn, 2008), "treeclim" (Zang and Biondi, 2015), and "pointRes" (van der Maaten-Theunissen et al., 2021).

3. Results

3.1. Datasets and weather-growth correlations

The measurement series showed similar trend and inter-annual variation and were successfully crossdated (except one), thus ensuring their quality (Fig. 1). The mean and, particularly, median HI followed the productivity of the clones (Table 2) indicating skewed, yet overlapping distributions. The strength of the common environmental forcing of increment was inversely related to the productivity of the clones; still, clone-specific variation was evident apart from the few common signatures (Fig. 1). In general, the slow-growing and the intermediate clones appeared more sensitive showing common tendencies (particularly decrease), as indicated by the mean interseries correlation, expressed populations signal, and signal-to-noise ratio (Table 2). The expressed population signal exceeded the 0.85 threshold (cf. Wigley et al., 1984) for the slow-growing and the intermediate clones, while being marginal (0.845) for the fast-growing one. The Gini coefficient and the first order autocorrelation were intermediate (0.22 and 0.54, respectively), and the mean sensitivity was (0.30) moderately high, indicating explicit variation.

The inter-annual variation of HI represented by the residual chronologies (Fig. 2) indicated the productivity-sensitivity relationships, with the less productive clones showing a higher range of indices. Still, the clonal differences, particularly in the unfavourable years (e.g., 2014, 2017, and 2019), decreased with time. The residual chronologies significantly correlated with ten of the 168 tested meteorological variables, yet the sets of the correlations were clone specifics (Fig. 3). The complete set of the individual correlations is shown in Supplementary material Fig. S2. The sets indicated carry-over effects of meteorological conditions, as the variables were dated with the period before the formation of increment. The meteorological variables related to moisture availability in the previous (year of the terminal bud formation) summer/autumn and those with the thermal regime in the preceding

Table 2
Statistics of the crossdated time series of height increment of maturing Norway spruce clones differing by productivity in a clonal trial in Latvia for the period of 1977–2020.

	Slow-growing (No. 17)	Intermediate (No. 13)	Fast-growing (No. 18)	Superior (No. 24)
Mean, mm	493	592	58	635
Median, mm	474	588	601	629
Standard deviation, mm	225	234	191	248
Gini coefficient	0.26	0.22	0.18	0.22
Mean first order autocorrelation ('ar1')	0.59	0.53	0.49	0.54
Mean sensitivity	0.35	0.29	0.27	0.29
Number of crossdated series	10	10	9	5
Mean interseries correlation	0.45	0.43	0.29	0.29
Expressed population signal	0.89	0.88	0.85	0.67
Signal-to-noise ratio	8.30	7.55	3.58	1.99

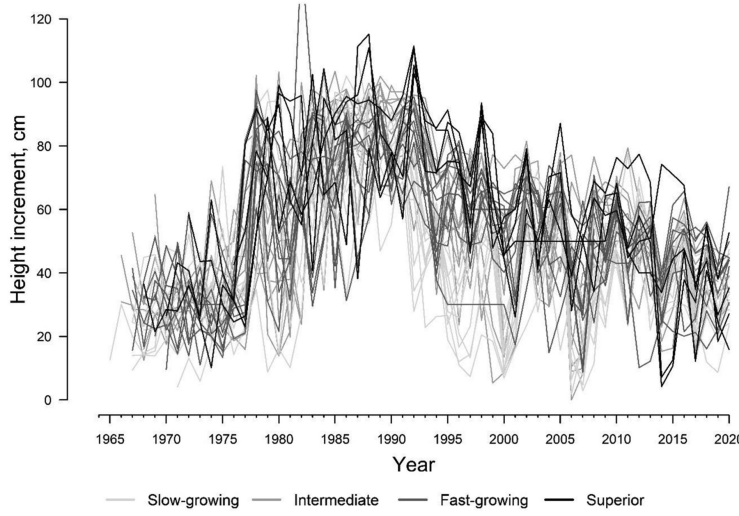

Fig. 1. Crossdated time series of height increment of clones of plus-trees of Norway spruce differing by productivity in a 55 years old clonal plantation in Latvia.

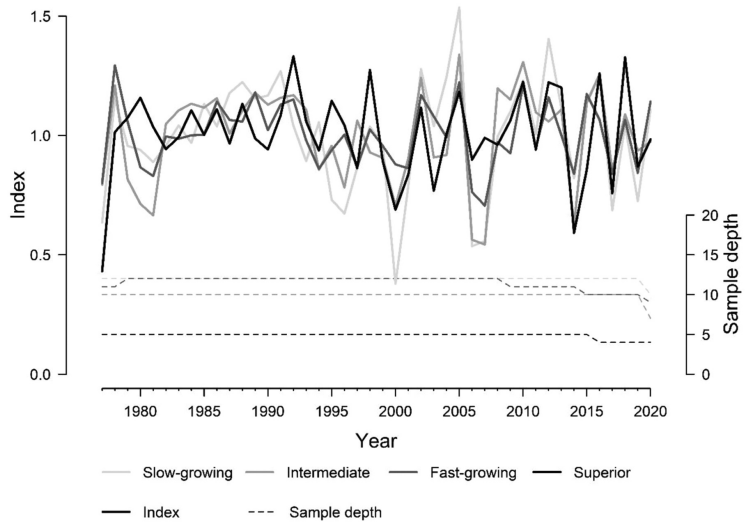

Fig. 2. Residual chronologies of clones of plus-trees of Norway spruce differing by productivity in a clonal plantation in Latvia for the period 1977–2020 (excluding juvenile/establishment growth).

dormancy period showed positive correlation; temperature in September before the bud formation (year before the previous) showed negative correlations.

The clonal differences in the sets and strength of the correlations indicated some genetic differences in growth sensitivity (Fig. 3). Meteorological variables related to the autumn moisture regime showed the strongest correlations with the increment of the superior clone; those with precipitation/SPEI and in the previous autumn and temperature in September before the bud formation were weaker. The intermediate and fast-growing clones showed the strongest correlation with temperature in the previous March. Additionally, the intermediate clone showed correlations with SPEI during the dormancy period and cloudiness in the previous June and September. The fast-growing clone showed a correlation also with precipitation related variables in June, July, and September of the previous year, and in September before the bud formation. The slow-growing clone showed generally weaker correlations, among which that with SPEI in the previous July was the strongest, followed by temperature in the previous March and precipitation in the previous September.

3.2. *Complex meteorological effects*

Complex meteorological controls of HI and sensitivity-productivity relationships were shown by the generalized additive models, which also highlighted uneven phenotypical plasticity of the clones (genotypes). Accordingly, the R^2 values of the models were inverse to the productivity of the clones (Table 3). Still, the strongest individual effects of the meteorological conditions (*F*-values) were estimated for the intermediate and fast-growing clones. The models were not overfitting the data, as the errors estimated for calibration and verification datasets during the cross validation were comparable, indicating their reliability. The random variance related to tree exceeded that of year, indicating temporarily stable, yet individual responses despite the genetic homogeneity of the material. The significant meteorological variables showed linear and nonlinear effects, as effective degrees of freedom of the responses equalled and exceeded 1.0, revealing varying degree of climatic dependency and plasticity of the responses. Two of the variables were significant for all clones and two of the variables were significant for three of the four clones, indicating the presence of common environmental drivers of increment. The responses to the remaining variables highlighted clonal differences in sensitivity. Nevertheless, the sets of the significant variables were mostly dated to the period before growth, thus indicating prevailing carry-over effects of meteorological conditions, none of which were collinear (Supplementary material, Table S1).

The minimum temperature in September before the bud formation, which had a significant negative effect on all clones and was the main driver of HI of the superior clone (Table 3), was estimated with linear or near linear responses (Fig. 4 A). In contrast, the minimum temperature in the previous March was estimated with a negative linear or near linear (superior clone) effect (Fig. 4 B), and was the strongest driver of HI for the slow-growing, intermediate, and fast-growing clones (Table 3). The superior clone, showed the mildest response, particularly regarding the coldest years. The effect of precipitation in the previous July was significant for all, but the superior clone, however, the responses differed by nature. The slow-growing clone showed a response with an optimum of 70–120 mm per month, yet a particularly steep slope in case of low precipitation (Fig. 4 E). The estimated spline for the intermediate clone indicated responsiveness to water shortage (< 100 mm per month), while the fast-growing clone showed a flatter, yet linear response.

All except the slow-growing clone were sensitive to temperature in May (Table 3), indicating direct meteorological effects on their HI, yet the responses were of a different nature (Fig. 4 I). The splines estimated for the intermediate and fast-growing clones indicated a threshold value

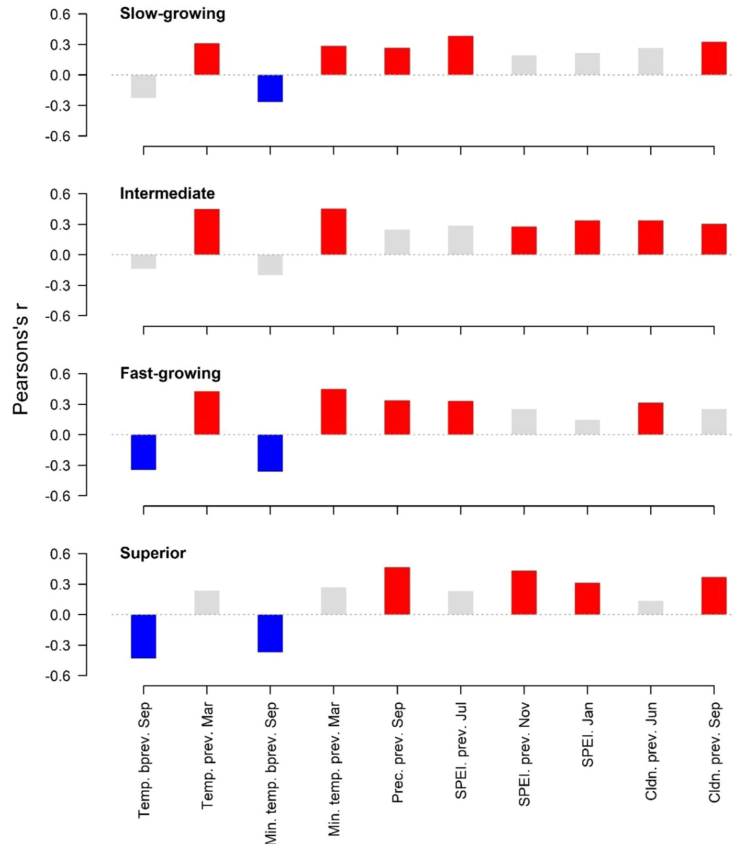

Fig. 3. Bootstrapped Pearson correlation coefficients between residual chronologies of height increment of Norway spruce clones of local plus-trees differing by productivity in a trial in Latvia and meteorological variables (monthly temperature, precipitation, standardized precipitation evapotranspiration indices, SPEI, and cloudiness) for the period 1977–2020. The significant correlations are shown in colour. Only the variables showing significant correlations are shown. Prev. – year of terminal bud formation, bprev. – year before the formation of terminal bud.

of 12 and 11°C, respectively, below which a positive response was observed. Such a response was steeper for the intermediate clone, while the superior clone showed a linear response of moderate steepness. The fast-growing clone was also significant to minimum temperature in April (Fig. 4 H), for which a negative response was estimated if temperature exceeded 0.5 °C.

The responses to the previous September precipitation, which were significant for the intermediate and superior clone (Table 3), were quadratic and indicated an optimum of 60–100 mm per month (Fig. 4 F). The effect of minimal temperature in the previous June was significant for the intermediate and fast-growing clones (Table 3), yet the responses were contrasting (Fig. 4 C). The intermediate clone showed a linear negative response, while the spline of the fast-growing clone had a threshold value of ca. 9.5 °C, above which a positive response was estimated. Sensitivity to the amount of solar radiation, as indicated by the significant effects of cloudiness in previous June and December, was estimated for the fast-growing and superior clone, respectively (Table 3), though the responses differed (Fig. 4 D, G). The fast-growing clone was sensitive to high cloudiness (exceeding 60%) in June, yet the superior clone showed a positive linear response.

3.3. *Pointer years and resilience components*

During the analysed period, several "significant" pointer years were identified revealing some abrupt changes in increment, yet a single of them was common for all clones (Fig. 5) indicating specifics of the

Table 3
Statistics of the mixed generalized additive models of responses of height increment of clones of local plus-trees of Norway spruce in a trial in Latvia to meteorological variables during the period 1977–2020. For the fixed effects the effective degrees of freedom, *F*-values (in brackets) and their significance are shown. Temp. – temperature, prec.–precipitation, Cldn.– cloudiness, SPEI – standardized precipitation evapotranspiration index, prev. – year of terminal bud formation, bprev. – year before the terminal bud formation. Significance codes, p-values: *< 0.05, ** < 0.01, *** <0.001.

	Slow-growing (No. 17)	Intermediate (No. 13)	Fast-growing (No. 18)	Superior (No. 24)
Fixed effects (χ^2)				
Min. temp. bprev. Sep	1.2 (5.7)*	1.0 (9.2)**	1.0 (19.5)***	1.2 (13.2)***
Min. temp. prev. Mar	1.0 (11.7)***	1.0 (48.2)***	1.0 (46.5)***	1.4 (7.2)*
Min. temp. prev. Jun	1.0 (0.8)	1.0 (9.5)**	1.6 (5.3)*	1.3 (0.4)
Cldn. prev. Jun	1.2 (0.5)	1.8 (2.4)	1.9 (7.4)***	1.0 (0.2)
Prec. prev. Jul	1.9 (10.5)***	1.7 (10.2)***	1.0 (14.3)***	1.6 (0.7)
Prec. prev. Sep	1.5 (0.5)	2.0 (11.3)***	1.8 (2.2)	1.9 (6.6)*
Cldn. prev. Dec	1.5 (0.3)	1.6 (0.6)	1.0 (0.1)	1.0 (4.2)*
Min. temp. Apr	1.8 (1.4)	1.3 (1.2)	1.7 (6.8)*	1.0 (2.0)
Temp. May	1.0 (0.8)	1.8 (6.3)**	1.6 (5.9)**	1.0 (6.2)*
Random effects, variance				
Year	0.0238	0.0054	0.0001	0.0001
Tree	0.0647	0.0574	0.0351	0.0584
Residual	0.0003	0.0002	0.0001	0.0001
General model statistics				
R^2 (marginal)	0.352	0.402	0.277	0.274
RMSE calibration	0.2814	0.2424	0.1833	0.2299
RMSE verification	0.2773	0.2258	0.2267	0.2446

genotypes. The abruptness of growth changes was, however, moderate, as the analysis was adjusted for trees growing under favourable site conditions (with the exception of meteorological extremes). Most of the positive pointer years occurred when the trees were young and increment increased rapidly (1968–1982; Fig. 1). Still, the sole common positive pointer year of 1979 might be associated with a cool and moist summer (Table 4). The negative pointer years were identified in the later part of the analysed period. The strongest negative pointer years common for two or three clones occurred in 1996, 2000, 2006, 2007, 2014, 2017, and 2019, years in which several temperature anomalies/records (in the preceding dormancy period, spring, and summer) generally coincided with warm and/or dry summers. This indicated direct meteorological effects on HI, as well as that only several stressors have caused abrupt changes in growth. Though positive pointer years for the less productive clones were estimated in 2010 irrespectively of hot summer. Nevertheless, the intensity of pointer year values suggested genetic (clonal) differences in height growth resilience.

The clones differed by the resilience components, particularly when responding to the negative pointer years, yet the effects were small, as shown by the low marginal R^2 values (Table 5). The resilience components varied temporally, as indicated by higher random variance related to year, as the underlying meteorological causes differed (Table 4). The random variance of tree for the resilience components was low (Table 5), showing diminished individuality under weather extremes. The clonal differences were significant for resistance, recovery, and relative resilience, and they corresponded to the productivity of the clones. The fast-growing and the superior clone showed significantly lower recovery and relative resilience, as the resistance was increased (Fig. 6).

4. Discussion

4.1. Plasticity of weather-growth responses

Common environmental forcing of HI shown by EPS (Table 2) highlighted the weather sensitivity of height growth of spruce (Mäkinen et al., 2018; Salminen and Jalkanen, 2005). The lower EPS (< 0.85) of the superior clone, however, was likely due to a smaller sample size (Wigley et al., 1984). The low/moderate interseries correlation indicated individuality of growth due to the effects of local density and competition (Klisz et al., 2019; Cavin and Jump, 2017). This was particular for the more productive clones, relating the productivity of genotypes to their plasticity (Lebourgeois et al., 2014; Chen et al., 2012). The individuality of increment might be also related to the scion-rootstock interaction in terms of gene expression and/or root development (Lopez-Hinojosa et al., 2021). The autocorrelation of HI (Table 2) was lower compared to tree-ring width (Matisons et al., 2021) indicating explicit inter-annual variation, despite the longer period of formation (Lanner, 1976). Alternatively, lower autocorrelation might be explained by the extended window of formation of HI allowing weather effects to be compensated (Cuny et al., 2019; Mäkinen et al., 2018; Salminen and Jalkanen, 2005). Autocorrelation has also been related to conservative growth strategy (Isaac-Renton et al., 2018). The mean sensitivity and Gini coefficients for HI were intermediate (Table 2) supporting the sufficiency of the datasets for weather-growth analysis (Hughes et al., 2019; Bunn, 2008; Cook, 1987).

The clone-specific weather-growth responses and resilience components (Figs. 4, 6) highlighted uneven phenotypic plasticity and fine scale local adaptation of the studied genotypes thus supporting the adaptability of the local peripheral population to changing environment (Forzieri et al., 2022; Liepe et al., 2022; Zeltiņš et al., 2022; Trujillo-Moya et al., 2018; Kapeller et al., 2017). Though, the clonal differences in the shape/nature of weather-growth responses (Figs. 4, 6) suggested uneven sustainability of local genotypes (Zeltiņš et al., 2019; Oboite and Comeau, 2019; Trujillo-Moya et al., 2018), which might increase the variability of height growth of trees within a stand (Liepe et al., 2022; Tei et al., 2017). Sensitive, yet plastic growth responses are an adaptation to changing environments improving long-term survival and competitiveness (Liepe et al., 2022; Cavin and Jump, 2017; Zeltiņš et al., 2019). This apparently has been the strategy of the intermediate clone, which had sensitive (Table 3) and resilient HI (Table 5; Fig. 6). On the contrary, the HI of the more productive clones was more resistant to environmental fluctuations, hence requiring lesser resilience (Schwarz et al., 2020; Jetschke et al., 2019; Lloret et al., 2011). Increased resistance relates to more efficient usage of resources (Liepe et al., 2022; Way and Oren, 2010), yet lower resilience might facilitate fatal damage in case of intensifying extremes (Forzieri et al., 2022; Schwarz et al., 2020; Prendin et al., 2018). The clonal differences in HI, however, tended to decrease with age (Fig. 2), likely as the maintenance costs and drought sensitivity of spruce increase (Prendin et al., 2018).

Decreased individuality and smaller clonal differences regarding the weather anomalies (Tables 3, 5), suggested the diminishing of genetic effects, as climatic conditions marginalize (van der Maaten-Theunissen et al., 2021; Klisz et al., 2019). This emphasizes the sensitivity of increment as a complementary trait when scrutinizing genotypes for commercial used (Breed et al., 2018; Housset et al., 2018; Jansson et al.,

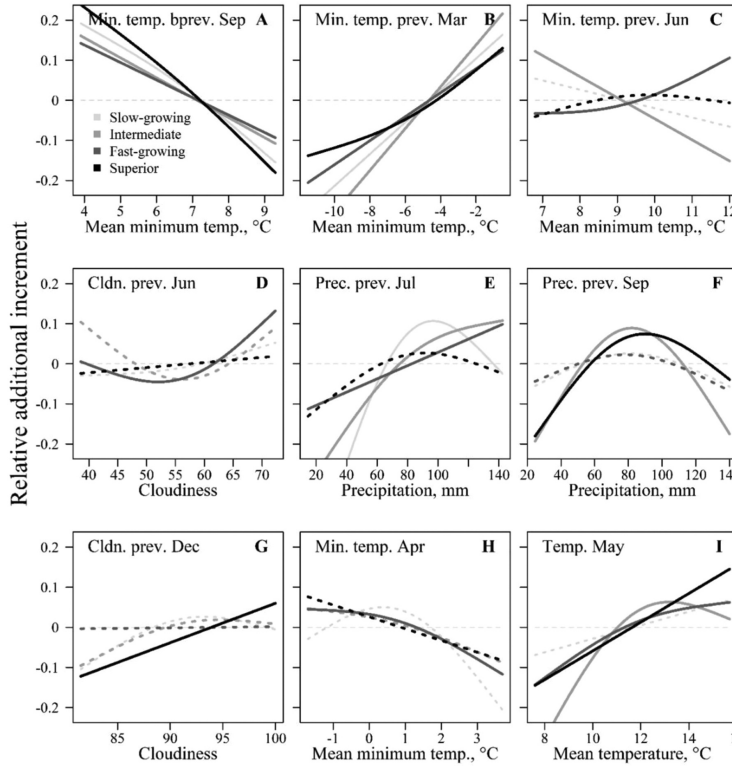

Fig. 4. The estimated (partial) responses splines of relative additional height increment (represented by indices of residual chronology) of clones of local plus-trees of Norway spruce differing by productivity to meteorological variables during the period 1977–2020 in a clonal trial in Latvia. Multiple regression was conducted for each clone. Confidence intervals for splines are not shown for clarity. Temp. – temperature, prec. – precipitation, SPEI –standardized precipitation evapotranspiration index, cldn. – cloudiness, min. – minimum, prev. – year of terminal bud formation, bprev. – year before the formation of terminal bud. Confidence intervals are not shown for clarity. The significant responses are shown by solid lines.

2017; Baliuckas et al., 2004). However, the studied clones were propagated plus-trees (Jansons et al., 2015a), hence the results might be biased regarding the general population (Klesse et al., 2018). Also, the dominant (taller) trees are more drought-sensitive (Prendin et al., 2018; Lebourgeois et al., 2014). On the other hand, the application of improved forest reproductive material is being advised for the sustainability of forests (Jansson et al., 2017; Keenan, 2015; O'Neill et al., 2014), thus emphasizing the relevance of the most competitive genotypes (Liepe et al., 2022; Jansson et al., 2017; Jansons et al., 2015a). Still, the limited set of genotypes studied must be acknowledged regarding the representation of the population.

At small spatial scales, nonlinear responses in tree growth have been related to close-to-marginal conditions (Lloyd et al., 2013), especially as the climatic changes extend climatic gradients (Meier et al., 2022; Wilmking et al., 2020; Klisz et al., 2019), particularly for locally adapted populations (Liepe et al., 2022; Svystun et al., 2021; Montwe et al., 2018). Accordingly, the observed common nonlinear responses (Fig. 4, Table 3) highlighted the extension of local climatic gradient, as the genotypes have been approaching the limit of adaptation (Wilmking et al., 2020; Cavin and Jump, 2017; Lloyd et al., 2013). The nonlinearity of the responses (Fig. 4) also indicates the effect of climate on the weather sensitivity of increment, thus highlighting the scalability of such relationships (Wilmking et al., 2020; Babst et al., 2018; Xu et al., 2017; Lloyd et al., 2013). The low effect (variance) of year (Table 3) suggested the stationarity of the HI responses (Wilmking et al., 2020) despite their dependence on tree size (Prendin et al., 2018). Though, the trees were still young, hence the age effects might not have manifested fully (de Micco et al., 2019; Hughes et al., 2019).

From the perspective of the genotypes, the differences in the type of the responses (linear or spline; Fig. 4) indicated uneven length of the meteorological gradients, and hence uneven phenotypical plasticity (Liepe et al., 2022; Housset et al., 2018). Accordingly, linear responses

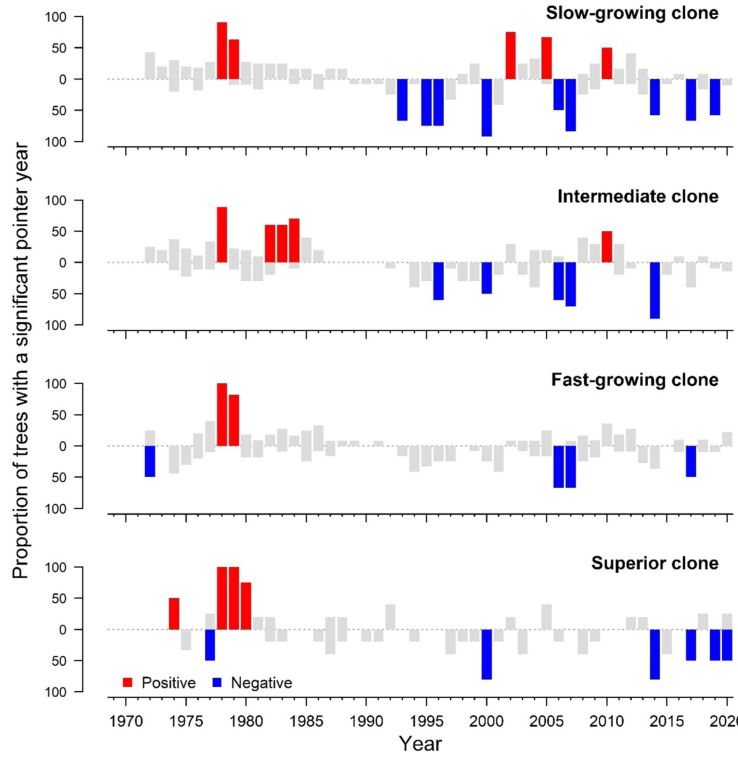

Fig. 5. Estimated pointer years of height increment of clones of local plus-trees of Norway spruce differing by productivity during the period 1969–2020 in a clonal trial in Latvia. The "significant" pointer years are shown in colour (higher intensity if in grayscale).

(Fig. 4) suggested the ability to cope with a wider spectrum of conditions (Wilmking et al., 2020; Lloyd et al., 2013), proposing local linearity as a proxy for conformity of genotype and climate (Way and Oren, 2010). A local nonlinear response could be considered indicative of increased sensitivity (Liepe et al., 2022) and marginalization of the conditions (Isaac-Renton et al., 2018; Montwe et al., 2018; Keenan et al., 2015). Furthermore, the clonal differences in weather-growth relationships (strength and type of spline) (Fig. 4; Table 3), indicated sensitivity-productivity relationships (Liepe et al., 2022; Harvey et al., 2020; Housset et al., 2018), with more productive clones being less sensitive, particularly to the unfavourable weather conditions (R^2, Tables 2, 3).

4.2. Weather drivers of height increment

The dependence of conifer HI on growth initials formed in the preceding year, their extension, as well as "free" growth (Lanner, 1976), complies with the complex of direct and carry-over effects of meteorological conditions (Tables 3, 5), supporting extended period of responsiveness (Matisons et al., 2021; Hughes et al., 2019; Jansons et al., 2015b, 2013; Salminen and Jalkanen, 2005; Mäkinen et al., 2001). The complexity of the weather-growth relationships can also be attributed to the interacting effects of weather conditions (Harvey et al., 2020; Wilmking et al., 2020; Isaac-Renton et al., 2018; Seidl and Rammer, 2017), as suggested by the underlying weather causes of pointer years (Tables 4, 5). Still, the prevailing carry-over effects of meteorological conditions (Fig. 4; Table 3), suggest that the formation of growth initials and availability of nutrient reserves (Schoonmaker et al., 2021; Mäkinen et al., 2018; Lanner, 1976) have been the principal source of the "normal" inter-annual variation of the increment (Cook, 1987). The generally stronger effect of the thermal regime during the dormancy period and the secondary effects of summer moisture availability (Table 3), however, suggested lower drought sensitivity of HI compared to radial increment (Matisons et al., 2021).

The positive effect of temperature in the previous March, which was the main weather driver of HI (excl. superior clone; Fig. 4 B), might be related to cold damage (Beck et al., 2004; Pearce, 2001), which was proportional to productivity, supporting the sensitivity-productivity

Table 4
Estimated "significant" pointer years of height increment of clones of local Norway spruce plus-trees differing by productivity in a clonal trial in Latvia for the period 1969–2020 and respective meteorological extremes according to the almanac of the Latvia Environment Geology and Meteorology Centre and gridded climatic data (30-year moving z-scores in brackets; variables with z-scores > 2 are shown). Temp. –temperature, prec.–precipitation, SPEI – standardized precipitation evapotranspiration index, prev. – year of terminal bud formation, bprev. – year before the terminal bud formation.

Year	Almanac	Gridded dataset
1978 (+)	Cool summer, strong temperature contrast in late autumn	Min. temp. bprev. Oct. (-3.27), Prec. prev. Jul. (2.19), Prec. Aug. (2.28)
1979 (+)	Cold winter, cool summer, temperature contrasts in autumn	Max. temp. prev. Nov. (2.42), Temp. prev. Dec. (-2.63), Max. temp. Jul. (-2.03), Prec. prev. Aug. (2.28), Prec. prev. Sep. (2.11), Prec. Mar (2.22)
1996 (-)	Cold records in winter-spring temperature contrasts in summer	Max. temp. bprev. Jul. (2.30), Prec. bprev. Jul, (-2.07)
2000 (-)	High temperature records throughout the year	Max. temp. bprev. Nov. (-2.21), Temp. prev. Apr. (2.04), Temp. prev. Jun. (2.28), Temp. Apr. (2.39)
2006 (-)	Cold January, heat records in summer	SPEI annual (-2.11)
2007 (-)	Warmth/heat records in winter and summer	Max. temp. prev. Dec. (2.33), Max. temp. Mar. (2.42)
2010 (+)	Cold January, hot summer	Min. temp. Jul. (2.41), Min. temp. Aug. (2.59), Temp. vegetation season (2.78), Max. temp. Jan. (-2.02)
2014 (-)	Heat records in summer, dry July	Min. temp. prev. May (2.14)
2017 (-)	Low temperature records and Temperature contrasts in summer	SPEI. bprev. Oct. (-2.36)
2019 (-)	Warm winter, and spring, cold records in summer	Temp. prev. May. (2.51), Max. temp. Jun. (2.19), SPEI bprev. Oct. (2.37)

Table 5
Statistics of the linear mixed models assessing clonal differences of resilience components of height increment of clones of local plus-trees of Norway spruce in a trial in Latvia to meteorological variables during the period 1977–2020. For the fixed effect (clone) their strength (Wald's χ^2 values are shown); for the random effects, variance is shown. Significance codes, p-values: *< 0.05, ** < 0.01, *** <0.001.

	Resistance	Recovery	Resilience	Rel. Resilience
Negative years (1996, 2000, 2006, 2014, 2017, and 2019)				
Fixed effects, χ2				
Clone	34.69***	19.60***	2.65	30.39***
Random effect, variance				
Tree	0.0001	0.0124	0.0001	0.0001
Year	0.0038	0.2927	0.0162	0.0265
Residual	0.0812	2.0669	0.0575	0.1042
Fit statistic				
$R^2_{marginal}$	0.12	0.09	0.01	0.13
$R^2_{conditional}$	0.16	0.21	0.24	0.30

relationships (Liepe et al., 2022; Housset et al., 2018; Xu et al., 2017). Conditions at the cessation of vegetation period affect the amount of nutrient reserves stored for growth in the following year (Schoonmaker et al., 2021; de Micco et al., 2019; Hughes et al., 2019). Hence, the negative effect of temperature in September before the bud formation (Fig. 4 A), might be related to the availability of nutrient reserves (Isaac-Renton et al., 2018; Prendin et al., 2018; Ericsson, 1978) and/or respiratory nutrient losses as trees start to cold harden (Beck et al., 2004). This tended to be stronger for the faster growing genotypes, which are investing in competitiveness, rather than stress tolerance (Oboite and Comeau, 2019; Prendin et al., 2018; Hartmann et al., 2013). Alternatively, this might be an artefact of the data. The intensifying summer droughts (Forzieri et al., 2022; Meier et al., 2022; Bosela et al., 2021; Matisons et al., 2021; Hughes et al., 2019) and extending vegetation season (Meier et al., 2022; Reyer et al., 2014) can explain the significant effect of previous July and September precipitation (Fig. 4 E, F). The nonlinear responses, however, indicated an optimum, implying the trade-off between sufficient moisture availability (Bosela et al., 2021) and assimilation (Schoonmaker et al., 2021; Strand et al., 2006) or excess of soil moisture (Zaerr, 1983). Still, the clonal differences suggested the relationships between drought tolerance and productivity (Liepe et al., 2022; Housset et al., 2018; Prendin et al., 2018).

The negative effect of the previous June temperature on the intermediate clone (Fig. 4 C) might be related to the temperature control over the growth-reproduction trade-offs, which can vary in a population (Hacket-Pain et al., 2019). The contrasting response of the superior clone particularly under warmer conditions might be related to increased assimilation (Salminen and Jalkanen, 2005; Hansen and Beck, 1994; Ericsson, 1978). The nonlinear effect of cloudiness in the preceding June on the fast-growing clone (Fig. 4 D), reflected the trade-off between assimilation (Mäkinen et al., 2018; Strand et al., 2006) and water loss in sunny/dry conditions (Prendin et al., 2018; Jyske et al., 2014; Hartmann et al., 2013). The positive linear effect of cloudiness in the previous December (superior clone; Fig. 4 G), might be related to cyclone activity, hence mildness of weather (Meier et al., 2022) and cold damage (Beck et al., 2004; Pearce, 2001).

The response to temperature in May (Fig. 4 I) indicated the direct effect of meteorological conditions on shoot elongation (Mäkinen et al., 2018; Salminen and Jalkanen, 2005; Lanner et al., 1976), particularly that of frosts (Svystun et al., 2021; Beck et al., 2004; Hansen and Beck, 1994). The positive linear response indicated a higher tolerance of the superior clone to the thermal regime in May. The fast-growing and intermediate clone only benefited from temperature in the case of cooler springs, suggesting that the responses reflected the trade-off between efficient xylogenesis and water loss (Mäkinen et al., 2018; Prendin et al., 2018). The negative response of the fast-growing clone to the above-average temperature in April (Fig. 4 H) might be related to premature frost dehardening or respiratory nutrient losses (Beck et al., 2004; Ögren, 1997). These responses also suggested asynchrony in the growth phenology among the genotypes (Nezval et al., 2021; Mäkinen et al., 2018).

The estimated relationships (Figs. 4, 6) differed from those shown for radial increment, which is sensitive to conditions in the year of formation, particularly summer moisture regime (Matisons et al., 2021; Hughes et al., 2019), indicating HI as a source of complementary information (Mäkinen et al., 2018; Metslaid et al., 2011). Such differences can be related to the asynchrony of primary and secondary growth (Nezval et al., 2021; Jyske et al., 2014) and the underlying mechanisms (Lanner et al., 1976). Nevertheless, considering the relations to productivity (Socha et al., 2021; Sharma et al., 2011; Skovsgaard and Vanclay, 2008), laborious HI measurements appeared reasonable particularly for scrutiny of experimental material (Jansons et al., 2015b; Metslaid et al., 2011). The prevailing low temperature limitation (Figs. 3, 4; Table 5) presumed positive effects of warming on HI (Dyderski et al., 2018; Reyer et al., 2017, 2014). However, such effects would likely be interacted by the intensifying disturbances and their legacy as stands mature (Knoke et al., 2021; Seidl and Rammer, 2017; Keenan et al., 2015). Nevertheless, the estimated clonal differences (Tables 3, 5) indicated sensitivity-productivity relationships (Babst et al., 2018; Zhang et al., 2018) and adaptive potential of the studied population (Liepe et al., 2022; Zeltiņš et al., 2022, 2019; Jansson et al., 2017; Baliuckas et al., 2004).

5. Conclusions

The long-term variability of HI indicated weather sensitivity of primary growth of Norway spruce implying responsiveness to changing climate. The effects of weather conditions differed among the clones indicating sensitivity-productivity relationships implying potential to

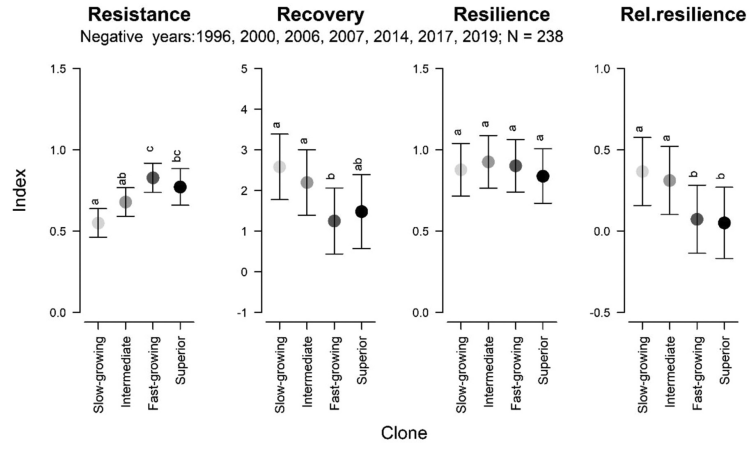

Fig. 6. The estimated mean resilience components of height increment of clones of local plus-trees of Norway spruce differing by productivity in responses to identified "significant" negative pointer years during the period 1969–2020 in a clonal trial in Latvia. The whiskers indicate a 95% confidence interval. Matching letters denote a lack of significant differences (at $\alpha = 0.05$) between the clones.

maintain productivity and sustainability of spruce forests in the eastern Baltic region. As the formation of HI is a two-year process, weather conditions prevailingly showed direct and particularly carry-over effects indicating complex climatic controls. Despite the drought sensitivity of Norway spruce, HI showed the strongest positive relationships with temperature during the dormancy period, while conditions in summer had secondary effects. Considering that narrow spatial scale and climatic gradient were analysed, diverse (linear and nonlinear) weather-growth responses were estimated within the local population. This indicated uneven phenotypic plasticity of the genotypes, as well as genetic adaptations in terms of environmental sensitivity, suggesting the adaptive potential of the local non-marginal population.

CRediT authorship contribution statement

Āris Jansons: Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Rolands Kāpostiņš:** Resources, Investigation, Formal analysis. **Kristaps Ozoliņš:** Writing – original draft, Investigation, Formal analysis, Data curation. **Pauls Zeltiņš:** Writing – review & editing, Writing – original draft, Validation, Software, Methodology, Data curation, Conceptualization. **Roberts Matisons:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Software, Methodology, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dendro.2024.126187.

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2018	"Forest tree and stand growth and dynamics: Multiple effects and problems when analysing data", Alnarp, Rootsi

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2020–2023	European Regional Development fund project No. 1.1.1.1/19/A/111: Decision support tool for increased forest productivity via efficient climate adjusted transfer of genetic gain

2020–2021	Latvian Council of Science Grant Agreement No. lzp-2020/2-0416: Local specialization and genetic control of plasticity of radial growth responses of Scots pine.
2015–2020	JSC Latvia's State Forests research programme (agreement No. 5.5-5.1_002u_101_15_58): Forest tree breeding to select genetically high value forest reproductive material 2.

LIST OF PUBLICATIONS

Indexed in Web of Science

Bāders, E., **Zeltiņš, P.,** Elferts, D., Ruņģis, D., Gailis, A., Jansons, Ā. 2024. Trends in genetic diversity of silver birch: Insights from varied planting scenarios. BALTIC FORESTRY, 30 (2), id759. DOI: 10.46490/BF759.

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