PROMOCIJAS DARBS
doktora grāda (Ph. D.) iegūšanai
lauksaimniecības, mežsaimniecības
un veterinārās zinātnēs

ĀRA BĒRZA (*Betula pendula* Roth.) SELEKCIJA LATVIJĀ

Arnis Gailis

BREEDING OF SILVER BIRCH (*Betula pendula* Roth.) IN LATVIA

DOCTORAL THESIS
for the doctoral degree
of Doctor of Science (Ph. D.) in Agriculture,
Forestry and Veterinary Sciences

LATVIJAS VALSTS MEŽZINĀTNES INSTITŪTS “SILAVA”
LATVIAN STATE FOREST RESEARCH INSTITUTE ‘SILAVA’

LATVIJAS BIOZINĀTŅU UN TEHNOLOĢIJU UNIVERSITĀTE
LATVIA UNIVERSITY OF LIFE SCIENCES AND TECHNOLOGIES

Mg. silv. **ARNIS GAILIS**

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Salaspils 2026

630(043)
Ga170

Promocijas darba zinātniskais vadītājs / *Supervisor*:
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The PhD thesis was prepared in Latvia State Forest Research Institute 'Silava'. The Ph. D. studies were carried out in Latvia University of Life Sciences and Technologies, Forestry Faculty in the period from 2010 to 2015. The work was developed within the framework of the research "Forest tree breeding studies for the creation of genetically high-value forest reproductive material sources" (LVM No. 5-5.9.1_0082_101_21_88) and "Development of a decision-making support tool for reducing the risk of wind damage in birch and aspen forest stands" (ERDF No. 1.1.1.1/18/A/134), data material was also collected in the studies "Establishment of a broadleaf tree seed database", "Characterization of broadleaf tree populations and seed supply", "Selection studies of economically important broadleaf tree species for the renewal of high-quality, productive and genetically diverse forest stands".

Oficiālie recenzenti / *Official reviewers:*
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3. Dr. biol. Ina ALSIŅA, Latvijas Biozinātņu un tehnoloģiju universitāte / *Latvia University of Life Sciences and Technologies.*

pISBN 978-9934-603-17-4
eISBN 978-9934-603-18-1

ANOTĀCIJA

Tuvākajās desmitgadēs sagaidāma saimniecisko bērza audžu platības samazināšanās, kas saistīta gan ar šīs koku sugas vecumstruktūras īpatnībām, gan platību ar vides aizsardzības un rekreācijas mērķiem pieaugumu. Vienlaikus pieaug pieprasījums pēc atjaunojamā resursa – koksnes, kas iegūta ilgtspējīgā mežsaimniecībā, un nepieciešamība kāpināt oglekļa uzkrājumu mežā un koksnes produktos. Tātad nepieciešams efektīvi izmantot meža zemes resursus, t.sk. atjaunojot audzes ar selekcionētu meža reproduktīvo materiālu. Mērķtiecīga meža atjaunošana nozīmīga arī klimata pārmaiņu negatīvās ietekmes mazināšanai: gan tieši – nodrošinot piemērotu genotipu ar augstu fenotipisko plastiskumu izmantošanu; gan pastarpināti – kombinācijā ar mežkopības metodēm kāpinot radiālo pieaugumu un mazinot nozīmīgāko abiotisko faktoru (t. sk. vēja) riskus. Promocijas darba mērķis ir raksturot āra bērza līdzšinējās selekcijas rezultātus un to efektīvas izmantošanas iespējas.

Promocijas darbā apkopota un vispusīgi izvērtēta bērza selekcija Latvijā, nodrošinot informācijas bāzi tās turpmākai attīstībai. Raksturota selekcijas potenciālā ietekme gan uz dažādām bērza fenotipisko pazīmju grupām, gan uz to apvienojošo pazīmi – stumbra monetāro vērtību, izmantojot nevis aprēķinātās, bet praksē (selekcijas stādījumos) sasniegtās selekcijas efekta vērtības. Iegūtie rezultāti pamato plašākas selekcionēta stādmateriāla izmantošanas nozīmību. Sagatavota tehnoloģija augstvērtīgāko bērza genotipu veģetatīvai pavairošanai, kas tieši izmantojama stādu ražošanā.

Promocijas darbā pirmo reizi bērzam raksturota pazīmju (t. sk. stumbra monetārās vērtības) ģenētiskā variācija stādījumā, kas sasniedzis galvenās cirtes parametrus, kā arī tieši novērtēta selekcijas ietekme uz finansiālajiem rādītājiem pirmajā retināšanā, kā arī pirmo reizi Latvijā detalizēti raksturoti bērza ātraudzību un stumbra kvalitāti nosakošo pazīmju ģenētiskie parametri un ar tiem saistītās provenienču reģionu atšķirības, nozīmīgi papildinot kopējo zinātnisko izpratni par bērza ģenētisko mainību Baltijas jūras reģionā.

Promocijas darbs sastāv no tematiski vienotām septiņām zinātniskajām publikācijām.

ABSTRACT

In the coming decades, a reduction in the area of commercial birch stands is expected. This trend is linked to both the age structure characteristics of this tree species and the increasing area designated for environmental protection and recreational purposes. At the same time, there is a growing demand for renewable resources – wood sourced from sustainable forestry – and a need to increase carbon sequestration in forests and wood products. Therefore, it is essential to use forest resources efficiently, including the regeneration of stands using genetically improved forest reproductive material. Targeted forest regeneration also plays an important role in mitigating the negative impacts of climate change: both directly – by ensuring the use of appropriate genotypes with high phenotypic plasticity – and indirectly – by combining with silvicultural methods to enhance radial growth and reduce risks from major abiotic factors, including wind. The aim of this doctoral thesis is to describe the results of silver birch breeding to date and the potential for their effective application.

The thesis compiles and comprehensively evaluates birch breeding in Latvia, providing a foundation for its further development. It characterizes the potential impact of breeding both on various groups of phenotypic traits and on a unifying trait – the monetary value of the stem – using not estimated, but empirically achieved realized breeding values from field trials. The obtained results support the importance of broader use of genetically improved planting material. A technology has been developed for the vegetative propagation of the superior birch genotypes, which can be directly used in production of planting material.

For the first time, this thesis characterizes the genetic variation of birch traits (including stem monetary value) in a plantation that has reached final harvest dimensions, as well as directly evaluates the financial effects of breeding during the first commercial thinning. Moreover, for the first time in Latvia, the genetic parameters of traits determining birch growth and stem quality are described in detail, along with the associated differences between provenance regions. These results significantly enhance the overall scientific understanding of birch genetic variability in the Baltic Sea region.

This doctoral thesis consists of seven thematically linked scientific publications.

SATURS / *CONTENTS*

PUBLIKĀCIJU SARAKSTS / *LIST OF PUBLICATIONS*

Promocijas darbā iegūtie rezultāti apkopoti septiņās publikācijās, uz kurām atsauces tekstā veidotas, izmantojot romiešu ciparus:

The thesis is based on seven publications, refered in the text with Roman numerals:

1. Selekcijas stādījumu novērtējums / *Evaluation of silver birch progeny trials*

I **Gailis A.**, Jansone B., Racenis E., Sisenis L., Jansons A. 2019. Assessment of silver birch (*Betula pendula* Roth.) geographical provenances in Latvia. In: 19th International Multidisciplinary Scientific Geoconference SGEM 2019: Conference Proceedings Vol. 19 "Water Resources. Forest, Marine and Ocean Ecosystems. Issue: 3.2 Soils, Forest Ecosystems", 30 June–6 July, 2019, Albena, Bulgaria, p. 625–632.

II **Gailis A.**, Zeltiņš P., Purviņš A., Augustovs J., Vīndedzis V., Zariņa I., Jansons Ā. 2020. Genetic parameters of growth and quality traits in open-pollinated silver birch progeny tests. Silva Fennica, 54(2), 10220; 10.14214/sf.10220.

III **Gailis A.**, Zeltiņš P., Matisons R., Purviņš A., Augustovs J., Vīndedzis V., Jansons Ā. 2021. Local adaptation of phenotypic stem traits distinguishes two provenance regions of silver birch in Latvia. Silva Fennica, 55(2), 10524; 10.14214/sf.10524.

2. Āra bērza veģetatīvā pavairošana un tās plašākas izmantošanas potenciāls / *Vegetative propagation of silver birch and its potential for mass propagation*

IV **Gailis A.**, Samsone I., Šēnhofa S., Girgžde E., Kāpostiņš R., Jansons Ā. 2021. Silver birch (Betula pendula Roth.) culture initiation in vitro and genotype determined differences in micropropagation. New Forests, 52, 791–806; 10.1007/s11056-020-09828-9.

V Zeltiņš P., Matisons R., **Gailis A.**, Jansons J., Katrevičs J., Jansons Ā. 2018. Genetic parameters of growth traits and stem quality of silver birch in a low-density clonal plantation. Forests, 9(2), 52; 10.3390/f9020052.

3. Finansiālais ieguvums no selekcionēta āra bērza izmantošanas / *Vegetative propagation of silver birch and its potential for mass propagation*

VI Jansons Ā., **Gailis A.**, Donis J. 2011. Profitability of silver birch (*Betula pendula* Roth.) breeding in Latvia. In: Gaile Z. (Ed.) Proceedings of the 17th International Scientific Conference "Research for Rural Development 2011", 18–20 May, 2011, Jelgava, Latvia. Jelgava: LUA, Vol. 2, p. 33– 38.

VII **Gailis A.**, Kārkliņa A., Purviņš A., Matisons R., Zeltiņš P., Jansons Ā. 2020. Effect of breeding on income at first commercial thinning in silver birch plantations. Forests, 11(3), 327; 10.3390/f11030327.

Autoru ieguldījums / *The contribution of the authors*

	I	**II**	**III**	**IV**	**V**	**VI**	**VII**
Ideja / *Original idea*	**AG**, ĀJ	**AG**, ĀJ	**AG**, ĀJ	**AG**, ĀJ	ĀJ	**AG**	ĀJ, **AG**
Pētījuma plāns / *Study design*	**AG**	**AG**, PZ	**AG**, PZ, RM	**AG**, IS	**AG**, PZ	**AG**	**AG**
Datu ievākšana / *Data collection*	ER, LS	AP, JA, VV	AP, JA, VV	SŠ, RK, GE	JK, JJ	ĀJ	AP
Datu analīze / *Data analysis*	**AG**, ER, LS	PZ, **AG**	PZ, **AG**	SŠ, **AG**	ĀJ, RM, PZ	ĀJ, JD, **AG**	**AG**
Manuskripta sagatavošana / *Manuscript preparation*	**AG**	**AG**, PZ, ĀJ	**AG**, PZ, RM, ĀJ	SŠ, **AG**, ĀJ	**AG**, ĀJ, RM, PZ	**AG**, JD, ĀJ	**AG**, AK, RM, PZ, ĀJ
Promocijas darba autora ieguldījums, % / *Contribution of author of the thesis, %*	80	60	65	65	55	75	70

AG – Arnis Gailis, AK – Annija Kārkliņa, AP – Andis Purviņš, ĀJ – Āris Jansons, BJ – Baiba Jansone, EG – Elva Girgžde, ER – Eduards Rācenis, IS – Ineta Samsone, IZ – Inga Zariņa, JA – Juris Augustovs, JD – Jānis Donis, JK – Juris Katrevičs, PZ – Pauls Zeltiņš, RK – Rolands Kāpostiņš, RM – Roberts Matisons, SŠ – Silva Šēnhofa, VV – Valts Vīndedzis.

PROMOCIJAS DARBA REZULTĀTU APROBĀCIJA / *APPROBATION OF RESEARCH RESULTS*

Ziņojumi par pētījuma rezultātiem prezentēti četrpadsmit starptautiskajās konferencēs:

Results of the study have been pressented in fourteen international scientific conferences:

1) Zeltiņš P., **Gailis A.**, Jansons Ā. 2022. Silver birch: breeding & growth modeling of improved material & effect of rot in Latvia. International Seminar, SNS "Stronger Together – Facilitating Efforts in Birch Breeding in the Baltic Sea Region", 7–8 September, 2022, Finland.
2) Zeltiņš P., **Gailis A.**, Jansons Ā. 2022. Tree breeding mitigates the potential adverse effect of climate change. International Conference, SNS Growth and Yield Researchers Network "Local Solutions for Regional and Global Forest Management Challenges", 7–9 June, 2022, Salaspils / Riga, Latvia.
3) **Gailis A.**, Jansons Ā. 2021. Forest tree breeding: its current and future importance. International Scientific Conference "Knowledge Based Forest Sector", 26–27 January, 2021, Riga, Latvia.
4) **Gailis A.**, Zariņa I., Zeltiņš P. 2021. Breeding perspectives of silver birch in Latvia. International Scientific Conference "Knowledge Based Forest Sector", 26–27 January, 2021, Riga, Latvia.
5) Zeltiņš P., **Gailis A.**, Matisons R. 2020. Local adaptation in silver birch growth and stem quality traits in Latvia. International Scientific Conference "Genetics to the Rescue. Managing Forests Sustainably in a Changing World", 27–31 January, 2020, Avignon, France.
6) **Gailis A.**, Purviņš A., Zeltiņš P., Jansons Ā. 2019. Impact of genetics on income at first commercial thinning in silver birch plantations. 25th International Scientific Conference "Research for Rural Development 2019", 15–17 May, 2019, Jelgava, Latvia.
7) Jansons Ā., **Gailis A.**, Zeltiņš P., Katrevičs J. 2019. Climate and fast growing trees. International Conference "Alders and Other Fast Growing Trees", 29–30 April, 2019, Kalsnava, Latvia.
8) **Gailis A.**, Jansone B., Rācenis E., Sisenis L., Jansons Ā. 2019. Assessment of silver birch (*Betula pendula* Roth.) geographical provenances in Latvia. 19th International Multidisciplinary Scientific Geoconference SGEM 2019, 29 June–6 July, 2019, Albena, Bulgaria.
9) **Gailis A.**, Samsone I., Zeltiņš P., Jansons Ā. 2019. Production potential of silver birch in Latvia: tree breeding, propagation and silviculture. SCAR Baltic Workshop on Bioeconomy Strategy, 5 April, 2019, Riga, Latvia.

10) **Gailis A.**, Samsone I., Giržgde E., Kāpostiņš R., Jansons Ā. 2018. Genetically determined differences in microclonal propagation of silver birch (*Betula pendula* Roth.). VII Baltic Genetics Congress, 24–27 October, 2018, Riga, Latvia.

11) **Gailis A.**, Jansons Ā. 2017. State and perspectives of silver birch breeding and propagation in Latvia. International Scientific Seminar, HealGenCar, 19–20 April, 2017, Riga, Latvia.

12) **Gailis A.**, Baumanis I., Bāders E., Puriņš M., Jansons Ā. 2016. Genetic differences in silver birch quality. IX Congress of the Latvian Society of Geneticists and Breeders, 15 July, 2016, Riga, Latvia.

13) **Gailis A.**, Augustovs J., Purviņš A., Jansons Ā. 2012. Differences of Latvia's silver birch (*Betula pendula* Roth.) provenances. SNS & IUFRO International Scientific Conference "Genetic Aspects of Adaptation and Mitigation: Forest Health, Wood Quality and Biomass Production", 3–5 October, 2012, Riga, Latvia.

14) Jansons Ā., **Gailis A.**, Donis J. 2011. Profitability of silver birch (*Betula pendula* Roth.) breeding in Latvia. 17th International Scientific Conference "Research for Rural Development 2011", 18–20 May, 2011, Jelgava, Latvia.

PĒTĪJUMĀ LIETOTIE SIMBOLI UN SAĪSINĀJUMI/ *ABBREVIATIONS*

BA – 6-benziladenīns / *6-benzyladenine*
BAP – 6-benzilaminopurīns / *6-benzylaminopurine*
BLUP – labākā lineārā nenobīdītā prognoze / *Best Linear Unbiased Predictors*
BV – selekcijas vērtība / *breeding value*
CV_A – aditīvās ģenētiskās variācijas koeficients / *coefficient of additive genetic variation*
CV_G – genotpiskās variācijas koeficients / *genotypic coefficient of variation*
d / *DBH* – krūšaugstuma caurmērs / *diameter at breast height*
dg / *Doubl* – dubultgalotne / *double leader*
DM – koksnes masa / *dry matter*
FEN – fenotipiskā selekcijas alternatīva /*phenotypic tree breeding alternative*
G × E – genotipa × vides mijiedarbība / *the genotype × environment interaction*
GCA – vispārējās kombinatīvās spējas / *general combining ability*
GEN – ģeneratīvā selekcijas alternatīva / *generative tree breeding alternative*
GG – selekcijas efekts / *genetic gain*
GLIMMIX – vispārināts lineārs jaukta tipa modelis / *Generalized Linear Mixed procedure*
ĢD – ģenētiskā daudzveidība / *genetic diversity*
h / *H* – koka augstums / tree height
h^2 – iedzimstamības koeficients šaurā nozīmē / *narrow-sense heritability coefficient*
H^2 – iedzimstamības koeficients plašā nozīmē / *broad-sense heritability*
h_{zz} – zemākā zaļā zara augstums
IRR – iekšējā atdeves likme / *internal rate of return*
KKC – krājas kopšanas cirte / *commercial thinning*
LVM – AS "Latvijas valsts meži" / *JSC 'Latvia's State Forests'*
MPS – Meža pētīšanas stacija / *Forest Research Station*
MRM – meža reproduktīvais materiāls / *forest reproductive material*
MS – kokaugu barotne / *Murashige and Skoog basal media*
MV – monetārā vērtība / *monetary value*
NAA – naftiletiķskābe / *naphthaleneacetic acid*
N_e – efektīvais klonu skaits / *effective number of clones*
N_s – statusa efektīvais skaitlis / *status effective number*
NWV – neto koksnes vērtība / *net wood value*
pad / *SpKn* – padēls / *spike knot*
PAR – fotosintēzes aktīvais reģions / *photosynthetically active radiation*
PCA – galveno komponenšu analīze / *Principal Component Analysis*
REML – ierobežotās maksimālās iespējamības pieeja / *restricted maximum likelihood approach*

r_g – ģenētiskā korelācija / *genotypic correlation coefficient*
RM – SIA "Rīgas meži" / *'Riga Forests' Ltd.*
r_p – fenotipiskā korelācija / *phenotypic correlation*
StStr – stumbra taisnums / *stem straightness*
TTV / *NPV* – tīrā tagadnes vērtība / *net present value*
V – stumbra tilpums / *stem volume*
VEG – veģetatīvā selekcijas alternatīva / *vegetative tree breeding alternative*
VM – valsts mežniecība / *forest district*
VMD – Valsts meža dienests / *State Forest Service*
VVM – valsts virsmežniecība / *regional forestry*
vvp / *MPC* – vainaga vidējā projekcija / *mean projection of crown*
WPM – kokaugu barotne / *woody plant medium*
zd / *BrD* – lielākā zara diametrs līdz 2 m stumbra augstumam / *diameter of the largest branch until the stem height of 2 m*
zg / LostTop – zaudēta galotne / *lost top*
zl / *BrA* – vidējais zaru leņķis / *mean branch angle*

ĀRA BĒRZA (*Betula pendula Roth*) SELEKCIJA LATVIJĀ

Tēmas izzinātības analīze

Bērzu sugas (*Betula* L.) ir nozīmīga Eiropas mēreno un boreālo mežu sastāvdaļa, kas veido aptuveni 11% no kopējās mežu platības Eiropā (Forest Europe 2020). Latvijā bērzi aizņem gandrīz trešdaļu no kopējās meža platības (MSI 2023) un ir izplatītākā ģints, kurā ir divas saimnieciski nozīmīgas sugas – āra bērzs (*Betula pendula* Roth) un purva bērzs (*Betula pubescens* Ehrh.). Abas sugas raksturojamas ar līdzīgu vainaga formu un baltu stumbru, kas var sasniegt 20–30 m augstumu, kā arī līdzīgu koksnes anatomiju, līdz ar to meža inventarizācijā, mežizstrādē un kokapstrādē šīs sugas netiek nodalītas atsevišķi. Āra bērzs raksturojams ar izteiktu kreves mizu stumbra lejasdaļā, dzinumi kārpaini (ar lenticelām), lapas smailas. Purva bērzam kreves mizas daļa uz stumbra neizteikta, lapas ovālas ar pūkainu apsarmi uz tām. Āra bērzs ir diploīda suga ar 28 hromosomām (2n = 28), bet purva bērzs ir tetraploīds (2n = 56; Helms & Jørgensen 1925). Lai gan bioķīmiskās nesaderības dēļ hibrīdi starp abām sugām ir reti sastopami (Hagman 1971), dažkārt tie var rasties (Jonsell & Karlsson 2000). Nereti morfoloģiskās atšķirības starp sugām nav izteiktas, kas apgrūtina to atšķiršanu dabā, tāpēc ir izstrādāta ķīmiska sugu identifikācijas metode to drošai nodalīšanai, kuras pamatā ir mizas ķīmiskās īpašības (Lundgren et al. 1995, Liepiņš et al. 2024).

Abas bērzu sugas atjaunojas bagātīgi ar sēklām, kuras ir mazas un vieglas, efektīvi izplatās ar vēju, var mērot lielus attālumus, veicinot sugas plašo izplatību, gēnu plūsmu un augstu ģenētisko daudzveidību (Jonsell & Karlsson 2000, Wagner et al. 2004). Bērzi ir vienmājas koki ar vīrišķām un sievišķām spurdzēm. Sēklas parasti veidojas koku savstarpējas apputeksnēšanās rezultātā bioķīmiskas pašnesaderības mehānisma dēļ (Hagman 1971). Bērzi zied vienlaikus ar lapu plaukšanu pavasarī, bet Ziemeļeiropā sēklas nogatavojas no jūlija līdz augustam (Sarvas 1952). Bērziem ir lielas atšķirības ikgadējā sēklu ražas apjomā un kvalitātē; Ziemeļeiropā raksturīgas bagātīgas sēklu ražas ar 2–3 gadu intervālu (Koski & Tallqvist 1978). Abas sugas spēj atjaunoties arī veģetatīvi, veidojot celma atvases. Šī spēja īpaši izteikta jauniem kokiem (līdz 20–30 gadu vecumam) un purva bērzam (Ferm & Kauppi 1990). Bērzs kā pioniersuga dabiski atjaunojas bagātīgi, ja ir pieejami sēklu avoti. Tomēr vēlamāka ir stādīšana, ja mērķis ir uzlabot nākamās paaudzes koku zarojuma vai stumbra kvalitāti, nodrošināt lielāku ātraudzību. Tas vienlīdz attiecas kā uz meža atjaunošanu, tā apmežošanu (Hynynen et al. 2010).

Bērza koksnes krāja Latvijā vidēji ir 261 m^3 ha^{-1}, taču variē reģionāli (224–301 m^3 ha^{-1}). Ražīgākas audzes sastopamas Austrumvidzemē un Zemgalē; ar augstu ražību izceļas Limbažu, Ogres un Jēkabpils populācijas. Audžu vidējā kvalitāte ir augstāka sausieņos, ņemot vērā, ka slapjaiņos ir mazāku dimensiju koki un lielāks nekvalitatīva purva bērza piemistrojums. Īpaši kvalitatīvas ir Naukšēnu, Svirlaukas, Ābeļu, Kupravas un Kandavas populācijas (Zālītis, 2006).

Bērza koksne tiek augstu novērtēta tās smalko šķiedru, gaišās krāsas un izturības dēļ, kas padara to piemērotu visdažādākajam pielietojumam, sākot no mēbelēm un grīdām līdz saplāksnim un finierim (Luostarinen & Verkasalo 2000, Verkasalo et al. 2017). Augstvērtīgie bērza sortimenti galvenokārt tiek izmantoti saplākšņa un zāģmateriālu ražošanā, tos tālāk pārstrādājot galdniecības izstrādājumos, paneļos un parketos. Priekšroka kokmateriālu ražošanā ir āra bērzam, jo tas ir ātraudzīgāks, ar labāku stumbra formu un lielāku koksnes blīvumu salīdzinājumā ar purva bērzu (Heräjärvi 2004). Salīdzinot āra un purva bērzu, konstatēts, ka Latvijā abu sugu vidējais augstums un caurmērs ir attiecīgi 25 un 22 m, un 35 un 32 cm (Zālītis 2006). Līdz ar to tieši āra bērzs ir bijis selekcijas programmu uzmanības centrā, lai uzlabotu šīs mežsaimnieciski nozīmīgās īpašības (Viherä-Aarnio & Velling 1999). Mazāka izmēra bērza sortimentus galvenokārt izmanto celulozes rūpniecībā, tomēr augstvērtīgi apaļkoku sortimenti ir galvenais meža apsaimniekošanas mērķis (Hynynen et al. 2010).

Tā kā klimata pārmaiņas ietekmē meža ekosistēmas, tad bērzu, īpaši – āra bērza, pielāgošanās spēja un ātraudzība veicina interesi par tā plašāku izmantošanu Baltijas jūras reģiona valstu mežsaimniecībā. Šīs sugas ir labi piemērotas izmantošanai adaptīvās meža apsaimniekošanas pieejā, kuras mērķis ir uzlabot meža noturību pret mainīgiem vides apstākļiem, piemēram, aizstājot nestabilākas skujkoku tīraudzes. Apmežošana var veicināt klimatneitralitāti, jaunizveidotajām audzēm uzkrājot atmosfēras oglekli, kā arī tajās iegūstot izejmateriālu ar augstu aizvietošanas efektu (Lutter et al. 2021). Āra bērza selekcijas programmu rezultāti atspoguļo sugas potenciālu liela apjoma augstas kvalitātes kokmateriālu ražošanā, padarot to par vienu no galvenajām sugām turpmākajā mežsaimniecības praksē. Latvijā visaptveroša āra bērza selekcija uzsākta 1990-to gadu vidū. Kā pamata selekcijas materiāls fenotipiski atlasīts 921 pluskoks un izcilie audžu koki 26 dabiskās audzēs visā valstī, un ierīkotas to pēcnācēju pārbaudes 1999. un 2000. gadā. Lai gan skujkoku sugu (parastās priedes *Pinus sylvestris* L. un parastās egles *Picea abies* (L.) H. Karst.) selekcijai Latvijā ir ilgāka vēsture, āra bērzs kā komerciāli nozīmīga koku suga ir iekļauts ilgtermiņa selekcijas programmā, kuras mērķis ir attīstīt sēklu ražošanu un paaugstināt mežu finansiālo vērtību (Jansons 2008). Mērķtiecīga meža atjaunošana ar šādu selekcionētu materiālu ir nozīmīga klimata pārmaiņu negatīvās ietekmes mazināšanai: gan tieši – nodrošinot piemērotu genotipu ar augstu fenotipisko plastiskumu izmantošanu, gan pastarpināti – kombinācijā ar mežkopības metodēm kāpinot radiālo pieaugumu un mazinot nozīmīgāko abiotisko faktoru (vēja) risku.

Promocijas darba mērķis ir raksturot āra bērza līdzšinējās selekcijas rezultātus un to efektīvas izmantošanas iespējas. Promocijas darba pētnieciskie uzdevumi ir:

1) raksturot saimnieciski nozīmīgo pazīmju ģenētiskos parametrus bērza selekcijas populācijā;
2) novērtēt ģenētikas ietekmi uz āra bērza veģetatīvās pavairošanas sekmēm;
3) novērtēt selekcijas ietekmi uz bērza stādījumu finansiālo vērtību un finansiālo ieguvumu no otrā selekcijas cikla.

1. ĀRA BĒRZA SELEKCIJA LATVIJĀ UN KAIMIŅVALSTĪS

1.1. Audžu vērtēšana un pluskoku atlase selekcijas un sēklkopības vajadzībām

Selekcijas sākums bērzam ir pēc noteiktām fenotipiskām pazīmēm pārāko indivīdu atlase. Meža selekcijā šādu koku meklēšana notiek iepriekš izvēlētās audzēs, paaugstinot varbūtību, ka fenotipiski konstatējamais pārākums ir iedzimstošs. Sākotnēji bērzu audzes atlasītas pēc to taksācijas rādītājiem – bonitāte ≥ I, tīraudzes vai mistraudzes ar citu sugu piemistrojumu ≤ 20%, platība ≥ 2 ha, vecums ≥ 30 gadi, izmantojot Valsts meža dienesta datu bāzi (atlases laikā – "Meža fonds"). Nākamais solis bija audžu vērtēšana pēc bērzu relatīvā zaru resnuma, zaru leņķa pret stumbru, stumbra taisnuma, bērzu veselības (1.1. tab.). Parauglaukumus šai vērtēšanai izvietoja subjektīvi noteiktās raksturīgākajās vietās. Parauglaukumu skaits bija atkarīgs no audzes vai audžu grupas (par grupu uzskatot un vienoti vērtējot audzes, kuras savstarpēji robežojas) platības un bija robežās no 2 līdz 6. Apļveida parauglaukumu veidoja visi koki, kas no parauglaukuma centra atradās redzamības robežās.

Vispirms audzē novērtē mīnuskoku īpatsvaru. **Mīnuskoki** ir audzes mazvērtīgākā daļa. Parasti tie ir augšanā atpalikušie koki, kurus izcērt starpcirtēs. Pie mīnuskokiem pieskaitāmi arī tādi, kuriem ir resni zari, plati vainagi, vairākas galotnes un līki stumbri. Šajā grupā ieskaita arī visus kokus ar slimības pazīmēm – nokaltušām galotnēm, trupi, putnu dobumiem u.c. Audzes, kurās vairāk nekā 50% koku ir ar resniem zariem, līkiem stumbriem un slimību pazīmēm, sauc par mīnusaudzēm, un tajās pluskoku atlase nav pieļaujama.

Audzi tālāk nevērtē, ja mīnuskoku īpatsvars pārsniedz 20% apļveida parauglaukuma redzamības robežās. Izvēlētajā apļveida parauglaukumā tiek uzskaitīti visi vērtējamie koki. Attiecinot kokus ar vainām pret kopējo redzamo novērtējamo koku skaitu, iegūst mīnuskoku īpatsvaru, kas attiecīgi samazina audzes vērtējumu: ja mīnuskoku īpatsvars ir 0–4% – vērtējums nesamazinās; ja 5–8% – vērtējums samazinās par 0,2 ballēm, un tālāk ik pa 4% audzes vērtējums samazinās par 0,2 ballēm. Bērziem par mīnuskokiem uzskata dihotomi zarotus, "piltuvveida", "slotveida", kokus ar padēliem un ļoti resniem zariem.

Audzes raksturošanu veic, par pamatu ņemot ideālo audzi ar novērtējumu piecas balles. Bērza ideālās audzes pazīmes: relatīvi tievi zari; zaru leņķis 60°–90°; taisni stumbri; audzē nav mīnuskoku. Audzes raksturojot, piezīmēs norāda dažādas īpatnības, apsaimniekošanas režīmu un citu interesējošu informāciju.

1.1. tabula

Audžu raksturošanas un vērtēšanas pazīmes

Pazīme	Vērtējums, balles				
	1	2	samazina audzes vērtējumu	3	samazina audzes vērtējumu
Zaru resnums	tievi	vidēji	–0,5	resni	–1
Stumbru taisnums	taisni	1 līkums	–0,5	≥ 2 līkumi	–1
Zaru leņķis pret stumbru *	ja zaru leņķis ir mazāks par 60°, tad par katriem 15° audzes balli samazina par 0,5 vienībām				

* nosaka katrā parauglaukumā, mērot to vainagu vidusdaļā.

Izvēlētajās audzēs meklēti **pluskoki** – valdaudzes augstākie un resnākie koki, kas starp blakus augošajiem kokiem vienvecuma audzē izceļas ar ātraudzību un augstu stumbra kvalitāti. Pluskoki audzē sastopami reti, tie ir ar taisniem, labi atzarotiem stumbriem, bez slimību pazīmēm, šauru vai vidēji platu vainagu un ar tieviem vai vidēji resniem zariem. Zaru novietojumam pret stumbru jābūt perpendikulāram vai tuvam tam.

Galvenie pamatprincipi pluskoku izvēlē visām koku sugām ir līdzīgi, tomēr katrai no tām piemīt savas īpatnības pazīmju vērtējumā un selekcijas mērķos. Dažādu koku sugu audžu resursi regulē izlases intensitāti. Pluskoku atlasei jāizvēlas labākās dabiski veidojušās audzes, ievērojot meža sēklu ieguves rajonus. Pluskoku izvēle pieļaujama arī stādītās audzēs, norādot to koku aprakstā. Pēc pluskoka atkārtotas izvērtēšanas (atestācijas) tas tiek definēts par **izcilo koku**.

Bērza pluskokus meklē par 30 gadiem vecākās augstākās bonitātes bērzu audzēs. Kā pluskokus izvēlas audzes garākos un resnākos kokus ar taisniem, gludiem un labi atzarotiem stumbriem, ar to lejasdaļā apaugušām zaru vietām. Nav piemēroti stumbri ar zaru atvasēm, stumbru bezzarainajai, gludajai apakšējai daļai jābūt iespējami garākai par stumbra zaraino vainaga daļu. Vainagam jābūt pēc iespējas šauram, ovālam vai piramidālam ar īsiem, tieviem zariem, kuri pret stumbru veido iespējami platāku leņķi. Pluskokiem jāražo daudz sēklu, tiem jābūt ar veselīgu lapojumu un veselīgu stumbru. Izvēloties pluskokus, jāņem vērā blakus esošo koku novietojums un to iespējamā ietekme uz atzarošanos.

Pirmie āra bērza 25 pluskoki, kas iekļauti pirmās bērza sēklu plantācijas izveidē, atlasīti no 1969. līdz 1971. gadam MPS "Kalsnava" (1), Limbažu MRS Liepupes, Vitrupes un Augstrozes mežniecībās (23) un Mazsalacas MRS Rūjupes mežniecībā (1). Informācija par 1970-tajos gados atlasītajiem pluskokiem glabājas LVMI "Silava" pluskoku reģistrā. Aptverot praktiski visus Latvijas reģionus, 1990-tajos gados pēc izstrādātajiem audžu vērtēšanas kritērijiem atlasītajās labākajās bērzu audzēs tika izraudzīti labākie koki. Ne visi tie uzskatāmi kā pluskoki klasiskā izpratnē, bet kā attiecīgās audzes labākie koki (skat. 1.2. att. nākamajā sadaļā), no kuriem vāca sēklas un uzsāka stādu ražošanu pēcnācēju pārbaužu ierīkošanai. Audzēs atlasītie koki dabā vairs neeksistē.

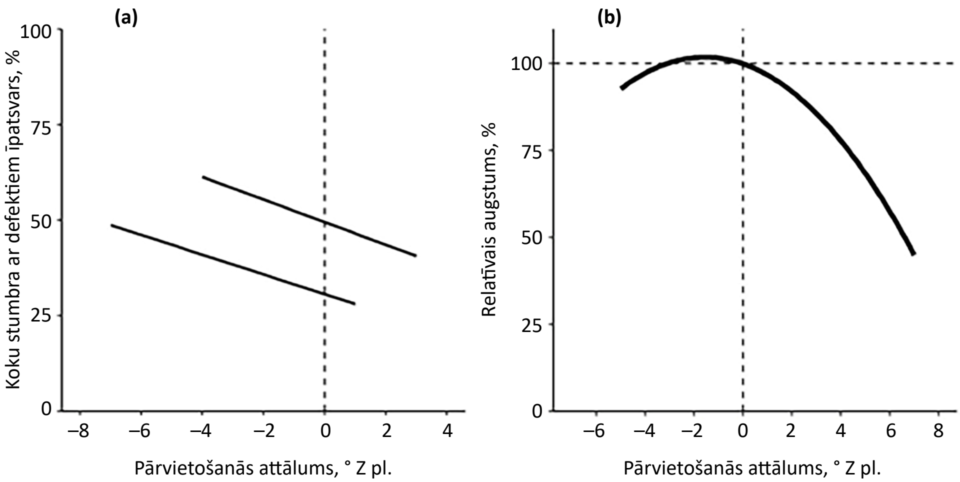
1.2. Āra bērza selekcijas stādījumi

Selekcijas materiāla izvērtēšanai un kandidātu atlasei pavairošanai un nākošajam selekcijas ciklam izmanto pēcnācēju pārbaudes. **Provenienču – koku sēklu izcelsmes ģeogrāfisko reģionu – salīdzināšanai** pirmais āra bērza pēcnācēju pārbaudes stādījums ierīkots 1975. gadā Vecumnieku pagastā ar 16 dažādas izcelsmes proveniencēm. Tomēr līdz šim trūkst pilnvērtīga provenienču izvērtējuma, lai konstatētu dažādas izcelsmes bērza reproduktīvā materiāla piemērotību Latvijas apstākļiem.

Vērtējot vispārīgās ģeogrāfiskās likumsakarības provenienču stādījumos, pētīta Somijas, Baltijas valstu un Krievijas izcelsmes bērza pēcnācēju saglabāšanās, stumbra kvalitāte un augšanas gaita izmēģinājumos Somijas dienvidu (60° Z pl.) un centrālajā daļā (63° Z pl.), ietverot 21 audzi un atsevišķus kokus, kuru izcelsme ir no 54° līdz 63° Z pl. Abos izmēģinājumos noteikts un salīdzināts koku augstums, caurmērs, krāja ha^{-1}, relatīvais stumbra raukums, koku ar defektiem (padēls, dubulta galotne) īpatsvars un saglabāšanās 22 gadu vecumā. Konstatētas nozīmīgas atšķirības starp izcelsmes vietām visām vērtētajām pazīmēm. Palielinoties sēklu izcelsmes vietas ģeogrāfiskajam platumam, lineāri statistiski būtiski samazinās koku ar stumbra defektiem īpatsvars (izmēģinājumā Somijas centrālajā daļā $p < 0{,}001$; dienvidu daļā $p = 0{,}002$); sēklu izcelsmes vietas ģeogrāfiskajam platumam samazinoties par 1 grādu, koku ar stumbra defektiem īpatsvars palielinājās par 3% (1.1. att.; Viherä-Aarnio & Velling 2008). Līdzīga sakarība novērota aļņu radītiem bojājumiem bērzu audzēs: palielinoties sēklu izcelsmes vietas ģeogrāfiskajam platumam un koku augstumam, bojājumu īpatsvars samazinās (Viherä-Aarnio & Heikkilä 2006).

Vērtējot plašāku ģeogrāfiskā platuma amplitūdu (54–67° Z pl.), konstatēts, ka vismazākais koku īpatsvars ar stumbra defektiem bija vietējas vai nedaudz vairāk uz ziemeļiem esošas izcelsmes kokiem, bet tas palielinājās, palielinoties pārvietošanas attālumam no dienvidiem (Viherä-Aarnio et al. 2013). Savukārt izcelsmes ģeogrāfiskā platuma saistība ar koksnes blīvumu netika novērota (Viherä-Aarnio & Velling 2017). Gan somu provenienču stādījumos (1.1. att.), gan 8–11 gadu vecos provenienču izmēģinājumos Lielbritānijā un Īrijā novērojama kopēja sakarība, ka provenienču pārvietošana uz ziemeļiem līdz diviem ģeogrāfiskā platuma grādiem uzlabo produktivitāti (lielāks koku augstums, caurmērs, lielāka krāja nekā vietējai izcelsmei) ilgāka fotoperioda dēļ, negatīvi neietekmējot saglabāšanos (Viherä-Aarnio et al. 2013, Lee et al. 2015, Viherä-Aarnio & Velling 2017). Jāņem vērā, ka pārvietošana uz dienvidiem vai uz ziemeļiem tālāk par 2° samazina ražību (Viherä-Aarnio et al. 2013).

Ziemeļvalstīs pirmie bērza **pēcnācēju pārbaužu stādījumi** ierīkoti Zviedrijā 1940-tajos gados, un *H. Johnsson* bija pirmais, kurš veica ģeogrāfiski attālas izcelsmes reģionu bērza ģimeņu augšanas gaitas salīdzinošos pētījumus un uzsāka arī bērza provenienču pētījumus, ierīkojot plašus stādījumus 1973.–1974. gadā (Viherä-Aarnio & Velling 2008). Uz šo izmēģinājumu pamata *L.-G. Stener* (1997),



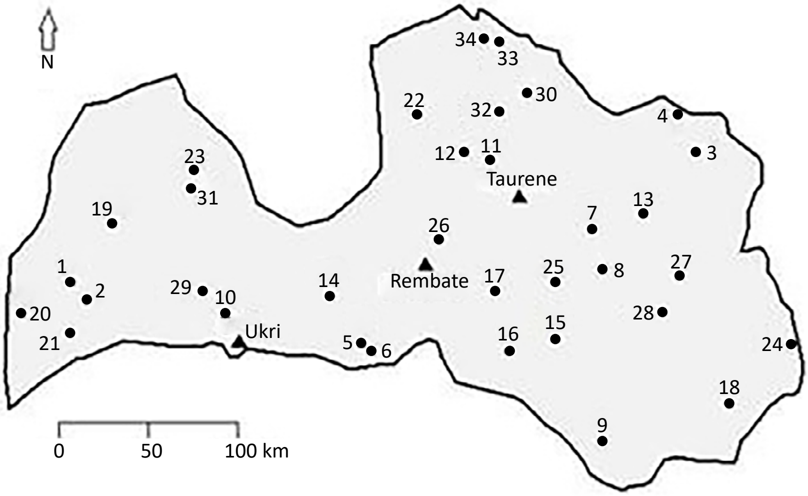
1.1. attēls. **Dažādu provenienču vidējais koku ar stumbra defektiem īpatsvars eksperimentā Somijas dienviddaļā (60° Z pl.) – augšējā līnija un centrālajā daļā (63° Z pl.) – apakšējā līnija (a) un ražība, ko raksturo relatīvais augstums (b), atkarībā no pārvietošanas attāluma ģeogrāfiskā platuma grādos**
(Viherä-Aarnio & Velling 2008, Viherä-Aarnio et al. 2013)

pētot ražības, stumbra kvalitātes un koksnes blīvuma atšķirības dažādu izcelsmju pēcnācējiem, izstrādāja bērza sēklu pārvietošanas noteikumus, Zviedrijas teritoriju iedalot četrās selekcijas zonās. Tomēr lielāka apjoma pēcnācēju pārbaužu ierīkošana uzsākta āra bērza selekcijas programmas ietvaros 1988.–1990. gadā, atlasot ap 1300 pluskoku, kuru brīvapputes pēcnācēju (pussibu ģimeņu) iedzimtības pārbaudes ierīkotas laika periodā no 1992. līdz 1998. gadam (Stener & Hedenberg 2003, Stener & Jansson 2005).

Somijā āra bērza selekcija sākās ar pluskoku atlasi 20. gadsimta 40-to gadu beigās, bet intensīvāk attīstījās 1960-to gadu beigās, kad tika izstrādāta metode sēklu masveida ražošanai polietilēna siltumnīcās (Lepistö 1973). Selekcijas pamatmateriālu veidoja aptuveni 1000 fenotipiski atlasītu pluskoku. Pirmā sēklu plantācija izveidota 1970. gadā (Haapanen 2024). Plaši provenienču pēcnācēju izmēģinājumi aizsākti 1960-tajos gados Somijas dienvidu un centrālajā daļā, un, pamatojoties uz tajos iegūtajiem rezultātiem, tika izstrādāti sēklu pārvietošanas principi (Raulo & Koski 1977).

Lietuvā ilgtermiņa selekcijas programma āra bērzam tika aizsākta 20. gadsimta 90-tajos gados, izvēloties ģenētisko resursu mežaudzes, atlasot sēklu audzes un pluskokus. Pirmā pēcnācēju pārbaužu sērija tika ierīkota 1999. gadā, bet pirmā sēklu plantācija – 2003. gadā, nodalot sēklu ražošanu diviem provenienču reģioniem (Baliuckienė 2009).

Latvijā, pieaugot interesei par lapu koku, tai skaitā āra bērza, selekciju, no 1990-tajos gados atlasītajiem mežaudžu labākajiem kokiem un pluskokiem, tos nocērtot ražas gadā, ievāca sēklas un uzsāka stādu audzēšanu, iegūstot materiālu



1.2. attēls. **Atlasīto bērza pluskoku un mežaudžu labāko koku izcelsmes vietas**

Skaitlis pie vietas atzīmes atbilst izcelsmes vietas numuram 1.3. tabulā

ļoti apjomīgu un plašu pēcnācēju pārbaužu ierīkošanai – Ogres novada Rembates pagastā (Nr. 54, šeit un turpmāk – numurs LVMI "Silava" Ilglaicīgo izmēģinājumu reģistrā), Auces novada Ukru pagastā (Nr. 55), Vecpiebalgas novada Taurenes pagastā (Nr. 589) >55 ha platībā, aptverot >900 brīvapputes ģimenes (ģimeņu izcelsme 1.2. att. un 1.3. tab.), kas kalpoja kā bāze turpmākai bērza selekcijai.

1998. gadā ierīkots provenienču pēcnācēju pārbaudes stādījums Rembates pagastā 3 ha platībā (Nr. 53) ar 15 dažādu provenienču pēcnācējiem, bet 2004. gadā ar MPS eksperimentālajā kokaudzētavā izaudzētajiem stādiem 5 ģeogrāfiski atšķirīgās vietās – MPS Kalsnavas, Mežoles, Auces un Šķēdes mežu novados un LVM "Sēklas un stādi" Latgales sēklkopības iecirkņa apsaimniekotajās platībās Sventes pagastā, ierīkotas provenienču pēcnācēju pārbaudes, katrā vietā 4 atkārtojumos ar 100 vai 50 stādiem parcelē, iekļaujot 17 āra un trīs pūkainā bērza provenineces, kopējā ierīkotā platība 15 ha (1.2. tab.).

Āra bērza pēcnācēju pārbaužu ierīkošana MPS mežu novados regulāri turpinās. No 2014. gada līdzās brīvapputes ģimeņu un kontrolēto krustojumu pēcnācējiem stādījumos iekļauti arī *in vitro* pavairoti klonu pēcnācēji. Šobrīd bērza selekcijas materiāla vērtēšanai ģeogrāfiski atšķirīgās vietās Latvijā ierīkoti 122 pēcnācēju pārbaužu stādījumi ar kopējo platību 274,3 ha. Stādījumos veidotas vienkoku, bloku vai rindu parceles, tās marķētas dabā. Kopsavilkums par bērza pēcnācēju pārbaužu stādījumu ierīkošanu – 1.4. tabulā, to izvietojums atbilstoši platības lielumam – 1.3. attēlā. Stādījumi reģistrēti LVMI "Silava" Ilglaicīgo izmēģinājumu reģistrā.

1.2. tabula

2004. gadā ierīkotie bērza provenienču pārbaužu stādījumi

Provenineces nosaukums	Kopējais stādu skaits stādījumu vietās				
	Šķēdes MN Nr. 310	Auces MN Nr. 315 *	Kalsnavas MN Nr. 236	Mežoles MN Nr. 333	Sventes pag. Nr. 752
Rūjupe	400	400	400	400	400
Šķēde	400	400	400	400	400
Saikava	400	400	400	400	400
Viesīte	400	-	400	240	400
Kalsnava	400	400	400	400	400
Naukšēni	400	400	400	400	400
Aizpute	400	400	400	400	400
Daliņi	400	-	275	-	-
Ziemeri	400	400	400	400	400
Kuldīga	400	200	400	200	400
Mālupe	400	120	400	-	400
Gaigalava	400	200	400	200	400
Medņi	400	-	200	150	200
Jaungulbene	400	150	200	-	200
Strenči	400	295	400	400	400
Gauja	400	200	400	300	400
Mērdzene	400	200	400	200	400
Kopā	6800	4165	6275	4490	6000
Rūjupe, pūk.	400	-	400	-	400
Naukšēni, pūk.	200	-	200	-	-
Gaigalava, pūk.	200	-	200	-	-
Pavisam kopā	7600	4165	7075	4490	6400
ha, (tīrā)	3,8	2,1	3,5	2,2	3,2

* stādījums gājis bojā.

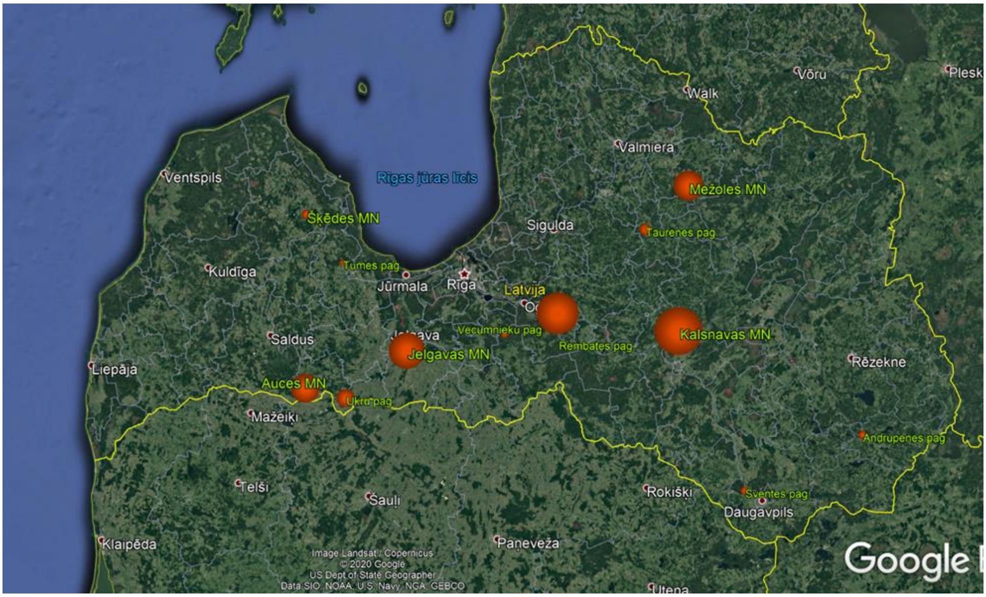
1.3. tabula

Bērza brīvapputes ģimeņu izcelsme pēcnācēju pārbaužu stādījumos

Nr. *	Izcelsme **	Ģimeņu skaits		
		Rembate Nr. 54	Ukri Nr. 55	Taurene Nr. 589
1	Aizputes VVM Aizputes VM (1998. g.)	-	17	10
2	Aizputes VVM Kalvenes VM	-	2	2
3	Alūksnes VVM Mālupes VM (1998. g.)	-	6	6
4	Alūksnes VVM Ziemeru VM (1998. g.)	-	5	5
5	Bauskas VVM Bauskas VM	24	24	24
6	Bauskas VVM Ceraukstes VM	21	23	13
7	Cesvaines VVM Cesvaines VM	46	46	14

Nr. *	Izcelsme **	Ģimeņu skaits		
		Rembate Nr. 54	Ukri Nr. 55	Taurene Nr. 589
8	Cesvaines VVM Saikavas VM (1998. g.)	-	12	12
9	Daugavpils VVM Sventes VM (1995. g.)	9	10	10
	Daugavpils VVM Sventes VM	34	4	10
10	Dobeles VVM Īles VM	23	-	-
11	GNP Gaujas VM	43	50	50
12	GNP Medņu VM	46	46	44
13	Gulbenes VVM Daukstu VM	29	31	20
14	Jelgavas VVM Garozas VM	21	21	8
15	Jēkabpils VVM Ābeļu VM	35	35	13
16	Jēkabpils VVM Viesītes VM (1998. g.)	-	8	8
17	Kokneses VVM Kokneses VM	13	17	12
18	Krāslavas VVM Dagdas VM	8	8	6
19	Kuldīgas VVM Kuldīgas VM	-	46	43
20	Liepājas VVM Grobiņas VM	25	-	-
21	Liepājas VVM Priekules VM	60	61	45
22	Limbažu VVM Limbažu s. pl.	8	1	-
23	LLU MPMS Šķēdes VM	20	20	13
	LLU MPMS Šķēdes VM (1998. g.)	-	20	20
24	Ludzas VVM Zilupes VM	9	9	9
25	MPS Kalsnavas VM (1998. g.)	-	18	13
26	Ogres VVM Suntažu VM (1995. g.)	10	11	9
	Ogres VVM Suntažu VM	22	23	17
27	Rēzeknes VVM Gaigalavas VM	-	46	41
28	Rēzeknes VVM Viļānu VM	25	7	7
29	Saldus VVM Blīdenes VM	3	3	-
30	Strenču VVM Strenču VM	23	24	9
31	Talsu VVM Andumu VM (1995. g.)	42	44	12
	Talsu VVM Andumu VM	8	10	8
32	Valmieras VVM Daliņu VM (1998. g.)	-	27	24
33	Valmieras VVM Naukšēnu VM	30	31	31
	Valmieras VVM Naukšēnu VM (1998. g.)	-	36	32
34	Valmieras VVM Rūjupes VM (1998. g.)	-	24	24
	Kopā	637	826	621

* kārtas numurs tabulā atbilst apzīmējumam kartē 1.2. attēlā;
** virsmežniecību un mežniecību nosaukumi atbilstoši sēklu ievākšanas gadā pastāvošajam iedalījumam.



1.3. attēls. **Āra bērza pēcnācēju pārbaužu stādījumu ierīkošanas vietas**

Ir pieejami pētījumu dati par citās valstīs ierīkotām āra bērza pēcnācēju pārbaudēm. Līdz šim Latvijā ierīkoto pēcnācēju pārbaužu stādījumu apjoms bērzam ir gana plašs un koku vecums tajos ir pietiekams pamatotu secinājumu ieguvei, tāpēc nepieciešama gadu gaitā iegūto datu detalizēta analīze un novērtējums.

1.4. tabula

Ierīkotie āra bērza pēcnācēju pārbaužu stādījumi

Eksperimentu ierīkošanas vieta	Ierīkošanas gads	Ierīkoto stādījumu skaits	Platība, ha	Uzmērīšanas gads	Variantu skaits			Eksperimenta Nr.
					kloni	ģim. / prov. / plant. vid. paraugs	krustojumi	
Auces MN	2007.	28	74,514	-	-	101	-	633; 634; 876
	2010.			-	-	2	96	736; 737
	2011.			2023.	-	99	145	754; 755
	2016.			2020.	16	-	-	928 *
	2019.			-	17	72	31	1374; 1375; 1376*
	2020.			-	44	-	-	1437 *; 1438 *
	2021.			-	34	4	-	1471*; 1472; 1473*
	2022.			-	20	129	69	1689; 1690; 1694; 1695; 1696; 1697; 1698*
	2023.			-	19	61	29	1750 *; 1751 *; 1752; 1753; 1754
Jelgavas MN	2010.	22	33,684	2013.; 2022.	-	3	189	738; 739
	2011.			2023.	3	108	147	761; 762
	2014.			2020.	5	-	-	872 *
	2016.			2020.	23	-	-	931 *; 932 *; 933 *; 934 *
	2017.			2020.	45	-	-	967 *; 978 *
	2018.			2020.	89	-	-	962 *; 963 *
	2019.			-	40	73	34	1409; 1410; 1411 *; 1412 *
	2020.			-	56	-	-	1434 *; 1435 *; 1436 *
	2021.			-	25	-	-	1474 *
	2022.			-	-	40	-	1708
Kalsnavas MN	2004.	37	47,946	2012.	-	20	-	236 **
	2007.			2012.; 2013.	-	139	-	629; 630; 807
	2010.			2013.; 2022.	-	2	169	727; 733
	2011.			2022.	3	69	124	757; 758; 759; 760
	2014.			2020.	5	-	-	892 *
	2016.			2020.	20	-	-	929 *; 930 *
	2017.			2020.	51	-	-	974 *; 975 *
	2018.			2020.	90	-	-	964 *; 965 *
	2019.			-	31	72	27	1386 *; 1387; 1388; 1389
	2020.			-	53	-	-	1439 *; 1440 *; 1441 *; 1442 *
	2021.			-	35	1	-	1523 *; 1524 *; 1525

Eksperimentu ierīkošanas vieta	Ierīkošanas gads	Ierīkoto stādījumu skaits	Platība, ha	Uzmērīšanas gads	Variantu skaits: kloni	Variantu skaits: ģim. / prov. / plant. vid. paraugs	Variantu skaits: krustojumi	Eksperimenta Nr.
	2022.			-	43	129	69	1667 *; 1668; 1673; 1675 *; 1676 *; 1677 *; 1678 *
	2023.			-	19	-	-	1762 *; 1763 *
Mežoles MN	2004.	26	52,51	-	-	14	-	333**
	2007.			-	-	85	-	631; 632; 877; 878
	2011.			-	-	4	35	756
	2019.			-	-	60	34	1382; 1383
	2020.			-	51	-	-	1432 *; 1433 *
	2021.			-	24	-	-	1533 *
	2022.			-	36	129	69	1719; 1720; 1721; 1722; 1727; 1728; 1732; 1733; 1734 *; 1735 *; 1736
	2023.			-	9	61	29	1758; 1759; 1760; 1761 *
Šķēdes MN	2004.	2	4,19	2013.	-	20	-	310 **
	2019.			-	25	-	-	1378*
Rembates pagasts	1998.	2	35,5	2007.	-	15	-	53
	1999.			2007.; 2008.; 2011.; 2012.; 2019.	-	637	-	54
Ukru pagasts	2000.	1	10,5	2008.; 2013.; 2021.	-	826	-	55
Taurenes pagasts	2000.	1	9,3	2008.; 2012.; 2021.	-	621	-	589
Sventes pagasts	2004.	1	3,2	-	-	17	-	752 **
Vecumnieku pagasts	1975.	1	0,5	-	-	16	-	769 **
Andrupenes pagasts	1998.	1	2,5	2011.	-	15	-	792
Kopā ierīkoti:	-	122	274,344	-	-	-	-	-

* veģetatīvi pavairoti stādi;
** provenienču stādījums.

1.3. Āra bērza pēcnācēju pārbaužu stādījumu novērtējums

Pēcnācēju pārbaužu izvērtēšanu un ģimeņu ranžēšanu veic pēc selekcijas indeksa. Pazīmju iekļaušanai indeksā būtiska:

a) ekonomiskā ietekme;
b) augsta ģenētiskā determinācija (lielākas iespējas to izmainīt ar selekcijas, nekā mežkopības metodēm);
c) pietiekama ģenētiski noteiktā variācija;
d) zema (un/vai no praktiskās izmantošanas viedokļa negatīva) korelācija ar citām pazīmēm, kuras jau ir selekcijas indeksā (Burdon 1989).

Stumbra caurmēra, koka augstuma un stumbra kvalitātes novērtējums ir noteicošais genotipu atlasē selekcijas populāciju un sēklu plantāciju izveidošanai. Turklāt selekcija pēc šāda principa netieši ietekmē arī ķīmiskajai pārstrādei būtiskās koksnes un šķiedru pazīmes. Bērza selekcijas darba īstenošanai praksē ir svarīgi, lai arī siltumnīcu sēklu plantācijās koki ziedētu agrīnā vecumā, bieži un bagātīgi un lai atlasīto klonu juvenīlā augšana būtu strauja un kloni būtu veģetatīvi pavairojami (Stener & Jansson 2005). Stumbra taisnums, apikālā dominance un atbilstošas zarojuma īpašības ir nozīmīgākās stumbra kvalitātes pazīmes, kuras kopā ar koksnes masu (DM – *dry matter*) tiek iekļautas selekcijas indeksā (Stener & Hedenberg 2003, Stener & Jansson 2005). Stumbra kvalitātes pazīmes – taisnums un apikālā dominance – ir svarīgākās no ekonomiskā viedokļa. Stumbra kvalitātes defektu – dakšošanos un padēlu veidošanos – sastopamību lielā mērā nosaka ģenētiskās īpašības, tomēr to izraisa arī vides faktori, kā sala, kukaiņu vai sēņu bojājumu, vai arī sausuma iniciēta vadošās galotnes nomaiņa (Stener & Jansson 2005).

Eksperimentālajā stādījumā Zviedrijas dienviddaļā vērtētas sakarības starp augšanas gaitas, stumbra un koksnes kvalitātes pazīmēm 11 gadus veciem mikroklonāli pavairotiem 30 klonu pēcnācējiem (Stener & Hedenberg 2003). Vērtēto pazīmju vidējās vērtības un ģenētiskie parametri parādīti 1.5. tabulā. Tā kā ģenētiskā variācija stumbra taisnumam bija tuvu nullei, tad šī pazīme tika izslēgta no tālākās analīzes.

1.5. tabula

Pazīmju vidējās vērtības, standartkļūdas un ģenētiskie parametri 30 mikroklonāli pavairotu klonu pēcnācējiem 11 gadu vecumā Zviedrijas dienvidos

(Stener & Hedenberg 2003)

Nr. p. k.	Pazīme	Mērvienība	H^2	SE (H^2)	CV_G, %
1	Augstums	dm	0,43	0,12	5,5
2	Caurmērs	mm	0,46	0,11	11,1
3	Stumbra tilpums	dm^3	0,43	0,12	22,7
4	Koksnes masa	kg	0,39	0,12	21,1
5	Formas koeficients	%	0,40	0,12	5,8
6	Apikālā dominance	balles (1–5)	0,17	0,12	-
7	Zaru resnums	balles (1–5)	0,18	0,12	-

Nr. p. k.	Pazīme	Mērvienība	H^2	SE (H^2)	CV_G, %
8	Zaru skaits	balles (1–5)	0,63	0,09	-
9	Zaru leņķis	balles (1–5)	0,10	0,12	-
10	Koksnes blīvums	kg m^{-3}	0,73	0,08	4,7
11	Šķiedru garums	mm	0,68	0,08	4,5
12	Šķiedru platums	µm	0,66	0,09	3,5
13	Šķiedru rupjums	mg m^{-1}	0,45	0,11	6,2

Saīsinājumi: H^2 – iedzimstamības koeficients plašā nozīmē; SE (H^2) – iedzimstamības koeficienta standartkļūda; CV_G, % – genotpiskās variācijas koeficients.

Augstas iedzimstamības koeficientu plašā nozīmē vērtības (H^2 = 0,43–0,73) konstatētas augšanas, koksnes un šķiedru pazīmēm, savukārt zemas – stumbra un zaru pazīmēm, izņemot zaru skaitu. Visaugstākais genotpiskās variācijas koeficients (CV_G) bija stumbra tilpumam (22,7%) un koksnes masai (21,1%), augsts – stumbra caurmēram (11,1%), turpretī koksnes blīvumam, šķiedru garumam un rupjumam (4,5–6,2%) tas bija līdzīgs kā koka augstumam (5,5%). Salīdzinot ar citiem pētījumiem, CV_G koku augstumam šajā pētījumā bija zemāks. Trijos klonu pārbaužu stādījumos Zviedrijas dienvidu daļā, kur vērtēti 78 kloni, tai skaitā arī 30 iepriekšminētie, CV_G koku augstumam bija no 6,3% līdz 7,9% (Stener & Hedenberg 2003). Savukārt, vērtējot 398 pluskoku pēcnācējus stādījumā Zviedrijas ziemeļu daļā, aditīvā ģenētiskā efekta noteiktais variācijas koeficients (CV_A) bija 9,5% (Stener & Wennström 2000). Tā kā uz konkurences palielināšanos jutīgāk reaģē stumbra caurmērs nekā koka augstums, tad šajā pētījumā (Stener & Hedenberg 2003) konstatēto ievērojamo atšķirību starp CV_G koku augstumam un stumbra caurmēram varētu izskaidrot ar koku savstarpējo konkurenci.

Starp koksnes blīvumu un augšanas pazīmēm būtiska ģenētiskā korelācija (r_g) bija tikai caurmēram (r_g = –0,53), pārējām vērtētajām pazīmēm tā nebija būtiska (1.6. tab.). Konstatētās ģenētiskās korelācijas starp augšanas un koksnes šķiedru pazīmēm bija tuvas nullei. Pārsvarā negatīvas un statistiski nebūtiskas ģenētiskās korelācijas bija starp augšanas un stumbra kvalitātes pazīmēm. Korelācija starp zaru skaitu un šķiedru garumu, kā arī korelācija starp šķiedru platumu un rupjumu bija pozitīva un statistiski būtiska; vājas un nebūtiskas ģenētiskās korelācijas konstatētas starp šķiedru pazīmēm un koksnes blīvumu, starp šķiedru pazīmēm un stumbra kvalitātes pazīmēm, starp dažādām koksnes šķiedru pazīmēm. Izņemot augšanas pazīmes, vāja bija arī fenotipiskā korelācija starp pazīmēm.

Ierasti, ka pētījumos koku sugām ar difūzi izkliedētiem koksnes vadaudiem netiek konstatēta korelācija starp koksnes blīvumu un augšanas pazīmēm, jo pārsvarā vērtētās pazīmes noteiktas fenotipiski. Vāja fenotipiskā korelācija (r_p = –0,23) starp koksnes blīvumu un stumbra caurmēru konstatēta arī šajā pētījumā.

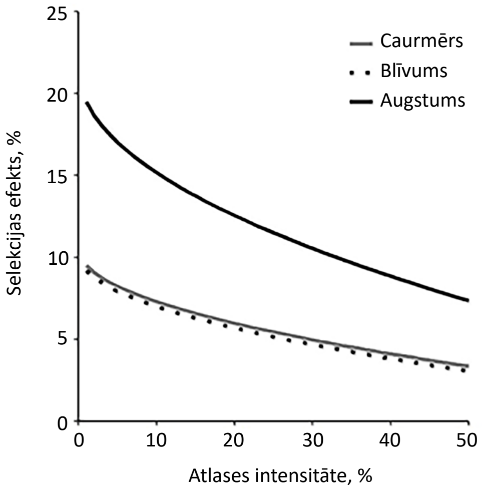
1.6. tabula

Ģenētiskā korelācija (augšējā daļā labajā pusē) un fenotipiskā korelācija (apakšējā, kreisajā pusē) starp pazīmēm

(Stener & Jansson 2005)

Pazīmes	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.
1. Augstums	-	0,57 *	0,71 *	0,75 *	0,65 *	–0,36	–0,13	0,30	0,83	–0,07	0,38	0,19	–0,11
2. Caurmērs	0,58	-	0,99 *	0,96 *	–0,08	–0,61	–0,58	–0,48	–0,01	–0,53 *	–0,14	–0,01	–0,13
3. Tilpums	0,69	0,97 *	-	0,98 *	0,09	–0,60	–0,43	–0,34	0,27	–0,48	–0,08	0,04	–0,15
4. Masa	0,69	0,95 *	0,98 *	-	0,18	–0,64	–0,42	–0,30	0,37	–0,30	–0,05	0,00	–0,17
5. Formas koeficients	0,23	–0,10	–0,05	–0,01	-	0,10	0,42	0,46 *	1,57	0,40	0,37	0,28	0,08
6. Apikālā domin.	–0,12	–0,28 *	–0,27 *	–0,27 *	0,22	-	0,39	0,63	0,71	–0,05	0,18	–0,21	–0,07
7. Zaru resnums	–0,10	–0,33 *	–0,28 *	–0,30 *	–0,06	0,03	-	0,89 *	0,88	0,12	–0,05	–0,04	–0,28
8. Zaru skaits	0,02	–0,40 *	–0,33 *	–0,31 *	0,29 *	0,18	0,34 *	-	1,16 *	0,30	0,41 *	0,04	–0,08
9. Zaru leņķis	–0,05	–0,23	–0,19	–0,18	0,21	0,03	0,36 *	0,51 *	-	0,33	0,31	0,17	0,25
10. Blīvums	0,01	–0,23	–0,20	–0,04	0,22	0,02	–0,04	0,14	0,11	-	0,14	–0,11	–0,05
11. Šķiedru garums	0,34	–0,05	–0,03	–0,01	0,25	0,06	–0,06	0,26	0,06	0,11	-	0,33	0,13
12. Šķiedru platums	0,16	0,10	0,08	0,05	0,13	–0,10	0,03	–0,05	–0,06	–0,14	0,32 *	-	0,74 *
13. Šķiedru rupjums	0,14	0,15	0,14	0,14	0,02	–0,09	–0,04	–0,05	–0,07	0,03	0,02	0,43 *	-

* $p < 0{,}05$.



1.4. attēls. **Selekcijas efekts trim pazīmēm, atkarībā no atlases intensitātes pēc šīm pašām pazīmēm**
(Stener & Hedenberg 2003)

Konstatētais selekcijas efekts bija līdzīgs, veicot atlasi pēc stumbra caurmēra vai koksnes blīvuma, taču aptuveni uz pusi mazāks nekā, veicot atlasi pēc koku augstuma (1.4. att.).

Pēc stumbra caurmēra veiktā atlasē stumbra tilpums un sausas koksnes masa tika nozīmīgi palielināti, vienlaicīgi nedaudz – par 2,5% (12 kg m^{-3}) – samazinot koksnes blīvumu. Atlasi veicot pēc koku augstuma, koksnes blīvuma samazinājums ir nebūtisks, taču selekcijas efekts stumbra tilpumam ir mazāks nekā, atlasot pēc stumbra caurmēra.

Mikroklonāli pavairotu bērza pluskoku klonu (~ 55%) un brīvapputes pēcnācēju (~ 45%) augšanu līdz 10 gadu vecumam 10 stādījumu vietās (pluskoku skaits 39–83) Zviedrijas dienvidu daļā analizējuši *L.-G. Stener* un *G. Jansson* (2005). Konstatēts, ka augšanas pazīmēm vairumā gadījumu ir augsta ģenētiskā kontrole un nozīmīga ģenētiskā variācija, kā arī augsts selekcijas efekts. Plašās robežās variē iedzimstamības koeficienta vērtības gan starp eksperimentu veidiem (klonu vai brīvapputes pēcnācēju), gan arī starp viena veida eksperimentiem – stādījumos H^2 koku augstumam variēja no 0,07 līdz 0,56 klonu pēcnācējiem, bet h^2 no 0,08 līdz 0,54 brīvapputes pēcnācējiem. Iedzimstamības koeficientu vērtības koku zarojuma pazīmēm bija vidējas vai augstas, vienlaikus stumbra taisnumam un apikālai dominancei – kopumā zemas.

Plašo iedzimstamības koeficientu variāciju augstumam un caurmēram lielā mērā var saistīt ar stādījumu ierīkošanas sekmēm. Bērzam, kā izteiktai pioniersugai, sevišķi raksturīga vides ietekme uz koeficienta vērtībām, un tā augšanu spēcīgi ietekmē stādījuma kopšanas intensitāte pirmajos gados pēc ierīkošanas. Piemēram, platībās ar spēcīgu konkurenci un zemu saglabāšanos arī augšanas pazīmju iedzimstamības koeficientu vērtības bija ļoti zemas, kamēr stādījumā, kurā pirmajos divos gados pēc ierīkošanas veikta regulāra kopšana, konstatēts ļoti augsts iedzimstamības koeficients šaurā nozīmē. Arī platībās, kas vides apstākļu ziņā vērtējamas kā homogēnas, ir augstāki iedzimstamības koeficienti. Tas ļauj secināt, ka iedzimstamības koeficientu vērtības atspoguļo eksperimenta efektivitāti un arī pazīmes ģenētisko nosacītību. Iedzimstamības koeficienta plašā nozīmē H^2 vērtībām vajadzētu būt augstākām nekā iedzimstamības koeficienta šaurā nozīmē h^2 vērtībām, kas gan nav konstatēts šajā pētījumā – atšķirības starp H^2 un h^2 nevienai no pazīmēm nebija būtiskas, mikroklonāli pavairotā materiāla atšķirīgā sākotnējā augstuma, kā arī nelielā novērojumu skaita dēļ tas bija sagaidāms. Savukārt genotpiskās variācijas koeficienti CV_G un CV_A augstumam (attiecīgi 7% un 9%) bija mazāki nekā caurmēram (attiecīgi 12% un 15%); būtiskas atšķirības starp brīvapputes un mikroklonāli pavairotiem pēcnācējiem netika konstatētas. Salīdzinājumam – brīvapputes pēcnācēju augstumam 9 gadu vecumā Zviedrijas ziemeļu daļā CV_A bija 9,5% (Stener & Wennström 2000).

Selekcijas efektivitātei noteicošais ir vecums, kurā var veikt atlasi. Interesējošo pazīmju augsta ģenētiskā korelācija vērtēšanas vecumā un mērķa vecumā dod iespēju sekmīgai agrīnās selekcijas veikšanai. Ģenētiskā korelācija starp pazīmes vērtību 10 gadu vecumā un 4 gadu vecumā koku augstumam *L.-G. Stener* un *G. Jansson* (2005) pētījumā bija 0,60, bet 10 gadu un 5 vai 6 gadu vecumā – 0,94. Tas liecina, ka ir iespējams atlasīt klonus ar labāko augstumu jau aptuveni 6 gadu vecumā, kad aptuvenais augstums ir 4 m. Secināms, ka bērza selekcijā iedzimtības pārbaudēm iespējams pielietot īsu pārbaudes periodu; tomēr jāņem vērā, ka atlasi veicot 4–6 gadu nevis 10 gadu vecumā, selekcijas efektivitāte (selekcijas efekts gadā) bija par 20–40% zemāka.

Aprēķinātās korelācijas starp kvalitātes pazīmēm (r_g vai r_a) pārsvarā gadījumu bija vājas un nebūtiskas. Taisnums un apikālā dominance ir savstarpēji ģenētiski korelējošas pazīmes, taču šo pazīmju ģenētiskā nosacītība ir zema, jo samērā zemas ir abu pazīmju iedzimstamības koeficientu vērtības. Tāpēc ar selekcijas metodēm uzlabot šīs pazīmes ir grūtāk nekā pazīmes, kam raksturīgas vidējas vai augstas iedzimstamības koeficientu vērtības, piemēram, zaru pazīmes. Augšanas un stumbra kvalitātes pazīmes ir ģenētiski samērā neatkarīgas, jo r_g vērtības starp tām ir zemas, kā rāda to ģenētiskās korelācijas analīze. Tomēr konstatēta gan no saimnieciskā viedokļa nevēlama vidēja līdz cieša korelācija starp stumbra caurmēru un zaru skaitu, gan (atsevišķos stādījumos) vēlama korelācija – starp augšanu un zaru leņķi. Pētījumā iegūti neviennozīmīgi rezultāti par sakarībām starp augšanas un kvalitātes pazīmēm, tāpēc ieteicams klonu vērtēšanā līdzās augšanas pazīmju vērtējumam izmantot vispārīgu stumbra kvalitātes vērtējumu (piemēram, 5 ballu skalā; Stener & Jansson 2005).

Kaut arī Zviedrijas dienviddaļā pašlaik bērzam nepastāv rudens salnu bojājumu risks, tomēr, ja selekcijā augstumu izmanto kā vienīgo atlases kritēriju, ilgtermiņā šāds risks varētu paaugstināties. Piemēram, starp augstumu un papildpieaugumu (pēc 8. augusta) konstatēta pozitīva korelācija ($r_G = 0,38$). Tāpēc papildus būtu nepieciešams arī kritērijs, kas saistīts ar pieauguma izbeigšanos, ja selekcijas rezultātus paredzēts izmantot salnu apdraudētās teritorijās. Tomēr ģenētiskā korelācija starp augšanu un augšanas apstāšanās laiku rudenī (*growth cessation*) bija vāja, no kā secināms, ka atlasīt klonus, kam raksturīgs gan augšanas pārākums, gan savlaicīga pieauguma izbeigšanās, ir iespējams. Pētījuma rezultāti liecina, ka genotipa × vides mijiedarbības ietekme ir vāja, uz ko norāda cieša ģenētiskā korelācija gan augšanas, gan stumbra kvalitātes pazīmēm. Šāda sakarība konstatēta pat stādījumos ar stipri atšķirīgiem vides apstākļiem, piemēram, meža un lauksaimniecības zemē, kā arī stādījumos ar atšķirīgiem klimatiskajiem apstākļiem. Mikroklonāli pavairotam materiālam saglabājies stabils klonu ranžējums (Stener & Jansson 2005).

Iegūtie rezultāti kopumā liecina, ka āra bērza augšanas pazīmēm raksturīga augsta ģenētiskā nosacītība, nozīmīga ģenētiskā variācija, lielākoties zema nevēlama ģenētiska saistība starp augšanas un kvalitātes pazīmēm un līdz ar to augsts selekcijas darba potenciālais efekts. Bērza selekcijas attīstība Latvijā vērtējama kā līdzīga citām Baltijas jūras reģiona valstīm, un tai ir nozīmīga bāze – selekcijas pamatpopulācija ar 929 atlasītiem kokiem, kā arī 34 proveniences ar plašu izcelsmes amplitūdu – kompleksai analīzei un tajā balstītu rezultātu iegūšanai. Šī bāze izmantojama gan selekcijas indeksa izstrādei un aktualizēšanai, gan fenotipiskai provenienču reģionu izdalīšanai un/vai to robežu precizēšanai.

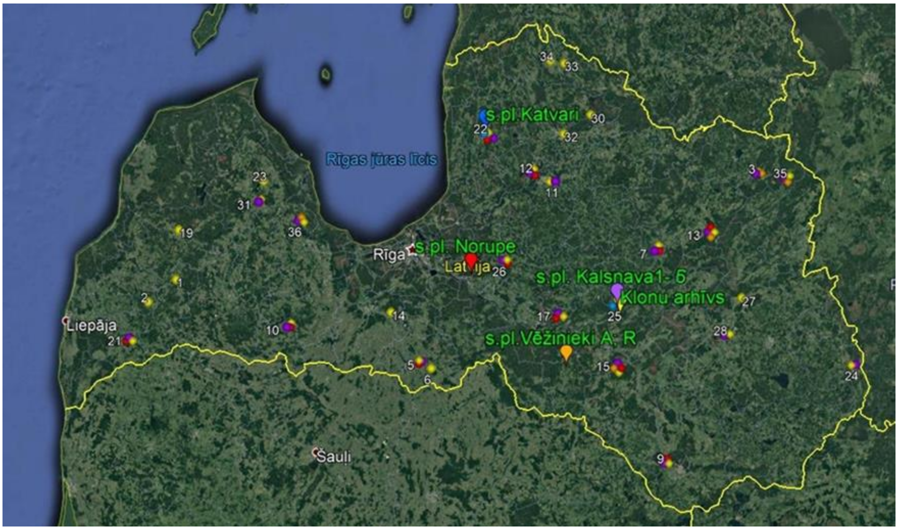
2. ĀRA BĒRZA PAVAIROŠANA

2.1. Bērza sēklu plantācijas

Pirmās kārtas bērza sēklu plantācijas ierīkotas, izmantojot fenotipiski atlasītu pluskoku potējumus. Latvijā pirmā āra bērza (*Betula pendula* Roth.) plantācija ar 22 pluskoku kloniem 1972. gadā ierīkota Limbažu novada Katvaros, koki izvietoti 5 × 5 m attālumā. Neveicot savlaicīgu vainagu veidošanu, tie saslēdzās jau 15– 20 gados, un apakšējie zari atmira, tādēļ ievākt sēklas plantācijā nebija iespējams. Sēklu plantācija šobrīd tiek izmantota kā klonu stādījums to augšanas gaitas vērtēšanai.

Nākamo pirmās kārtas plantāciju ierīkošana (potējumu audzēšana) MPS "Kalsnava" uzsākta 1997. gadā (2.1. tab.). Izmantojot sagatavoto materiālu, 2001. gadā Jaunkalsnavā akciju sabiedrības "Latvijas valsts meži" struktūrvienībā "Sēklas un stādi" tika ierīkotas divas slēgta tipa bērza sēklu plantācijas (siltumnīcas), katra 0,08 ha platībā; izveidoti atsevišķi plantāciju bloki tajā laikā definētajiem Ziemeļu (Kalsnava 1A) un Rietumu (Kalsnava 2R) sēklu ieguves apgabaliem. 2003. gadā ievākta pirmā raža.

2007. gadā akciju sabiedrībā "Latvijas valsts meži", Viesītes novadā ierīkotas āra bērza sēklu plantācijas – klonu arhīvi "Vēžinieki R" un "Vēžinieki A", balstoties uz 1996.–1998. gadā veiktu klonu izvēli. Papildus šim darbam 2007. gadā izveidots klonu komplekts "Kalsnava 3" – atlasīti un atkārtoti pavairoti ražojošie sēklu plantāciju



2.1. attēls. **Āra bērza sēklu plantāciju, klonu arhīva un iekļauto klonu izcelsmes vietas**

Skaitlis pie izcelsmes vietas un krāsojums atbilst izcelsmes vietas numuram un iekrāsojumam klonu izcelsmei attiecīgajai sēklu plantācijai 2.2. tabulā

2.1. tabula

Āra bērza sēklu plantācijas

Vieta	Apsaim-niekotājs	Plantācija	Ierīkošanas gads	Stādīšanas attālums, m	Platība, ha	Klonu skaits	Plantācijas kārta	MRM kategorija	MRM pieliet. apgabals	Sēklu ieguve
Limbažu nov.	LVM	Katvari	1972.	5 × 5	5,0	22	1	-	-	nav vāktas
Kalsnavas pag.	LVM	Kalsnava – 1A	2001.	3,4 × 3,7	0,08	55	1	uzlabots	Z	2003.–2014.
	LVM	Kalsnava – 2R	2001.	3,4 × 3,7	0,08	55			R	
Viesītes nov.	LVM	Vēžinieki A	2007.	4 × 5	0,7	88	1	uzlabots	A; R	sākot ar 2012.
	LVM	Vēžinieki R	2007.	4 × 5	0,5	58			R	
Ogres nov.	RM	Norupe	2009.	7 × 7	1,1	48	2	pārāks	A; R	sākot ar 2018.
Kalsnavas pag.	LVM	Kalsnava –3A *	2016.	-	0,015	50	1	uzlabots	A	sākot ar 2017.
	LVM	Kalsnava – 4R	2016.	3,4 × 3,7	0,08	25	3	pārāks	R	
	LVM	Kalsnava – 5A	2016.	3,4 × 3,7	0,08	36		pārāks	A	
	MPS	Klonu arhīvs *	2016.	-	-	97	3	pārāks	A; R	sākot ar 2018.
	LVM	Kalsnava – 6A	2024.	3,6 × 3,75	0,25	32	3	pārāks	A	-

* klonu rameti aug podos.
Saīsinājumi: LVM – AS “Latvijas valsts meži”, RM – SIA “Rīgas meži”, MPS – Meža pētīšanas stacija.

“Kalsnava 1A” un “Vēžinieki A” 50 kloni. Izveidotais klonu komplekts izmantots 2016. gadā ierīkotajā “Kalsnava 3A” sēklu plantācijā, klonu rametus audzējot podos.

Norupe ir pirmā sēklu plantācija, kurā izmantota informācija un materiāls no pēcnācēju pārbaudēm (fenotipiski labākie koki no augstvērtīgākajām ģimenēm), ierīkota 2009. gada rudenī SIA “Rīgas meži” Daugavas mežniecības teritorijā. Izvērtējot 921 brīvapputes ģimeni pēcnācēju pārbaudēs (Nr. 54, 55, 589), atlasītas augstvērtīgākās un to ietvaros izvēlēti fenotipiski labākie koki Rietumu (25 kloni) un Austrumu (36 kloni; 2.2. tab. un 2.1. att.) provenienču reģionam piemērotu sēklu plantāciju ierīkošanai. Pēc veiktās potēšanas 2014. gadā, jaunās – 3. kārtas – sēklu plantācijas “Kalsnava – 4R” un “Kalsnava – 5A” ierīkotas 2016. gadā, un jau 2019. gadā tajās ievākta pirmā nozīmīgā sēklu raža. Vienlaikus ar klonu atlasi sēklu plantāciju vajadzībām, izvēlēti arī potenciālai veģetatīvi pavairotu stādu ražošanai atbilstoši kloni, kam veiktas turpmākas pārbaudes *in vitro*.

Meža pētīšanas stacijas stādaudzētavā Jaunkalsnavā 2016. gadā sākta klonu arhīva ierīkošana, kur 50 l podos audzēti āra bērza selekcijas materiāla 2013.–2018. gadā potēto un *in vitro* pavairotu 188 klonu 607 rameti (2019. g.) ziedēšanas stimulēšanai kontrolētās krustošanas veikšanai. Ziedēšana 2018., 2019. un 2020. gadā nodrošināja iespēju veikt kontrolēto krustošanu nākamā selekcijas cikla vajadzībām. Pēc tās daļa klonu kolekcijas vairs netiek uzturēta, šobrīd tajā ir 97 klonu 344 rameti. Klonu skaits ir mainīgs, jo augi periodiski tiek atjaunoti, daži no sākotnējiem kloniem vairs netiek uzturēti.

2024. gada jūnijā akciju sabiedrības “Latvijas valsts meži” stādaudzētavā “Mežvidi” Jaunkalsnavā nodota ekspluatācijā jaunākā 3. kārtas siltumnīcas tipa bērza sēklu plantācija “Kalsnava 6A” (2.2. att.) ar 32 kloniem (65% *in vitro* pavairotiem, 35% potētiem), kuri, pēcnācēju pārbaudēs no augstvērtīgākajām ģimenēm atlasot fenotipiski labākos kokus, šobrīd atzīti par piemērotākajiem Austrumu provenienču reģionam.

2.2. attēls. **Trešās kārtas āra bērza sēklu plantācija “Kalsnava 6A”**
(Foto: Ā. Jansons)

2.2. tabula

Āra bērza sēklu plantācijās iekļauto klonu izcelsmes vietas

Izcelsmes vietas Nr. *	Izcelsme **	Sēklu plantācija										
		Katvari	Kalsnava – 1	Kalsnava – 2	Kalsnava – 3A	Kalsnava – 4	Kalsnava – 5	Kalsnava – 6A	Vēžinieki A	Vēžinieki R	Norupe	Klonu arhīvs
1	Aizputes VVM Aizputes VM	-	-	-	-	-	-	-	-	-	-	1
2	Aizputes VVM Kalvenes VM	-	-	-	-	-	-	-	-	-	-	-
3	Alūksnes VVM Mālupes VM	-	36	-	21	-	-	-	43	-	-	-
5	Bauskas VVM Bauskas VM	-	-	-	-	-	6	-	-	-	7	4
6	Bauskas VVM Ceraukstes VM	-	-	-	-	-	-	-	-	-	-	2
7	Cesvaines VVM Cesvaines VM	-	-	-	-	5	-	4	-	-	1	9
9	Daugavpils VVM Sventes VM	-	-	-	-	3	-	3	-	-	2	5
10	Dobeles VVM Īles VM	-	-	-	-	-	5	-	-	-	4	1
11	GNP Gaujas VM	-	-	-	-	2	-	2	-	-	-	9
12	GNP Medņu VM	-	-	-	-	3	-	5	-	-	7	9
13	Gulbenes VVM Daukstu VM	-	-	-	-	4	-	3	1	-	3	6
14	Jelgavas VVM Garozas VM	-	-	-	-	-	-	-	-	-	-	2
15	Jēkabpils VVM Ābeļu VM	-	-	-	19	6	-	4	22	-	6	5
17	Kokneses VVM Kokneses VM	-	-	-	-	1	-	1	-	-	1	1
19	Kuldīgas VVM Kuldīgas VM	-	-	-	-	-	-	-	-	-	-	2
21	Liepājas VVM Priekules VM	-	-	-	-	-	9	-	-	-	3	6
22	Limbažu VVM Limbažu sēklu plant.	21	-	-	-	1	-	1	-	-	2	1
23	LLU MPMS Šķēdes VM	-	-	-	-	-	-	-	-	-	-	5

Izcelsmes vietas Nr. *	Izcelsme **	Sēklu plantācija										
		Katvari	Kalsnava – 1	Kalsnava – 2	Kalsnava – 3A	Kalsnava – 4	Kalsnava – 5	Kalsnava – 6A	Vēžinieki A	Vēžinieki R	Norupe	Klonu arhīvs
24	Ludzas VVM Zilupes VM	-	-	-	-	1	-	1	-	-	-	1
25	MPS Kalsnavas VM	1	-	-	-	-	-	-	-	-	-	-
26	Ogres VVM Suntažu VM	-	-	-	-	8	-	7	-	-	11	7
27	Rēzeknes VVM Gaigalavas VM	-	-	-	-	-	-	-	-	-	-	2
28	Rēzeknes VVM Viļānu VM	-	-	-	-	2	-	1	-	-	-	2
30	Strenču VVM Strenču VM	-	-	-	-	-	-	-	-	-	-	-
31	Talsu VVM Andumu VM	-	-	-	-	-	5	-	-	-	-	4
32	Valmieras VVM Daliņu VM	-	-	-	-	-	-	-	-	-	-	-
33	Valmieras VVM Naukšēnu VM	-	-	-	-	-	-	-	-	-	-	7
34	Valmieras VVM Rūjupes VM	-	-	-	-	-	-	-	-	-	-	1
35	Alūksnes VVM Liepnas VM	-	19	-	10	-	-	-	22	-	-	-
36	Tukuma VVM Kaives VM	-	-	55	-	-	-	-	-	58	-	-
	Cita	-	-	-	-	-	-	-	-	-	-	5
	Kopā kloni	22	55	55	50	36	25	32	88	58	47	97

* kārtas numurs un iekrāsojums tabulā atbilst apzīmējumam kartē 2.1. attēlā;
** virsmežniecību un mežniecību nosaukumi atbilstoši sēklu ievākšanas gadā pastāvošajam iedalījumam.

Izveidojot bērza sēklu plantācijas, nodrošināta iespēja praksē izmantot meža selekcijas rezultātus, meža atjaunošanā un ieaudzēšanā pielietojot kategoriju "uzlabots" un "pārāks" stādus.

2.2. Āra bērza veģetatīvā pavairošana

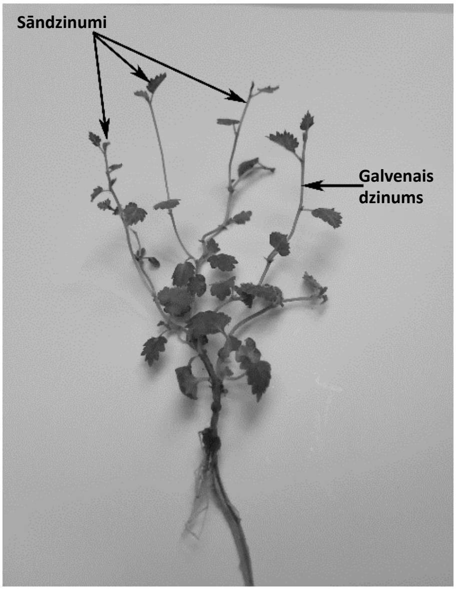
Veģetatīvā pavairošana rada iespēju praksē realizēt visu sasniegto selekcijas efektu, izmantojot tikai nelielu skaitu pašus augstvērtīgākos genotipus. Tāpat šī pieeja nodrošina iespēju saīsināt laiku no selekcijas darba rezultātu iegūšanas (atlasītas genotipu kopas ar vēlamajām pazīmēm) līdz šo rezultātu praktiskai izmantošanai meža atjaunošanā, jo nav jāgaida līdz sēklu plantācijas ražošanas sākumam. Tomēr bērzam, salīdzinot ar, piemēram, egli, šis ieguvums ir visai neliels, jo pirmās sēklu ražas mērķtiecīgi apsaimniekotā plantācijā iespējams iegūt no ievērojami jaunākiem rametiem. Meža selekcijai nozīmīgākais ieguvums no veģetatīvās pavairošanas ir augstāka pēcnācēju pārbaužu precizitāte (samazinot lokālo apstākļu variācijas ietekmi uz ģenētisko parametru novērtējumu) un īsāks to realizācijas laiks. Augstāko selekcijas efektu iespējams sasniegt, pēc kontrolētās krustošanas no katras sibu ģimenes izmantojot lielāku skaitu kandidātu un katru no tiem pārbaudot ar nelielu (6–10) rametu skaitu katrā no 3–4 stādījuma vietām (Danusevicius & Lindgren, 2002a,b, 2004, Isik et al. 2003, 2004, 2005, Dieters et al. 2004, Stener & Jansson 2005).

Liela apjoma stādu ražošana no veģetatīvi pavairotiem pārāku ģimeņu krustojumiem vai indivīdiem, kas raksturojami ar saimnieciski vēlamu pazīmju kompleksu (ideotipiem), ir bijusi saistoša kopš mikropavairošanas tehnoloģijas radīšanas (Naujoks et al. 2002). Galvenās bērzu masveida veģetatīvās pavairošanas metodes ir organoģenēze un somatiskā embrioģenēze. Organoģenēzes procesā jaunu augu inducēšana notiek no auga orgāniem – pumpuriem, dzinumiem, lapām, zieda daļām. Šajā procesā nepieciešami divi dažādi hormonālie signāli, lai izraisītu dzinuma orgānu un sakņu attīstību. Somatiskā embrioģenēze ir augu embriju attīstība, diferencējoties somatiskajām šūnām. Somatiskais embrijs satur gan dzinuma, gan saknes meristēmu, tāpēc ierosināšanai nepieciešams viens hormonāls signāls. Izmantojot somatisko embrioģenēzi, iespējams iegūt lielu skaitu ģenētiski vienādu embriju un izveidot mākslīgās sēklas, kuru izmaksas būtu pielīdzināmas parastajām sēklām. Augšanu veicinošās rizobaktērijas, minerālelementus un pesticīdus būtu iespējams iekļaut mākslīgo sēklu apvalkos. Metode ir perspektīva, tomēr līdz šim nav tik tālu attīstīta, lai būtu pielietojama praktiskā meža stādu ražošanā (Rihan et al. 2017).

Mikroklonālās pavairošanas procesā notiek augu organoģenēze mākslīgā barotnē sterilos apstākļos. Pētījumi par kokaugu mikroklonālo pavairošanu pasaulē notiek kopš 20. gs. 30-tajiem gadiem. Bērzi ir vieni no pirmajiem mikroklonāli pavairotajiem kokiem (Jacquiot 1955 citēts pēc McCown 1989). Skandināvijas valstīs un citviet Eiropā bērzu mikroklonālās pavairošanas pētījumi sākās 20. gs. 80-tajos gados ar mērķi apgūt metodes izvēlētā genotipa pavairošanai apmežošanas nolūkos, kā arī selekcijas procesa paātrināšanai (Welander 1988). LVMI "Silava" Augu fizioloģijas laboratorijā bērza mikroklonālās pavairošanas iespēju apgūšana tika uzsākta 2006. gadā. Pašlaik bērzu *in vitro* kolekcijā ir vairāk nekā 150 īpaši atlasīti bērzu genotipi.

Mikroklonālā pavairošana sākas ar materiāla ievākšanu no izvēlētajiem kokiem (genotipiem) un ievadīšanu mākslīgā (laboratorijas) vidē – barotnē, kas satur visas augam nepieciešamās minerālvielas, ogļhidrātus, vitamīnus, aminoskābes, fitohormonus. Šai audu kultūras uzsākšanai izvēlētajiem genotipiem ievāc iespējami juvenīlākas augu daļas. Svarīgs faktors kultūras iniciācijai ir eksplantu ņemšanas laiks, mātes auga vecums un fizioloģiskais stāvoklis. Sākotnējā kultūras attīstība ir atkarīga no atbilstošas barotnes izvēles. Svarīgākie ir augšanas regulatori, galvenokārt citokinīni un auksīni. Citokinīni veicina šūnu dalīšanos un bremzē to novecošanos, bet auksīni – šūnu attīstību. Augšanas regulatori pilda arī specifiskas regulējošas funkcijas. Tie var ietekmēt enzīmu darbību, gēnu ekspresiju un mainīt pat šūnu membrānu īpašības.

Pēc *in vitro* kultūras stabilizācijas var uzsākt nākamo mikroklonālās pavairošanas etapu – pašu mikropavairošanu. Tās vajadzībām augi tiek ievietoti proliferācijas barotnēs, kas stimulē auga sānpumpuru plaukšanu un adventīvo dzinumu veidošanos, kā arī nodrošina optimālos temperatūras un gaismas režīmus. Lai nodrošinātu šīs metodes efektivitāti stādu ražošanā, jāpanāk maksimāla augu galvenā dzinuma un sānu dzinumu augšana garumā un sānu dzinumu skaita pieaugums (2.3. att.). Tas nodrošina, ka pēc noteikta laika (bērzam 4–5 nedēļas), sadalot pa dzinumiem un katru dzinumu iestādot atsevišķi, iegūst vairākus augus. Lai pavairošanas process būtu efektīvs, iegūstamo jauno augu skaits nedrīkstētu būt mazāks par pieciem. Definētais minimālais skaits (pavairošanas koeficients) būs atkarīgs no ražošanas izmaksām un stādu tirgus vērtības.



2.3. attēls. **Mikroklonāli pavairots āra bērzs**

Klons (genotips) ir nozīmīgs pavairošanas koeficientu ietekmējošs faktors (Koski & Rousi 2005) – tātad ne visus tos genotipus, kas ir ar vēlamajām īpašībām, būs iespējams efektīvi pavairot veģetatīvi. Tāpat ir konstatēts, ka dažādiem kloniem labāki rezultāti sasniedzami atšķirīgās proliferācijas barotnēs – tātad nepieciešams un tiek realizēts eksperimentālais darbs, lai atrastu tieši konkrētajiem ražīgākajiem un kvalitatīvākajiem kloniem piemērotākās barotnes.

Noslēdzošā šīs veģetatīvās pavairošanas metodes fāze ir augu aklimatizācija augšanai nesterilā vidē. Tos stāda kūdras substrātā, sākotnēji siltumnīcā ar miglas iekārtu, nodrošinot augstu (> 80%) gaisa mitrumu un precīzi kontrolējot augu audzēšanas režīmu, vēlāk stādus pārskolo lielāka izmēra konteineros un pārvieto ārvidē (uz poligonu).

Mikroklonālās pavairošanas metodei ir arī trūkumi. Tā ir dārga, jo ir nepieciešams ilgs manuāls darbs sterilos apstākļos un kvalificēts personāls. Atsevišķos gadījumos augšanas regulatori, kas ir pievienoti barotnēs, var izraisīt somaklonālas mutācijas. To gan var novērst, ierobežojot kultūras ilgumu *in vitro* apstākļos, jo izmaiņas uzkrājas laikā.

Veģetatīvi pavairoto koku augšana mežā neatšķiras no atbilstoša selekcijas efekta ģeneratīvi pavairotiem indivīdiem, par ko liecina plaši un ilgstoši pētījumi (Meier-Dinkel 1992, Viherä-Aarnio 1994). Iegūstamais rezultāts ir paredzamāks – ar mazāku variāciju – un ar iespēju praksē realizēt augstāku selekcijas efektu. Mikroklonāli pavairotu stādu plašākā praktiskā izmantošana notikusi Somijā, vairāku uzņēmumu sadarbības ietvaros, sākot ar 1989. gadu, kad tika saražoti pa 30 000 stādi no 30 dažādiem kloniem (Viherä-Aarnio & Ryynänen 1994). 1990. gada sākumā bija saražoti vairāk nekā miljons stādu, tomēr lielāka mēroga mikroklonālā pavairošana tika pārtraukta 1994. gadā (Viherä-Aarnio & Velling 2001). Šādam lēmumam bija vairāki iemesli. Samērā strauji auga darbaspēka izmaksas, sadārdzinot stādmateriālu; tāpat strauji palielinājās pārnadžu bojājumi bērzu jaunaudzēs, samazinot interesi (un jēgu) šo koku sugu stādīt. Taču nozīmīgākais iemesls bija pavairotais materiāls – kloni, kas tika izmantoti projektā, nebija raksturojami ar pozitīvu selekcijas efektu. Somu pētnieki norāda, ka, izvēloties klonus pavairošanas programmai, netika veikta korekta to atlase pēcnācēju pārbaužu stādījumos; nereti darbu veica personas bez atbilstošām zināšanām (Viherä-Aarnio & Velling 2001). Desmit pēcnācēju pārbaužu stādījumos 17 ha platībā Dienvidsomijā, kopumā ietverot 29 000 kokus, salīdzināti 6–7 gadus veci 11 klonu mikropavairoti pēcnācēji un 10 ģimeņu sējeņi. Tika secināts, ka stādmateriāla veidam nav būtiskas ietekmes uz saglabāšanos, augstuma pieaugumu un biotiskajiem riska faktoriem (grauzēju un pārnadžu bojājumi, vēzis u. tml.), toties ievērojamas atšķirības šīm pazīmēm tika konstatētas starp kloniem. Tiek rekomendēta rūpīgi pārbaudītu labāko klonu izvēle izmantošanai plaša mēroga mikropavairošanai (Viherä-Aarnio & Ryynänen 1994, Viherä-Aarnio & Velling 2001).

Zviedrijā mikropavairošana stādu ražošanai pagaidām netiek izmantota. Selekcijas programmā tikusi veikta pluskoku pavairošana augu audu kultūrās, tomēr lielu daļu klonu nav bijis iespējams šādi pavairot. Kā atsevišķu privātu uzņēmumu iniciatīvu piemēru var minēt pētniecības un tehnoloģiju attīstību kompāniju "SweTree

Technologies", kas attīsta automatizētas veģetatīvās pavairošanas tehnoloģijas. Šīs kompānijas veiktā pētījumā vērtēta *Betula pendula* eksplantu kultivēšana jaunā pagaidu iegremdēšanas bioreaktoru sistēmā, demonstrējot potenciālu paplašināt un automatizēt mikropavairošanu komerciālai izmantošanai (Businge et al. 2017).

Arī Krievijā tiek veikti pētījumi augstas kvalitātes bērza konteinerstādu ražošanai ar klonu mikropavairošanu, attīstot metodes stādu aklimatizācijas nodrošināšanai. Tas ļautu izvairīties no izmaksām, kas saistītas ar mākslīgās miglas aprīkojumu un reizē nodrošinātu 90–95% *in vitro* kultūrās iegūto stādu saglabāšanos, tos izstādot *ex vitro*. Stādu audzēšana tiek veikta un vērtēta augstā biezībā (660–900 stādi m^{-2}) mazās šūnās (20 ml), kas samazina izmaksas (Lebedev et al. 2017). Lietuvā vērtēta eksplantu kultūras uzsākšana un uzturēšana *in vitro*, lai sagatavotu praktiskus ieteikumus tālākai mikroklonālās pavairošanas izmantošanai stādu ražošanā (Vaičiukynė et al. 2017).

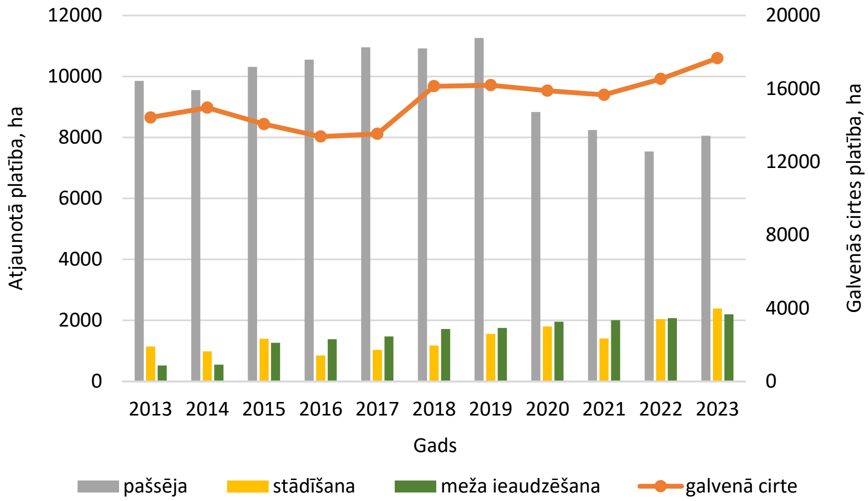
Eiropas Savienības dalībvalstīm ir atļauts regulēt veģetatīvi pavairota meža reproduktīvā materiāla ražošanu un pielietošanu meža atjaunošanā vai ieaudzēšanā. Tā kā Baltijas un Fenoskandijas reģionā kopumā šāds materiāls tiek ražots un izmantots maz, detalizēti ierobežojumi tiek piemēroti reti. Latvijā vienīgais ierobežojums – kloniem, kuri reģistrēti kategorijas "uzlabots" reproduktīvā materiāla ražošanai, ar veģetatīvās pavairošanas metodi iegūstamo pēcnācēju (rametu) maksimālais skaits ir viens miljons izaudzētu stādu. Kloniem, kuri reģistrēti kategorijas "pārāks" reproduktīvā materiāla ražošanai, maksimālo iegūstamo pēcnācēju (rametu) skaitu neierobežo (MK Noteikumi par meža reproduktīvo materiālu Nr. 159).

Kopumā var secināt, ka bērza mikroklonālā pavairošana meža atjaunošanai šobrīd nedz Latvijā, nedz kaimiņvalstīs netiek praktizēta, tomēr ir skaidri tās principi. Praktiskai to pielietošanai nozīmīgi izstrādāt tehnoloģiju, ietverot arī kloniem specifisku, pielāgotu barotņu sastāvu.

2.3. Bērza audžu atjaunošana un ieaudzēšana

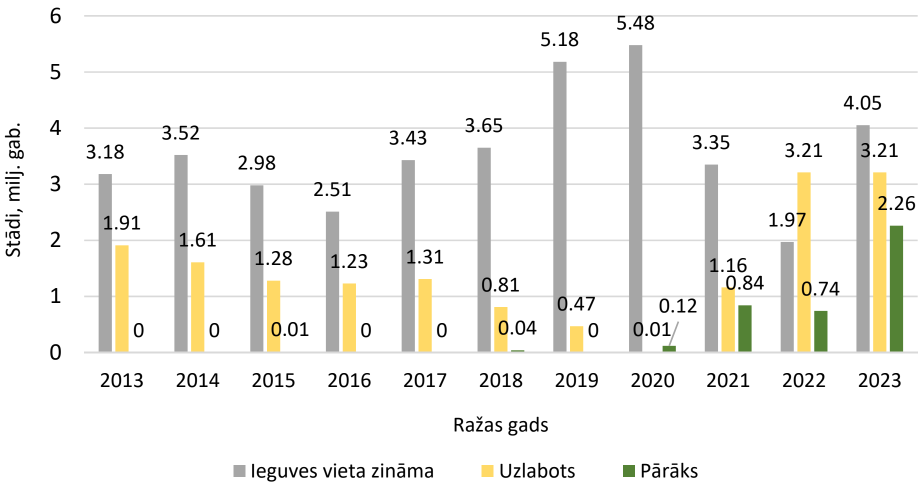
Selekcija nodrošina praktisku ieguldījumu tautsaimniecībā tikai tad, ja tās rezultāti tiek izmantoti meža atjaunošanā un ieaudzēšanā. Bērza audzēs galvenajā cirtē vidēji gadā nocērt 15,3 tūkst. ha (VMD statistika 2013.–2023. gadam), no kuriem lielākā daļa (74–100%) tiek atjaunota ar bērzu. Tomēr gan valsts, gan pārējos mežos bērza audžu atjaunošanā dominē paššēja (2.4. att.). Šāds stāvoklis saistīts kā ar zemākām atjaunošanas izmaksām, tā bērza stādu trūkumu.

Valsts meža dienesta meža reproduktīvā materiāla (MRM) ieguves avotu reģistrā no 134 āra bērzam reģistrētiem ieguves avotiem 100 ir zemākās kategorijas "ieguves vieta zināma", viens – kategorijas "atlasīts", 30 – kategorijas "uzlabots" (5 sēklu plantācijas, 7 kloni un 18 ģimeņu vecāki) un trīs sēklu plantācijas kategorijā "pārāks" (VMD dati par 2023. g.). No 2013.–2023. gadam bērzam dominē zemākās kategorijas MRM ražošana – stādu audzēšana no mežaudzēs iegūtām sēklām (2.5. att.), uz pusi sarucis kategorijas "uzlabots" saražotais MRM apjoms, bet kategorijas "pārāks" sēklu materiāls kļuvis pieejams pēdējos gados un saražotā MRM apjoms ir neliels.



2.4. attēls. **Bērza galvenā cirte un meža atjaunošana un ieaudzēšana ar bērzu visos mežos kopā**

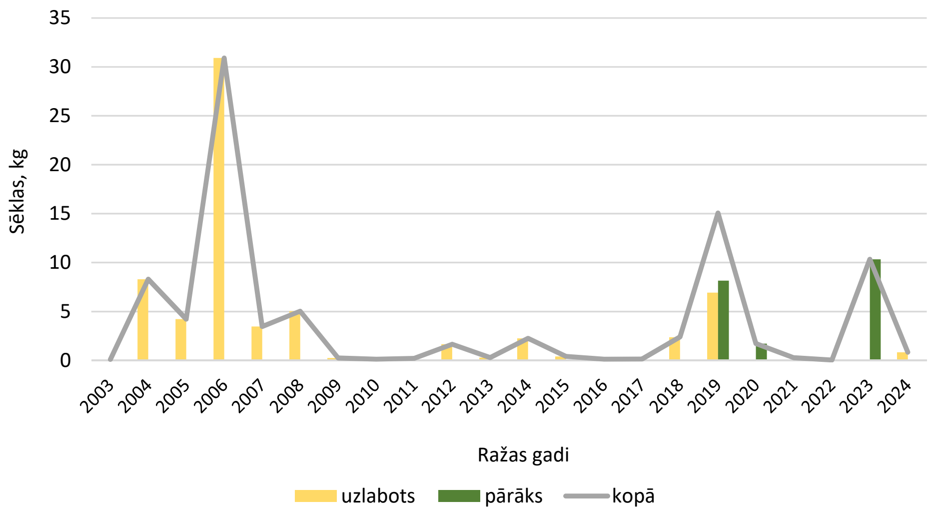
(Avots: VMD)



2.5. attēls. **Āra bērza meža reproduktīvā materiāla ražošana pa kategorijām**

(Avots: VMD)

Kā visām koku sugām, arī āra bērzam sēklu ražas apjoms atšķiras gadu no gada gan mežaudzēs, gan sēklu plantācijās (2.6. att.). Siltumnīcu tipa plantācijās ir iespēja veikt ziedēšanas stimulēšanu, piemēram, izmantojot CO_2, kas var palielināt sēklu ražu un līdz ar to padarīt pieejamākas bērza augstākās kategorijas sēklas stādu ražošanā.



2.6. attēls. **Akciju sabiedrības "Latvijas valsts meži" bērza sēklu plantācijās iegūtais sēklu apjoms**

(Avots: LVM "Sēklas un stādi")

Pēdējos gados (2019., 2020. un 2023. gadā) ražot sākušām LVM 3. kārtas āra bērza sēklu plantācijām "Kalsnava – 4" un "Kalsnava – 5" ir potenciāls ražību palielināt un nodrošināt stādu ražotājus ar augstvērtīgām kategorijas "pārāks" sēklām (2.6. att.).

Selekcijas rezultātu pārnese meža atjaunošanā ir ļoti ierobežota, kas saistīts galvenokārt ar sēklu ražošanas izaicinājumiem, bet ne pašu selekcijas rezultātu (klonu ar noteiktām, pārbaudītām pazīmēm) pieejamību.

3. FINANSIĀLĀ IEGUVUMA NO SELEKCIJAS UN IETEKMES UZ ĢENĒTISKO DAUDZVEIDĪBU NOTEIKŠANA

3.1. Finansiālais ieguvums

Salīdzinot materiālu no sēklu plantācijām un kā kontroli izmantojot mežaudžu pēcnācējus, bijušajā lauksaimniecības zemē ierīkotos pēcnācēju pārbaužu stādījumos Somijas dienvidu daļā pētīta ģenētisko faktoru ietekme uz stumbra kvalitāti un augšanas pazīmēm bērzam 8–12 gadu vecumā. Sēklu plantāciju pēcnācēju pārākums konstatēts, vērtējot gan produktivitāti, gan stumbra kvalitāti. Realizētais selekcijas efekts 8–12 gadu vecumā sēklu plantāciju pēcnācējiem sasniedza 26,3– 29,3% stumbra tilpumam, 9,7–13,6% stumbra raukumam un 6,1–10,1% relatīvajam zara diametram; prognozēts, ka relatīvās atšķirības saglabājas līdz vismaz 30 gadu vecumam (Hagqvist & Hahl 1998). Brīvapputes ģimeņu pēcnācēju vērtēšana 13 gadu vecumā Somijas dienvidos uzrādīja par 20–30% labāku augšanu un stumbra kvalitāti labākajiem genotipiem, salīdzinot ar stādījumu vidējiem rādītājiem (Raulo & Koski 1977, Koski & Rousi 2005). Šo pašu ģimeņu augšanas atšķirību amplitūda saglabājās 32 gadu vecumā, labāko ģimeņu stumbra tilpumam un krājai pārsniedzot stādījumu vidējos rādītājus par attiecīgi 13–28% un 24–28%. Savukārt brīvapputes ģimeņu krāja 32 gadu vecumā bija par 12–16% augstāka nekā mežaudžu pēcnācējiem (Viherä-Aarnio & Velling 1999). Jāmin, ka Somijā, kur bērza selekcija uzsākta jau 1961. gadā, selekcionētam bērzam ir visaugstākais īpatsvars stādmateriāla ražošanā (teju 100%; Jansson et al. 2017). Somijā analizēta arī sēklu plantāciju rentabilitāte, kā indikatoru izmantojot tīro tagadnes vērtību (TTV; Ahtikoski 2000). Aprēķinātā TTV bija pozitīva pie 4% diskonta likmes un prognozētā selekcijas efekta – 20% Dienvidsomijā un 14% Centrālsomijā.

Realizētais selekcijas efekts vērtēts 19 sēklu plantāciju pēcnācējiem 34 pēcnācēju pārbaužu stādījumos Somijas dienvidos un centrālajā daļā 9–24 gadu vecumā. Sēklu plantāciju pēcnācēji uzrādīja visu vērtēto pazīmju uzlabojumu, salīdzinot ar kontroles materiālu no paššējas mežaudzēm, bet rezultāti būtiski atšķīrās pa sēklu plantācijām, jaunākajām no tām uzrādot labākus rādītājus. Realizētais selekcijas efekts augstumam, caurmēram un stumbra tilpumam bija attiecīgi 1,6–12,1%, 0,6– 9,4% un 1,0–31,1%. Selekcionētiem kokiem bija vidēji par 6,8% (līdz 26,7%) mazāk padēlu un par 16,2% (līdz 57,6%) mazāk dubultgalotņu nekā kontrolei (Haapanen 2024).

Dienvidzviedrijā realizētais selekcijas efekts kloniem 9 gadu vecumā, salīdzinot ar lēnaudzīgāko genotipu, bija vidēji 22% augstumam un 16% caurmēram; 26 gadu vecumā šis efekts sasniedza 32% šķērslaukumam un 56% krājai (Liziniewicz et al. 2022).

Labākās bērza ģimenes no Somijas un Zviedrijas selekcijas programmām Norvēģijā uzrādīja 10% augstuma pārākumu pār vietējo provenienču materiālu

(Kohmann 1998). Norvēģijā deviņu brīvapputes ģimeņu dialēlo krustojumu stādījuma lauksaimniecības zemē krāja 37 gadu vecumā (pēc divām kopšanas cirtēm) bija 308 m^3 ha^{-1}, un ģimeņu līmenī novērtēts ļoti atšķirīgs īpatsvars kopējā krājā – produktīvākās ģimenes pēcnācēju krāja bija trīs reizes lielāka nekā krustojumiem, kuros pārstāvēta lēnaudzīgākā ģimene (Skrøppa & Solvin 2019). Šajā pēcnācēju pārbaužu stādījumā augstas korelācijas starp ģimeņu augstuma un caurmēra mērījumiem sešu un 37 gadu vecumā arī apstiprina, ka labāko ģimeņu atlase iespējama agrīnā vecumā, kad koki sasnieguši 2,5–3 m augstumu.

Lietuvā analizēti sešus gadus veci vietējās izcelsmes 100 brīvapputes ģimeņu pēcnācēji, un to selekcijas efekts novērtēts, atlasot 30% labāko ģimeņu pēc saglabāšanās, augstuma, caurmēra, stumbra taisnuma un zaru resnuma (augstumam pielietots koeficients 1,5; Baliuckiené 2009). Koku saglabāšanās selekcijas efekts sasniedza nepilnus 60%; augstumam un caurmēram tas bija robežās no 20 līdz 40%; uzlabojums stumbra taisnumam sasniedza 10%. Selekcijas efekts zaru resnumam bija neliels (līdz 5%) vai nebūtiski negatīvs, atkarībā no selekcijas zonas.

Āra bērzs ir iekļauts meža koku selekcijas programmās Lietuvā, Zviedrijā un Somijā, kā arī, kā papildu suga ar mazāku nozīmi, Norvēģijā.

Jāņem vērā, ka realizēto selekcijas efektu nosaka ne tikai pats atlases process, bet arī veids, kā šis selekcijas efekts tiek pārnests praksē. Piemēram, bērza sēklu plantācija zem plēves seguma ir efektīvāka par brīvapputes sēklu plantāciju, kurā ieguvumu līdz pat divām reizēm var mazināt fona putekšņi (Ruotsalainen 2014).

Ierasti pieņemts, ka selekcijas efekts realizējas ilgākā laika periodā pēc stādīšanas – krājas kopšanas un galvenās cirtes laikā. Tomēr ir tūlītējs ieguvums no selekcionēta stādmateriāla izmantošanas, jo tā ļauj samazināt sākotnējo stādīšanas biezumu augstākas stumbra kvalitātes dēļ, tādā veidā samazinot sākotnējo investīciju apjomu (Ruotsalainen 2014).

Reizē ar selekcijas mērķi paaugstināt produktivitāti un uzlabot augstvērtīgu sortimentu iznākumu panākama arī oglekļa piesaistes palielināšana par aptuveni 10–20% (Ameray et al. 2021). Selekcija, intensīva apsaimniekošana un atbilstošs rotācijas ilgums ilgmūžīgu koksnes produktu ražošanai kopā ir svarīgi instrumenti, lai palielinātu oglekļa piesaisti. Piemēram, *Pinus taeda* stādījumos ASV dienvidos aplēsts, ka selekcionētas šīs sugas priedes raksturojamas ar par 17% augstāku krāju un par 13% augstāku oglekļa piesaisti nekā neselekcionēti koki (Aspinwall et al. 2012). Stādītajām audzēm piesaistot oglekli, tām būs liela nozīme oglekļa tirgū, vairojot meža īpašnieka ienākumus. Pētījumā Somijā novērtēts, ka, izvirzot par meža apsaimniekošanas mērķi gan koksnes ražošanu, gan oglekļa uzkrāšanu, finansiālie ieguvumi selekcionētās audzēs ir augstāki, nekā, izvirzot par mērķi tikai koksnes ieguvi (Ahtikoski et al. 2020).

Meža apsaimniekošanai oglekļa piesaistei mainīgos klimatiskajos apstākļos nepieciešamas pielāgošanās darbības (adaptīva mežsaimniecība). Mainīgs klimats apdraud mežu spēju piesaistīt oglekli, paaugstinoties temperatūrai un izmainoties nokrišņu sezonalitātei, kā arī dabisko traucējumu, piemēram, sausuma, vēja vai meža kaitēkļu bojājumu biežuma un smaguma pieauguma dēļ (Seidl et al. 2017, Ontl et al. 2020). Meža apsaimniekošanas pārtraukšana ar nolūku maksimāli palielināt oglekļa daudzumu ekosistēmā uzskatāma par nereālu tādos reģionos kā Baltija un Ziemeļvalstis, kur mežsaimniecībai ir nozīmīga loma tautsaimniecībā, tādēļ tāda adaptīvā mežsaimniecība kā, piemēram, produktīvas stādītas audzes ar selekcionētu reproduktīvo materiālu un ar zemāku sākotnējo biezumu to stabilitātes veicināšanai, var paaugstināt izturību pret, piemēram, vēja bojājumu risku, un tādējādi ilgtermiņā samazināt oglekļa zuduma riskus (Jandl et al. 2015). Ņemot vērā, ka selekcionēts stādmateriāls parasti tiek izmantots sugai piemērotākajās augsnēs (augsta bonitāte), kur vislabāk izpaužas tā papildu ieguldījums augšanā (Zeltiņš et al. 2024), svarīga ir selekcijas efekta mijiedarbība ar citām mežkopības darbībām risku mazināšanā. Proti, selekcionētu stādu izmantošana, zemāks sākotnējais audzes biezums un laicīga retināšana gan paaugstina audzes stabilitāti, gan saīsina rotācijas ilgumu līdz mērķa caurmēra sasniegšanai, tādā veidā samazinot laiku, kad koki ir pakļauti vēja un citu bojājumu riskam, un reizē palielinot finansiālo ieguvumu (Donis et al. 2020, Samariks et al. 2020).

Līdz šim trūkst bērza selekcijas radītā finansiālā ieguvuma krājas kopšanas cirtēs novērtējuma, kas ļauj noteikt ieguvumus meža īpašniekam jau pirms galvenās cirtes vecuma sasniegšanas. Tāpat salīdzinoši ir maz vērtēts ieguvums no selekcijas galvenās cirtes vecumā, kā arī visam selekcijas ciklam kopumā.

3.2. Ģenētiskā daudzveidība

Selekcijas populācijas un veģetatīvi pavairota materiāla plašākas izmantošanas kontekstā būtiski ir ņemt vērā ģenētisko daudzveidību (ĢD), kas ir pamats bioloģiskajai daudzveidībai gan sugas, gan ekosistēmas līmenī (Koskela et al. 2007, de Vries et al. 2015). ĢD nodrošina dzīvo organismu, t.sk. koku saglabāšanos un evolūciju mainīgā vidē.

ĢD selekcijas populācijā svarīga, jo:

a) nodrošina iespējas selekcijas mērķu maiņai nākotnē;
b) novērš (mazina) gēnu dreifu un tuvradniecisko krustošanos un ar tiem saistīto negatīvo ietekmi;
c) uzlabo selekcionēta materiāla adaptācijas potenciālu, kas īpaši nozīmīgi strauji mainīgā vidē.

ĢD ir mainīga arī cilvēka neietekmētās koku populācijās (populāciju daļās), tādēļ ir komplicēti definēt kādas skaitliskas indikatoru vērtības, kas raksturotu augstu vai pietiekamu tās apmēru. Precīzāko priekšstatu par ĢD saglabāšanu selekcijas populācijā nodrošina salīdzinājums ar neselekcionētu autohtonu materiālu. Vairāki autori kā mērķi ĢD saglabāšanai selekcijas populācijā norāda vismaz 95% no saimnieciskās darbības neskartās populācijās (to daļās, kā vecas mežaudzes, kas nav atjaunotas stādot vai sējot selekcionētu materiālu) konstatējamā alēļu skaita, tam tērējot mazāko iespējamo resursu (Thomas et al. 2014).

Pavairošanai – stādu ražošanai un stādīšanai mežā – tiek izmantota tikai neliela daļa no selekcijas populācijas: pēc noteiktas pazīmju kopas, kas ietilpst selekcijas indeksā, izvēlēti genotipi. Nozīmīgi, lai ĢD šajā kopā būtu pietiekama konkrētas sugas daudzveidības saglabāšanai ilgtermiņā meža ainavā. Sēklu plantācijās šāda ĢD līmeņa raksturošanai bieži vien tiek izmantots efektīvais klonu skaits (N_e) – īpatņu skaits ideālā populācijā (kura atrodas Hardija-Weinberga līdzsvara stāvoklī), kam ir tāds pats inbrīdinga koeficients (vai dispersija) kā dotajai populācijai (Falconer, Mackay 1996). N_e ietekmē gan klonu skaits un to savstarpējā radniecība, gan atšķirīga to pārstāvētība plantācijas pēcnācēju kopā, kas saistīts ar ziedēšanas fenoloģijas atšķirībām, ziedēšanas intensitātes un dzimuma attiecības atšķirībām, kopējās sēklu ražas un tās kvalitātes atšķirībām (Charlesworth 2009). Kopā ar mutāciju biežumu N_e determinē ģenētiskās daudzveidības līmeni (lielākoties neitrālo daudzveidību, kas maz vai nekādā veidā neietekmē dabisko selekciju). Ir pieradīts, ka gēnu dreifa (nejaušam kādas alēles vai alēļu zudumam no populācijas, mainoties paaudzēm un aizejot bojā indivīdam, kuram vienīgajam ir konkrētā alēle vai alēles) ietekme nav nozīmīga, ja $N_e > 25$. Šādu vai pat ievērojami mazāku ($N_e = 10–16$) vērtību iesaka izmantot sēklu plantācijā (apskats: Jansons 2008). Mazāka vērtība lielākoties tiek saistīta ar faktu, ka plantācijas ražo relatīvi īsu laiku (pēc kura notiek klonu sastāva nomaiņa) un nav sagaidāms, ka nākamajās paaudzēs plantāciju pēcnācēji krustoties tikai savā starpā. Krustošanās ar blakus audžu kokiem paaugstinās efektīvo klonu skaitu un novērsīs ĢD zudumu. Tieši šie paši argumenti ir spēkā, arī vērtējot veģetatīvi pavairota materiāla (klonu) izmantošanu meža atjaunošanā.

Veģetatīvā pavairošana un klonu izmantošana Baltijas jūras reģionā ir salīdzinoši maz izplatīta (Högberg & Varis 2016), tādēļ saikni starp klonu izmantošanu un ģenētisko daudzveidību iespējams analizēt teorētiski vai izmantojot piemērus no citiem reģioniem, kur tā lietota plašāk. Piemēram, aptuveni puse no eikaliptu audzēm Brazīlijā ir klonu stādījumi (Wu 2019). Tāpat iespējams vērtēt audzes, kuras atjaunojas ar sakņu un/vai celmu atvasēm. Šādās dabiski atjaunojušās audzēs konstatējamas ievērojamas heterogēnu vides apstākļu noteiktas koku fenotipiskās atšķirības pat tad, ja tie ir tikai 3–5 klonu rameti (Bradshaw et al. 2019) – tātad ārējās vides faktori, kas negatīvi ietekmē kādu klona rametu, neatstās šādu ietekmi uz citu. Tādējādi audzes ar nelielu klonu skaitu var pastāvēt ļoti ilgu laiku. Paleoekoloģiskajos pētījumos secināts, ka daļā Eiropas bijis ilgs periods ar šādām melnalkšņa un parastās liepas klonu audzēm, kas radušās agrīnajā holocēnā (Giesecke et al. 2017). Šo periodu pārtraukusi antropogēnā ietekme ar nozīmīgiem mājlopu radītiem bojājumiem, kas ierobežoja turpmāku atjaunošanos ar atvasēm un iznīcināja klonus, kas varētu būt bijuši vairākus tūkstošos gadu veci. Uz šādu klonu vecumu norāda arī *Cook* (1985). Vecākā zināmā parastā egle (Old Tjikko, > 9000 gadi), kas konstatēta Zviedrijā, arī eksistējusi kā klons, periodiski atjaunojoties tās virszemes daļai (Öberg & Kullman 2011).

Vērtējot informāciju par 45 augu sugu, tostarp kokaugu, ģenētiskās daudzveidības sadalījumu, konstatēts, ka daudzi to genotipi acīmredzami ir ierobežoti sastopami tikai vienā populācijā, kurā reti kad sastopami vairāk par 25 genotipiem (Widén et al. 1994). Parastajai apsei (*Populus tremula* L.) pētījumā Latvijā aprēķinātais vidējais klonu skaits uz ha bija robežās no 6,1 līdz 26,8 ar vidējo distanci starp rametiem 48 ± 9,5 m, maksimālajai vidējai distancei sasniedzot 85,6 m (Zeps et al.

2017). Līdzīgi rezultāti iegūti arī Somijā (Suvanto & Latva-Karjanmaa 2005). Intensīva savstarpējā konkurence, kā arī ārējie faktori (piemēram, pārnadžu bojājumi), pirmajos augšanas gados ievērojami samazina genotipu skaitu audzē (Krasny & Johnson 1992, Watkinson & Powell 1993, Edenius & Ericsson 2007).

Dabā ģenētiskās daudzveidības samazināšanās bieži vien saistīta ar kādu reģionāla mēroga un/vai vēsturisku būtisku vides pārmaiņu ietekmi. Piemēram, ledus laikmetu, kurā Skandināvijā skujkoki izdzīvojuši tikai ļoti nelielās platībās (Parducci et al. 2012), sugai lielākoties pēc ledus laikmeta tajā ienākot no citām teritorijām. Dabiskās egles populācijas Zviedrijā un Norvēģijā ir ar zemāko ģenētisko mainību Eiropā, taču ar augstu fenotipisko plastiskumu (Bradshaw et al. 2019) un spēju izdzīvot kā skarbos, tā mainīgos vides apstākļos. Tas atkārtoti apliecina, ka starp ģenētisko daudzveidību un adaptācijas spēju nav liekama vienādības zīme.

Klonu izplatība dabiskās populācijās norāda uz to, ka skarbos apstākļos tā ir dabiska izdzīvošanas stratēģija, līdz ar to piemērotu klonu izmantošana klimata pārmaiņu kontekstā būtu uzskatāma par sava veida dabas procesu atdarināšanu. Savukārt ierobežotais genotipu skaits dabiskās populācijās, kurās raksturīga veģetatīvā vairošanās, norāda, ka audzes līmenī var nebūt nepieciešams liels klonu skaits.

Klonu izmantošanas ietekmi uz ģenētisko daudzveidību nosaka (Ingvarsson & Dahlberg 2019):

1) tas, cik pilnvērtīgi dotā selekcijas populācija pārstāv esošo sugas ģenētisko daudzveidību konkrētajā teritorijā (t.i., no kādas kopas tiek atlasīti piemērotākie genotipi);
2) cik klonu un cik daudz rametu no šiem kloniem tiks izmantoti;
3) kopējā platība, kas apstādīta ar (noteiktu) klonālo materiālu.

Riskus, kas saistīti ar potenciālu daudzveidības noplicināšanu, iespējams vadīt:

1) selekcijas indeksā klonu atlasei ietverot noturību nosakošas pazīmes (kuru noteikšanai var būt nepieciešamas plašākas pārbaudes daudzveidīgākos apstākļos un/vai ilglaicīgākas pārbaudes);
2) nodrošinoties pret nezināmiem (iespējamiem) nākotnes riskiem, saglabājot sugas genofondu ilgtermiņa selekcijai, piemēram, klonu arhīvos un ģenētisko resursu mežaudzēs (Hoban & Schlarbaum 2014, Hoban et al. 2018, Rosvall et al. 2019, Proschowsky et al. 2020).

Klonu izmantošanas ietekme uz ģenētisko daudzveidību (un citiem daudzveidības līmeņiem) vērtējama divos telpiskajos līmeņos – atsevišķas audzes (plantācijas) un ainavas (meža masīva).

Klonu izmantošanas **audzes līmenī** ietekme būs atkarīga no:

1) izmantotā klonu skaita;
2) specifiskām šo klonu īpašībām;
3) mežsaimniecības prakses šajās audzēs.

Vērtējot izmantoto klonu skaitu un izsakot heterozigotitātes vai adaptīvās ģenētiskās mainības zudumu kā funkciju no efektīvā populācijas īpatņu skaita, $N_e \approx 10$ pirmajā paaudzē nodrošina aptuveni 95% no sākotnējās ģenētiskās mainības populācijā (Roberds et al. 1990). Trešās paaudzes tējas koka selekcijas populācijas pētījumā

Austrālijā netika novērotas atšķirības heterozigotitātē starp dažāda skaita klonu komplektiem (10, 15 un 20 indivīdi atkārtoti izvēlēti (10 reizes) no 114 koku selekcijas populācijas). Tomēr 10 klonu komplektā konstatēta samazināta heterozigotitāte, salīdzinot ar 20 indivīdu komplektu un selekcijas populāciju. Inbrīdinga koeficients 20 klonu komplektam ir būtiski mazāks nekā 10 klonu komplektam. Kā sagaidāms, komplekta lielums lielā mērā ietekmē iekļauto alēļu skaitu, mazākai paraugkopai saturot mazāk reto alēļu. Tomēr alēļu daudzveidība visiem komplektiem ir līdzvērtīga, izvēloties 7 indivīdus no visām populācijām (Voelker & Shepherd 2020).

Ģenētiskās mainības kontekstā, svarīgi arī atšķirt ģenētisko daudzveidību un genotipisko daudzveidību. Ģenētiskā daudzveidība attiecas uz ģenētisko mainību populācijā un ir atkarīga no atšķirīgo alēļu skaita un biežuma. Genotipiskā daudzveidība attiecas uz unikālajiem genotipiem, kas ir sastopami. Piemēram, 10 unikāli kloni nodrošina līdzvērtīgu ģenētisko daudzveidību kā visi to iespējamie pēcnācēji, kas rodas, izmantojot šos kokus kā vecākus. Tomēr genotipiskā daudzveidība šiem 10 kloniem ir zemāka, nekā stādot pēcnācējus, kas radušies, nejauši krustojot šos klonus. Šajā gadījumā atkārtota kombinācija, kas saistīta ar mejozi, nodrošina, ka praktiski visiem pēcnācējiem būs unikāli genotipi, pat tad, ja tos rada tik ierobežots vecāku skaits. Tiklīdz pietiekams skaits klonu tiek izmantots meža atjaunošanā, ģenētiskās daudzveidības zudums būs minimāls. Tomēr genotipiskā daudzveidība tiek būtiski samazināta pat tad, ja tiek izmantots liels skaits unikālu klonu (Ingvarsson & Dahlberg 2019).

D. Lindgren (2009) parastajai eglei Zviedrijas apstākļos iesaka izmantot 25 klonu maisījumu ar minimālo gēnu daudzveidību, izteiktu kā statusa efektīvu skaitli (*status effective number*) $N_s = 4$. Tas līdzvērtīgs gēnu daudzveidībai divās bezgalīgi lielās sibu ģimenēs ar četriem neradniecīgiem vecākiem vai vienai lielai pussibu ģimenei, t.i., viens mātes koks un bezgalīgi liels skaits tēva koku. Ilgtermiņā šāds klonu maisījums ar $N_s = 4$ nodrošina 87,5% no sākotnējās gēnu daudzveidības (Wu 2019). Eikaliptu plantācijās tiek izmantoti 5–14 kloni, kas ir pietiekams efektīvais skaits, lai nodrošinātu nepieciešamo ĢD (Rosvall et al. 2019). Eiropā sugām pašlaik praksē bieži tiek izmantoti 10–20 kloni (Lelu-Walter et al. 2013). Vērtējot klonu plantācijas bojāejas iespējamību, atšķirības starp riska pakāpēm ir ļoti nelielas, ja tiek izmantoti 13–25 kloni (Roberds et al. 1990, Roberds & Bishir 1997). Modelējot situāciju ar kompleksu rezistenci (daudzu gēnu noteiktu) pret zināmiem un nezināmiem nākotnes kaitēkļiem, rezultāti lielā mērā apstiprina šo tendenci – aptuveni 18 genotipi ir optimums, lai samazinātu nākotnes nezināmos riskus, lai gan atšķirības starp 6, 18 un 30 genotipiem ir ļoti mazas (Yanchuk et al. 2006). Šie rezultāti ir vispārināmi un attiecināmi uz boreālo mežu koku sugām ar garu aprites ciklu (Wu 2019).

Visas pieejas minimālā klonu skaita noteikšanā norāda uz vienādu tendenci – genotipu skaita palielināšana virs noteikta sliekšņa maz ietekmē ĢD samazināšanās varbūtību: 5– 30 kloni nodrošina tikpat augstu “drošību” pret sagaidāmajiem nākotnes riskiem kā bezgalīgi liela populācija, un optimālais daudzveidības līmenis eksistē 18 genotipu lielā populācijā (Wu 2019). Praksē klonu maisījumā vērts izmantot nedaudz vairāk klonu, iekļaujot vairāk klonu no augstvērtīgākajām (pēc selekcijas indeksa) ģimenēm (Weng et al. 2012). Regulējot klonu īpatsvaru maisījumā, iespējams uzlabot gan ražību, gan tās stabilitāti telpā un laikā, šādā veidā mazinot riskus (Weng et al. 2013). Stādot klonu maisījumu, ieteicams sajaukt visus klonus kopā, lai samazinātu viena klona rametu telpisku saistību (Prospero & Cleary 2017). Vērtējot iebildumus pret izmainītu (samazinātu) ĢD, kas argumentēti ar palielinātu patogēnu un dendrofāgo kukaiņu ietekmi (Aitken et al. 2008), jāatceras, ka šie faktori var nozīmīgi ietekmēt arī platības ar augstu ģenētisko daudzveidību un ģenētisko mainību starp audzēm (Jump et al. 2009, Prospero & Cleary 2017), kardināli samazinot indivīdu skaitu ne tikai konkrētās sugas audzes (piemēram, vienas egļu audzes), bet arī meža masīva vai pat reģiona līmenī (piemēri: goba un osis Eiropā). Tātad jāanalizē relatīvās riska izmaiņas.

Kloni izmantojami ne tikai intensīvā mežsaimniecībā. Tā var būt daļa no kombinētas atjaunošanas, atbilstoši dabai tuvākas mežsaimniecības pieejai. Piemēram, atlasīti genotipi ar tieviem zariem var tikt stādīti retākā izvietojumā, sasniedzot vēlamās dimensijas bez kopšanas cirtēm un radot atvērtākus apstākļus bagātīgākai pameža veģetācijai un lielākai tās sugu daudzveidībai.

Kritika klonu izmantošanai, tāpat kā jebkuram citam ģenētiski uzlabotam meža reproduktīvajam materiālam, ir saistīta arī ar "ģenētisko piesārņojumu" apkārtējās mežaudzēs ar stādījuma ziedputekšņiem vai sēklām. Tomēr šajā aspektā nav reālas ietekmes, ciktāl stādījumā izmantotais reproduktīvais materiāls nav ģenētiski modificēts un ir iegūts no plašu ģenētisko daudzveidību uzturošas selekcijas populācijas vietējiem apstākļiem piemērotām un/vai vietējām koku sugām (Bradshaw et al. 2019).

Darbības, kas veicamas, lai audzē nodrošinātu sugu daudzveidībai nozīmīgas struktūras (kā atmirusī koksne, iepriekšējās paaudzes koki u.c.), nav atkarīgas no stādmateriāla pavairošanas veida vai klonu skaita (Ratcliffe & Peterken 1995, Felton et al. 2010). Taču parasti sugu daudzveidības vai atsevišķu sugu sastopamības pētījumos "plantācija" – ar to saprotot klonu stādījumu, parasti lielā, homogēnā platībā – tiek analizēta kā vienots kopums, nenodalot ģenētikas (klonu) un mežsaimniecības ietekmes. Šādās "plantācijās" parasti konstatējama samazināta, vai tāda pati sugu (kopumā vai konkrētas grupas) daudzveidība un blīvums, kā paššējas ceļā izveidojušās audzēs (Peterken & Game 1984, Humphrey et al. 2002, Plue et al. 2017).

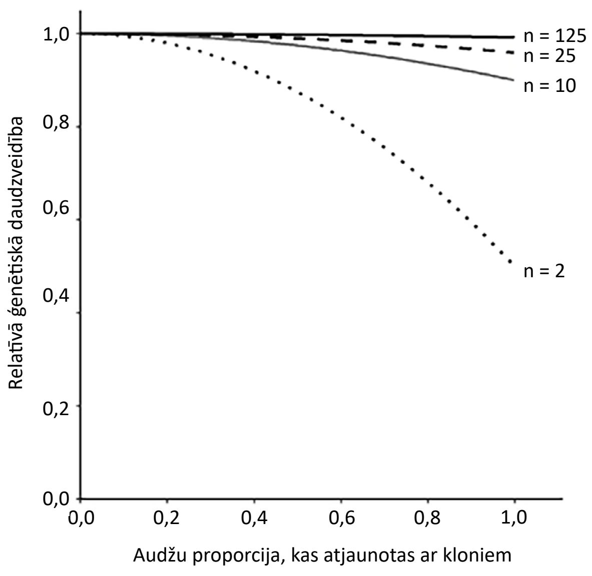
Viendabīgi augšanas apstākļi un intensīva, standartizēta mežsaimniecība ir faktori, kas rada vienveidību klonu plantācijās un līdz ar to nelielu dzīvotņu skaitu un ar tām saistīto sugu daudzveidību (Bradshaw et al. 2019). Taču negatīvo ietekmi uz daudzveidību iespējams mazināt vai pilnībā novērst, veidojot nelielas (2–20 ha) un meža masīvā starp dažādu koku sugu un mežsaimniecisko mērķu audzēm izvietotas plantācijas. Šāda pieeja būtu ļoti piemērota Latvijā, kur tāpat ļoti reti sastopamas lielākas homogēnas, augstas ražības meža audzēšanai piemērotas vienlaidus platības.

Kopumā **meža ainavas (masīva)** plantāciju izvietojumam iespējamas divas pieejas:

1) koncentrācija lielā, homogēnā platībā. Šāda pieeja nodrošina augstu mežsaimniecības efektivitāti, darbu mehanizācijas un pat automatizācijas iespējas. Turklāt iespējams iegūt visu nepieciešamo koksnes apjomu relatīvi

nelielā daļā no kopējās meža teritorijas. Piemēram, Jaunzēlandē, kas reģionāli ir nozīmīga koksnes un tās produktu ražotāja un eksportētāja, absolūti lielākais vairums koksnes (> 99%) tiek iegūta plantācijās, kas aizņem ap 7% no tās platības (New Zealand Forest ... 2023). Tātad pārējā mežu platība var tikt izmantota citām vajadzībām, un mežsaimnieciskajiem mērķiem nav nozīmīgas ietekmes uz mežu bioloģisko daudzveidību valstī. Līdzīgi ASV dienvidos, kas ir reģions ar pasaulē lielākajām meža plantāciju platībām, liela daļa koksnes tiek iegūta no audzēm, kas atjaunojušās paššējas ceļā (Bettinger et al. 2009): tātad ir ļoti lielas arī šādu mežu platības. Šī pieeja piemērota un tiek izmantota vietās, kur pieejamas plantāciju mežu izveidei piemērotas lielas vienlaidus platības un kur raksturīgs tāds klimats, kas nodrošina iespēju veidot īsu aprites ciklu (6–26 gadi);

2) izvietojums izklaidus plašākā teritorijā. Heterogenitāte ainavas mērogā tiek uzturēta ar ģenētisko mainību starp audzēm, t.i., dažādi klonu maisījumi tiek izmantoti dažādās audzēs ainavas līmenī (Lindgren 1993), kā arī blakus atrodas paššējas ceļā atjaunojušās audzes un klonu stādījumi (plantācijas). Pat neliels klonu skaits katrā plantācijā, ja šādu plantāciju īpatsvars saglabājas zems (2 kloni – līdz ~ 10%, 10 kloni – līdz ~ 35%), nodrošina iespēju saglabāt līdzvērtīgu ģenētisko daudzveidību meža masīva līmenī kā tad, ja šādu plantāciju tajā nebūtu (3.1. att.). Kā redzams, arī izmantojot šo pieeju (plantācijas



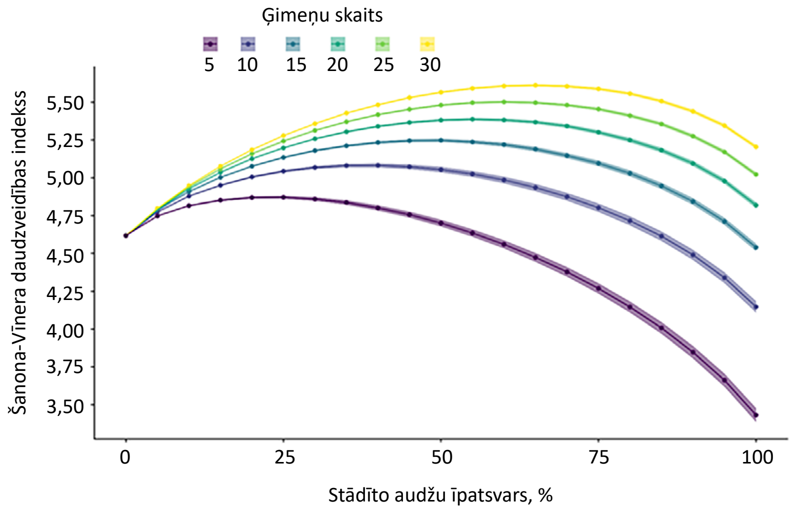
3.1. attēls. **Relatīvā ģenētiskā daudzveidība pret situāciju, kad kloni netiek izmantoti**

Tiek pieņemts, ka audzē ir 2000 koki un tās atjaunošanā izmantoti 125, 25, 10 un 2 kloni. Pieņemts, ka dažādas audzes tiek stādītas, izmantojot dažādus klonu komplektus no selekcijas populācijas, kas ir liela un nemainīga laikā (Ingvarsson & Dahlberg 2019) izvietojot izklaidus), ekoloģiskā ietekme lielā mērā atkarīga no tā, cik liela daļa platības (īpatsvars) ir atvēlēta intensīvai vai klonu mežsaimniecībai (Bettinger et al. 2009, Bradshaw et al. 2019). Pētījumos Zviedrijā novērtēts, ka pat pie visintensīvākā apsaimniekošanas scenārija, puse no egļu populācijas atjaunosies pašsējas ceļā (Rosvall 2019), un tas nodrošinās iespējas pielietot klonu stādījumus pārējā teritorijā, vienlaikus uzturot ĢD (Ingvarsson & Dahlberg 2019). Tāpat jāņem vērā, ka ainavā ilgstoši netiek izmantots viens un tas pats klonu maisījums – katrā selekcijas ciklā vai pat biežāk tiek izvēlēti jauni, labāki (pēc selekcijas indeksa vērtības) kloni, kas nomaina iepriekšējos. Kopējo sugas ģenētisko daudzveidību uztur arī ģenētisko resursu mežaudzes, kas iesaistītas reti sastopamu alēļu saglabāšanā un šādu alēļu pārnesē selekcijas populācijā, nodrošinot potenciālu piemērotu (ražīgu) genotipu atlasei arī ļoti mainīgos vai skarbos apstākļos (Maxted et al. 2007, Trethowan & Mujeeb-Kazi 2008, Khoury et al. 2010, Hanso & Drenkhan 2012, McCouch et al. 2012). Analīze liecina, ka pašsējas ceļā atjaunojušos vai stādītu (sēklu plantāciju pēcnācēji) mežaudžu saglabāšanās meža masīvā ir svarīga, lai varētu izvērst plaša mēroga klonu mežsaimniecību (Wu 2019).

Analīzes rezultāti liecina, ka boreālajos apstākļos, kuros raksturīga bagātīga bērza, egles un citu koku sugu pašatjaunošanās un brīva to savstarpējā krustošanās arī starp attālām audzēm, klonu plantācijām ir relatīvi maza ietekme uz kopējo genofondu, kamēr šīs plantācijas neveido lielāko daļu audžu ainavā un kamēr satur daudzveidīgus genotipu komplektus (Rosvall 2019). Vairums no alēlēm, kas sastopamas populācijā citās mežaudzēs, būs arī klonu maisījumā, tikai ar dažādu biežumu. Klonu maisījums spēj ietvert plašu genofondu arī ar ierobežotu genotipu skaitu (Ingvarsson & Dahlberg 2019).

Latvijas apstākļos, modelējot stādītu selekcionēta āra bērza audžu (pirmās kārtas sēklu plantāciju brīvapputes pēcnācēji) proporcijas meža masīva līmenī un izmantoto ģimeņu skaita (5 līdz 30 ģimenes) stādmateriāla ražošanā ietekmi uz ģenētisko daudzveidzību, novērtēts, ka ģenētiskās daudzveidības indikatori (Šanona-Vīnera daudzveidības indekss un sagaidāmā heterozigotitāte) ir visaugstākie, kad 50–55% audžu ir stādītas un tiek izmantotas vismaz 20 ģimenes (3.2. att.). Savukārt, izmantojot atlasītas piecas labākās ģimenes, ģenētiskā daudzveidība ir salīdzināma ar dabiskajā atjaunošanā sastopamo, ja stādītu audžu proporcija ainavā nepārsniedz 55% (Bāders et al. 2024).

Secināms, ka pētījumi atbalsta ierobežota skaita (5) labāko genotipu izmantošanu intensīvā mežsaimniecībā, ja šādu stādītu audžu īpatsvars starp dabiski atjaunotajām mežaudzēm ainavā nepārsniedz aptuveni 55%. Šī pieeja nodrošina līdzsvaru starp produktivitāti un ģenētiskās daudzveidības saglabāšanu apsaimniekotās meža ekosistēmās.



3.2. attēls. **Ģimeņu skaita un to stādījumu īpatsvara meža masīvā ietekme uz ģenētisko daudzveidību**
(Bāders et al. 2024)

Kopsavilkums

Latvijā, līdzīgi kā citās Baltijas jūras reģiona valstīs, ir ierīkotas plaša apjoma pēcnācēju pārbaudes, kas ir sasniegušas vecumu, lai tiktu veikts līdz šim trūkstošs detalizēts to vērtējums un analīze pamatotu secinājumu ieguvei. Vērtējama no saimnieciskā viedokļa svarīgo pazīmju ģenētiskā determinācija, kā arī savstarpējās genotipiskās korelācijas, kas var dažādās populācijās atšķirties.

Balstoties uz pēcnācēju pārbaudēm, atlasāmi kloni ne tikai sēklu plantāciju ierīkošanai, bet arī potenciāli veģetatīvajai pavairošanai atbilstoši genotipi stādu ražošanai, veicot turpmākas pārbaudes *in vitro*. Genotips ir būtisks faktors veiksmīgai bērza mikropavairošanai, tādēļ tās pielietošanai praksē ir svarīgi izstrādāt tehnoloģiju ar kloniem specifisku, pielāgotu barotņu sastāvu. Savukārt pamatotai veģetatīvi pavairota stādmateriāla izmantošanai praksē (ar ko praktiska pieredze ir, piemēram, Somijā) ir nepieciešams līdz šim trūkstošs vērtējums visam aprites ciklam, kas būtu iegūstams mērķa caurmēru sasniegušā plantācijā.

Selekcijas finansiālo efektu nosaka iegūstamā papildu produktivitāte (ņemot vērā arī uzlabotu izturību pret dažādiem vides riskiem) un augstāka stumbra kvalitāte augstvērtīgāku sortimentu īpatsvara paaugstināšanai galvenajā cirtē, kā arī aprites cikla saīsināšanas pozitīvā ietekme. Taču līdz šim ir maz vērtēts finansiālais ieguvums krājas kopšanas cirtēs.

4. MATERIĀLI UN METODES

4.1. Selekcijas stādījumu novērtējums (I, II un III publikācija)

Promocijas darba atsevišķās nodaļās analizētas daļas no kopumā 122 bērza selekcijas stādījumiem, kuru kopējā platība kopš to ierīkošanas uzsākšanas 1975. gadā sasniegusi 274, ha (1.4. tab.). Stādījumu vietās klimatiskie apstākļi nedaudz atšķiras, kontinentalitātei palielinoties no Baltijas jūras krasta uz iekšzemi (Laiviņš & Melecis 2003). Saskaņā ar Latvijas Vides, ģeoloģijas un meteoroloģijas centra datiem pēdējās desmitgadēs vidējā gada gaisa temperatūra Latvijā ir +6,4°C. Tā svārstās no +5,2…+5,3°C iekšzemes augstienēs līdz +6,8…+7,4°C Baltijas jūras piekrastē. Siltākais gada mēnesis ir jūlijs ar vidējo gaisa temperatūru +17,4°C un vidējo maksimālo temperatūru +22,3°C. Aukstākajā mēnesī februārī vidējā gaisa temperatūra ir –3,7°C, un vidējā minimālā temperatūra ir –6,6°C. Vidējais gada nokrišņu daudzums Latvijā ir 692 mm. Lietainākie mēneši ir jūlijs un augusts: 76–77 mm nokrišņu, bet sausākais – aprīlis: 34 mm.

4.1.1. Datu ievākšanas metodika

Provenienču stādījums ierīkots Latvijas centrālajā daļā ar sākotnējo biezumu 4200 koki ha^{-1} (stādīšanas shēma 2 × 1,2 m), platībā ar mezotrofu augsni un normālu mitruma režīmu. Tajā iekļautas 16 provenieces – 8 no Latvijas, 4 no Somijas un 4 no Polijas (izcelsmes vietas ģeogrāfiskā platuma intervālā 51°–61° Z pl.). Izmēģinājums ierīkots pilnīgi randomizētos blokos ar 24 koku bloku parcelēm, sešos atkārtojumos. Uzmērīts 37 gadu vecumā, pirms mērījumiem retināšana netika veikta. Katram kokam uzmērīts augstums (h) un krūšaugstuma caurmērs (d). Tika novērtēta arī padēlu un vairāku galotņu veidošanās. Paraugkopa ar 10 kokiem, kas pārstāvēja d diapazonu, tika nozāģēta, un dati par zaru un stumbra biomasu tika iegūti, sadalot stumbru 1 m garās sekcijās. Šie dati tika izmantoti, lai aprēķinātu koku masas centra augstumu.

Apjomīgākajiem darbā analizētajiem **brīvapputes pēcnācēju pārbaužu stādījumiem** sēklas tika ievāktas no 1995. līdz 1998. gadam no pluskokiem 26 mežaudzēs visā Latvijā. Stādījumi ierīkoti Taurenē (57°06’ Z, 25°38’ A), Ukros (56°22’ Z, 23°07’ A) un Rembatē (56°46’ Z, 24°8’ A) neizmantotā lauksaimniecības zemē platībās ar mezotrofu augsni un normālu mitruma režīmu. Ukros un Taurenē eksperimentālais dizains bija randomizēti izvietoti bloki ar vienkoku parcelēm, attiecīgi 10– 93 un 10–77 atkārtojumos, ar 2 × 2,5 m stādīšanas attālumu. Rembates stādījums ierīkots ar pilnīgi randomizētu bloku dizainu, kur katrai ģimenei bija 32 koku bloku parceles trīs līdz piecos atkārtojumos un ar 2 × 2 m stādīšanas attālumu. Rembates izmēģinājums tika izveidots 1999. gada pavasarī, bet Ukru un Taurenes izmēģinājumi – 2000. gada pavasarī, izmantojot viengadīgus konteinerstādus. Eksperimenta ierīkošanas laika atšķirības ņemtas vērā uzmērīšanā, nodrošinot, ka šie darbi norit vienādā koku vecumā, tādējādi visu trīs stādījumu dati izmantojami kopējā analīzē.

Stādījumos uzmērījumi veikti 10 un 14 gadu vecumā. Pirmajā vērtēšanā analīzei bija pieejami mērījumi no 68 256 kokiem (9643 koki Ukros, 11 917 koki Taurenē un 46 696 koki Rembatē), otrajā 82 367 koki (18 371 koks Ukros, 10 964 koki Taurenē un 53 032 koki Rembatē). Pirmajā vērtēšanas reizē katram kokam tika mērīts: a) koka augstums (h), b) lielākā zara diametrs līdz 2 m stumbra augstumam (zd), un c) vidējais zaru leņķis (zl). Tāpat tika atzīmēta padēlu (pad), dubultgalotņu (dg) un zaudētas galotnes (zg) esamība (1 – ir, 0 – nav), kā arī tika novērtēts stumbra taisnums (izliekts, nedaudz izliekts, taisns) un kopējā stumbra kvalitāte (slikta, vidēja, laba) trīs ballu skalā. Otrajā – h un d (izņemot Rembati, kur h netika mērīts). Pēc tam tika aprēķināts stumbra tilpums (V) saskaņā ar I. Liepas formulu (1996). Rembates izmēģinājumā tika mērīts zl, bet Ukros un Taurenē tas tika novērtēts, izmantojot trīs ballu skalu (1 – no 65° līdz 90°; 2 – no 45° līdz 60°; 3 – no 0° līdz 40°). pad, dg, zg esamība un stumbra taisnums un kvalitāte tika novērtēti, kā aprakstīts iepriekš.

4.1.2. Datu statistiskā apstrāde

Provenienču pārbaužu stādījumā aprēķināti koku produktivitātes rādītāji (stumbra tilpums, šķērslaukums un krāja ha^{-1}), to atšķirību būtiskums, kā arī sagaidāmās šo rādītāju vērtības laikā, kad koki sasniegtu mērķa caurmēru (25 cm). Šis laiks noteikts, izmantojot LVMI “Silava” izstrādātu augšanas modeli (Donis et al. 2024).

Pēcnācēju pārbaužu stādījumu nepārtraukto datu (uzmērītās pazīmes) dispersijas un kovariācijas komponentes tika novērtētas, izmantojot SAS MIXED procedūru ar ierobežotās maksimālās iespējamības pieeju (REML; Littel et al. 2006). Diagnostikas diagrammas tika izmantotas, lai pārbaudītu atlikumu normālo sadalījumu. Binārajām pazīmēm tika pielāgots vispārējais lineārais jaukta tipa modelis ar binomālo atlikumu sadalījumu un *logit* saistības funkciju. Ordinālajām pazīmēm tika izmantota ordināla loģistiskā regresija. Binārās/kategoriskās pazīmes tika analizētas, izmantojot vispārinātu lineāru jaukta tipa modeli (GLIMMIX; Littell et al. 2006). Standarta kļūdas tika aprēķinātas, izmantojot Dikersona aproksimācijas metodi (Dickerson 1969). Analizējot kopā Ukru un Taurenes stādījumus ar līdzīgu eksperimentālo dizainu un ģimeņu komplektu, tika izmantots sekojošs modelis:

$$y_{ijkl} = \mu + S_i + B_j + F_k + SF_{ik} + \varepsilon_{ijkl} \ , \qquad (4.1.)$$

kur:

y_{ijk} – *l*-tā koka no *k*-tās ģimenes novērojums *j*-tajā atkārtojumā *i*-tajā stādījumā;

μ – vidējais rādītājs;

S_i un B_j – attiecīgi fiksētie *i*-tās vietas un *j*-tā atkārtojuma *i*-tajā stādījumā efekti;

F_k un SF_{ik} – attiecīgi *k*-tās ģimenes un *i*-tā stādījuma un *k*-tās ģimenes mijiedarbības randoma efekti, un ε_{ijkl} ir randoma atlikuma efekts.

Individuālu stādījumu analīzei Ukros un Taurenē tika izmantots modelis:

$$y_{jkl} = \mu + B_j + F_k + \varepsilon_{jkl} \ , \qquad (4.2.)$$

kur:

y_{jkl} – *l*-tā koka no *k*-tās ģimenes novērojums *j*-tajā atkārtojumā.

Individuālai Rembates stādījuma analīzei modelis tika papildināts ar atkārtojuma un ģimenes mijiedarbības efektu (bloku parceles efektu):

$$y_{jkl} = \mu + B_j + F_k + BF_{jk} + \varepsilon_{jkl} \ , \qquad (4.3.)$$

kur:

BF_{jk} – randoma *j*-tā atkārtojuma un *k*-tās ģimenes mijiedarbības efekts.

Individuālais koka iedzimstamības koeficients šaurā nozīmē (h^2) katrai pazīmei tika aprēķināts, izmantojot dispersijas komponentes no iepriekš aprakstītajiem analītiskajiem modeļiem (Falconer & Mackay 1996). Iedzimstamības koeficients apvienotajā Ukru un Taurenes stādījumu analīzē tika aprēķināts kā:

$$h^2 = \frac{4 \cdot \hat{\sigma}_f^2}{\hat{\sigma}_f^2 + \hat{\sigma}_{fs}^2 + \hat{\sigma}_\varepsilon^2} \ , \qquad (4.4.)$$

kur:

h^2 – iedzimstamības koeficients šaurā nozīmē;

$\hat{\sigma}_f^2$, $\hat{\sigma}_{fs}^2$ un $\hat{\sigma}_\varepsilon^2$ – attiecīgi ģimenes, ģimenes un stādījuma mijiedarbības un atlikuma dispersijas komponentes.

Individuālai Ukru vai Taurenes stādījumu analīzei tika izmantota formula:

$$h^2 = \frac{4 \cdot \hat{\sigma}_f^2}{\hat{\sigma}_f^2 + \hat{\sigma}_\varepsilon^2} \qquad (4.5.)$$

Bloku parceļu dizainam Rembatē tika izmantota formula:

$$h^2 = \frac{4 \cdot \hat{\sigma}_f^2}{\hat{\sigma}_f^2 + \hat{\sigma}_{fb}^2 + \hat{\sigma}_\varepsilon^2} \ , \qquad (4.6.)$$

kur:

$\hat{\sigma}_{fb}^2$ – ģimenes × atkārtojuma mijiedarbības dispersijas komponente.

Aditīvo ģenētisko variācijas koeficientu (CV_a) aprēķināja kā (Falconer & Mackay 1996):

$$CV_a = \sqrt{4\hat{\sigma}_f^2} \cdot \frac{100}{\bar{x}} \ , \qquad (4.7.)$$

kur:

$\bar{x}$ – vidējais fenotipiskais rādītājs.

Ģenētiskās korelācijas (A-tipa) starp pazīmēm vai dažādiem vecumiem vienai pazīmei tika aprēķinātas, izmantojot formulu:

$$r_G = \frac{\widehat{Cov}_{(xy)}}{\sqrt{\hat{\sigma}_{(x)}^2 \cdot \hat{\sigma}_{(y)}^2}} \ , \qquad (4.8.)$$

kur:

$\hat{\sigma}_{(x)}^2$ un $\hat{\sigma}_{(y)}^2$ – a) genotipiskās dispersijas *x* un *y* pazīmēm, vai b) tās pašas pazīmes dispersijas dažādos vecumos;

$\widehat{Cov}_{(xy)}$ – genotipiskā kovariācija starp *x* un *y* pazīmēm vai starp diviem vienas un tās pašas pazīmes mērījumiem.

Genotipa × vides mijiedarbība (G × E) pazīmēm tika novērtēta, aprēķinot B-tipa ģenētiskās korelācijas (r_B) starp diviem stadījumiem (Burdon 1977). Ņemot vērā līdzīgu eksperimentālo dizainu un to pašu ģimeņu kopu, korelācija starp Ukru un Taurenes stādījumiem tika aprēķināta kā (Lu & Charrette 2008):

$$r_B = \frac{\widehat{Cov}_{(a1a2)}}{\sqrt{\hat{\sigma}^2_{(a1)} \cdot \hat{\sigma}^2_{(a2)}}} \ , \tag{4.9.}$$

kur:

$\widehat{Cov}_{(a1a2)}$ – genotipisko efektu kovariācija vienām un tām pašām pazīmēm dažādos stādījumos;

$\hat{\sigma}^2_{(a1)}$ un $\hat{\sigma}^2_{(a2)}$ – genotipiskās dispersijas tām pašām pazīmēm katrā stādījumā.

Gan r_G, gan r_B un to standartkļūdas tika novērtētas, izmantojot daudzdimensiju REML ar SAS MIXED procedūru (Piepho & Möhring 2011), paplašinot iepriekš aprakstītos jaukta tipa modeļus.

Selekcijas vērtības (BV) tika aprēķinātas katrai pazīmei, lai noteiktu selekcijas efektu labāko ģimeņu atlasei. Iegūtas vispārējās kombinatīvās spējas (GCA) vērtības, izmantojot labāko lineāro nenobīdīto prognozi (BLUP), iegūtu ar iepriekš definētajiem analītiskajiem modeļiem. Tā kā vecāks var nodot tikai pusi no saviem gēniem pēcnācējiem, ģimeņu selekcijas vērtības tika aprēķinātas kā divkārši BLUP (Falconer & Mackay 1996). Tā kā lineārie mainīgie binārajām pazīmēm no vispārinātajiem jauktajiem modeļiem tika aprēķināti *logit* skalā, stumbra defektu prognozētās varbūtības ģimenēm tika novērtētas, pielietojot apgriezto funkciju (Littell et al. 1996). Selekcijas efekts, pieņemot selekcijas intensitāti 10% (kā tas parasti tiek izmantots koku selekcijas praksē Latvijā), tika aprēķināts no BV kā procenti virs izmēģinājuma vidējiem rādītājiem.

Galveno komponenšu analīze (PCA) tika veikta kopā Ukru un Taurenes stādījumā, lai novērtētu bērzu izcelsmes vietu (provenienču; 1.2. att.) standartizēto fenotipisko pazīmju variāciju un lai to sasaistītu ar izcelsmes vietu. Novērtētie provenienču vidējie rādītāji tika iegūti no jauktajiem efektu modeļiem:

$$y_{ijklm} = \mu + P_i + F_j + S_k + b_l + sf_{jk} + \varepsilon_{ijklm} \ , \tag{4.10.}$$

kur:

y_{ijklm} – novērojums;

μ – vidējais rādītājs;

P_i, F_j un S_k – fiksētie provenineces, ģimenes un stādījuma vietas efekti;

b_l un sf_{jk} – randoma, attiecīgi, bloka un stādījuma vietas × ģimenes mijiedarbības efekti;

ε_{ijklm} – randoma atlikuma efekts.

Galveno komponenšu (PC) nozīmīgums tika noteikts, izmantojot Montekarlo (randomizācijas) testu, veicot 1000 iterācijas. Pētīto pazīmju un ģeogrāfiskā platuma/garuma attiecības ar pirmajām divām galvenajām komponentēm tika novērtētas, izmantojot Pīrsona korelācijas analīzi. Katram ar PCA analīzi noteiktajam provenienču reģionam vērtētajām pazīmēm tika aprēķinātas dispersijas komponentes pēc 4.1. vienādojuma un tika aprēķināts h^2 un CV_a.

4.2. Āra bērza veģetatīvā pavairošana un tās plašākas izmantošanas potenciāls (IV un V publikācija)

4.2.1. Datu ievākšanas metodika

Pētāmais materiāls **āra bērza *in vitro* kultūras uzsākšanai un genotipiski noteikto atšķirību pārbaudei mikropavairošanā** tika ievākts 15 gadu vecumā pēcnācēju pārbaužu stādījumā Rembatē (aprakstīts 4.1.1. apakšnodaļā). Lai novērtētu mātes koka vecuma ietekmi uz dzinumu iniciēšanu *in vitro*, klona 54–95 eksplanti Rembatē tika salīdzināti ar vienu gadu veciem tā paša klona potējumiem (gadu veci potzari uz divus gadus veca potcelma) Kalsnavā (56°40′ N, 25°58′ E); visi paraugi tika ievākti martā. Klona 54–95 jaunie dzinumi Rembatē tika ievākti no vainaga apakšējās daļas četros dažādos laikos: martā un aprīlī (pavasarī), kā arī jūnijā (vasaras vidū) un septembrī (rudenī), lai novērtētu eksplantu ievākšanas laika ietekmi. Kopā katram variantam (ontoģenēzes vecumam un ievākšanas laikam) *in vitro* kultūru iniciācija uzsākta no 100 eksplantiem. Kultūru iniciācija veikta, sagriežot dzinumus ~ 1,5 cm garos segmentos tā, lai uz katra būtu viens pumpurs. Pumpurus sākotnēji mehāniski notīrīja ar zobu birsti un ziepjūdeni, pēc tam kārtīgi noskalojot zem tekoša ūdens. Mehāniski attīrītus pumpurus tālāk dezinficēja, 10 minūtes mērcējot 0,1% (w/v) $HgCl_2$ šķīdumā, kam pievienoti daži pilieni *Tween* 20 detereģenta, un trīs reizes skaloja dejonizētā ūdenī. Pēc tam dezinficētos segmentus ar pumpuriem izpreparēja un novietoja uz 3 mL iniciācijas barotnes, kas iepildīta stikla mēģenēs (18 × 180 mm garas, ar alumīnija korķi). Iniciācijai izmantota *Woody Plant Medium* (WPM; Lloyd & McCown 1980) tipa barotne, kas papildināta ar 1,0 mg L^{-1} 6-benzilaminopurīnu (BAP), 0,05 mg L^{-1} naftiletiķskābi (NAA), 20 g L^{-1} saharozi un 6 g L^{-1} agaru. Gatavās barotnes pH noregulēts uz 5,8 pirms autoklavēšanas (15 minūtes 121°C temperatūrā zem 110 kPa spiediena). Mēģenes ar pumpuriem novietotas audzēšanas telpā, kur tika uzturēta 23 ± 1°C temperatūra un apgaismojumam izmantotas fluorescentās (*cool-white*) spuldzes, nodrošinot apgaismojuma intensitāti fotosintēzes aktīvajā reģionā (PAR; 400– 750 nm) 40 ± 10 µmol m^{-2} s^{-1}, ar 16/8 h (diena/nakts) fotoperiodu. Pēc 30 dienu ilga inkubācijas perioda veikts kultūru iniciācijas novērtējums (cik daudzi no pumpuriem ir izplaukuši un veido dzinumus).

Pavairošanas un dzinumu augšanas spēju novērtēšanai izmantotas jau ievadītas un nostabilizētas *in vitro* kultūras, kuras iniciētas no 50 genotipiem, kas ievākti Rembates stādījumā. Pavairošanu veica, sagriežot reģenerētus mikrospraudeņus ~ 1,5 cm garos eksplantos un novietojot uz 3 mL svaigas barotnes mēģenēs. Pavairošanai izmantota *Murashige & Skoog* (MS) tipa barotne (Murashige & Skoog 1962), kas papildināta ar 0,2 mg L^{-1} zeatīnu, 20 g L^{-1} saharozi un 6 g L^{-1} agaru. Gatavās barotnes pH noregulēts uz 5,8 pirms autoklavēšanas (15 minūtes 121°C temperatūrā zem 110 kPa spiediena). Mikrospraudeņus kultivēja tādos pašos apstākļos, kā aprakstīts iniciācijas etapā. Pēc 30 dienu ilgas kultivēšanas veikti mērījumi –

noteikts galvenā dzinuma garums, saskaitīti sāndzinumi (visi, kas garāki par 0,5 cm). Kultūrām noteikts pavairošanas koeficients – cik 1,5 cm garus, jaunus mikrospraudeņus var iegūt no viena reģenerēta auga (vitrificētie dzinumi netika ņemti vērā). Kopumā nomērīti 500 reģenerēti mikrospraudeņi (10 mikrospraudeņi no katra klona). Ņemot vērā veiktos mērījumus, noteikti pavairošanas koeficienti un vitrificēto dzinumu proporcija katram klonam, un atbilstoši šiem rādītājiem tālākai analīzei tie iedalīti grupās.

Lai pārbaudītu pavairošanai izmantotās barotnes un dažāda veida citokinīnu ietekmi dažādās kombinācijās, no katras grupas nejauši izvēlēti trīs kloni, kas kultivēti mēģenēs uz dažādām barotnēm: (1) WPM barotne ar zeatīnu 0,1 mg L^{-1}, (2) WPM barotne ar zeatīnu 0,5 mg L^{-1}, (3) MS barotne ar zeatīnu 0,1 mg L^{-1}, (4) MS barotne ar zeatīnu 0,5 mg L^{-1}, (5) MS barotne ar zeatīnu 1,0 mg L^{-1}, (6) MS barotne ar BAP 0,5 mg L^{-1}, un (7) MS barotne ar BAP 1,0 mg L^{-1}. Barotne sagatavota un autoklavēta pēc iniciācijas etapā aprakstītās procedūras un katra klona katram variantam izmantoti 24 mikrospraudeņi. Pēc 30 dienu ilgas kultivēšanas katram reģenerētam augam noteikts galvenā dzinuma un sāndzinumu garums, sāndzinumu skaits (garāki par 0,5 cm), kā arī pavairošanas koeficients. Kopumā nomērīti 2016 augi, pēc kuriem aprēķināts kopējais pavairošanas koeficients katram klonam, kā arī vitrificēto augu proporcija.

Ģenētiskie parametri āra bērza veģetatīvi pavairotu klonu augšanas un stumbra kvalitātes pazīmēm tika vērtēti zema sākotnējā biezuma plantācijā, kas atrodas Latvijas centrālajā daļā (57°32′ N, 24°44′ E); ierīkota 1972. gadā bijušajā lauksaimniecības zemē ar mezotrofu smilšmāla augsni (atbilst vērim). Gadu pēc potēšanas 22 bērza pluskoku kloni no Latvijas centrālās daļas (56°37′–57°28′ N, 24°50′–26°24′ E) tika iestādīti 5 × 5 m attālumā (400 koki ha^{-1}); 13–56 rameti no klona. Sākotnēji plantācija tika paredzēta kā sēklu plantācija, bet drīz pēc tam tika pamesta, tāpēc nekāda apsaimniekošana, izņemot agrotehnisko kopšanu, netika veikta. Plantācijas platība bija 1,8 ha (720 stādvietas). 40 gadu vecumā katram kokam tika mērīts: (1) d, (2) h, (3) zemākā zaļā zara augstums (h_{zz}, m), (4) zl, (5) vainaga vidējā projekcija (vvp, m), novērtēta (6) pad, (7) dg un (8) stumbra plaisu sastopamība (ir/nav), kā arī 6 ballu skalā vērtēts (9) stumbra taisnums un (10) zarainība.

4.2.2. Datu statistiskā apstrāde

Āra bērza ***in vitro*** pētījumā tika izmantots Hī kvadrāta (χ^2) tests, lai novērtētu iniciēto dzinumu skaita atšķirības atkarībā no eksplanta ievākšanas laika un donorkoka vecuma. Lai novērtētu mērīto pazīmju (galvenā dzinuma garuma, sāndzinumu garuma un skaita, pavairošanas koeficientu un vitrificēto augu proporcijas) atšķirības starp kloniem un klonu grupām, veikta dispersijas analīze (ANOVA) un Tjūkija (*Tukey's HSD*) tests. Saistību starp galvenā dzinuma garumu un sānu dzinumu skaitu noteikšanai, kā arī, lai novērtētu galvenā dzinuma garuma, sānu dzinumu skaita, sānu dzinumu garuma un kopējā pavairošanas koeficienta ietekmi uz vitrificēto dzinumu skaitu, tika izmantoti vispārējie lineārie modeļi ar Puasona sadalījumu. Attiecību starp galvenā dzinuma garumu un sānu dzinumu garumu novērtēšanai tika izmantots lineārais modelis. Visi aprēķini veikti R 3.5.1 (R Core Team 2018) ar būtiskuma līmeni α = 0,05.

Zemas biezības āra bērza klonu plantācijā katram kokam tika aprēķināts V, izmantojot I. Liepas formulu (Liepa 1996). Katram kokam iegūtais sortimentu rezultāts tika aprēķināts, izmantojot R. Ozoliņa izstrādāto modeli (Ozolins 2002) ar J. Doņa modifikācijām (Donis et al. 2024). Koksnes defekti un stumbra kvalitātes rādītāji tika ņemti vērā, nosakot stumbra sortimentu struktūru (saskaņā ar mežsaimniecības praksi Latvijā). Pamatojoties uz aprēķināto sortimentu apjomu, katra paraugkoka stumbra koksnes monetārā vērtība (MV) tika aprēķināta kā integrējošs parametrs. Sortimentu cenas pēc tievgaļa diametra, kuras izmantotas MV aprēķinā, bija 20, 26, 45, 60 un 70 EUR m^{-3} attiecīgi malkai (< 13 cm), papīrmalkai (< 13 cm), zāģbaļķiem 14–18 cm, zāģbaļķiem 19–25 cm un zāģbaļķiem > 26 cm.

Vērtētajām pazīmēm tika aprēķināti individuālie iedzimstamības koeficienti H^2 plašā nozīmē (Falconer & Mackay 1996):

$$H^2 = \frac{\sigma_G^2}{\sigma_P^2} \ , \tag{4.11.}$$

kur:
σ_G^2 – genotipiskā dispersija;
σ_P^2 – fenotipiskā dispersija, kas sastāv no genotipiskās un vides dispersijas komponentēm.

Selekcijas efekts tika novērtēts pēc formulas (Falconer & Mackay 1996):

$$R = S \cdot H^2 \ , \tag{4.12.}$$

kur:
S – selekcijas starpība, kas ir izvēlēto klonu vidējais fenotipiskais vērtējums, izteikts kā novirze no izmēģinājuma vidējā.

Katram mainīgajam tika novērtēta trīs labāko klonu pārākuma pakāpe pret izmēģinājuma vidējo. Pētāmajām pazīmēm tika aprēķinātas fenotipiskās klonu vidējo vērtību Pīrsona korelācijas un ģenētiskās korelācijas (Falconer & Mackay 1996). Ģenētiskās korelācijas starp pazīmēm tika aprēķinātas, izmantojot 4.8. formulu, un to standartkļūdas tika iegūtas ar delta metodi (Lynch & Walsh 1998). Genotipiskais variācijas koeficients (CV_g) tika aprēķināts pēc formulas:

$$CV_g = \sqrt{\sigma_G^2} \cdot \frac{100}{\bar{x}} \ , \tag{4.13.}$$

kur:
$\bar{x}$ – fenotipiskā vidējā vērtība.

Genotipiskās un vides dispersijas attiecīgās komponentes tika iegūtas, izmantojot modeli:

$$y_{ij} = \mu + c_i + \varepsilon_{ij} \ , \tag{4.14.}$$

kur:
y_{ij} – katras pazīmes novērojums i-jam kokam;
μ – vidējā vērtība;
c_i – randoma klona efekts.

Kvantitatīvajiem mainīgajiem (d, h) tika izmantots lineārs jaukta tipa modelis. Binomiālajiem mainīgajiem (saglabāšanās, stumbra plaisas) tika pielāgots vispārināts lineārs jaukta tipa modelis, izmantojot binomiālo atlikuma sadalījumu un *logit* saistības funkciju. Abiem modeļiem tika izmantota R pakotne "lme4" (Bates et al. 2014). Stumbra taisnumam un zarojumam tika pielietota ordinālā loģistiskā regresija (Long 1997), izmantojot R pakotni "ordinal" (Christensen 2015). Saistības funkcijas vides dispersija tika noteikta kā $\pi^2/3$ jeb 3,29. Ģenētiskā kovariācija $\sigma_{G(x,y)}$ starp jebkurām divām pazīmem x un y tika novērtēta, izmantojot funkciju *varcomp* pakotnē "lme4". Datu analīze tika veikta programmā R, v. 3.3. (R Development Core Team 2016).

4.3. Finansiālais ieguvums no selekcionēta āra bērza izmantošanas (VI un VII publikācija)

4.3.1. Datu ievākšanas metodika

Finansiālais ieguvums no āra bērza selekcijas Latvijā tika vērtēts, ņemot vērā visu selekcijas populāciju, kuras materiāls iedalīts divās grupās:

1) 921 atlasīts koks, kam ir uzmērīti brīvapputes pēcnācēju pārbaužu stādījumi (4.1.1. apakšnodaļa);
2) pēcnācēji, kas līdz analīzes veikšanai vēl nebija sasnieguši uzmērīšanai un novērtēšanai piemērotu vecumu, no 360 kontrolētiem krustojumiem no 100 nepārbaudītiem (fenotipiski atlasītiem) kloniem.

Lielākajai daļai materiāla (pirmajai grupai) plānots izveidot divas selekcijas populācijas, balstoties uz noteiktajiem provenienču reģioniem (Austrumu un Rietumu), izmantojot kopumā 150 kokus – fenotipiski atlasītus pēcnācējus no produktīvākajām un kvalitatīvākajām brīvapputes ģimenēm, jo mātes koki vairs nav pieejami. Starp selekcijas populācijas indivīdiem veicama dubultpāru krustošana. Turpmākajām darbībām tika salīdzinātas trīs dažādas alternatīvas: (1) fenotipiskā (FEN) atlase labāko indivīdu atlasīšanai ģimenes ietvaros, (2) klonālā (VEG – veģetatīvā) testēšana, kur tiek veikta kandidātu atlase ģimenes ietvaros un to veģetatīvā pavairošana, kam seko klonālo pēcnācēju izmēģinājumu izveide un divu labāko kandidātu atlase katrai ģimenei, (3) pēcnācēju (GEN – ģeneratīvā) testēšana, kur tiek veikta kandidātu fenotipiskā atlase ģimenes ietvaros un to ziedēšanas stimulēšana, lai iegūtu sēklas, kam seko brīvapputes pēcnācēju izmēģinājumu ierīkošana un divu labāko kandidātu atlase katrai ģimenei.

Āra bērza selekcijas ietekme uz ienākumiem pirmajā krājas kopšanas cirtē tika vērtēta izmēģinājumā Rembatē (stādījums aprakstīts 4.1.1. apakšnodaļā). Tika novērtētas tikai tās ģimenes, kas bija pārstāvētas vismaz trīs atkārtojumos (kopā 524). 2014. gadā, kad kokiem bija 14 gadi, katram dzīvajam kokam pirms ciršanas tika uzmērīts d un h, un pēc ciršanas tika atzīmēti izņemtie koki. Kopumā līdz ciršanai bija saglabājušies 84% sākotnēji stādīto koku; katrā atkārtojumā bija no 24 līdz 32 kokiem. Kopšana tika veikta ar motorzāģiem, lai mazinātu bojājumus atlikušajiem kokiem; koksne tika transportēta ar forvarderu. Tika veikta retināšana no apakšas, samazinot šķērslaukumu no 14,62 līdz 7,52 m^2 ha^{-1}.

4.3.2. Datu statistiskā apstrāde

Finansiālā ieguvuma no āra bērza selekcijas analīzei plānotās darbības, kas pētījumā nav tieši analizētas, bet kuru izmaksas ir iekļautas katrai no alternatīvām:

1) pirmajai selekcijas materiāla grupai pirms otrā selekcijas cikla sākuma: daļas pārbaužu stādījumu atkārtota mērīšana, individuālo koku atlase izcilās ģimenēs;
2) otrajai selekcijas materiāla grupai: pēcnācēju pārbaužu stādījumu kopšanas darbi, mērījumi, individuālo koku atlase izcilās ģimenēs.

Alternatīvu salīdzinājums ir balstīts uz diferenciālu pieeju, t.i., tiek ņemti vērā tikai tie ienākumu un izmaksu posteņi, kas atšķiras starp divām atjaunošanas metodēm – dabisko atjaunošanu un selekcionēta materiāla stādīšanu (Ahtikoski 2000). Analīzē diferenciālās izmaksas ir balstītas uz 2010. gada cenām un ietver:

1) koku selekcijas darbību izmaksas, iegūtas no praktiskās pieredzes LVMI "Silava" atbilstoši darbībām, kas nepieciešamas katras alternatīvas (FEN, VEG, GEN) īstenošanai;
2) sēklu plantāciju izveides un uzturēšanas izmaksas, iegūtas no AS "Latvijas valsts meži", kam pieder bērza sēklu plantācijas Latvijā;
3) atjaunošanas izmaksas: stādi, augsnes sagatavošana, stādīšana un divas papildu agrotehniskās kopšanas reizes, informācija no AS "Latvijas valsts meži" iepirkumu rezultātiem.

Diferenciālais ieguvums tika attēlots kā papildu pieaugums un īsāks rotācijas laiks (ciršana pēc mērķa caurmēra, ja iespējams) mežaudzēm, kas atjaunotas ar selekcionētu reproduktīvo materiālu. Selekcijas efekta vērtības katrai no alternatīvām, selekcijas darbu apjoms un laiks daļēji tika novērtēti, izmantojot programmu "Breeding Cycle Analyser" (Danusevicius & Lindgren 2002a,b), ar mērķi maksimizēt selekcijas efektu vienā laika vienībā (4.1. tab.). Selekcionētas mežaudzes selekcijas efekts, izteikts salīdzinājumā ar neselekcionētas mežaudzes caurmēra un augstuma pieaugumu, tika aprēķināts, izmantojot nemainīga proporcionālā uzlabojuma pieeju (Ahtikoski 2000).

Pamatojoties uz P. Zālīša un J. Jansona (2009) ieteikumiem, tika izvēlēti augšanas modeļi tradicionālajām (liela sākotnējā biezuma, ar novēlotām, zemas intensitātes kopšanām) un mērķtiecīgām (maksimāla vidējā caurmēra un kopējās krājas sasniegšana galvenās cirtes vecumā; raksturojamas ar zemu sākotnējo biezumu) mežkopības sistēmām un kopšanas režīmiem, kas ir vienādi gan dabiski atjaunotai, gan stādītai (selekcionētai) mežaudzei. Tika aprēķināta sortimentu struktūra krājas kopšanā un galvenajā cirtē; sortimentu cenas par 2006.–2010. gadu tika iegūtas no Centrālās statistikas pārvaldes un AS "Latvijas valsts meži". Sortimenti tika noteikti šādi: pirmās šķiras zāģbaļķi (tievgaļa diametrs pārsniedz 25,9 cm, garums 4,9 m), otrās šķiras zāģbaļķi (18–25,9 cm, 4,9 m), trešās šķiras zāģbaļķi (14–17,9 cm, 4,9 m), papīrmalka (6–13,9 cm, 3 m), malka (3,0–5,9 cm, 2 m).

Sēklu plantācijas platība tika noteikta, balstoties uz minimālo klonu skaitu, lai nodrošinātu ģenētisko daudzveidību, kā arī prognozēto sēklu nepieciešamību, pieņemot, ka visi bērzu meži auglīgās augsnēs tiks nocirsti atjaunošanas cirtē un atjaunoti ar uzlabotu materiālu. Izvēlētais klonu komplekts paredzēts 24 gadu izmantošanai, jo neviena no alternatīvām nevar ātrāk pāriet uz jaunu augstākas ģenētiskās kvalitātes klonu komplektu.

4.1. tabula

Koku selekcijas darbu apjoms un laiks, balstoties uz analīzē izmantotajām dažādajām alternatīvām

Selekcijas materiāla apjoms un dažādu posmu ilgums		Selekcijas alternatīva		
		FEN	VEG	GEN
Aktivitātes ilgums, gadi	Rekombinācija	6	6	6
	Stādu audzēšana	2	4	2
	Pēcnācēju pārbaudes	25	12	14
	Ziedēšanas stimulēšana, sēklu ieguve	-	-	5
	Stādu audzēšana	-	-	2
	Kandidātu pārbaudes	-	-	12
	Kopējais laiks	33	22	41
Selekcijas materiāla apjoms, gab.	Ģimeņu skaits	150	150	150
	Koku skaits ģimenē	300	100	120
	Kandidātu skaits	-	40	25
	Kandidāta pēcnācēju/rametu skaits	-	40	35

Lai nodrošinātu objektīvu salīdzinājumu starp atjaunošanas metodēm un selekcijas alternatīvām, tika aprēķināta tīrā tagadnes vērtība (TTV) ar procentu likmi 3%. Lai **novērtētu selekcijas ietekmi uz ienākumiem pirmajā krājas kopšanā āra bērza plantācijā**, tika aprēķināts stumbra tilpums un sortimentu iznākums no katra nocirstā koka. Lai parādītu tirgus svārstību ietekmi uz ienākumiem, tika izmantotas zemas (2014. gada) un augstas (2018. gada) koksnes cenas (4.2. tab.).

4.2. tabula

Sortimentu klases pēc tievgaļa diametra un monetārā vērtība pie zemām un augstām koksnes cenām

Apaļkoku sortiments	Garums, m	Tievgaļa diametrs, cm	Cena, EUR m^{-3}		Nocirstā apjoma proporcija, %
			zema (2014. g.)	augsta (2018. g.)	
Zāģbaļķi	3,0	12,0	47	56	1,3
Taras kluči	3,0	10,0	37	50	14,3
Papīrmalka	3,0	6,0	35	54	59,3
Malka	3,0	3,0	22,5	30	25,1

Ģenētiskie parametri tika aprēķināti, izmantojot trīs lielākos (pēc d) kokus katrai ģimenei un atkārtojumam. Lai novērtētu pazīmju (d, stumbra vērtība un sortimentu īpatsvars) iedzimstamību, dispersijas un kovariances komponentes (σ) tika noteiktas, izmantojot jaukta tipa modeļa analīzi ar ierobežotās maksimālās iespējamības pieeju programmā SAS (Versija 9, SAS Institute, Cary, NC, USA; Littel et al. 2006) saskaņā ar 4.3. formulu. Ņemot vērā izmēģinājuma izlases bloku dizainu, iedzimstamības koeficients (h^2) tika novērtēts pēc 4.6. formulas. Aditīvās ģenētiskās variācijas koeficients (CV_a), kas raksturo kvantitatīvo īpašību ģenētisko mainību (Falconer & Mackay 1996), tika aprēķināts pēc 4.7. formulas. Selekcijas efekts (GG) tika aprēķināts, izmantojot 10% atlases intensitāti (i; Falconer & Mackay 1996). Neto koksnes vērtība (NWV), tīrā tagadnes vērtība (TTV) un iekšējā atdeves likme (IRR) tika aprēķinātas kā ekonomiskie rādītāji nocirstajai koksnei. Lai novērtētu selekcijas ekonomisko efektu, rādītāji tika aprēķināti gan izmēģinājuma vidējām vērtībām, gan labākajām un sliktākajām 10% ģimenēm, kas ranžētas pēc d selekcijas efekta.

Katram kokam ienākumi no zāģbaļķiem tika aprēķināti kā:

$$NWV = I_{income} - H_{costs} \ , \tag{4.15.}$$

kur:

I_{income} – ienākumi no ciršanas;

H_{costs} – ciršanas izmaksas (Centrālā statistikas pārvalde 2016).

Ienākumi un izmaksas tika iekļauti analīzē, aprēķinot tīro tagadnes vērtību kā nākotnes sagaidāmo neto naudas plūsmas diskontēto vērtību:

$$NPV = \frac{NWV - E_{costs}}{(1+r)^n} \ , \tag{4.16.}$$

kur:

E_{costs} –ierīkošanas izmaksas (zemas un augstas cenas);

r – diskonta likme (3% un 5%);

n – gadu skaits (14).

Ierīkošanas izmaksas tika iegūtas no Centrālās statistikas pārvaldes.

Lai novērtētu potenciālās investīcijas rentabilitāti, iekšējā atdeves likme (IRR) tika aprēķināta, izmantojot formulu:

$$NPV = \frac{NWV - E_{costs}}{(1+r)^n} \ , \tag{4.17.}$$

kur:

r_a – zemākā diskonta likme (3%);

r_b – augstākā diskonta likme (5%);

NPV_a – NPV pie r_a;

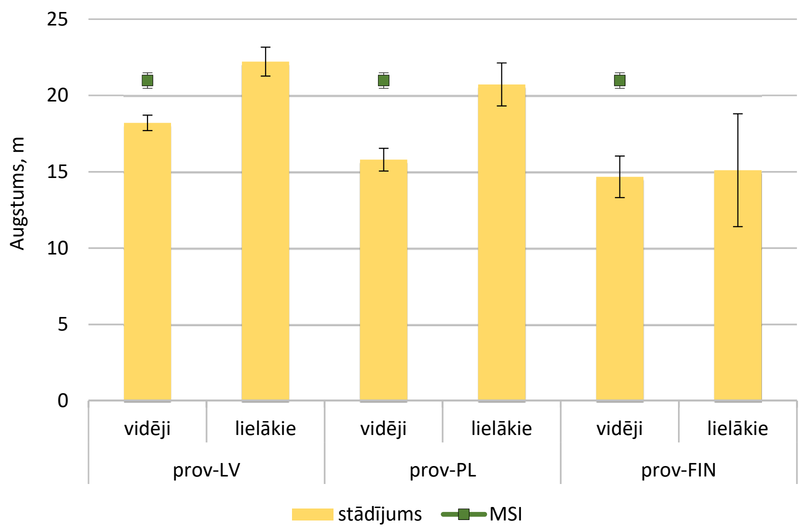
NPV_b – NPV pie r_b diskonta likmes.

5. REZULTĀTI UN DISKUSIJA

5.1. Selekcijas stādījumu novērtējums (I, II un III publikācija)

Provenienču pārbaudēs izcelsme bija nozīmīgs faktors, kas ietekmēja koku saglabāšanos. Noteiktām proveniencēm saglabājušos koku īpatsvars bija robežās no 11% līdz 63%; viszemākā saglabāšanās bija Somijas izcelsmei (vidēji 16%), augstāka – bērziem no Polijas (42%), bet augstākā – vietējas izcelsmes bērziem (50%). Provenience arī bija nozīmīgs faktors, kas ietekmēja h (5.1. att.), d un līdz ar to arī V, tomēr padēlu sastopamība neuzrādīja būtiskas atšķirības starp proveniencēm. Korelācija starp provenienču vidējo augstumu piecu gadu vecumā (agrākie mērījumi) un 37 gadu vecumā bija statistiski nozīmīga (r = 0,78).

Provenienču vidējā krāja svārstījās no 24 m^3 ha^{-1} līdz 405 m^3 ha^{-1} un bija vidēji 204 m^3 ha^{-1}. Lielākā audzes krāja bija vietējam (Latvijas) bērzam, mazāka bērzam no Polijas un vismazākā – no Somijas. Proveniences ar vislabākajiem rādītājiem, vadoties pēc h un d (5.1. tab., 5.2. att.), bija no Latvijas, tomēr tām bija sastopama augsta pazīmju variācija, un atsevišķu Polijas provenienču bērzu atlase varētu sasniegt līdzīgus rezultātus kā vietējās proveniences. Tādējādi materiālu, kas atrodas līdzīgā selekcijas cikla posmā (sēklu plantāciju pēcnācēji vai kloni), varētu papildus pārbaudīt, lai noskaidrotu genotipus ar augstākiem rezultātiem esošajos (Latvijā) un nedaudz siltākos (šobrīd Polijā) apstākļos. Rezultāti bērziem no Somijas bija ievērojami zemāki, un tikai pārāko genotipu (piemēram, ļoti ātraudzīgo klonu) pārbaudes varētu būt pamatotas.



5.1. attēls. **Augstums provenienču grupām izmēģinājumos salīdzinājumā ar vidējiem rādītājiem bērzu audzēs Latvijā**

(± 95% ticamības intervāls; avots: MSI)

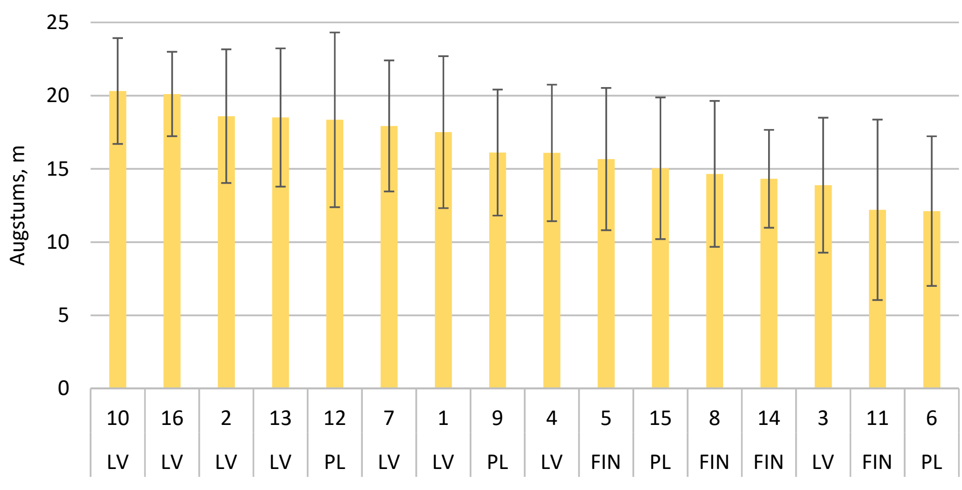
5.1. tabula

Dažādu valstu provenienču grupu meža inventarizācijas parametri

Vidējie – uzmērītie meža inventarizācijas parametri; augstākie – parametri augstākajiem kokiem, kas atbilst noteiktajam mežaudzes biezumam (521 koks uz hektāru)

Provenienču grupa	Vidējie			Augstākie		
	biezums, koki ha^{-1}	augstums, m	caurmērs, cm	biezums, koki ha^{-1}	augstums, m	caurmērs, cm
Latvija (LV)	2064	17,9	13,0	521	22,2	17,0
Somija (FIN)	669	14,2	9,5	521	15,1	10,0
Polija (PL)	1691	15,4	10,0	521	20,7	15,0

Lai gan uzmērīšanas vecumā konstatētās h un d atšķirības šķietami bija nelielas, tomēr tās ievērojami ietekmē prognozējamo mērķa caurmēra sasniegšanas vecumu (5.2. tab.). Zemāka biezuma audzē (521 koks ha^{-1}), pieņemot labāko augšanu un labus apstākļus āra bērzam Latvijā (27 gadi, augstākie), šo caurmēru var sasniegt jau 48 gadu vecumā. Šādi rezultāti ir tuvu uzmērītajam zema biezuma bērzu klonu stādījumā Latvijā (**IV**), kur vidējais caurmērs 40 gadu vecumā pārsniedza 28 cm, tomēr biezums bija mazāks (sākotnēji: 400 koki ha^{-1}). Polijas provenienes mērķa caurmēru sasniegtu 57 gadu vecumā, un tām būtu līdzīga krāja, kā Latvijas proveniencēm 10 gadus agrāk (attiecīgi 272 m^3 ha^{-1} un 263 m^3 ha^{-1}), izmantojot līdzīgus modeļa ievades parametrus. Bērzi no Somijas nevienā no analizēto parametru kombinācijām nevar sasniegt mērķa caurmēru agrāk nekā 100 gadu vecumā, kas ir ievērojami vēlāk par likumā noteikto ciršanas vecumu Latvijā (71 gads). Esošajos apstākļos mērķa caurmēru nevar sasniegt pirms ciršanas vecuma. Pieņemot, ka ir labāki augšanas apstākļi, ar uzmērītajiem ievades datiem prognozējams, ka 67 gadu



5.2. attēls. **Provenienču vidējais augstums izmēģinājumā**

Latvijas provenienes Nr. atbilst 2.1. attēlā minētajiem numuriem vecumā paredzēto mērķa caurmēru var sasniegt tikai vietējās proveniences, ja tiek veikta kopšanas cirte.

Modelētajai krājas kopšanas cirtei bija būtiska ietekme, palielinot caurmēra pieaugumu (5.3. att.). Tomēr ietekme varētu būt pārvērtēta augstas biezības dēļ, kas samazina zaļā vainaga garumu audzē. Proveniences no Polijas un Somijas nesasniedza minimālo šķērslaukumu, kas nepieciešams, lai veiktu krājas kopšanas cirti, tāpēc tā netika plānota.

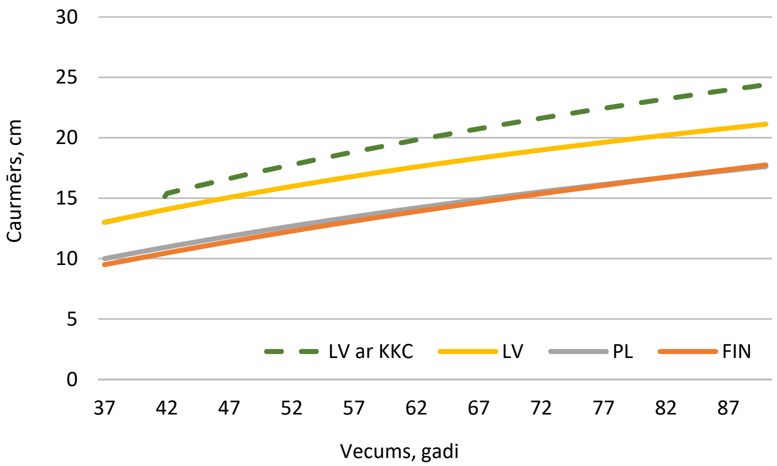
5.2. tabula

Vecums, kad tiks sasniegts mērķa caurmērs (25 cm) dažādām provenienču grupām

Provenienču grupas	Dati	Vecums	
		27	37
Latvija (LV)	Visi koki	91	127
Latvija (LV)	Visi koki *	67	94
Somija (FIN)	Visi koki	111	157
Polija (PL)	Visi koki	127	167
Latvija (LV)	Augstākie koki	48	67
Somija (FIN)	Augstākie koki	100	143
Polija (PL)	Augstākie koki	57	81

* veikta krājas kopšanas cirte; citi saīsinājumi saskaņā ar 2.1. tabulu.

Straujākas koku augšanas dēļ masas centrs Latvijas proveniencēm bija augstāks, jo tā relatīvais augstums attiecībā pret koku augstumu bija diezgan stabils. Tas var radīt lielāku vēja postījumu risku Latvijas izcelsmes bērzam, ņemot vērā līdzīgus rotācijas periodus proveniencēm no dažādām valstīm (izņemot modelētu augšanu bērzam labos augšanas apstākļos). Lai sīkāk novērtētu šo ietekmi, jāveic papildu pētījumi.



5.3. attēls. **Modelētā krūšaugstuma caurmēra attīstība dažādām proveniencēm**
Pārtraukta līnija – veikta krājas kopšanas cirte (KKC); citi saīsinājumi saskaņā ar 2.1. tabulu

Vērtētajās **brīvapputes āra bērza pēcnācēju pārbaudēs** saglabāšanās bija augsta abās uzmērīšanas reizēs stādījumā Rembatē (>80%) un Ukros (>90%), bet zemāka – Taurenē (>60%), ko, visticamāk, ietekmēja nepietiekamais mitrums sausajā vasarā pēc iestādīšanas, jo stādījuma vietā Taurenē bija smalkas tekstūras augsne (Sutinen et al. 2002). Pirmos gadus pēc stādīšanas tika veikta nepieciešamā agrotehniskā kopšana, lai novērstu turpmāku koku mirstību, ko izraisa apauguma konkurence (Ferm et al. 1994, Hynynen et al. 2010). Desmit gadu vecumā vidējais h Taurenē un Ukros bija vienāds (6,7 m), un citas uzmērītās pazīmes, kā arī koku īpatsvars ar stumbra defektiem bija līdzīgi. Rembatē h bija zemāks (5,5 m), un koku īpatsvars ar pad bija apmēram trīs reizes zemāks nekā abos pārējos stādījumos. Vidējais h 14 gadu vecumā bija nedaudz augstāks Ukros, salīdzinot ar Taureni (attiecīgi 12,3 m un 11,5 m), tomēr citas pazīmes bija līdzīgas. Rembatē koku īpatsvars ar pad bija palielinājies un bija augsts (aptuveni 60%), līdzīgi kā abos pārējos stādījumos. Visos stādījumos koku īpatsvars ar pad un zg bija diezgan augsts (>50%), bet tikai 6–12% kokiem bija dg, ko šķietami neietekmēja pētīto stādījumu atšķirīgā kontinentalitāte (Laiviņš & Melecis 2003). *A. Viherä-Aarnio* un *P. Velling* (1999) ziņoja par 13% koku ar pad. Līdzīgi kā *A. Viherä-Aarnio* un *P. Velling* (1999) pētījumā, lielākajai daļai koku bija vismaz viegla stumbra līkumainība.

Baltijas jūras reģionā bieži sastopamo meža koku sugu – parastās priedes un parastās egles – augšanas un kvalitātes iedzimstamības rādītāji svārstās no 0,05 līdz 0,25 (Velling 1982, Haapanen et al. 1997, Hannrup et al. 1998, Olsson & Ericsson 2002, Jansons et al. 2006). Šajā pētījumā novērtētā iedzimstamība šaurā nozīmē (h^2) bija atšķirīga vērtētajām āra bērza pazīmēm, esot augstākai augšanas pazīmēm nekā stumbra kvalitātei (5.3. tab.), līdzīgi kā agrākā pētījumā Latvijā (Zeltiņš et al. 2018). Augstākā h^2 vērtība novērtēta h, d, V (0,30–0,64), izņemot zemo vērtību caurmēram (0,12) Rembatē. Tāpat augsta h^2 bija StStr (0,35–0,45), bet stumbra kvalitātei zd un dg bija kopumā zemākas vērtības (0,04–0,35). zl iedzimstamība ievērojami svārstījās (0,25–0,83) atkarībā no stādījuma vietas un gada, bet zg uzrādīja kopumā zemākās vērtības (0,02–0,12). Salīdzinoši augsts CV_a bija aprēķināts V, kas svārstījās no 25,3% Rembatē līdz 40,3% Ukros. Visos izmēģinājumos zaru leņķis uzrādīja zemu ģenētiskās variācijas pakāpi (3,7–6,4%; 5.4. tab.). Aprēķinātais r_G starp augšanas pazīmēm visos stādījumos bija līdzīgs un augsts (0,90–0,99; 5.5. tab.), taču bija galvenokārt zems līdz viduvējs starp augšanas un stumbra kvalitātes pazīmēm ($–0,10 < r_G < 0,40$). Zaru leņķim bija vidēja līdz augsta negatīva korelācija ar stumbra taisnumu un kvalitāti ($–0,67 < r_G < –0,45$), kas savstarpēji cieši korelēja (0,83–0,84). Tika konstatētas diezgan augstas pozitīvas korelācijas starp pad un dg (0,60–0,74). Tomēr stumbra kvalitātes rādītāji parasti bija ar zemu līdz vidēju ģenētisko korelāciju savā starpā (5.5. tab.).

5.3. tabula

Iedzimstamības koeficienti šaurā nozīmē (h^2) un B-tipa ģenētiskās korelācijas (r_B) ar standartkļūdām (SE)

(visi r_B ir būtiski $p < 0,01$)

Stādījums	$h^2 \pm SE$								$r_B \pm SE$
	Taurene		Ukri		Rembate		Ukri un Taurene kopā		
Vecums, gadi	10	14	10	14	10	14	10	14	14
h	0,37 ± 0,03	0,45 ± 0,04	0,47 ± 0,04	0,64 ± 0,04	0,30 ± 0,07	na	0,37 ± 0,03	0,52 ± 0,03	0,94 ± 0,02
d	na	0,45 ± 0,04	na	0,52 ± 0,03	na	0,12 ± 0,02	na	0,42 ± 0,03	0,89 ± 0,03
V	na	0,41 ± 0,03	na	0,53 ± 0,03	na	na	na	0,41 ± 0,03	0,97 ± 0,03
zd	0,24 ± 0,03	na	0,20 ± 0,03	na	0,10 ± 0,03	na	0,17 ± 0,02	na	na
zl	0,33 ± 0,03	0,83 ± 0,19	0,27 ± 0,03	0,61 ± 0,07	0,30 ± 0,03	0,31 ± 0,03	0,25 ± 0,02	0,37 ± 0,1	0,78 ± 0,12
pad	0,07 ± 0,02	0,08 ± 0,02	0,06 ± 0,02	0,05 ± 0,01	0,04 ± 0,03	0,07 ± 0,02	0,07 ± na	0,06 ± 0,02	na
dg	0,29 ± 0,07	0,05 ± 0,06	0,04 ± 0,03	0,19 ± 0,04	0,08 ± 0,04	0,27 ± 0,05	0,1 ± na	na	na
zg	0,09 ± 0,03	0,04 ± 0,02	0,06 ± 0,03	0,05 ± 0,01	0,12 ± 0,03	0,06 ± 0,02	0,05 ± 0,04	0,02 ± 0,01	na
Stumbra taisnums	0,45 ± 0,05	0,35 ± 0,05	0,41 ± 0,05	0,45 ± 0,05	0,32 ± 0,05	0,39 ± 0,05	0,40 ± 0,06	0,4 ± 0,05	0,97 ± 0,05
Stumbra kvalitāte	0,15 ± 0,03	0,35 ± 0,05	0,11 ± 0,03	0,21 ± 0,03	0,14 ± 0,03	0,26 ± 0,04	0,10 ± 0,03	0,23 ± 0,03	0,89 ± 0,08

Saīsinājumi: h – augstums, d – krūšaugstuma caurmērs, V – stumbra tilpums, pad – padēli, dg – dubultgalotnes, zg – zaudētas galotnes, zd – zara diametrs, zl – zara leņķis, na – nav datu.

5.4. tabula

Kvantitatīvo pazīmju aditīvās ģenētiskās variācijas koeficients (CV_a) pētītajos brīvapputes āra bērza pēcnācēju pārbaužu stādījumos 10 un 14 gadu vecumā

Vecums (gadi)	Stādījums					
	Taurene		Ukri		Rembate	
	10	14	10	14	10	14
h	10,4	8,5	11,4	5,5	7,5	na
d	na	18,7	na	10,3	na	4,7
V	na	32,5	na	20,1	na	na
zd	16,2	na	12,6	na	4,3	na
zl	4,4	na	4,7	na	3,2	1,9

Saīsinājumi: h – augstums, d – krūšaugstuma caurmērs, V – stumbra tilpums, zd – zaru diametrs, zl – zaru leņķis, na – nav datu.

Ņemot vērā, ka gēni, kas kontrolē katru augšanas pazīmi, var būt cieši savstarpēji saistīti (Searle 1961), atlase var tikt balstīta uz koku augstumu, kas uzrādīja visaugstāko h^2. Agrākos pētījumos norādītās h^2 un iedzimstamības plašā nozīmē (H^2) vērtības atbilstošajām āra bērza pazīmēm ir ļoti atšķirīgas – no zemām līdz augstām (Nepveu & Velling 1983, Malcolm & Worrell 2001, Stener & Jansson 2005, Zeltiņš et al. 2018). Norvēģijā h^2 sešus gadu vecām brīvapputes ģimenēm ir diezgan zems, t. i., 0,09 un 0,17 attiecīgi h un d (Skrøppa & Solvin 2019). Šajā pētījumā augstas iedzimstamības koeficientu vērtības un zemā variācija augšanas pazīmēm starp stādījumiem varētu norādīt uz relatīvi homogēniem augšanas apstākļiem bijušajās lauksaimniecības zemēs, kā arī uz pietiekamu stādījuma kopšanu pēc ierīkošanas. Tādējādi ģenētiski noteiktas atšķirības izpaudās labāk, salīdzinot ar meža zemēm (Haapanen 1996, Hannrup et al. 2004). Lai gan h^2 vērtības, kas iegūtas individuālu stādījuma vietu analīzē, parasti ir pārvērtētas un augstākas salīdzinājumā ar kopā vērtētu stādījumu vietu aprēķiniem (Hodge & White 1992, Haapanen 2001, Wu et al. 2008), ģenētiskie parametri Ukros un Taurenē kopā bija līdzīgi rādītājiem, analizējot eksperimentus atsevišķi. Turpretim nepietiekama kopšana, nevienmērīga saglabāšanās un heterogēni augšanas apstākļi samazina iedzimstamības koeficientu un tā precizitāti, samazinot ieguvumus no koku selekcijas (Haapanen 1996, Mäkinen 1996, Talbot 1997, Nummi 1999, Olsson & Ericsson 2002, Koski & Rousi 2005). Tomēr galvenokārt zems h^2 tādiem stumbra defektiem kā pad, dg un zg sakrīt ar agrākiem pētījumu rezultātiem (Stener & Hedenberg 2003, Zeltiņš et al. 2018), kas liecina par relatīvi vāju ģenētisko kontroli un tādu vides faktoru kā sausums, sals vai biotiskie bojājumi dominējošo ietekmi (Malcolm & Worrell 2001, Stener & Hedenberg 2003). Zviedru pētījumā (Stener & Jansson 2005) ziņots par zemām h^2 un H^2 vērtībām (0,09–0,27) stumbra taisnumam vairākos līdz 10 gadus vecu āra bērza klonu un pēcnācēju izmēģinājumos. Stādījumos Latvijā kopējai stumbra kvalitātei bija zemas h^2 vērtības (0,10–0,15), tomēr atsevišķām ar sortimentu iznākumu saistītām kvalitātes pazīmēm – vidējas un augstas (0,21– 0,45). Šie rezultāti kombinācijā ar diezgan vāju ģenētisko korelāciju starp kvalitāti un ātraudzību raksturojošām pazīmēm (5.5. tab.) liecina par būtisku stumbra kvalitātes uzlabošanas iespēju.

5.5. tabula

Ģenētiskās korelācijas (iekavās standartkļūdas) kopā analizētajos Ukru un Taurenes (augšējā diagonālā daļa) un Rembates (apakšējā diagonālā daļa) brīvapputes āra bērza pēcnācēju pārbaužu stādījumos 14 gadu vecumā

Pazīme	d	v	pad	dg	zg	Stumbra taisnums	zl	Stumbra kvalitāte
h	0,92 (0,01)	0,94 (0,01)	0,43 (0,07)	0,23 (0,07)	0,05 (0,09)	–0,10 (0,05)	0,26 (0,06)	0,16 (0,06)
d	-	0,99 (0,00)	0,39 (0,07)	0,20 (0,07)	0,10 (0,09)	–0,06 (0,05)	0,22 (0,06)	0,17 (0,06)
V	na	-	0,39 (0,07)	0,23 (0,07)	0,06 (0,09)	–0,06 (0,05)	0,23 (0,06)	0,17 (0,06)
pad	0,13 (0,13)	na	-	0,60 (0,11)	0,08 (0,20)	–0,29 (0,08)	–0,02 (0,09)	–0,51 (0,07)
dg	–0,10 (0,11)	na	0,74 (0,11)	-	–0,51 (0,11)	0,03 (0,08)	–0,12 (0,09)	–0,16 (0,08)
zg	0,10 (0,13)	na	–0,06 (0,14)	–0,49 (0,11)	-	–0,69 (0,09)	0,52 (0,11)	–0,58 (0,09)
Stumbra taisnums	0,02 (0,09)	na	–0,39 (0,10)	–0,08 (0,09)	–0,71 (0,09)	-	–0,67 (0,05)	0,83 (0,03)
zl	0,00 (0,25)	na	–0,01 (0,10)	0,09 (0,09)	0,28 (0,10)	–0,57 (0,06)	-	–0,45 (0,07)
Stumbra kvalitāte	0,40 (0,24)	na	–0,67 (0,09)	–0,28 (0,08)	–0,62 (0,08)	0,84 (0,04)	–0,48 (0,07)	-

Saīsinājumi: h – augstums, d – krūšaugstuma caurmērs, V – stumbra tilpums, pad – padēli, dg – dubultgalotnes, zg – zaudētas galotnes, zl – zara leņķis, na – nav datu.

Turklāt vidēji stipra negatīva korelācija starp stumbra kvalitāti un stumbra defektiem liecina, ka atlase, kuras pamatā ir vispusīgs stumbra kvalitātes vērtējums, var samazināt stumbra defektu sastopamību, neraugoties uz to zemo iedzimstamību, tādējādi uzlabojot kokmateriālu kvalitāti un palielinot lietkoksnes apjomu (Agestam et al. 1998, Möttönen 2005). Galvenokārt vājas ģenētiskās korelācijas, kas novērotas starp kvalitātes pazīmēm, kā arī starp augšanas un kvalitātes pazīmēm, varētu būt saistītas ar diezgan zemu kvalitātes pazīmju genotipisko dispersiju (Koski & Rousi 2005, Stener & Jansson 2005). Skotijā taisni stumbri bērzam bija saistīti ar lielāku stumbra tilpumu (Malcolm & Worrell 2001), tomēr mūsu pētījumā šāda saistība netika novērota. Līdzīgi kā iepriekšējos pētījumos Zviedrijā un Latvijā (Stener & Jansson 2005, Zeltiņš et al. 2018), zd un zl uzrādīja augstu iedzimstamību. Tomēr ievērojamās negatīvās korelācijas starp zl un stumbra taisnumu rezultātā var palielināties zaru resnums taisnākiem stumbriem, tādējādi samazinot kokmateriālu kvalitāti (Niemistö 1995a). Ātraudzīgiem bērziem raksturīgi nevēlami lielāki zd (Niemistö 1995b, Stener & Jansson 2005), ko rekomendē mazināt ar stādīšanas biezumu ar vismaz 1600 kokiem ha^{-1}, lai veidotos mazāka izmēra zari un uzlabotos koksnes stiprība (Niemistö 1995a, Dunham et al. 1999). Tomēr 40 gadus vecā zema biezuma āra bērza klonu plantācijā Latvijā konstatēts, ka iegūstami augstas kvalitātes finierkluči, pielietojot lielus (5 × 5 m) sākotnējos stādīšanas attālumus (Zeltiņš et al. 2018). Papildus iedzimstamībai, ievērojamais CV_a (20,1–32,5%) liecināja par selekcijas potenciālu uzlabot V. Zemākas CV_a vērtības stumbra kvalitātes pazīmēm salīdzinājumā ar augšanas pazīmēs saskan ar rezultātiem Lietuvā, kur CV_a stumbra taisnumam un zl bija apmēram 13% (Baliuckienė & Baliuckas 2006). Nesenā zema sākotnēja biezuma klonu plantācijas pētījumā (Zeltiņš et al. 2018) aprēķinātais CV_g augstumam bija gandrīz trīs reizes zemāks (3,2%) nekā CV_a pašreizējā pētījumā (vidēji apmēram 8%). To daļēji varētu izskaidrot ar ievērojami atšķirīgajiem sākotnējās stādīšanas attālumiem (5 × 5 m klonu plantācijā un 2 × 2,5 m šī pētījuma stādījumos), jo genotipiskā dispersija var būt lielāka pie mazākiem attālumiem (Franklin 1979, Euler et al. 1992). Tomēr līdzīgs CV_a augstumam konstatēts Zviedrijas ziemeļos (Stener & Jansson 2005). Kopumā augstākas aprēķinātās CV_a vērtības d un h bija līdzīgas Zviedrijas pēcnācēju pārbaudēs iegūtajiem rezultātiem (attiecīgi 14% un 8%; Stener & Jansson 2005).

Attiecībā uz augšanas rādītājiem, augstvērtīgāko 10% ģimeņu izlases GG % vērtības h un d bija 9,6–26,6%, bet V sasniedza 25,3–61,6%. Līdzīgi h^2 vērtībām, GG % vairumā gadījumu bija zemāks stumbra kvalitātes pazīmēm: 8,6–21,2% stumbra taisnumam, 5,5–10,3% stumbra kvalitātei, 6,9–18,2% zd, 1,6–9,1% zl. Aprēķinātie GG % stumbra defektiem (pad un zg ievērojami atšķīrās starp izmēģinājumiem un gadiem, svārstoties no 5,2 līdz 58,3%. Aprēķinātie GG % apstiprināja galvenās tendences, ko iepriekš uzrādīja h^2 un CV_a, sasniedzot augstākās vērtības V (25,3– 61,6%), kamēr viszemākās vērtības uzrādīja stumbra kvalitāte (1,6–21,2%). Šis selekcijas efekts noteikts pret eksperimenta vidējo vērtību, nevis kopējo populāciju, jo trūkst kontrolparauglaukumu ar neselekcionētu materiālu, un tādējādi ieguvumi, salīdzinot ar mežaudzēm, varētu būt lielāki (Malcolm & Worrel 2001). Tomēr genotipu atlasei būtu jāpanāk balanss starp uzlabotu produktivitāti un pietiekamu stumbra kvalitāti, kā arī uzlabotu sniegumu dažādos augšanas apstākļos (Matheson & Cotterill 1990), jo īpaši, ja mērķis ir ražot augstas kvalitātes āra bērza kokmateriālus finiera rūpniecībai (Hynynen et al. 2010). Kā norāda atsevišķu pazīmju selekcijas efekts, CV_a vērtības (5.4. tab.) un galvenokārt vājā r_G starp augšanas un kvalitātes pazīmēm (5.5. tab.), turpmāka indeksa izstrāde vienlaicīgai augšanas un stumbra kvalitātes pazīmju atlasei var būt iespējama.

Pētītās pazīmes uzrādīja zemu G × E mijiedarbību, par ko liecināja spēcīga B-tipa korelācija visām pētītajām pazīmēm ($r_B \geq 0,78$) starp Ukru un Taurenes izmēģinājumiem (5.3. tab.). Iepriekš publicēti pretrunīgi rezultāti: sākot ar spēcīgu korelāciju starp izmēģinājumiem pat diezgan atšķirīgos augšanas apstākļos (Stener & Hedenberg 2003, Stener & Jansson 2005) līdz ievērojamai genotipa un stādījuma vietas mijiedarbībai (Baliuckienė 2009). Tomēr r_B precizitāte var nebūt augsta (Burdon 1977, Haapanen 1996), bieži ir saistīta ar nepiemērotu pēcnācēju pārbaužu eksperimentālo dizainu, kam ir nepietiekams atkārtojumu skaits, neievērojot augšanas apstākļu dažādību (Haapanen 1996). Augstas B-tipa korelācijas ar diezgan zemām standartkļūdām un attiecīgo pazīmju nelielu h^2 variāciju šajā pētījumā liecināja par snieguma stabilitāti dažādās vidēs, kā arī par atbilstošu eksperimenta dizainu.

Vēl viens būtisks jautājums attiecībā uz eksperimenta dizainu ir vienkoku vai vairāku koku (bloku) parceļu izmantošana. Galvenokārt vienkoku parcelēm Ukros un Taurenē bija augstākas aprēķinātās augšanas pazīmju un zl iedzimstamības nekā bloku parcelēm Rembatē (5.3. tab.). Vienkoka parceles daudzos atkārtojumos ļauj statistiski efektīvi novērtēt genotipiskās atšķirības (White et al. 2007), jo pluskoku pēcnācēji ir pārstāvēti iespējami dažādos konkurences un augšanas apstākļos viena izmēģinājuma ietvaros (Haapenen 1992, 1995). Tomēr koku konkurence starp dažādiem genotipiem var pārspīlēt noteikto ģenētisko dispersiju augšanas pazīmēm, izceļot sākotnēji ātraudzīgās ģimenes (Malcolm & Worrell 2001, Vergara et al. 2004, Gould & Marshall 2010). Šajā pētījumā augšanas pazīmes zināmā mērā varētu ietekmēt konkurence vienkoku parceļu izmēģinājumos Ukros un Taurenē, jo aprēķini no bloku parcelēm Rembatē bija nedaudz zemāki. Tomēr vispārīgiem secinājumiem būtu vajadzīgi aprēķini no vairāk izmēģinājumiem.

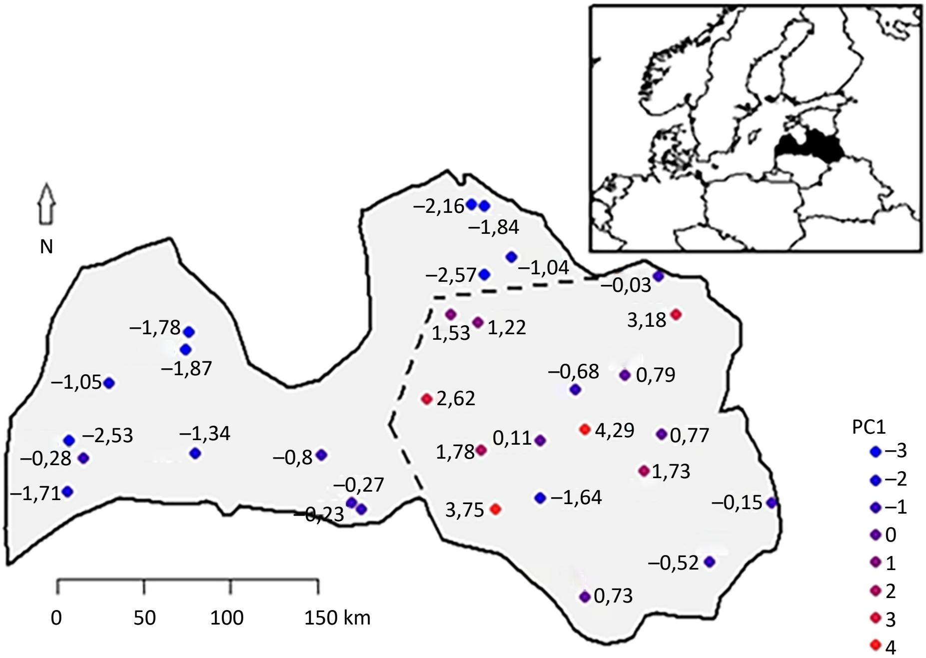
L.-G. Stener un *Ö. Hedenberg* (2003) uzsvēra vispārīgu informācijas trūkumu par āra bērza ģenētiskajām korelācijām dažādos vecumos. Šajā pētījumā ģenētiskās korelācijas 10 un 14 gadu vecumā visos stādījumos galvenokārt bija ciešas (> 0,78), norādot uz precīzu atlasi kā pirmajā, tā otrajā uzmērīšanas reizē, lai gan augsta korelācija starp tik tuviem vecumiem nav īpaši informatīva par ilgtermiņa tendencēm. Tomēr spēcīgas ģenētiskās korelācijas V ir novērotas līdz pat trim desmitgadēm Somijas dienvidos (Hagqvist & Hahl 1998). Augstumam ir ziņots par korelāciju, kas svārstās no 0,75 līdz 0,86 starp vecumu 9 un 26 gadi, korelāciju 0,94 starp vecumu 5 un 10 gadi un 0,84 starp vecumu 11 un 18 gadi (Stener & Hedenberg 2003). *L.-G. Stener* un *G. Jansson* (2005) konstatēja vidējas līdz ciešas ģenētiskās korelācijas (0,60– 0,99) starp dažādiem vecumiem h un kvalitātes pazīmēm.

Fenotipiskais plastiskums un vietējā (ģenētiskā) specializācija ir galvenie faktori, kas ietekmē koku pielāgošanās spējas mainīgajam klimatam, un līdz ar to tie ir būtiski klimata pārmaiņām pielāgotas meža apsaimniekošanas stratēģijas elementi (Aitken & Bemmels 2016, Moran et al. 2017). Analizējot Ukros un Taurenē pārstāvētās ģimenes izcelsmju līmenī, tika novērota izteikta vietējā specializācija, īpaši augšanas pazīmēm. Iekšzemes reģiona bērzi uzrādīja labāku augšanu. Skaidri izteiktais piekrastes-iekšzemes gradients un atšķirīga ģenētiskās kontroles intensitāte atbilda reģiona klimatiskajam zonējumam (Laiviņš & Melecis 2003, Reitalu et al. 2013). Vērtējot provenienienču fenotipisko pazīmju grupēšanos ar PCA analīzi, pirmie divi galvenie komponenti (PC) bija nozīmīgi ($p < 0{,}001$) un aptvēra 57,6% no kopējās pētīto pazīmju variācijas. Pirmais PC bija cieši saistīts ar augšanas pazīmēm, norādot uz reģionālajām atšķirībām produktivitātē. Otrais PC bija saistīts ar kvalitātes pazīmēm un liecina par dažādiem augšanas un kvalitātes variāciju avotiem. Trešais PC aptvēra 19,8% no variācijas un bija saistīts ar stumbra defektiem. Ordinācijas telpā proveniences veidoja vienu grupu, norādot uz nepārtrauktu pazīmju variācijas gradientu. Tomēr pirmais PC ievērojami korelēja ar izcelsmes ģeogrāfisko garumu ($r = 0{,}46$, $p = 0{,}01$), kas liecina par augšanas atšķirībām starp piekrastes un valsts iekšzemes daļām, savukārt otrais PC neuzrādīja korelāciju ($r = 0{,}02$, $p = 0{,}92$).

Korelācijas starp PC un izcelsmes platuma grādiem bija vājas ($|r| < 0{,}22$, $p > 0{,}24$), norādot uz ziemeļu–dienvidu gradienta neesamību. Pamatojoties uz provenienču pirmā PC saistību ar to ģeogrāfisko izvietojumu, iespējams Latvijā izdalīt divus reģionus (5.4. att.). Piekrastes reģions ietvēra valsts rietumu un ziemeļu daļu, savukārt iekšzemes reģions aptvēra centrālo un austrumu daļu (5.4. att.). Iekšzemes reģionā bija ievērojami ($p < 0{,}01$) lielāki h, d un V. Vidējais stumbra taisnums, vispārējā stumbra kvalitāte un zl starp reģioniem neatšķīrās.

Vidēja līdz augsta iedzimstamība ($h^2 > 0{,}20$) tika noteikta pētītajām pazīmēm abos reģionos, izņemot stumbra defektus ($h^2 < 0{,}15$). Tika novērota ģeogrāfiski mainīga pazīmju ģenētiskās kontroles intensitāte: h iedzimstamība iekšzemes reģionā bija vairāk nekā divas reizes augstāka nekā piekrastē (attiecīgi 0,61 ± 0,061 un 0,28 ± 0,037), savukārt V un d iedzimstamība atšķirības sasniedza 31,3–41,4%. Piekrastes reģionā augsta iedzimstamība ($h^2 \geq 0{,}45$) tika novērtēta stumbra taisnumam un zaru leņķim, savukārt šīm pazīmēm iekšzemē tika konstatēta vidēja iedzimstamība ($0{,}26 \leq h^2 \leq 0{,}30$). Turklāt aprēķinātais aditīvais ģenētiskās variācijas koeficients (CV_a) bija nedaudz augstāks (par 0,97–4,06%) iekšzemē, salīdzinot ar piekrasti, kas norāda uz nelielām atšķirībām plastiskumā. Spēja reaģēt uz dabisko atlasi, ko raksturo CV_a, bija aptuveni trīs reizes augstāka V, salīdzinot ar h abos reģionos.

Ģenētiskā specializācija bija izteiktāka kontinentālajā klimatā iekšzemes reģionā, izraisot augstāku heterogenitāti un izskaidrojot augstāku augšanas pazīmju h^2 un CV_a, salīdzinot ar piekrastes reģionu. Augstā iedzimstamība, visticamāk, norādīja uz lielākām atšķirībām starp dažādu provenienču genotipiem, salīdzinot ar vides apstākļu izraisītu variāciju genotipa ietvaros (Griffiths et al. 2000). Aprēķinātā h^2 augšanas pazīmēm bija augstāka iekšzemē un zemāka piekrastes proveniencēs,



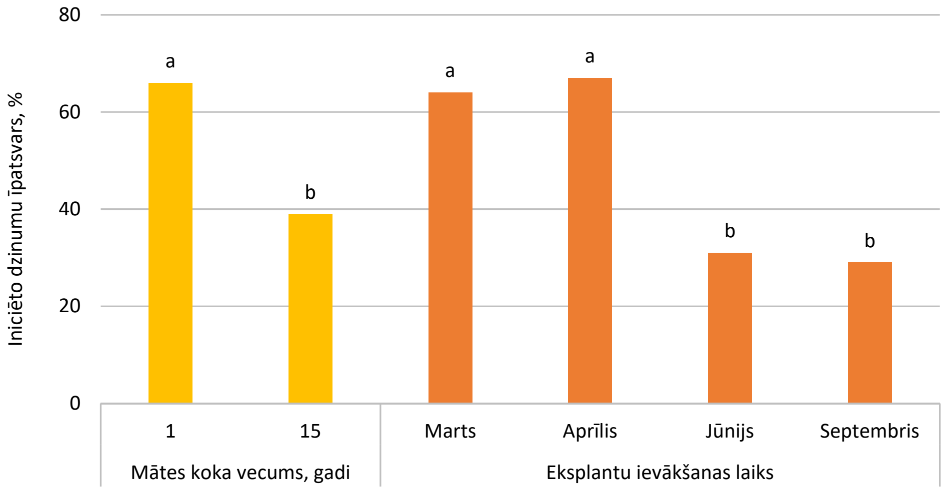
5.4. attēls. **Vērtēto bērza pēcnācēju fenotipisko pazīmju izcelsmju (provenienču) līmeņa pirmā galvenā komponenta (PC1) vērtības**

Pārtrauktā līnija norāda divu izdalīto āra bērza provenienču reģionu robežu – piekrastes (rietumu) un iekšzemes (austrumu) reģionu

salīdzinot ar visu selekcijas populāciju (h^2 = 0,41–0,52), norādot uz labāku atlases efektivitāti iekšzemes reģionā.

5.2. Āra bērza veģetatīvā pavairošana un tās plašākas izmantošanas potenciāls (IV un V publikācija)

Iniciācijas fāze ir viens no būtiskākajiem klonālās mikropavairošanas etapiem, kas būtiski ietekmē tālāko procesu norisi. Vienlaicīgi daudzgadīgajiem augiem tā ir arī viena no problemātiskākajām fāzēm. Viens no galvenajiem limitējošajiem faktoriem ir eksplantu inertums jeb nereaģēšana uz mehāniskajām un ķīmiskajām manipulācijām *in vitro* vidē (Benson 2000). Eksplantu jutību pret manipulācijām var ietekmēt tādi faktori kā materiāla ievākšanas periods, donorauga vecums, pozīcija, no kuras ievākti pumpuri (vainaga augša, vidus u.c.), genotips, uzglabāšana un priekšapstrāde, kā arī iniciācijai izmantotās barotnes sastāvs (Welander 1988, 1993, McCown 2000, Vaičiukynė et al. 2017). Šajā pētījumā (**IV**) *in vitro* kultūru iniciāciju būtiski ($p < 0,01$) ietekmēja donorauga vecums un pumpuru ievākšanas laiks (5.5. att.).



5.5. attēls. **Iniciēto kultūru īpatsvars atkarībā no donorauga vecuma un eksplantu ievākšanas laika**

Statistiski būtiskas atšķirības starp vecuma grupām un eksplantu ievākšanas laika grupām attēlotas ar atšķirīgiem burtiem (abiem mainīgajiem $p \leq 0{,}001$)

Augiem ir sarežģīts dzīves cikls, raksturojams ar reproduktīvo un veģetatīvo attīstības fāzi, morfoģenēzi. Turklāt mērenās klimata joslas sugām raksturīgi miera periodu cikli, kas nosaka sekojošo aktīvās augšanas fāžu un šūnu dalīšanās norisi. Attiecīgi, augi uzrāda sezonālas *in vitro* kultūru iniciācijas sekmju variācijas atkarībā no perioda, kad ievākts augu materiāls (Benson 2000). Eksplantiem, kas ievākti no viengadīga donorauga, novērota iniciācija 66% gadījumu, kamēr eksplantiem, kas ievākti no 15-gadīga donorauga, iniciēto kultūru proporcija bija 39%. Augstākā iniciēto kultūru proporcija novērota eksplantiem, kas ievākti pavasarī (64% martā un 67% aprīlī), kamēr jūnijā un septembrī ievāktiem eksplantiem iniciēto kultūru proporcija bija būtiski zemāka (attiecīgi, 31% un 29%; 5.5. att.). Šie rezultāti atbilst bieži novērotai tendencei, ka visaugstākās kultūru iniciācijas sekmes var panākt, augu materiālu ievācot pēc miera perioda beigām pavasarī līdz vasaras sākumam (George et al. 2008a).

Līdzīgas tendences novērotas arī citām mērenās klimata joslas kokaugu sugām. Parastajai apsei *Populus tremula* L. augstākā iniciācija novērota pumpuriem, kas ievākti februāra beigās/marta sākumā, kamēr agrāk ievākti pumpuri attīstījās būtiski lēnāk, ar mazākiem kallusiem, savukārt no vēlāk ievāktiem pumpuriem vairums aizgāja bojā infekciju rezultātā (Peternel et al. 2009). Parastajam ozolam *Quercus robur* L. augstākā pumpuru iniciācija novērota eksplantiem, kas ievākti no maija līdz jūlijam (Civínová & Sladský 1990), kas, iespējams, saistīts ar vēlāku pumpuru plaukšanu salīdzinājumā ar parasto apsi un āra bērzu (Linkosalo 2000, Lange et al. 2016). Tajā pašā laikā citos pētījumos novērots, ka āra bērza kultūru sekmīga iniciācija panākama, ievācot augu materiālu rudenī un ziemā (Jokinen & Törmälä

1991), un pumpuru apstrāde ar miera periodu ierosinošām procedūrām rezultējās ar augstāku plaukstošu pumpuru proporciju un dzinumu attīstību (Welander 1993), norādot, ka ne tikai eksplantu ievākšanas periods, bet arī citi faktori ietekmē kultūru iniciācijas sekmes.

Augšanas regulatori jeb fitohormoni, kas pievienoti iniciācijas barotnei, ietekmē pumpuru plaukšanu un dzinumu attīstību (Magnusson et al. 2009). Piemēram, *Q. robur* eksplantiem, kas ievākti februārī un martā, visaugstākā iniciācija un dzinumu attīstība novērota, izmantojot zemu BAP koncentrāciju (0,2 mg L^{-1}), kamēr maijā un jūlijā ievāktiem pumpuriem sekmīgākā iniciācija norisinājās pie augstākām BAP koncentrācijām (1 un 2 mg L^{-1}; Civínová & Sladský 1990). Maijā un jūlijā ievāktiem pumpuriem novērotas arī augstākas reģenerācijas spējas nekā februārī un aprīlī ievākto pumpuru kultūrām, tomēr meristēmu stimulēšanai bija nepieciešamas augstākas BAP koncentrācijas (Civínová & Sladský 1990).

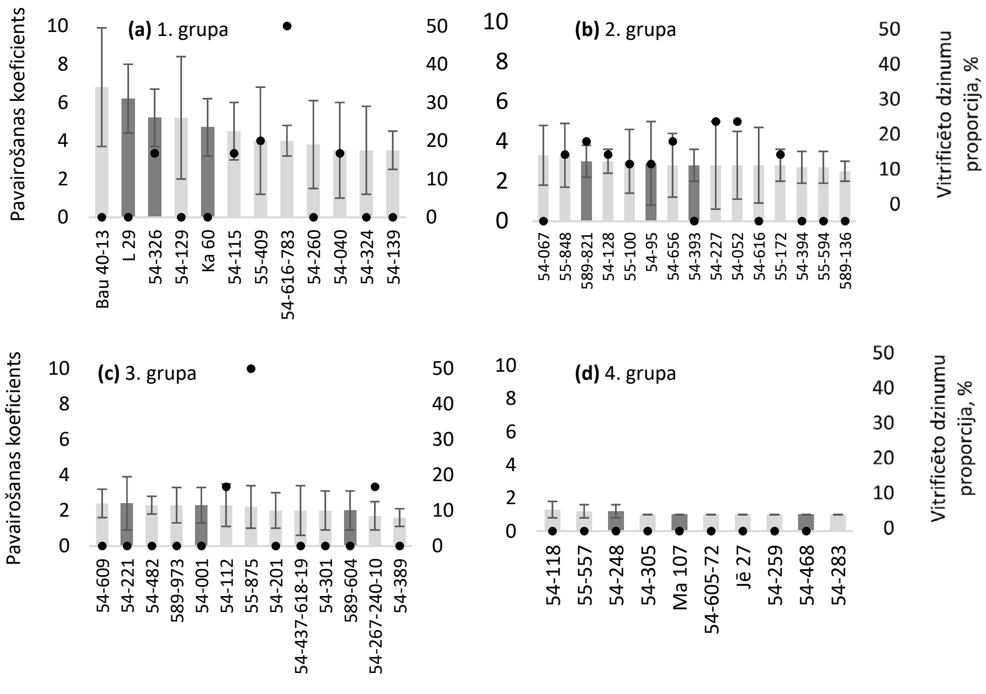
Sterilitātes kontekstā augstākas iniciācijas sekmes pavasarī ievāktiem eksplantiem varētu būt attiecināmas uz mikroorganismu sezonālo dinamiku. Miera periodā ievākti pieaugušu *B. lenta* L. koku eksplanti uzrādīja zemāku inficēto paraugu proporciju nekā eksplanti, kas ievākti pavasarī (Rathwell et al. 2016). Līdzīgi rezultāti novēroti ar *Platanus occidentalis* L., kam infekciju attīstība pieauga no 14% janvārī vāktiem eksplantiem līdz 48% jūlijā vāktiem eksplantiem (Tao et al. 2007). Infekciju attīstības novēršanai *Ulmus americana* L. vispiemērotākais laiks kultūru iniciācijai bija pavasaris (Shukla et al. 2012), kamēr miera periodā ievāktiem eksplantiem infekciju attīstība bija visaugstākā. Pretēji, tīras *Pinus sylvestris* L. kultūras attīstījās no maija līdz oktobrim ievāktiem eksplantiem, kamēr no decembra līdz aprīlim ievāktiem eksplaniem attīstījās būtiski vairāk infekciju, kas, visticamāk, skaidrojams ar labāku audu noturību aktīvās augšanas fāzē (Hohtola 1988).

Dabiskās attīstības gaitā kokaugiem pārejot no veģetatīvās augšanas (juvenilās) fāzes uz ģeneratīvo jeb nobriedušo fāzi, būtiski samazinās eksplantu iniciācijas un kultūru mikropavairošanas spējas (von Aderkas & Bonga 2000). Juvenili audi no sējeņiem parasti iniciācijai pakļaujas vieglāk nekā audi no nobriedušiem/pieaugušiem kokiem (George et al. 2008a). Turklāt kultūru uzsākšana ar materiālu no nobriedušiem kokiem parasti ir problemātiska, jo tiem raksturīgs augstāks infekciju risks, audu brūnēšana (oksidācija) un inertums (George et al. 2008a). Viens no veidiem, kā panākt donorauga daļēju juvenilizāciju, ir potēšana (Benson 2000). Lai gan šajā pētījumā netika veikts izmantoto potzaru juvenilizācijas novērtējums, eksplanti, kas ievākti no vienu gadu veca potēta auga, uzrādīja būtiski augstākas iniciācijas sekmes nekā eksplanti, kas ievākti no 15 gadus veca, nepotēta donorauga (5.5. att.). Līdzīgi, augstākas pumpuru iniciācijas sekmes (80%) iegūtas, kā donoraugu izmantojot trīs gadus vecus *B. lenta* L. stādus, kamēr eksplanti, kas iegūti no pieaugušiem kokiem, neizplauka un neveidoja dzinumus (Rathwell et al. 2016). Jāatzīmē, ka lielākajai daļai *Betula* dzimtas sugu *in vitro* kultūras bez lielām grūtībām var tikt iniciētas neatkarīgi no izejmateriālu vecuma (Welander 1993), un vairākos pētījumos veiksmīga iniciācija ir panākta, izmantojot pumpurus no veciem, nobriedušiem bērza donoraugiem (Ryynänen & Ryynänen 1986, Jones et al. 1996, Aubakirova & Kalashnikova 2011).

Šajā pētījumā datu interpretācijas iespējas ierobežo fakts, ka izmantots tikai viens genotips (klons 54–95), kas neļauj pilnībā novērtēt eksplantu ievākšanas laika un donorauga vecuma ietekmi. Genotips kultūru iniciācijas sekmes bieži ietekmē vairāk nekā iepriekšminētie faktori (Jokinen & Törmälä 1991), savukārt genotipa izpausmes nosaka konkrētā klona heterogenitāte jeb fenotipiskais plastiskums (Civínová & Sladský 1990). Tomēr šie limitējošie faktori var tikt pārvarēti, ja konkrētais klons kopumā izrāda jutību pret *in vitro* manipulācijām (Jokinen & Törmälä 1991).

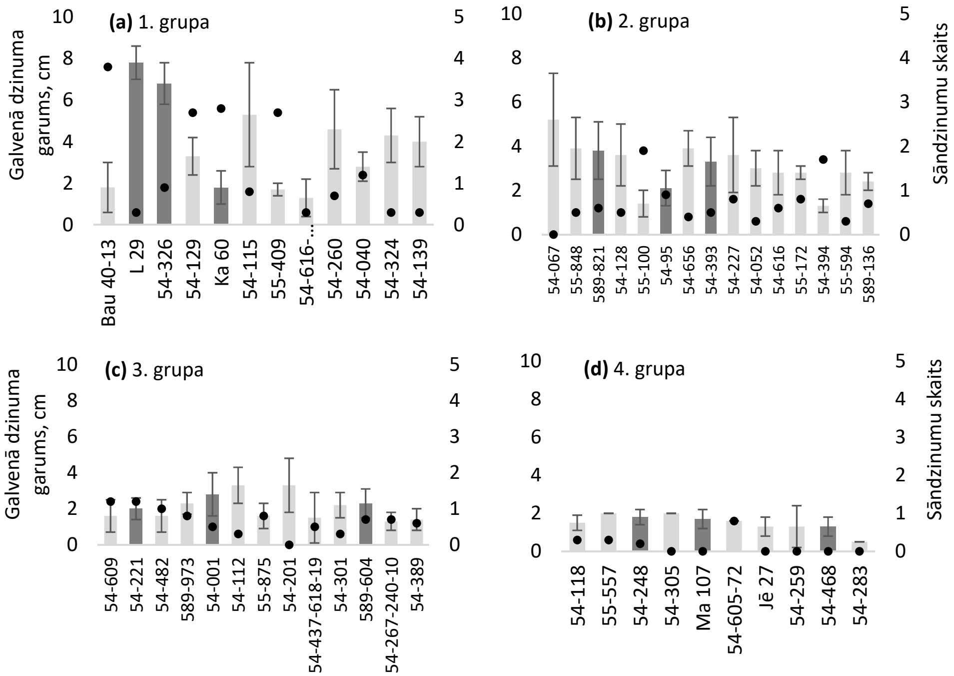
Kad kultūra ir iniciēta un nostabilizēta, sezonalitāte un attīstības fāžu nomaiņa to vairs neietekmē (McCown 2000). Šajā momentā kultūru augšanu lielā mērā ietekmē klonu īpašības, kas var ievērojami atšķirties. Šajā pētījumā pavairošanas koeficienti svārstījās no 1,0 (nepavairojas) līdz 6,8 (5.6. att.), un galvenā dzinuma garums svārstījās no 1,3 līdz 7,8 cm (5.7. att.). Katra mikrospraudeņa sāndzinumu skaits novērots robežās no 0 līdz 3,8. Līdzīgas pavairošanas sekmes (koeficienti no 1,6 līdz 7,4) konstatētas 10 genotipiem no Zviedrijas, Somijas un Vācijas (Ewald et al. 2002). Augstākus pavairošanas koeficientus (2 līdz 20), bet ar lielāku rezultātu izkliedi, novēroja *Jokinen* and *Törmälä* (1991), analizējot 100 genotipus.

Šajā pētījumā kloni uzrādīja dažādas augšanas tendences; vairākiem genotipiem veidojās izteikti spēcīgs galvenais dzinums ar vāji attīstītiem sāndzinumiem



5.6. attēls. **Pavairošanas koeficienti (stabiņi; ± standartkļūda) un vitrificēto dzinumu proporcija (apļi) kloniem: (a) 1. grupā, (b) 2. grupā, (c) 3. grupā un (d) 4. grupā**

Ar tumši pelēku krāsu atzīmēti kloni, kas izvēlēti dažādu apstrādes veidu ietekmes novērtēšanai



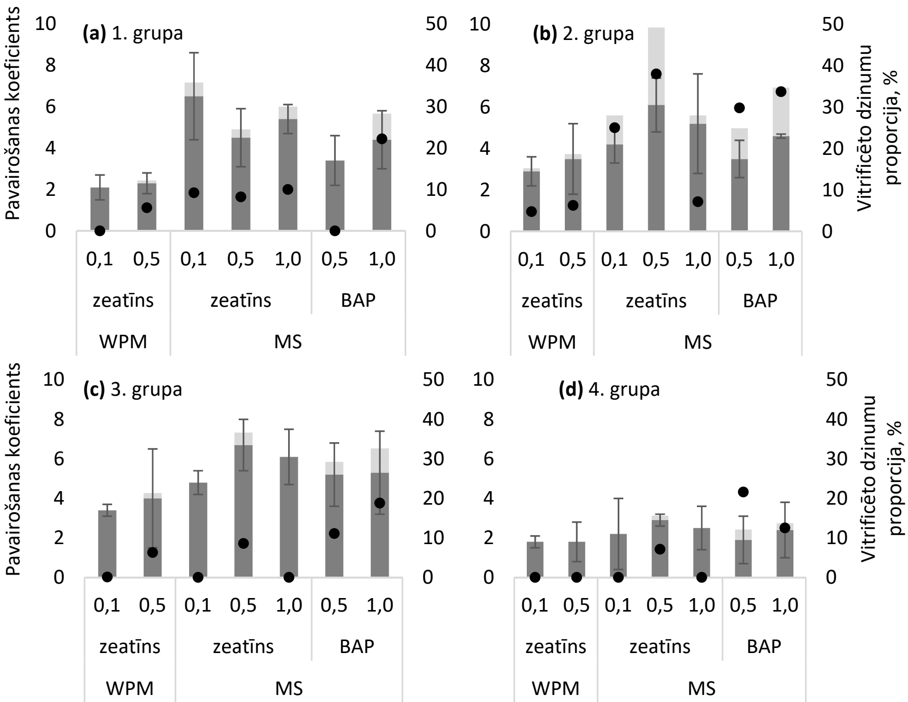
5.7. attēls. **Galvenā dzinuma garums (stabiņi; ± standartkļūda) un sāndzinumu skaits (aplīši) kloniem: (a) 1. grupā, (b) 2. grupā, (c) 3. grupā un (d) 4. grupā**

Ar tumši pelēku krāsu atzīmēti kloni, kas izvēlēti dažādu apstrādes veidu ietekmes novērtēšanai

(piemēram, klons L 29; 5.7.(a) att.), kamēr citiem veidojās īss galvenais dzinums un liels skaits sāndzinumu (piemēram, klons Bau 40-13; 5.7.(a) att.). Pavairošanas sekmes nebija atkarīgas no šīm augšanas tendencēm – kā viena, tā otra augšanas stratēģija varēja rezultēties ar augstu pavairošanas koeficientu. Neskatoties uz augstu variāciju, sāndzinumu skaits uzrādīja negatīvu sakarību ar galvenā dzinuma garumu ($p < 0{,}01$, regresijas koeficients $-0{,}11 \pm 0{,}04$). Gandrīz ceturtdaļai klonu konstatētas zemas pavairošanas spējas: 12 kloniem pavairošanas koeficienti bija < 2, kamēr 7 kloni nepavairojās (pavairošanas koeficients < 1). Rezultāti varētu būt skaidrojami ar ierobežoto pētījuma periodu. Parasti bērza kultūru iniciācijai nepieciešamas 4 līdz 10 nedēļas atkarībā no eksplanta veida, donorauga fizioloģiskā stāvokļa un vecuma, un genotipa (Welander 1993), tāpēc izvēlētais iniciācijas etapa ilgums varētu būt bijis par īsu, lai panāktu pilnīgu kultūru uzsākšanu.

Genotipu pavairošanas spējas atkarīgas arī no barotnes sastāva un pievienotajiem augšanas regulatoriem. Optimālais barotnes sastāvs atkarīgs no pavairojamās sugas un konkrētā genotipa, un, lai gan daļa augu aug vienlīdz labi uz dažādām barotnēm, daļai var būt ievērojamas atšķirības (McCown & Sellmer 1987). Pavairošanai piemēroto klonu skaitu var palielināt, modificējot kultūru barotni un pievienojot dažāda veida augšanas regulatorus, piemēram, citokinīnus (Jokinen & Törmälä 1991). Lai kultūras optimāli attīstītos, barotnei jānodrošina augi ar nepieciešamajām barības vielām, minerālelementiem. Bērza pavairošanai visbiežāk izmanto MS vai WPM tipa barotnes, tomēr var tikt izmantotas arī citas minerālvielu kombinācijas (Ewald et al. 2000, Iliev et al. 2003). Pavairošanas spējas uz minētajām barotnēm audzētām kultūrām šajā pētījumā svārstījās no 1,8 līdz 6,7 (vidēji 3,9). Visās klonu grupās augstāki pavairošanas koeficienti konstatēti uz MS barotnes audzētiem augiem (5.8. att.), kamēr garāki dzinumi veidojās kultūrām, kas audzētas uz WPM barotnes. Izteiktākās atšķirības šiem diviem parametriem novērotas 1. grupai (5.8.(a) att.), un pakāpeniski samazinājās līdz 4. grupai (5.8.(d) att.). Uz WPM barotnes audzētām kultūrām novērota zemāka vitrificēto augu proporcija no 0 līdz 6,3 (vidēji 2,9), kamēr uz MS barotnes audzētām kultūrām tā bija 0 līdz 38,0 (vidēji 13,2). Sāndzinumu skaits un garums neuzrādīja izteiktu sakarību ar izmantotās barotnes tipu.

Līdzīgi, vājāka attīstība uz WPM barotnes novērota *B. lenta* L. kultūrām. Augiem, kas kultivēti uz WPM barotnes, parādījās sarkana pigmentācija, tie bija īsāki un veidoja mazāk posmu nekā uz MS barotnes kultivēti augi, tomēr pavairošanas koeficients netika būtiski ietekmēts (Rathwell et al. 2016). Šie rezultāti tiek saistīti



5.8. attēls. **Pavairošanas koeficienti (tumši pelēks; ± standartkļūda) un vitrificēto dzinumu skaits (gaiši pelēks), un vitrificēto dzinumu proporcija (aplīši) atkarībā no barotņu sastāva: (a) 1. grupa, (b) 2. grupa, (c) 3. grupa, and (d) 4. grupa**

WPM – *Woody Plant medium* tipa barotne, MS – *Murashige* & *Skoog* tipa barotne, BAP – 6-benzilaminopurīns ar sāļu koncentrācijām dažādos bazālo sāļu barotņu veidos, jo, piemēram, amonija nitrāta (NH_4NO_3) koncentrācija WPM barotnē ir par apmēram ¼ zemāka nekā MS barotnē. Zemas slāpekļa koncentrācijas limitējošā ietekme konstatēta konkrētam *Populus* hibrīda genotipam. Sākotnēji uz WPM barotnes audzētas kultūras uzrādīja zemu dzīvotspēju, bet pēc pārstādīšanas uz MS tipa barotnes varēja tikt uzturētas ilgstoši. Augšana uz WPM barotnes būtiski uzlabojās un kļuva pielīdzināma kultivēšanai uz MS barotnes, kad NH_4NO_3 koncentrācija tika paaugstināta līdz MS barotnes līmenim (McCown & Sellmer 1987). Pretēji, četriem *Betula platyphylla* Sukatchev var. *japonica* (Miq.) Hara × *B. pendula* genotipiem ilgstoši vislabākā augšana konstatēta, kultivējot uz WPM barotnes pretstatā MS, iegūstot vidējos pavairošanas koeficientus attiecīgi 3,7 un 2,8 (Meier-Dinkel 1992).

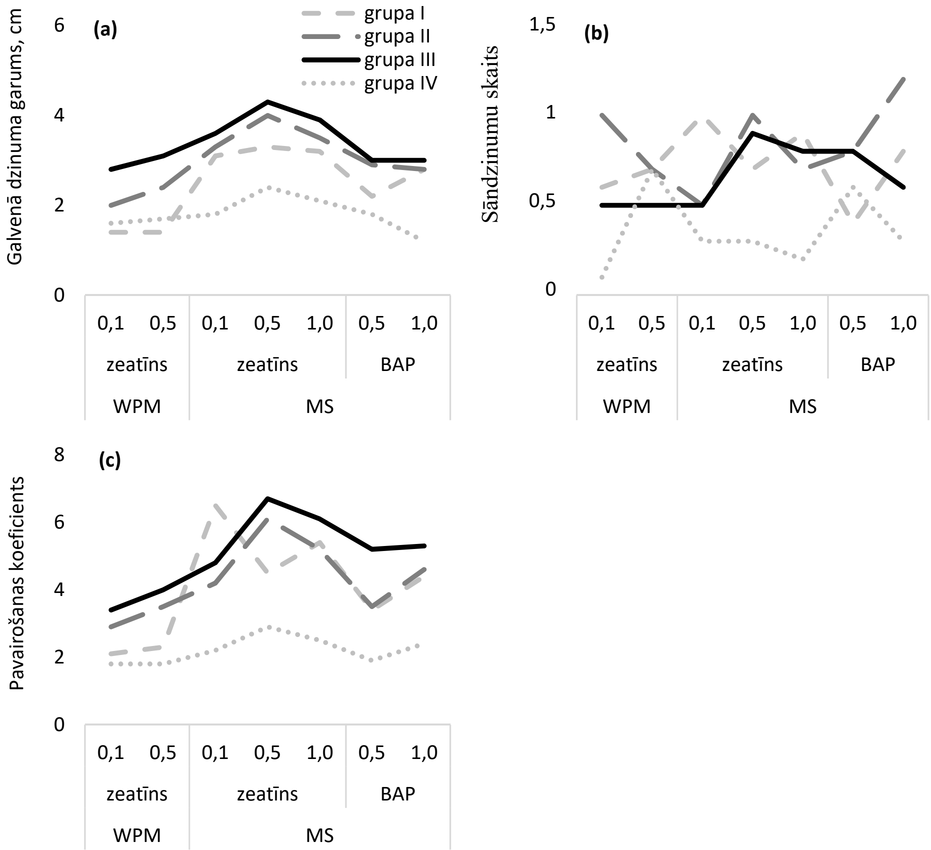
Augšanas regulatoriem ir būtiska loma bērza *in vitro* kultūru iniciācijā un tālākā kultivēšanā. Visbiežāk tiek lietoti citokinīni, kas stimulē šūnu dalīšanos, sekmējot morfoģenēzi (George et al. 2008b). Pavairošanās spēju uzlabošanai barotnei visbiežāk tiek pievienots BAP vai zeatīns koncentrācijās, attiecīgi, 0,2 līdz 5,0 mg L^{-1} un 1,0 līdz 5,0 mg L^{-1}, vai BAP koncentrācijā no 0,7 līdz 2,0 mg L^{-1} kombinācijā ar auksīniem zemās koncentrācijās (Meier-Dinkel 1992). Dažādos pētījumos viens un tas pats citokinīns tiek aprakstīts ar diviem dažādiem nosaukumiem – BA (6-benziladenīns) un BAP (6-benzilaminopurīns; Teixeira da Silva 2012), tāpēc vieglākai uztveramībai šeit un turpmāk tiks izmantots apzīmējums BAP, neatkarīgi no apzīmējuma, kāds lietots oriģinālajā avotā.

Konkrēta citokinīna ietekmi jānovērtē eksperimentāli un jāņem vērā, ka atbildes reakcijas vienlaikus nosaka izmantotais savienojums, kultūras veids, genotips un audu ontoģenētiskā attīstības stadija (George et al. 2008b). Piemēram, divi *B. pendula* genotipi uzrādīja atšķirīgas atbildes reakcijas uz citokinīna pievienošanu barotnei. Viens no kloniem veidoja daudz, bet īsus dzinumus, ievērojami palielinot pavairošanas koeficientu, kamēr otru klonu citokinīna pievienošana būtiski neietekmēja. Vienlaicīgi otrais klons uzrādīja augstāko dzinumu skaitu gan uz kontroles barotnes, gan arī barotnes ar pievienotu BAP (Vaičiukynė et al. 2017). Vairākām *Betula* sugām citokinīnu neiekļaušana barotnes sastāvā rezultējās ar vāju augšanu (Cheng et al. 2000) vai arī – ekstrēmos gadījumos – augšana apstājās un eksplanti aizgāja bojā (Magnusson et al. 2009, Rathwell et al. 2016, Girgžde & Samsone 2017). Visbiežāk augstākās pavairošanas sekmes var iegūt, izmantojot citokinīnus relatīvi šaurā koncentrācijas diapazonā. Šajā pētījumā (**IV**) citokinīnu ietekme uz augšanas parametriem pētīta, audzējot kultūras gan uz WPM, gan MS bazālajiem sāļiem veidotas barotnes. Uz MS tipa barotnes, neatkarīgi no koncentrācijas, kultūras visās klonu grupās uzrādīja augstākos pavairošanas koeficientus un galvenā dzinuma garumu, ja tika izmantots zeatīns (5.8. att.). Grupu ietvaros vidējā pavairošanas koeficientu atšķirība starp apstrādi ar zeatīnu un BAP bija 11% līdz 29%, kamēr atšķirība galvenā dzinuma garumiem bija 21% līdz 29%. No apstrādes variantiem, kur zeatīns pievienots MS tipa barotnei, augstākais pavairošanas koeficients konstatēts pie koncentrācijas 0,5 mg L^{-1} visām klonu grupām, izņemot pirmo (5.8. att.). Šādas zeatīna koncentrācijas izmantošana arī rezultējās ar garākajiem galvenajiem dzinumiem visās grupās. Variantos, kur pievienots BAP, relatīvi augstāki pavairošanas koeficienti novēroti, izmantojot salīdzinoši augstākas citokinīna koncentrācijas, tomēr tendences nebija statistiski būtiskas augstās rezultātu variācijas dēļ.

Uz WPM bazālo sāļu barotnes zeatīna koncentrācijas 0,5 mg L^{-1} ietekmē kultūrām bija līdzīgi vai nedaudz augstāki pavairošanas koeficienti un garāki galvenie dzinumi nekā audzējot ar zeatīnu koncentrācijā 0,1 mg L^{-1}, tomēr šīs atšķirības nebija tik izteiktas kā tad, ja izmantota MS barotne. Vidējais sāndzinumu skaits vienam augam bija no 0,1 līdz 1,2 (vidēji 0,6), un netika novērota specifiska sakarība starp sāndzinumu garumu un skaitu, un izmantotā citokinīna veidu.

Vairākos pētījumos pārbaudītas dažādas citokinīnu koncentrācijas *Betula* genotipu pavairošanai. BAP ietekme pārbaudīta uz *B. platyphylla* šķirnēm. Izmantojot 2,2 µM BAP (apmēram 0,5 mg L^{-1}), iegūts četras reizes augstāks pavairošanas koeficients nekā izmantojot 1,1 µM BAP (apmēram 0,25 mg L^{-1}), un divas reizes augstāks pavairošanas koeficients nekā audzējot uz barotnes ar 4,4 µM BAP (apmēram 1,0 mg L^{-1}; Cheng et al. 2000). Konkrētam *B. pendula* genotipam, audzējot kultūru uz barotnes ar 1,0 mg L^{-1} BAP, iegūti dzinumi, kas bija vienlīdz gari kā uz zeatīna dažādās koncentrācijās (0,5–1,0 mg L^{-1}) audzētām kultūrām. Tomēr uz 1,0 mg L^{-1} BAP audzētām kultūrām attīstījās divreiz vairāk sāndzinumu, rezultējoties ar augstāku pavairošanas koeficientu, salīdzinot ar citām apstrādēm (Girgžde & Samsone 2017). Pētījumā ar *B. lenta* visaugstākās dzinumu augšanas sekmes novērotas BAP apstrādei, salīdzinājumā ar 2-izopentiladenīna (2-iP) un tidiziaurona (TDZ) apstrādēm, un visaugstākais pavairošanas koeficients iegūts, audzējot uz BAP koncentrācijas 5,0 µM (apmēram 1,1 mg L^{-1}; Rathwell et al. 2016). *B. platyphylla* and *B. papyrifera* Marsh kultūrām augstākās pavairošanas sekmes novērotas, barotnei pievienojot BAP 10 līdz 20 µM koncentrācijā (apmēram 2,3–4,5 mg L^{-1}) un TDZ 4 līdz 8 µM koncentrācijā (Magnusson et al. 2009). Dažādas atbildes reakciju izpausmes intensitātes varētu būt saistītas ar endogēno augšanas regulatoru sezonālo dinamiku, attiecīgi, saistāmas ar iniciācijai paredzēto eksplantu ievākšanas laiku. *B. Civínová* un *Z. Sladský* (1990) konstatēja, ka *Q. robur* kultūru iniciēšanai no eksplantiem, kas ievākti no maija līdz jūlijam, nepieciešamas augstākas BAP koncentrācijas (2 mg L^{-1}) nekā tad, ja eksplanti ievākti periodā no februāra līdz aprīlim (0,5 mg L^{-1}).

Galvenā dzinuma garums uzrādīja būtisku sakarību ar sāndzinumu garumu ($p < 0{,}001$, regresijas koeficients 1,68 ± 0,24) un sāndzinumu skaitu ($p < 0{,}01$, regresijas koeficients 0,23 ± 0,06), kā arī konsekventu ranžējumu starp klonu grupām (5.9.(a) att.). Tomēr sāndzinumu skaits starp variantiem bija izteikti svārstīgs (5.9.(b) att.), ietekmējot pavairošanas koeficienta ranžējumu (5.9.(c) att.). Neatkarīgi no barotnes sastāva vai izmantotā citokinīnu veida gan augstākie pavairošanas koeficienti, gan garākie galvenie dzinumi konstatēti 3. grupai, kam sekoja 2. grupa un 1. grupa. Kā sagaidāms, 4. grupa, kas sastāvēja no vissliktāk augošajiem genotipiem, uzrādīja vājākos rezultātus visām mērītajām pazīmēm (5.8. un 5.9. att.). Lai gan parasti pavairošanas koeficienti kloniem saglabājas stabili vairākas pārstādīšanas pēc kārtas (Jokinen & Törmälä 1991), šajā pētījumā konstatētas klonu grupu ranga apgrieztas izmaiņas, salīdzinot pirmo un pēdējo pārstādīšanas reizi. Šīs klonu



5.9. attēls. **Grupu vidējie (a) galvenā dzinuma garumi, (b) sāndzinumu skaiti, un (c) pavairošanas koeficienti atkarībā no barotņu sastāva**

WPM – *Woody Plant Medium* tipa barotne, MS – *Murashige* & *Skoog* tipa barotne, BAP – 6-benzilaminopurīns

grupu pavairošanas spēju atšķirības starp pārstādīšanas reizēm skaidri demonstrē vajadzību rūpīgi izvēlēties pareizo barotnes sastāvu.

Augstākām citokinīnu koncentrācijām ir stimulējošs efekts, līdz tiek sasniegts taksonam specifiskais slieksnis, pēc kura pārsniegšanas citokinīnu koncentrācijas tālāka palielināšanās izraisa attīstības anomālijas. Eksplantam var sākt veidoties daudzi mazi neattīstīti dzinumi, kas nestiepjas garumā, vai arī veidojas nestandarta formas lapas (George et al. 2008b). Piemēram, augstas zeatīna koncentrācijas izraisīja anormālu dzinumu veidošanos *B. pendula* kultūrām. Zeatīna lietošana koncentrācijā 5 mg L^{-1} rezultējās ar 3,4% fasciētu dzinumu veidošanos, kamēr dzinumi attīstījās normāli, ja izmantotas zemas zeatīna koncentrācijas (2 mg L^{-1}) vai arī tas netika pievienots barotnei vispār (Iliev et al. 2003). Citā pētījumā BAP izmantošana augstā koncentrācijā (5,3 µM; apmēram 1,2 mg L^{-1}) rezultējās ar dažāda garuma, vitrificētu un hlorotisku dzinumu veidošanos (Cheng et al. 2000). Vitrifikācija ir bieži novērota deformācija *in vitro* pavairošanas procesā, kam raksturīga caurspīdīgu, ūdeņainu (stiklam līdzīgu), hipolignificētu augu veidošanās (Gaspar 1991, Debergh et al. 1992). Dzinumi veidojas resni, ar īsiem posmiem, savukārt lapas biezas, pagarinātas, sarullētas un trauslas (Franck et al. 1995).

Šajā pētījumā ap 34% klonu veidoja vitrificētus dzinumus (5.6. att.), robežās no 0% līdz 50% no dzinumu skaita. Skatoties klonu līmenī, diviem kloniem novērota augsta (50%) vitrificēto dzinumu proporcija. Viens no kloniem ietilpa grupā ar augstu pavairošanas koeficientu (klons 54-616-783; 5.6.(a) att.), savukārt otrs – grupā ar zemu pavairošanas koeficientu (klons 55-875; 5.7. att.). Vidēji izteikta vitrifikācija (14–25% no kopējā dzinumu skaita) bija raksturīga 15 no 20 kloniem. Klonu līmenī netika novērotas būtiskas ($p > 0,05$) sakarības starp vitrificēto dzinumu skaitu un galvenā dzinuma garumu vai sāndzinumu skaitu. Tomēr pastāvēja būtiska pozitīva sakarība ($p < 0,001$, regresijas koeficients $0,56 \pm 0,04$) starp vitrificēto dzinumu skaitu un kopējo pavairošanas koeficientu. Dažādos barotnes sastāvos vitrificēto dzinumu skaitam novērotas pozitīvas sakarības ar visiem dzinumu augšanu raksturojošajiem parametriem: galvenā dzinuma garumu ($p < 0,001$, regresijas koeficients $0,77 \pm 0,07$), sāndzinumu skaitu ($p < 0,001$, regresijas koeficients $3,11 \pm 0,07$) un garumu ($p < 0,001$, regresijas koeficients $0,98 \pm 0,21$). Attiecīgi, pastāv būtiska sakarība ($p < 0,001$, regresijas koeficients $0,44 \pm 0,02$) starp pavairošanas koeficientiem un vitrificēto dzinumu īpatsvaru. Šie rezultāti saskan ar *Gaspar* (1991) novēroto, ka pastiprināta dzinumu vitrifikācija saistīta ar intensīvu pavairošanu (biežām pārstādīšanām, uzturot augstus pavairošanas koeficientus). Tajā pašā laikā donorauga fizioloģiskais stāvoklis eksplantu ievākšanas laikā vitrifikāciju neietekmēja.

Vitrifikācija tiek saistīta ar specifiskiem *in vitro* kultivēšanas apstākļiem un rodas eksplantu nespējas pielāgoties stresa faktoriem (ievainojums, pārāk augstas jonu koncentrācijas, nepietiekams apgaismojums, temperatūra) dēļ (Kevers et al. 2004). Visām pētītajām grupām zemāks vitrificēto dzinumu īpatsvars konstatēts zeatīna apstrādes variantiem (2,4% līdz 23,4% no dzinumu skaita), kamēr BAP apstrādes variantiem 11,1% līdz 31,8% dzinumu bija vitrificējušies. Jāatzīmē, ka augsts vitrificēto dzinumu īpatsvars konstatēts arī variantam, kur apstrāde veikta ar zeatīnu koncentrācijā 0,5 mg L^{-1} (variants, kam konstatēts visaugstākais pavairošanas koeficients).

Vērtētajā zema biezuma āra bērza klonu plantācijā saglabāšanās 40 gadu vecumā bija 84,4%. Koku vidējais h (± standartnovirze) un d bija attiecīgi 26,2 ± 2,2 m un 27,7 ± 5,6 cm. Kopējā krāja stādījumā bija 210 m^3 ha^{-1}, un vidējais ikgadējais stumbra koksnes pieaugums bija 5,25 m^3 ha^{-1} $gads^{-1}$. Novērtētā MV bija aptuveni 9600 EUR ha^{-1}, ko galvenokārt nodrošina mazāka, vidēja un liela izmēra baļķi (attiecīgi 44%, 25% un 21%).

Aprēķinātais H^2 un CV_g vērtētajām pazīmēm atšķīrās (5.6. tab.). Visaugstākā iedzimstamība tika aprēķināta zaru leņķim, vidējai vainaga projekcijai, zarainumam un stumbra taisnumam ($0,40 \leq H^2 \leq 0,29$), bet viszemākās iedzimstamības bija saglabāšanās, padēlu un plaisu iespējamībai (< 0,08). Vidēji augsts $H^2 = 0,16$ MV bija līdzīgs h, h_{zz} un d (attiecīgi 0,14, 0,14 un 0,21). Kvantitatīvo rādītāju CV_g variēja no

3,2% līdz 21,8% attiecīgi koku augstumam un MV caurmēram un zemākā zaļā zara augstumam CV_g bija ~ 9%, bet zl un vvp tas bija attiecīgi 14,8% un 19,2%.

Aprēķinātais H^2 (5.6. tab.) norāda, ka iespējams būtiski uzlabot augšanu un stumbra kvalitāti, līdz ar to bērzu plantāciju ražību ar meža selekcijas metodēm (Stener & Hedenberg 2003). Tomēr H^2 pazīmēm bija atšķirīgs (5.6. tab.), kas norāda uz nevienlīdzīgu īpašību uzlabošanas potenciālu (Falconer 1996). Zaru leņķis, zarainums, vainaga projekcija un stumbra taisnums, kas lielā mērā ietekmē kokmateriālu kvalitāti (Savill et al. 1997), bija lielā mērā ģenētiski noteikti un tiem bija vidēji CV_g (5.6. tab.), kas norādīja uz ievērojamu uzlabojumu potenciālu (Falconer 1996). Augsts CV_g MV (21,8%) norādīja uz iespējamiem finansiāliem ieguvumiem no koku selekcijas.

Noteiktās ģenētiskās korelācijas starp vērtētajām pazīmēm bija līdzīgas fenotipiskajām klonu vidējām Pīrsona korelācijām (5.7. tab.). Korelācija starp h, d un MV bija augsta ($r > 0{,}63$); tomēr d un MV ($r > 0{,}66$) korelēja ar vvp. Zarainums pozitīvi korelēja ar d ($r = 0{,}79$), tomēr ne ar h ($p = 0{,}41$). Vidējas līdz augstas ($0{,}30 < |r| < 0{,}78$) negatīvas korelācijas tika novērotas zemākā zaļā zara augstumam ar vairākām citām pazīmēm – d, pad, stumbra taisnumu, zarainumu un vvp. Dubultgalotņu sastopamība uzrādīja vidēju vai ciešu korelāciju ar stumbra taisnumu, zarainumu un vvp (r = attiecīgi 0,70, 0,67 un 0,56), bet negatīvu korelāciju ($r = -0{,}68$) ar padēliem. Galvenokārt tika novērotas vājas un nenozīmīgas korelācijas starp stumbra plaisām un zaru leņķi, kā arī citiem mainīgajiem lielumiem.

Spēcīgā korelācija starp zarainumu un d, vvp un stumbra taisnumu liecināja par iespējamu negatīvu ietekmi uz stumbra kvalitāti, izvēloties ātraudzīgus kokus ar taisniem stumbriem (5.7. tab.). Turklāt h_{zz} bija ievērojamas negatīvas korelācijas ar tiem pašiem mainīgajiem lielumiem, pamatojot iepriekš minēto apsvērumu. Agrāki pētījumi ziņoja par vidēji augstu korelāciju starp d un zaru skaitu (Stener & Hedenberg 2003, Stener & Jansson 2005). Būtiska negatīva ģenētiska korelācija starp produktivitātes pazīmēm un stumbra taisnumu (r_G no –0,45 līdz –0,72) tika novērota Zviedrijā (Stener & Jansson 2005). Tomēr citas stumbra kvalitātes pazīmes, piemēram, pad, stumbra plaisas un dg, neliecināja par būtisku saistību ar produktivitātes pazīmēm un MV, kas liecina par iespējamu vienlaicīgu pazīmju uzlabojumu (Viherä-Aarnio & Velling 1999, Stener & Jansson 2005).

5.6. tabula

Statistiskie rādītāji, iedzimstamības koeficienti (H^2) un genotipiskās variācijas koeficienti (CV_g, %) vērtētajām pazīmēm un koksnes monetārajai vērtībai (MV) 40 gadus veciem potētiem bērza pluskoku pēcnācējiem zema biezuma plantācijā

Stumbra koksnes vērtība aprēķināta, ņemot vērā stumbra kvalitāti

Pazīme	Vidējais	Min	Max	Standartnovirze	Iedzimstamības koeficients H^2 ± standartkļūda	Genotipiskās variācijas koeficients CV_g ± standartkļūda, %
Kvantitatīvie mainīgie						
Stumbra krūšaugstuma caurmērs, cm	27,7	14,2	45,8	5,6	0,21 ± 0,06	9,5 ± 1,5
Koka augstums, m	26,2	15,3	31,6	2,2	0,14 ± 0,05	3,2 ± 0,5
Zemākā zaļā zara augstums, m	11,2	1,8	18,0	2,7	0,14 ± 0,05	9,3 ± 1,4
Zaru leņķis, °	43,2	15,0	80,0	10,4	0,40 ± 0,08	14,8 ± 2,3
Vidējā vainaga projekcija, m	2,9	1,1	6,3	0,8	0,39 ± 0,08	19,2 ± 3,0
Stumbra koksnes vērtība, EUR	28,2	3,7	95,4	14,6	0,16 ± 0,05	21,8 ± 3,4
Kvalitatīvie mainīgie						
Saglabāšanās, % koku *	84,4	59,6	100,0	-	0,08 ± 0,03	-
Padēli, % koku *	23,2	5,2	42,8	-	0,02 ± 0,02	-
Dubultgalotnes, % koku *	34,9	6,0	75,1	-	0,14 ± 0,05	-
Stumbra taisnums, balles *	3,2	2,5	4,7	-	0,29 ± 0,07	-
Zarainums, balles *	3,3	2,5	5,3	-	0,33 ± 0,08	-
Stumbra plaisas, % koku *	24,9	0,0	50,3	-	0,08 ± 0,03	-

* vidējās klonu vērtības.

5.7. tabula

Genotipiskās korelācijas (standartkļūdas iekavās) augšējā diagonālajā daļā un fenotipiskās klona vidējās Pīrsona korelācijas (statistiski būtiskas korelācijas ar *p* ≤ 0,05 treknrakstā) apakšējā diagonālajā daļā

Pazīme	Koka augstums	Stumbra krūšaugstuma caurmērs	Stumbra plaisas	Zemākā zaļā zara augstums	Zaru leņķis	Dubultgalotnes	Padēli	Stumbra taisnums	Zarainums	Vidējā vainaga projekcija	Stumbra koksnes vērtība
Koka augstums	**1**	0,65 (0,16)	0,02 (0,30)	0,14 (0,27)	0,43 (0,21)	0,03 (0,27)	0,17 (0,45)	−0,16 (0,25)	0,16 (0,25)	0,35 (0,22)	0,79 (0,11)
Stumbra krūš-augstuma caurmērs	0,63	**1**	0,11 (0,29)	−0,56 (0,19)	0,23 (0,23)	0,35 (0,23)	−0,23 (0,43)	0,44 (0,20)	0,79 (0,10)	0,86 (0,07)	0,93 (0,03)
Stumbra plaisas	0,03	0,10	**1**	−0,11 (*)	0,08 (0,02)	−0,68 (0,20)	0,38 (0,44)	−0,60 (0,21)	−0,30 (0,27)	−0,20 (0,27)	0,47 (*)
Zemākā zaļā zara augstums	0,17	**−0,51**	0,07	**1**	0,29 (0,23)	−0,75 (0,13)	0,90 (0,37)	−0,76 (0,12)	−0,85 (0,24)	−0,77 (0,11)	−0,32 (0,25)
Zaru leņķis	0,36	0,22	0,15	0,25	**1**	−0,37 (0,22)	0,67 (0,31)	−0,09 (0,23)	−0,25 (0,07)	0,27 (0,22)	0,29 (0,23)
Dubultgalotnes	0,05	0,35	**−0,51**	**−0,69**	−0,34	**1**	−1,19 (0,35)	0,78 (0,12)	0,74 (0,13)	0,60 (0,17)	−0,10 (*)
Padēli	0,06	−0,07	0,29	0,40	**0,46**	**−0,68**	**1**	−0,47 (0,43)	−0,64 (0,40)	−0,35 (0,22)	0,06 (0,48)
Stumbra taisnums	−0,15	**0,42**	−0,41	**−0,71**	−0,08	**0,70**	−0,15	**1**	0,87 (0,07)	0,60 (0,14)	0,12 (0,25)
Zarainums	0,19	**0,79**	−0,22	**−0,78**	−0,05	**0,67**	−0,26	**0,82**	**1**	0,93 (0,03)	0,28 (0,28)
Vidējā vainaga projekcija	0,36	**0,86**	−0,15	**−0,71**	0,26	**0,56**	−0,16	**0,70**	**0,93**	**1**	0,65 (0,14)
Stumbra koksnes vērtība	0,74	**0,93**	0,32	−0,30	0,28	0,14	0,03	0,14	**0,54**	**0,66**	**1**

* aprēķināšana pārtraukta bezgalīgas iespējamības dēļ.

Saglabāšanās H^2 bija zema (5.6. tab.), kas liecina par mikrovides dominējošo ietekmi, kā to norāda *L.-G. Stener* un *G. Jansson* (2005) bērzam Zviedrijā. Vides faktori var spēcīgi ietekmēt sugas augšanu, maskējot ģenētisko efektu un rezultējoties zemos iedzimstamības rādītājos (Koski & Rousi 2005). Aprēķinātie ģenētiskie parametri (5.6. tab.) varētu būt ietekmēti jau ar stādmateriāla ar uzlabotām zarošanās un stumbra īpašībām priekšatlasi (pluskoku), jo stādījums sākotnēji bija plānots kā sēklu plantācija. Lai gan potēta āra bērza izmantošana praktiskajā mežniecībā nav izplatīta prakse, stādījums sniedza iepriekš trūkstošu informāciju par ģenētiskajiem parametriem vidējā vecumā. Neprecizitātes ģenētiskajos parametros var būt izraisītas nekontrolēta potcelma × potzara mijiedarbības efekta dēļ. Lai gan šis jautājums ir maz pētīts attiecībā uz meža koku sugām (Jayawickrama et al. 1991), tomēr *Pinus taeda* potcelma × potzara efekts ir bijis niecīgs salīdzinājumā ar klona un vides faktoru ietekmi (Jayawickrama et al. 1997). Mūsu pētījumā laba potējumu saglabāšanās liecināja par saderību starp potcelmiem un potzariem. Ciklofīzes negatīvā ietekme, ko var izraisīt dažādi potcelmu un potzaru bioloģiskie vecumi (Olesen 1978, Greenwood & Hutchison 1993, Viherä-Aarnio & Ryynänen 1994, Wendling et al. 2014), netika novērota, par ko liecināja plantācijas produktivitāte. Līdzīgi vāja ciklofīzes ietekme uz veģetatīvi pavairota āra bērza augšanu un saglabāšanos konstatēta boreālajos apstākļos (Jones et al. 1996, Viherä-Aarnio & Velling 2001). Tomēr potējumiem varētu būt zemāks zarainums un zaru resnums (Viherä-Aarnio & Ryynänen 1995).

Vienkoka parceļu dizains plantācijā, iespējams, ir ietekmējis arī pazīmju ģenētiskos parametrus, jo šādu parceļu mērījumus ietekmē konkurence starp dažādiem genotipiem (Vergara et al. 2004). Tomēr zemais stādījuma biezums, iespējams, veicinājis vēlāku starpkoku konkurences sākumu, tādējādi samazinot augšanas pazīmju genotipiskās dispersijas pārvērtēšanu aprēķinos (Malcolm & Worrell 2001, Stener & Hedenberg 2003, Stener & Jansson 2005). Tādējādi aprēķinātais H^2 un CV_g bija nedaudz zemāki nekā ziņots iepriekšējos pētījumos, kur H^2 bija 0,07–0,56 koku augstumam un 0,11–0,59 d, bet CV_g šīm pazīmēm bija attiecīgi 5–14% un 9–21% (Malcolm & Worrell 2001, Stener & Hedenberg 2003, Stener & Jansson 2005). Tomēr augstuma un d iedzimstamība dažādos pētījumos ir ļoti atšķirīga (Stener & Jansson 2005). Ņemot vērā pētāmo pazīmju atšķirīgo ģenētisko kontroli, MV H^2 un CV_g bija vidēji (0,16 un 21,8), līdzīgi kā tas novērots Zviedrijā (Stener & Hedenberg 2003).

Āra bērzam tiek ziņots par ~ 10% selekcijas efektu augstumam un 20% d augstvērtīgākajiem 10% kloniem 7–11 gadu vecumā (Stener & Hedenberg 2003, Stener & Jansson 2005), bet atbilstošs realizētais selekcijas efekts šī pētījuma stādījumā iespējamās galvenās cirtes brīdī bija attiecīgi aptuveni 17 un 5 reizes mazāks. Katram mainīgajam lielumam trīs labāko klonu atlase deva attiecīgi 3,8%, 0,6% un 2,7% selekcijas efektu d, h un MV. Tas var liecināt par vājām korelācijām starp dažādiem vecumiem, kā arī atspoguļo zemāku iedzimstamību un augstu mainību, ko rada spēcīga vides ietekme. Tomēr nebija pieejami agrāki mērījumi pētītajā stādījumā, lai veiktu salīdzināšanu.

Vērtētā plantācija bija sasniegusi galvenās cirtes kritērijus pēc caurmēra jau 40 gadu vecumā. Augstāks ražīgums (līdz 8,90 m^3 ha^{-1} $gads^{-1}$ (Oikarinen 1983), salīdzinot ar 5,25 m^3 ha^{-1} $gads^{-1}$ pētītajā stādījumā) un laba stumbra kvalitāte varētu tikt sasniegta tradicionālajās plantācijās ar augstāku stādīšanas biezumu (Niemistö 1995a), lai gan stādīšanas attāluma palielināšana neietekmē augstuma pieaugumu (Niemistö 1995b). Tomēr samazinātā konkurence un iepriekš atlasītā stādāmā materiāla izmantošana acīmredzami uzlaboja vērtētā bērza sortimentu struktūru, nobīdot tā sadalījumu uz augstvērtīgākiem sortimentiem, tādējādi norādot uz zemas biezības klonu plantācijas efektivitāti apaļkoksnes ražošanai un iespējamu turpmāku ekonomisku uzlabojumu zemas biezības īscirtmeta plantācijās. Zemākas ierīkošanas izmaksas lielāka stādīšanas attāluma dēļ kopā ar atlasītu stādmateriālu varētu būt faktors, lai izvēlētos zemāka biezuma stādījumus. Lielāku vērtību rada ne tikai koksnes apjoma pieaugums, bet arī uzlabota stumbru kvalitāte, kas rezultējas ar vērtīgākiem sortimentiem (Moore et al. 2018). Selekcijas efekts produktivitātei varētu nebūt pilnībā izteikts biezās audzēs, jo bērzs saglabā spēcīgu augšanu, ja tam ir zema konkurence audzē (Hynynen et al. 2010).

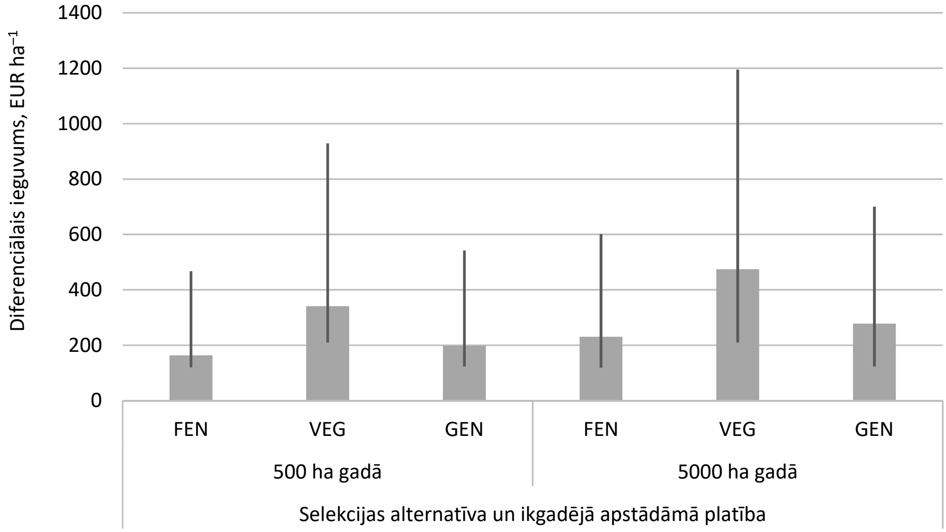
Latvijā nav īpaša regulējuma izcilo koku veģetatīvi pavairotu klonu praktiskai izmantošanai. Klonu vai klonu maisījumu stādīšana atļauta bez īpašiem ierobežojumiem. Veģetatīvā pavairošana tiek regulēta, līdzīgi kā lielākajā daļā ES valstu. Veģetatīvi pavairot drīkst tikai meža reproduktīvo materiālu no kategorijām “atlasīts”, “uzlabots” un “pārāks”. Kloniem un klonu maisījumam kategorijā “uzlabots” maksimālais pavairošanas apjoms (pēcnācēju vai rametu skaits) ir viens miljons pieaugušu augu. Materiālam no “pārāks” kategorijas nav pavairošanas daudzuma ierobežojumu.

5.3. Finansiālais ieguvums no selekcionēta āra bērza izmantošanas (VI un VII publikācija)

Āra bērza selekcijas finansiālā ieguvuma analīzes rezultāti liecina, ka visaugstākā koku selekcijas izmaksu NPV ir VEG alternatīvai, kam seko GEN (60% no VEG izmaksām) un FEN (40%). FEN alternatīvas selekcijas efekts ir aptuveni 79% no pārējām alternatīvām, kas ir saskaņā ar teoriju (Falconer & Mackay 1996) un atspoguļo palielinātu atlases precizitāti, pamatojoties uz pēcnācēju pārbaudēm. Vērtētajā situācijā (2010. gada cenas un izmaksas, bērza stādīšana vidēji nedaudz zem 500 ha gadā, paredzamais selekcijas efekts augstumam un caurmēram 14% (FEN) un 18% (VEG un GEN), mērķtiecīga un tradicionāla mežkopība pielietota vienādās platību proporcijās) vislielākais diferenciālais ieguvums tiek panākts VEG alternatīvā, kam seko GEN un FEN (5.10. att.).

Rezultāti parāda, ka selekcijas pārākums, pamatojoties uz klonu testēšanu (VEG), saglabājas visā selekcijas efekta līmeņu amplitūdā, kas pārsniedz 10%, un pieaug absolūtā vērtībā, jo augstāks ir selekcijas efekts. Tas saskan ar *L.-G. Stener* un *G. Jansson* (2005) secinājumiem, kuros arī tika atzīmēts veģetatīvās (klonu) pārbaudes pārākums.

Šajā pētījumā izmantotie selekcijas efekta rādītāji atbilst citiem publicētiem aprēķiniem: 10 gadu vecumā āra bērzam konstatēts 10% ieguvums augstumam un

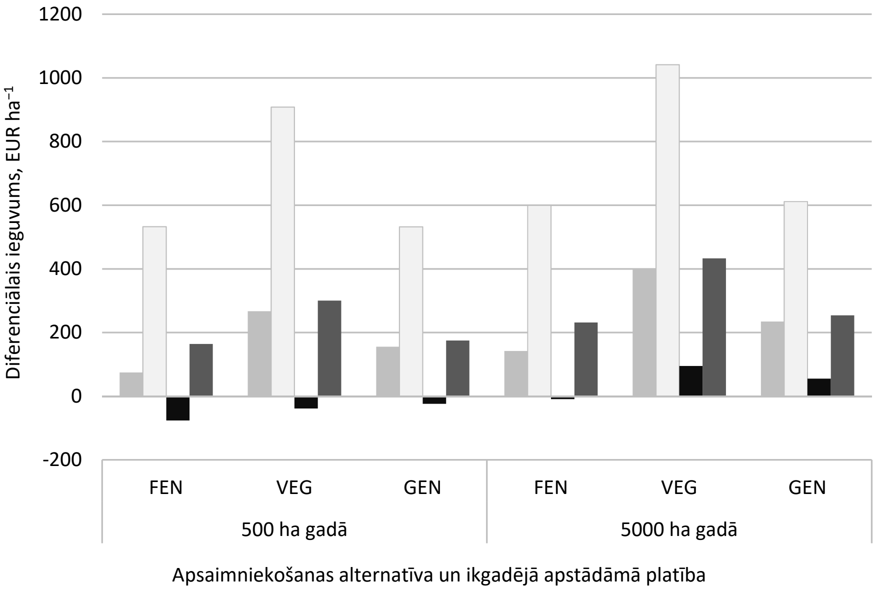


5.10. attēls. **Diferenciālā ieguvuma salīdzinājums selekcijas alternatīvām, EUR atbilstoši 2023. gada cenu līmeņa indeksam**

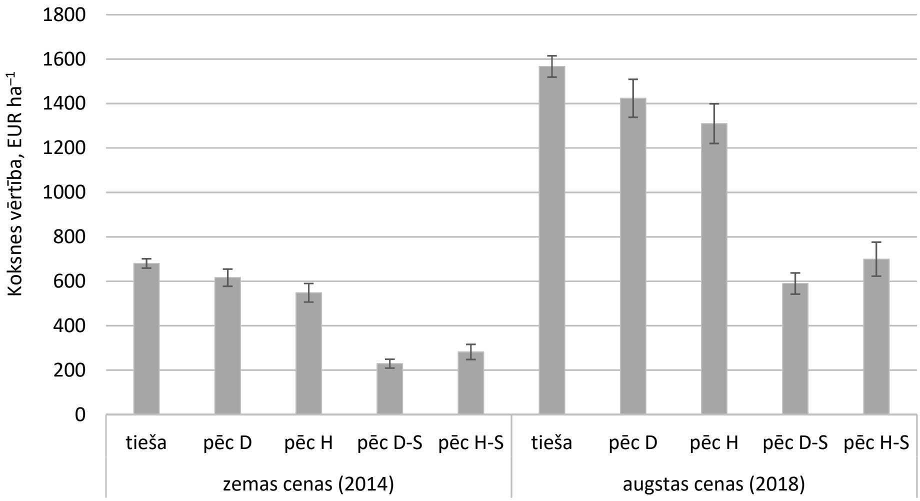
Stabiņi norāda vērtību pie vidējās apaļkoku sortimentu cenas; izkliedes rādītāji – minimālā un maksimālā apaļkoku sortimentu cena vērtētajā periodā (2006.–2010. gads). Selekcijas efekts augstumam un caurmēram 14% FEN, un 18% VEG un GEN alternatīvām, pieņemot, ka mērķtiecīga un tradicionāla mežkopība pielietota vienādās platību proporcijās

18% caurmēram (Stener & Jansson 2005). Citi pētījumi liecina, ka selekcijas efektam nav vērā ņemamu atšķirību 10 un 20–36 gadu vecumā, absolūtā vērtība krājai ir 29% (Hagqvist & Hahl 1998), kas aptuveni atbilstu 14% augstuma un caurmēra pieaugumam. Parastajai priedei aprēķināts 10–25% selekcijas efekts 21–32 gadu vecumā (augstumam) un prognozēts 20% krājai pieaugušā vecumā (Ståhl & Jansson 2002, Andersson et al. 2006, Jansson 2007) pirmajā selekcijas ciklā. Ir konstatēta ievērojama ģenētiskās variācijas samazināšanās starp savvaļas populāciju un atlasītiem pluskokiem, bet nākamajos selekcijas ciklos vērojamas tikai nelielas izmaiņas, pamatojoties uz pēcnācēju pārbaudēm (Bouffier et al. 2008). Tāpēc var pieņemt, ka nākamajā selekcijas ciklā turpmākas uzlabošanas iespēja paliek tāda pati kā pirmajā.

Diferenciālā ieguvuma vērtības ietekmē ne tikai selekcijas efekts, bet arī ikgadējā iestādītā platība un sortimenta cenu svārstības (5.11. un 5.12. att.). Ikgadējā iestādītā platība būtiski ietekmē diferenciālā ieguvuma vērtību: tai palielinoties no 500 ha gads^{-1}, kas vidēji iestādīts desmitgades laikā, līdz 5000 ha gads^{-1}, diferenciālais ieguvums vidēji palielinās par 60%, svārstoties no 25% līdz vairāk nekā 200%. Tas saistīts ar nemainīgām izmaksām, kas iekļautas vienādojumā – jo platība kļūst lielāka, jo zemākas ir sēklu plantācijas ierīkošanas un uzturēšanas izmaksas uz vienu hektāru, ja materiālu audzē no selekcionētām sēklām. Spēcīgo saikni starp koku selekcijas procesa ekonomisko vērtību un platības lielumu, kurā izmanto selekcionētu meža reproduktīvo materiālu, atzīmē arī citi autori (Ledig & Porterfield 1982).



5.11. attēls. **Mežkopības sistēmas izmantošanas ietekme uz diferenciālo ieguvumu no mežsaimniecības gadā ar augstām (2007. g.) un zemām (2009. g.) koksnes cenām, EUR atbilstoši 2023. gada cenu līmeņa indeksam:**
2007 tradicionālā 2007 mērķtiecīga 2009 tradicionālā 2009 mērķtiecīga
Selekcijas efekts augstumam un caurmēram 14% FEN, un 18% VEG un GEN alternatīvām



5.12. attēls. **Kopšanas cirtes koksnes vērtība (atskaitot mežistrādes izmaksas) 14 gadu vecumā, balstoties uz zemām un augstām koksnes cenām un 10% augstvērtīgāko vai sliktāko (-S) ģimeņu tiešas (pēc pazīmes) vai netiešas (pēc caurmēra vai augstuma 10 gadu vecumā) atlases**

Koksnes cenu svārstības būtiski ietekmē diferenciālo ieguvumu vērtību: starpība starp zemāko un augstāko cenu aprēķinu vienai un tai pašai alternatīvai un ikgadējai iestādītajai platībai svārstās 2,4–5,0 reizes. Tas norāda, ka svarīgi ir izvēlēties pareizu galvenās cirtes laiku, pamatojoties uz tirgus apstākļiem, lai gūtu visaugstākos ienākumus no selekcionētā materiāla izmantošanas meža atjaunošanā. Rezultāti arī pierāda, ka diezgan konservatīvs selekcijas efekta aprēķins nodrošina pozitīvu diferenciālo ieguvumu no koku selekcijas un selekcionēta materiāla izmantošanas, pat ar vismazāk izdevīgo alternatīvu un gados ar viszemākajām koksnes cenām.

Mežkopības sistēma būtiski ietekmē audzes parametrus. Rezultāti liecina, ka audzes ar "mērķtiecīgu" apsaimniekošanas režīmu, kas ietver tikai vienu krājas kopšanas cirti, nodrošina ievērojami augstāku diferenciālo ieguvumu nekā audzes ar "tradicionālo" apsaimniekošanas režīmu, neatkarīgi no selekcijas alternatīvām vai koksnes cenu apstākļiem (5.11. att.). Galvenais iemesls tam ir lielāks caurmēra pieaugums "mērķtiecīgā" apsaimniekošanā, sniedzot iespēju saīsināt rotācijas periodu, kā arī iegūt lielāku vērtīgāko sortimentu īpatsvaru. Pētījumā nevarēja aplūkot genotipa × mežkopības sistēmas mijiedarbības aspektus (piemēram, sākotnējo stādīšanas attālumu, jaunaudžu kopšanas ciršu intensitāti utt.). Šajā reģionā veikti tikai daži šī aspekta pētījumi, izmantojot ļoti ierobežotu parastās priedes materiālu. Tie norāda, ka genotipa-sākotnējās stādīšanas attāluma mijiedarbībai var būt praktiska nozīme (Persson 1994, Roth et al. 2007). Sortimentu izvēle mūsu pētījumā balstās tikai uz dimensijām, un kvalitāte netiek ņemta vērā. Tomēr pētījumi liecina, ka finierkluču īpatsvaru līdz pat 90% nosaka zaru kvalitāte (Hagqvist 2001). Ģenētika ir pat svarīgāka nekā mežkopība, nosakot bērza kvalitātes pazīmes, piemēram, dabisko atzarošanos (Zālītis & Zālītis 2002), zara diametru un leņķi (Hagqvist & Hahl 1998), koksnes kvalitāti (Koski & Rousi 2005). Ģenētikai ir būtiska ietekme arī uz koku slaidumu (Kroon et al. 2008). Tāpēc lielāka vērtīgāko sortimentu kvalitāte un īpatsvars varētu būt nozīmīga diferenciālā ieguvuma daļa no selekcionētā materiāla izmantošanas un varētu tikt apskatīta tālākos pētījumos, tiklīdz būs pietiekami daudz datu no Nacionālā meža monitoringa un vecākiem bērzu izmēģinājumiem. Augstākās klases apaļkoku vidējo īpatsvaru varētu noteikt arī, izmantojot vienādojumus, ko izstrādājis P. Zālītis un kolēģi (Zālītis et al. 2002), taču tas neļauj ņemt vērā papildu ieguvumu no kvalitātes uzlabošanas. Mūsu pētījumā tiek izmantota nemainīga proporcionāla uzlabojuma pieeja, kas pieņem vienādu selekcijas efektu jebkurā vecumā. Tomēr selekcijas efekts dažādos vecumos var būt atšķirīgs, un kopšanas režīmu varētu optimizēt, lai iegūtu vislielākos ieguvumus no selekcionēta materiāla izmantošanas.

Ņemot vērā iepriekš minēto – kopšanas režīms nav optimizēts, kvalitātes pazīmes nav aprēķinātas un augstākās klases finiera sortiments nav vērtēts –, kā arī varbūtību, ka nebūs nepieciešama papildu kopšana stādītajām audzēm salīdzinājumā ar dabīgi atjaunotajām, var teikt, ka šī pētījuma rezultāti ir tuvu zemākajai diferenciālo ieguvumu aprēķina robežai no selekcionēta materiāla izmantošanas. Šajā pētījumā izmantotā procentu likme (3%) var šķist diezgan zema, taču tā atbilst vērtībai, ko parasti izmanto mežsaimniecības ekonomiskajā analīzē (Pesonen & Hirvelä 1992, Pentinten 1999).

Stādījumā, kurā tika pētīta **selekcijas ietekme uz ienākumiem pirmajā krājas kopšanas cirtē**, vidējais d un h (± ticamības intervāls) 14 gadu vecumā bija attiecīgi 9,1 ± 0,2 cm un 13,4 ± 0,2 m; audzes krāja bija 91 ± 1,9 m^3 ha^{-1}. Iedzimstamība kokmateriālu vērtībai un ierastajai atlases pazīmei d bija ļoti līdzīga (5.8. tab.). Tomēr lietkoksnes īpatsvaram bija mazāka iedzimstamība. Selekcijas efekta vērtībām bija līdzīga tendence kā CV_a. Selekcijas efektam no tiešas atlases vai no atlases pēc d bija nelielas atšķirības.

Aprēķinātā iedzimstamība (5.8. tab.) nozīmē augstu potenciālu d un kokmateriālu vērtības palielināšanai ar selekcijas metožu palīdzību (Stener & Hedenberg 2003). Tā bija augstāka nekā novērots bērziem Norvēģijā (0,23; Skrøppa & Solvin 2019) un Zviedrijā (0,32; Stenner & Jansson 2005). Augstākas selekcijas efekta vērtības, iespējams, saistītas ar daudzveidīgu bērza populāciju struktūru Latvijā (Gailis et al. 2012), kas ir veģetācijas postglaciālā perioda rekolonizācijas rezultāts Ziemeļeiropā. Attiecīgi augstāka ģenētiskā daudzveidība ļāva iegūt plašāku fenotipu spektru, tādēļ materiāla intensīvā atlase bija efektīva (Palmé et al. 2003).

5.8. tabula

Iedzimstamības koeficients (h^2), aditīvās ģenētiskā variācijas koeficients (CV_a) un selekcijas efekts (GG_10%) āra bērza pluskoku pēcnācēju plantācijā 14 gadu vecumā

Pazīme	Iedzimstamības koeficients h^2 ± standartnovirzes	Aditīvās ģenētiskās variācijas koeficients CV_a, %	Selekcijas efekts GG_10% tiešā atlasē	Selekcijas efekts GG_10% atlasē pēc caurmēra
Caurmērs	0,49 ± 0,08	8,4	8,9	8,9
Lietkoksnes īpatsvars	0,18 ± 0,07	3,7	1,7	1,6
Koksnes vērtība (zemas cenas)	0,49 ± 0,08	22,7	26,9	26,3
Koksnes vērtība (augstas cenas)	0,50 ± 0,075	20,0	22,9	22,5

Aditīvās ģenētiskās variācijas koeficienti (CV_a) svārstījās attiecīgi no 3,7% līdz 22,7% lietkoksnes īpatsvaram un koksnes vērtībai (5.8. tab.). CV_a caurmēram bija salīdzinoši zems, ko varētu izskaidrot ar audzes konkurences ietekmi (Stenner & Jansson 2005, Egbäck et al. 2018, Zeltiņš et al. 2018), bet augstāks koeficients koksnes vērtībai varētu tikt skaidrots ar d un h kumulatīvo efektu. Tomēr aprēķinātā selekcijas efekta tendence augstvērtīgākajām 10% ģimenēm bija līdzīga CV_a tendencei un bija līdzīga rezultātiem citos pētījumos. Piemēram, *L.-G. Stener* un *G. Jansson* (2005), un *R. Hagqvist* un *J. Hahl* (1998) konstatēja 18% un 11% uzlabojumu d, salīdzinot pirmās kārtas plantāciju pēcnācējus ar mežaudžu pēcnācējiem 7 līdz 12 gadu vecumā. Šāds selekcijas efekts pamato genotipu atlases efektivitāti (Zeltiņš et al. 2018).

Kopšanas cirtē izzāģēto koku d un h bija attiecīgi 8,0 ± 0,3 cm un 13,0 ± 0,4 m. Atstāto koku vidējais d un h bija attiecīgi 10,0 ± 0,3 cm un 10,0 ± 0,4 m. Iegūto apaļkoku sortimentu apjoms vidēji bija 28,0 ± 0,8 m^3 ha^{-1}.

Ienākumi no krājas kopšanas cirtes ievērojami atšķīrās atkarībā no kokmateriālu tirgus svārstībām: pie zemām kokmateriālu cenām tie vidēji bija 1275 ± 29 EUR ha^{-1}, pie augstām cenām – 1863 ± 33 EUR ha^{-1} (5.9. tab.). Līdzīgas atšķirības novēroja ar NWV (5.12. att.): augstvērtīgākās ģimenes sasniedza 1424 ± 86 EUR ha^{-1} pie augstām kokmateriālu cenām un 616 ± 39 EUR ha^{-1} pie zemām cenām; atbilstošie vidējie rādītāji brīvapputes pluskoku pēcnācēju stādījumā bija statistiski ievērojami mazāki: attiecīgi 1030 ± 25 EUR ha^{-1} un 426 ± 11 EUR ha^{-1}. Atlasītajām ģimenēm bija pozitīva NPV (ar 3% diskonta likmi) no 370 līdz 741 EUR ha^{-1}. Turklāt augstvērtīgākajām ģimenēm NPV pie augstām kokmateriālu cenām un zemu diskonta likmi bija par 50% augstāka salīdzinājumā ar izmēģinājuma vidējo rādītāju; pie zemām kokmateriālu cenām uzlabojums bija 35%. Vismaz daļēji to varētu skaidrot ar zemām ierīkošanas izmaksām: augstas kvalitātes stādmateriāls nodrošināja nepieciešamību tikai pēc vienas agrotehniskās kopšanas. Salīdzinot ar neselekcionētas parastās priedes audzēm Zviedrijā (Ahtikoski et al. 2018), aprēķinātā NPV augstvērtīgākajām āra bērza ģimenēm 14 gadu vecumā bija augsta: 2305 un 1488 EUR ha^{-1}, attiecīgi pie augstām un zemām kokmateriālu cenām. Tas liecina par lielu potenciālu uzlabota bērza reproduktīvā materiāla izmantošanai mežsaimniecībā, radot iespēju gūt arī agrus ienākumus no ieguldījumiem. *R. Simonsen* et al. (2010) un *G. Jansson* et al. (2017) norāda, ka ģenētiski uzlabots materiāls ievērojami palielina koku augšanu ar zemākām investīciju izmaksām. Tomēr *G. Jansson* et al. (2017) norādīja, ka ar IRR 5,3% ienākumi joprojām ir zemi, jo pieaug ierīkošanas un mežistrādes izmaksas, ko, iespējams, nevar kompensēt ar uzlabotu augšanu.

5.9. tabula

Selekcionēta āra bērza finanšu rādītāji pirmajā krājas kopšanas cirtē 14 gadu vecumā

Koksnes cenas	Izmēģinājuma vidējais				Augstvērtīgākās 10% ģimenes			Mazvērtīgākās 10% ģimenes		
	WV, EUR ha^{-1}	NPV		IRR, %	NPV		IRR, %	NPV		IRR, %
		3%	5%		3%	5%		3%	5%	
Augstas (2018. g.)	1863 ± 33	741	451	8,1	1484	1018	9,4	106	–33	4,5
Zemas (2014. g.)	1275 ± 29	370	171	6,7	780	484	8,3	–7	–117	2,9

Saīsinājumi: WV – kopējā iegūtās koksnes vērtība.

Tomēr Latvijā ierīkošanas un apsaimniekošanas izmaksas nepalielinātos tik strauji kā Zviedrijā. Aprēķinātais IRR vidējiem un atlasīto ģimeņu rādītājiem uzrādīja labu rentabilitāti pat pie zemām koksnes cenām, svārstoties no 6,7% līdz 8,3% (5.9. tab.), tādējādi pārsniedzot dabiski atjaunojušos audžu vērtības (Jansson et al. 2017). Sliktāko ģimeņu IRR sasniedza 2,9% nelabvēlīgā kokmateriālu tirgus situācijā un 4,5% labvēlīgā tirgus situācijā. Kopumā šie rādītāji var būt mazāki zemākas krājas dēļ, ja tiek izmantots lielāks stādīšanas attālums. Tāpat vērtība samazinātos ar vēl agrāku krājas kopšanas cirti, tiecoties uzlabot paliekošo bērzu augšanu. Tādēļ būtu lietderīgi veikt papildu aprēķinus, izmantojot augšanas modeļus, lai optimizētu stādīšanas attālumu. Šī pētījuma galvenā vērtība ir parādīt praktisko ieguvumu, kas iegūts no lielas (23,1 ha) krājas kopšanas cirtes platības agrā vecumā, un faktisko pievienoto vērtību, ko dod meža selekcija.

SECINĀJUMI UN REKOMENDĀCIJAS

Secinājumi

1) Augstvērtīgu un mainīgam klimatam piemērotu bērza genotipu efektīvāka atlase veicama izdalītajā Austrumu provenienču reģionā, kas raksturojams ar augstāku ģenētisko mainību (iedzimstamību) vērtētajām bērza fenotipiskajām pazīmēm, kā arī augstāku produktivitāti. Ir lietderīgi saglabāt izdalītos bērza provenienču reģionus, jo pēcnācēju pārbaužu analīzes rezultāti apliecina ar ātraudzību saistīto pazīmju vērtību atšķirības starp šiem reģioniem.
2) Selekcija var nodrošināt nozīmīgu bērza ātraudzības un stumbra kvalitātes pieaugumu, par ko liecina augstas iedzimstamības koeficienta vērtības koku augstumam, caurmēram, stumbra tilpumam (vidēji $h^2 = 0{,}43$), kā arī zarojumu un stumbra taisnumu raksturojošām pazīmēm (vidēji $h^2 = 0{,}32$) jaunaudzes vecumā. Līdzīgi rezultāti iegūti arī galvenās cirtes kritērijiem atbilstošā stādījumā (attiecīgi vidēji $H^2 = 0{,}18$ un $H^2 = 0{,}31$). Zema genotipa × vides mijiedarbības ietekme un augsta ģenētiskā korelācija starp stādījumiem vairākumam analizēto pazīmju liecina par iegūto rezultātu vispārināmību.
3) Iespējams vienlaikus nodrošināt augstu selekcijas efektu gan ātraudzību, gan stumbra kvalitāti (zarojumu) raksturojošajām pazīmēm, ko apliecina relatīvi augsta ģenētiskā variācija (vidēji attiecīgi $CV_a = 13{,}0\%$ un $CV_a = 6{,}8\%$ jaunaudzēs, un $CV_g = 6{,}4\%$ un $CV_g = 14{,}3\%$ vecākā stādījumā) un vāja savstarpējā ģenētiskā korelācija starp šīm pazīmju grupām.
4) Augstvērtīgāko (10%) ģimeņu atlase pēc dažādiem selekcijas indeksiem pirmajā retināšanā nodrošina par 27%–60% augtāku iegūstamās koksnes vērtību un, atkarībā no koksnes cenas, par 16–23 procentpunktiem augstāku iekšējās atmaksāšanās likmi investīcijām stādījuma ierīkošanā un kopšanā. Bērza ģenētiskajām īpašībām ir būtiska ietekme uz bērza audzes finansiālo vērtību kā pirmās retināšanas, tā galvenās cirtes kritērijiem atbilstošā stādījumā.
5) Noskaidrots, ka atsevišķu klonu pavairošanas sekmes ietekmē barotnes sastāvs.
6) Diferenciālais ieguvums no bērza selekcijas otrā cikla realizācijas ir pozitīvs, ja selekcijā, sēklu plantāciju apsaimniekošanā un meža stādīšanā ieguldītajiem līdzekļiem tiek piemērota 3% reālā interešu likme. Tā vērtība palielinās proporcionāli selekcijas darba rezultātu realizācijai praksē, t.i., ikgadējai iestādītajai platībai.

Rekomendācijas

Rekomendējams palielināt mērķtiecīgi atjaunoto āra bērza audžu īpatsvaru, īpaši platībās, kur augšanas apstākļi ir piemērotākie augstražīgām mežaudzēm, tādējādi nodrošinot gan augstāku finansiālo atdevi no investīcijām meža selekcijā, gan efektīvāku meža zemes izmantošanu. Papildus audžu ražības paaugstināšanai rekomendējams izmantot meža reproduktīvā materiāla kategorijas "pārāks" veģetatīvi pavairotu stādmateriālu.

Otrā selekcijas cikla realizāciju rekomendējams veikt saskaņā ar ģimeņu-klonu atlases shēmu, pēcnācēju pārbaužu galējo novērtējumu paredzot jau 10 gadu vecumā un, lai būtu iespējams veikt precīzu stumbra kvalitāti ietekmējošo pazīmju novērtēšanu, nodrošinot stādījuma ietvaros iespējami homogēnus apstākļus.

Rekomendējams selekcijas populācijā iekļaut lielāku genotipu īpatsvaru no Austrumu provenienču reģiona, kā arī adaptācijas pazīmju uzlabošanai ietvert bērzus no Polijas ziemeļu daļas (53–54° Z pl.). Nav pieļaujama bērza reproduktīvā materiāla ar izcelsmi uz ziemeļiem no Latvijas vai uz dienvidiem no 53° Z pl. izmantošana meža atjaunošanā bez speciālu konkrētā materiāla augšanas un kvalitātes novērtējuma stādījumu ierīkošanas mūsu valstī.

Rekomendējams izmantot promocijas darba ietvaros pēcnācēju pārbaužu stādījumos atlasītos pluskokus (61), kā klonus sēklu ieguves plantāciju ierīkošanai kategorijas "pārāks" meža reproduktīvā materiāla ražošanai.

Rekomendējams izmantot promocijas darba ietvaros izstrādāto tehnoloģiju un atlasītos āra bērza klonus veģetatīvai pavairošanai stādmateriāla ražošanai.

BREEDING OF SILVER BIRCH (*Betula pendula* Roth) IN LATVIA

Analysis of the knowledge of the theme / literature review

Birch species (*Betula* L.) is an important component of Europe's temperate and boreal forests, accounting for around 11% of the total forest area in Europe (Forest Europe 2020). In Latvia, birch covers almost a third of the total forest area (MSI 2023) and is the most common genus with two economically important species: silver birch (*Betula pendula* Roth) and downy birch (*Betula pubescens* Ehrh.). The two species are characterised by a similar shape and a white stem, which can reach a height of 20–30 m, as well as a similar anatomy of wood, so there is no distinction between them in forest inventory, logging and woodworking. The silver birch is characterised by a pronounced rugged bark at the bottom of the stem, with warts on the young shoots and pointed leaves. For the downy birch, the bottom part of the stem is much smoother, leaves are oval with downy stalks. Silver birch is a diploid species with 28 chromosomes (2n = 28), while downy birch is a tetraploid (2n = 56; Helms & Jørgensen 1925). Although hybrids between the two species are rare due to biochemical incompatibility (Hagman 1971), they can sometimes occur (Jonsell & Karlsson 2000). Morphological differences between species are often not pronounced, which makes it difficult to distinguish them in nature, so a chemical method of identifying species has been developed for their safe separation based on the chemical characteristics of the bark (Lundgren et al. 1995, Liepiņš et al. 2024).

Both birch species regenerate abundantly with seeds that are small and light, spread efficiently with wind, can cover long distances, contributing to the species' wide spread, gene flow and high genetic diversity (Jonsell & Karlsson 2000, Wagner et al. 2004). Birches are monoecious trees with male and female flowers. Seeds are usually formed by cross-pollination of trees due to a biochemical mechanism of self-incompatibility (Hagman 1971). Birch blooms at the same time as leaves appear in spring, while in northern Europe the seeds ripen from July to August (Sarvas 1952). Birch trees vary widely in the volume and quality of the annual seed crop; in northern Europe rich seed crop every 2–3 years (Koski & Tallqvist 1978). Both species are also able to regenerate vegetatively by forming coppice shoots. This ability is particularly distinct in young trees (under 20–30 years) and for downy birch (Ferm, Kauppi 1990). Birch, as a pioneering species, naturally regenerates abundantly when seed sources are available. However, planting is preferable if the aim is to improve the quality of the tree branching or stems of the next generation, to ensure greater fast-growth. This applies equally to regeneration and afforestation (Hynynen et al. 2010).

Birch standing volume (yield) in Latvia is on average 261 m^3 ha^{-1}, but varies regionally (224–301 m^3 ha^{-1}). More productive stands are found in the Eastvidzeme and Zemgale; the populations of Limbaži, Ogre and Jēkabpils stand out with high yields. The average quality of the stands is higher on fresh mineral soils, given that on wet mineral soils the trees are smaller and with a higher admixture of poor-quality downy birch. The populations of Naukšēni, Svirlauka, Ābele, Kuprava and Kandava are of the highest quality (Zālītis 2006).

Birch wood is prized for its fine fibre, light colour and durability, which makes it suitable for a wide range of applications, from furniture and floors to plywood and veneer (Luostarinen & Verkasalo 2000, Verkasalo et al. 2017). The high-value birch assortments are mainly used in the production of plywood and sawn timber, further processed into carpentry products, panels and parquets. Silver birch prevails in timber production because it is more fast-growing, with better stem shape and higher wood density compared to downy birch (Heräjärvi 2004). Comparing silver and downy birch, it has been found that the average height and diameter of the two species are 25 and 22 m, and 35 and 32 cm, respectively (Zālītis 2006). It is therefore the silver birch that has been the focus of breeding programmes in order to improve these forestry-relevant characteristics (Viherä-Aarnio & Velling 1999). Smaller birch assortments are mainly used in the pulp industry, but high-quality roundwood assortments are the main goal of forest management, taking into account their value (Hynynen et al. 2010).

As climate change affects forest ecosystems, the adaptability and fast-growth of birches, especially silver birch, stimulates interest in its wider use in forestry in the Baltic Sea region. These species are well suited for use in an adaptive forest management approach aimed at improving forest resilience to changing environmental conditions, for example by replacing more unstable coniferous tree pure stands. Afforestation can contribute to climate neutrality by accumulating atmospheric carbon in newly created stands, as well as producing raw material with a high substitution effect (Lutter et al. 2021). The results of silver birch breeding programmes reflect the potential of the species in the production of large-scale high-quality timber, making it one of the main species in future forestry practices. In Latvia, comprehensive silver birch breeding was started in the mid-1990s. As basic breeding material, 921 plus trees and superior stand trees have been phenotypically selected in 26 natural stands across the country, and progeny trials have been established in 1999 and 2000. Although breeding of coniferous species (Scots pine *Pinus sylvestris* L. and Norway spruce *Picea abies* (L.) H. Karst.) in Latvia has a longer history, silver birch as a commercially important tree species is included in a long-term breeding programme aimed at developing seed production and increasing the financial value of forests (Jansons 2008). Targeted regeneration with such improved material is important to mitigate the negative impacts of climate change: both directly, by ensuring the use of suitable genotypes with high phenotypic plasticity, and indirectly, in combination with forestry methods, by increasing radial growth and reducing the risk of major abiotic factors (wind).

The objective of the doctoral thesis is to describe the results of the breeding of silver birch so far and the possibilities for its effective use. The research tasks of the doctoral thesis are:

1) Characterise the genetic parameters of economically significant traits of the birch breeding population;
2) To evaluate the effect of genetics on the success of vegetative propagation of silver birch;
3) To evaluate the impact of breeding on the financial value of birch plantations and the profitability of the second breeding cycle.

1 BREEDING OF SILVER BIRCH IN LATVIA AND NEIGHBOURING COUNTRIES

1.1 Evaluation of stands and selection of plus trees for breeding and seed production

The beginning of breeding is based on the selection of superior individuals for certain phenotypic traits. In forest breeding, the search for such trees takes place in pre-selected stands, increasing the probability that the phenotypically detectable superiority is hereditary. Initially, birch stands were selected on the basis of their inventory parameters – site index ≥ I, pure or mixed stands with other species ≤ 20%, area ≥ 2 ha, age ≥ 30 years – using the State Forest Service database (at the time of selection: 'Forest Fund'). The next step was evaluating the stands by the relative branch thickness, branch angle, stem straightness, visible presence of diseases (Table 1.1). Plots for this assessment were placed in subjectively defined characteristic locations. The number of plots varied depending on the area of the stand or group of stands (considered as such and evaluated together, if adjacent to each other) and ranged from 2 to 6. A circular plot was formed by all trees within sight of the plot center.

First, the proportion of minus trees is estimated. **Minus trees** are the least valuable part of the stand. These are usually trees lagging in growth that are felled in thinnings. Minus trees also include those with thick branches, wide crowns, multiple tops and crooked stems. All trees with signs of disease – dead tops, rot, bird cavities, etc. are also included in this group. Stands with more than 50% of trees with thick branches, crooked stems and signs of disease are called minus stands, and no selection of plus trees is allowed in them.

The stand is not further evaluated if the number of minus trees exceeds 20% within the visibility of a circular plot. The selected circular plot lists all the trees to be evaluated. By applying the defected trees to the total number of evaluated trees, gives the percentage of "minus trees", which reduces the score of the stand accordingly: if the number of minus trees is 0–4% – 0.0 points – the score does not decrease; if 5–8% – a reduction in the score by 0.2 points, and then every 4% more – the score of the stand decreases by 0.2 points. For birches, minus trees are considered: trees with dichotomy branching, "funnel shape", "broom shape", trees with spike knots and thick branches.

Characterisation of the stand is carried out on the basis of the ideal stand with a score of five points. The ideal traits of a birch stand: thin branches; branch angle of 60° to 90°; straight stems; there are no minus trees in the stand. In the evaluation of the stands, the notes shall indicate different features, management regime and other information of interest.

Table 1.1

Stand characterisation and evaluated traits

Trait	Evaluation, points				
	1	2	reduces the score of stand	3	reduces the score of stand
Branch thickness	thin	average	–0.5	thick	–1
Stem straightness	straight	1 bend	–0.5	≥ 2 bends	–1
Branch angle *	if the angle of branches is less than 60°, the score of the stand is reduced by 0.5 units for each 15°				

* Determined in each sample plot, measuring it in the middle of crowns.

In the selected stands **plus trees** were identified – the tallest and thickest trees of the dominant storey of stand, which, among the adjacent growing trees of the same age, stand out for fast-growth and high stem quality. Plus trees are rare in stands, they are with straight, well self-pruned stems, no signs of disease, with narrow to medium-width crown and with thin to medium-thick branches. Branches must be perpendicular (or close to that) to the stem.

The main fundamentals of the selection of plus trees are similar for all tree species, but each has its own particularities in the assessment of traits and breeding objectives. The resources of the different tree species regulate the intensity of the selection. For the selection of plus trees, the best naturally formed stands should be selected, taking into account the forest seed production districts. The selection of plus trees may also be allowed in planted stands, indicating it in the description of the trees. After reassessment (attestation) of the plus tree, it is defined as a **superior tree**.

Birch plus trees are sought in 30–70-year-old birch stands of the highest site index. The tallest and thickest trees of the stand are chosen as plus trees, with straight, smooth and well-pruned stems, with occluded branches at the bottom part. Stems with epicormic shoots are not suitable, their branch-free smooth bottom part must be as long as possible relative to the crown part of the stem. The crown must be as narrow, oval or pyramidal as possible, with short, thin branches forming the widest possible angle against the stem. Plus trees must produce lots of seeds, have healthy foliage and a healthy stem. When choosing plus trees, the position of adjacent trees should be taken into account and their potential impact on self-pruning.

The first 25 silver birch plus trees included in the establishment of the first birch seed orchard were selected from 1969 to 1971 in the Forest Research Station “Kalsnava” (1), in Liepupe, Vitrupe and Augstroze forestries of the Limbaži forest district (23), and in the Rūjupe forestry of Mazsalaca forest district (1). The information regarding the plus trees selected in the 70s is stored in the register of plus tree in the Latvian State Forest Research Institute ‘Silava’ (LSFRI ‘Silava’). Covering virtually all regions of Latvia, in the 90s following the established criteria for the evaluation of the stands, the best trees were selected in the selected best birch stands (not all of them are considered classic plus trees, but as the best trees of the respective stand (Fig. 1.2), from which seeds were harvested and seedlings produced for progeny trials). The trees selected in the stands no longer exist in nature.

1.2 Progeny trials of silver birch

Progeny trials are used for the evaluation of breeding material and selection of candidates for propagation and next selection cycle. For the **comparison of provenances – the geographical regions of origin of tree seeds** – the first progeny trial plantation of silver birch was established in 1975 in Vecumnieki Parish with 16 provenances of different origins. However, until now, there is a lack of a full evaluation of provenances in order to determine the suitability of birch reproductive material of different origins for Latvian conditions.

In evaluation of the overall geographical relationships in provenance trials, the survival, stem quality and growth rate of birch progenies originating in Finland, the Baltic States and Russia have been studied in trials in southern Finland (60° N) and central Finland (63° N), including 21 stands and individual trees originating from 54° to 63° N. In both trials tree height, diameter, standing volume ha^{-1}, relative stem taper, proportion of trees with stem defects (spike knots, double leaders) and survival were determined and compared at the age of 22. Significant differences have been identified between the provenances for all the traits assessed. As the geographical latitude of the seed provenance increases, the proportion of trees with stem defects decreases linearly and statistically significantly (in the trial in central Finland $p < 0.001$; in the southern part $p = 0.002$); as the geographical latitude

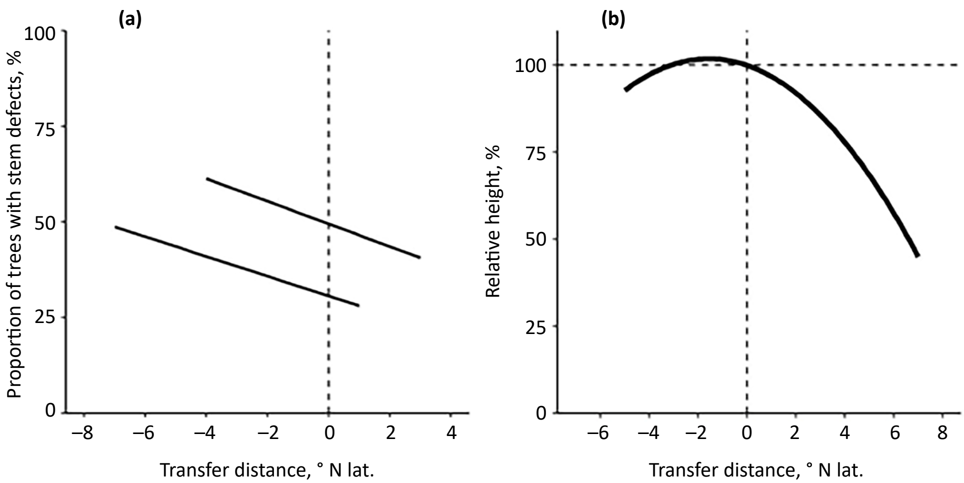


Figure 1.1 **Average percentage of trees with stem defects (a) and produtivity, characterised by relative height (b) of the various provenances, depending on the transfer distance in degrees of latitude**
(Viherä-Aarnio & Velling 2008, Viherä-Aarnio et al. 2013)

of the seed provenance decreased by 1 degree, the proportion of trees with stem defects increased by 3% (Fig. 1.1; Viherä-Aarnio & Velling 2008). A similar relationship has been observed with elk damage in birch stands: as the geographical latitude of the seed provenance and the height of the trees increase, the proportion of damage decreases (Viherä-Aarnio & Heikkilä 2006).

The evaluation of a wider range of latitude (54–67° N) showed that the lowest incidence of stem defects were for local or slightly more northern provenance trees, but increased as the distance from the south increased (Viherä-Aarnio et al. 2013). On the other hand, the relationship between the geographical latitude of origin and the wood density was not observed (Viherä-Aarnio & Velling 2017). There is a common relationship between Finnish provenance trials (Fig. 1.1) and provenance trials aged 8–11 in Great Britain and Ireland that transfering provenance north by two degrees of latitude improves productivity (higher tree height, diameter, higher yield than for local provenance) due to longer photoperiod without negative effect on survival (Viherä-Aarnio et al. 2013, Lee et al. 2015, Viherä-Aarnio & Velling 2017). It should be noted that transfer south or north beyond 2° reduces productivity (Viherä-Aarnio et al. 2013).

In the Nordic countries, the first birch **progeny trials** were established in Sweden in the 1940s, and H. Johnsson was the first to carry out comparative studies of the growth of birch families in geographically remote regions of origin and also began studies of birch provenances, establishing extensive plantations in 1973–1974 (Viherä-Aarnio & Velling 2008). On the basis of these trials, L.-G. Stener (1997), when studying differences in yield, stem quality and wood density among progenies of different origins, developed rules for the transfer of birch seeds, dividing Swedish territory into 4 breeding zones. However, the establishment of larger-scale progeny tests was started as part of the silver birch breeding programme in 1988–1990, selecting around 1,300 plus trees whose open-pollinated progeny (half-sib families) tests were established between 1992 and 1998 (Stener & Hedenberg 2003, Stener & Jansson 2005).

In Finland, silver birch breeding began with the selection of plus tree in the late 1940s, but developed more intensively in the late 60s when the method of mass production of seeds in polyethylene greenhouses (Lepistö 1973) was developed. The basic breeding material consisted of about 1,000 phenotypically selected plus trees. The first seed orchard was established in 1970 (Haapanen 2024). Extensive provenance progeny trials began in the 1960s in southern and central Finland and based on the results obtained, principles for seed transfer (Raulo & Koski 1977) were developed.

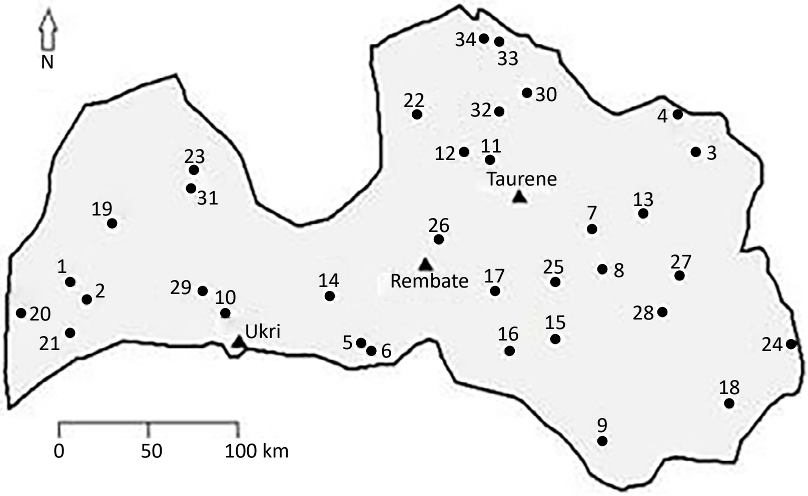


Figure 1.2 **Place of origin of the selected birch plus trees and best trees of forest stands**

Explanation: the number at the spot mark corresponds to the origin number in Table 1.3

In Lithuania, the long-term breeding programme for silver birch was launched in the 1990s, choosing forest stands for genetic resources, selecting seed stands and plus trees. The first series of progeny tests was established in 1999 and the first seed orchard was established in 2003, separating seed production for two provenance regions (Baliuckienė 2009).

In Latvia, with growing interest in the selection of deciduous trees, including silver birch, in the 90s the best trees and plus trees of forest stands were selected, they were felled to harvest seeds and begin growing seedlings, obtaining material for the establishment of very large and extensive progeny tests in Ogre municipality in Rembate parish (No. 54), Auce municipality in Ukri parish (No. 55), Vecpiebalga municipality in Taurene parish (No. 589), in area > 55 ha, covering > 900 open-pollinated families (origin of families in Fig. 1.2 and Table 1.3), which served as a base for future birch breeding.

Table 1.2

Provenance trials of silver birch established in 2004

Name of provenance	Total number of plants in				
	Šķēde MN No. 310	Auce MN No. 315 *	Kalsnava MN No. 236	Mežole MN No. 333	Svente par. No. 752
Rūjupe	400	400	400	400	400
Šķēde	400	400	400	400	400
Saikava	400	400	400	400	400
Viesīte	400	-	400	240	400
Kalsnava	400	400	400	400	400
Naukšēni	400	400	400	400	400

Name of provenance	Total number of plants in				
	Šķēde MN No. 310	Auce MN No. 315 *	Kalsnava MN No. 236	Mežole MN No. 333	Svente par. No. 752
Aizpute	400	400	400	400	400
Daliņi	400	-	275	-	-
Ziemeri	400	400	400	400	400
Kuldīga	400	200	400	200	400
Mālupe	400	120	400		400
Gaigalava	400	200	400	200	400
Medņi	400		200	150	200
Jaungulbene	400	150	200		200
Strenči	400	295	400	400	400
Gauja	400	200	400	300	400
Mērdzene	400	200	400	200	400
Total	6,800	4,165	6,275	4,490	6,000
Rūjupe **	400	-	400	-	400
Naukšēni **	200	-	200	-	-
Gaigalava **	200	-	200	-	-
Total	7,600	4,165	7,075	4,490	6,400
Trial net area, ha	3.8	2.1	3.5	2.2	3.2

* plantation has not survived; ** downy birch (for comparison).

In 1998, a provenance progeny trial was established in Rembate parish with an area of 3 ha (No. 53) with progenies of 15 different provenances, but in 2004, using plants grown in the experimental tree nurseries of Forest Research Station in 5 geographically different areas – provenance progeny trials were established in Forest Research Stations in the forest districts of Kalsnava, Mežole, Auce and Šķēde, and JSC 'Latvia's State Forests' unit 'Seeds and Seedlings' managed areas of Latgale seed nursery in Svente parish, with 4 replications in each site with block design with 100 or 50 seedlings, including 17 silver birch and 3 downy birch provenances, with the total area of 15 ha (Table 1.2).

The establishment of silver birch progeny trials in forest districts of Forest Research Station continues on a regular basis. From 2014, *in vitro* propagated progenies of clones have been included alongside progenies of open-pollinated families and controlled crossings. Currently 122 progeny trials with a total area of 274.3 ha have been established in Latvia for the assessment of birch breeding material in geographically different places. Planted in single-tree, block or row designs, marked in nature. Summary of the establishment of birch progeny trials in Table 1.4, their layout in Figure 1.3. The plantations have been registered in the Register of long-term trials of LSFRI 'Silava'.

Table 1.3

Origin of birch open-pollinated families in progeny trials

No. *	Origin **	Number of families		
		Rembate No. 54	Ukri No. 55	Taurene No. 589
1	Aizpute VVM Aizpute VM (1998)	-	17	10
2	Aizpute VVM Kalvene VM	-	2	2
3	Alūksne VVM Mālupe VM (1998)	-	6	6
4	Alūksne VVM Ziemeri VM (1998)	-	5	5
5	Bauska VVM Bauska VM	24	24	24
6	Bauska VVM Ceraukste VM	21	23	13
7	Cesvaine VVM Cesvaine VM	46	46	14
8	Cesvaine VVM Saikava VM (1998)	-	12	12
9	Daugavpils VVM Svente VM (1995)	9	10	10
	Daugavpils VVM Svente VM	34	4	10
10	Dobele VVM Īle VM	23	-	-
11	GNP Gauja VM	43	50	50
12	GNP Medņi VM	46	46	44
13	Gulbene VVM Dauksti VM	29	29	20
14	Jelgava VVM Garoza VM	21	21	8
15	Jēkabpils VVM Ābeles VM	35	35	13
16	Jēkabpils VVM Viesīte VM (1998)	-	-	8
17	Koknese VVM Koknese VM	13	13	12
18	Krāslava VVM Dagda VM	8	8	6
19	Kuldīga VVM Kuldīga VM	-	-	43
20	Liepāja VVM Grobiņa VM	25	25	-
21	Liepāja VVM Priekule VM	60	60	45
22	Limbažui VVM Limbaži s. pl.	8	8	-
23	LLU MPMS Šķēde VM	20	20	13
	LLU MPMS Šķēde VM (1998)	-	20	20
24	Ludza VVM Zilupe VM	9	9	9
25	MPS Kalsnava VM (1998)	-	18	13
26	Ogre VVM Suntaži VM (1995)	10	11	9
	Ogre VVM Suntaži VM	22	23	17
27	Rēzekne VVM Gaigalava VM	-	46	41
28	Rēzekne VVM Viļāni VM	25	7	7
29	Saldus VVM Blīdene VM	3	3	-
30	Strenči VVM Strenči VM	23	24	9
31	Talsi VVM Andumi VM (1995)	42	44	12
	Talsi VVM Andumi VM	8	10	8
32	Valmiera VVM Daliņi VM (1998)	-	27	24
33	Valmiera VVM Naukšēni VM	30	31	31
	Valmiera VVM Naukšēni VM (1998)	-	36	32

No. *	Origin **	Number of families		
		Rembate No. 54	Ukri No. 55	Taurene No. 589
34	Valmiera VVM Rūjupe VM (1998)	-	24	24
	Total	637	826	621

* The serial number in the table corresponds to the marks on the map in Fig. 1.2;
** Names of regional forestries (VVM) and districts within (VM) according to the division in the year of harvesting.

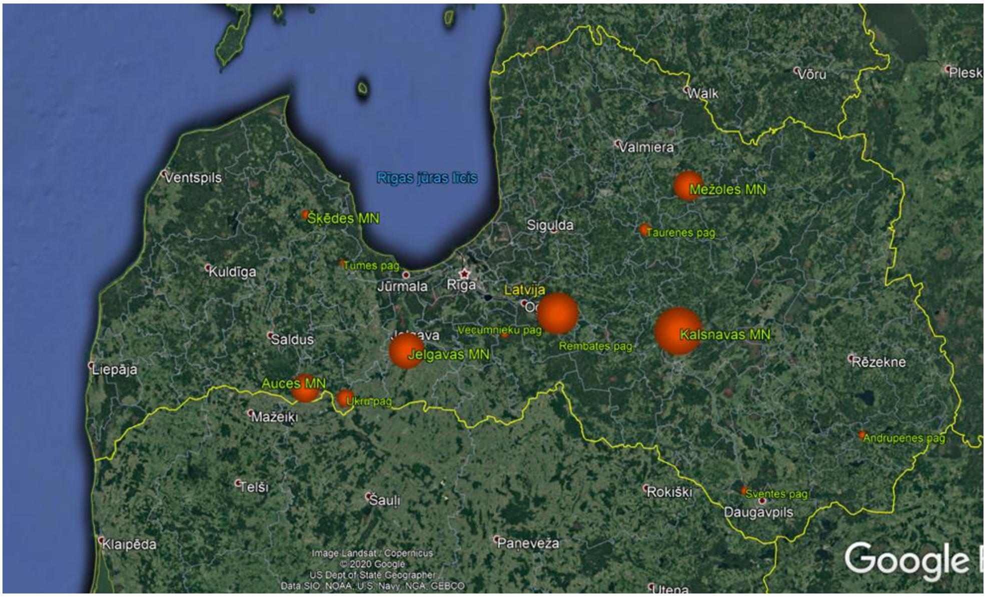


Figure 1.3 **Locations of silver birch progeny trials**

Research data on progeny trials of silver birch established in other countries are available. Until now, the amount of progeny trials established in Latvia for birch is wide enough and the age of trees is sufficient for obtaining valid conclusions, therefore a detailed analysis and evaluation of the data obtained over the years is necessary.

Table 1.4

The established progeny trials of silver birch

Location of site	Year of establishment	Number of trials	Area, ha	Year of measurement	Number of clones	Number of families / provenances / average samples of seed orchard	Number of crosses	No. of experiment
Auce MN	2007	28	74.514	-	-	101	-	633; 634; 876
	2010			-	-	2	96	736; 737
	2011			2023	-	99	145	754; 755
	2016			2020	16	-	-	928 *
	2019			-	17	72	31	1374; 1375; 1376*
	2020			-	44	-	-	1437 *; 1438 *
	2021			-	34	4	-	1471*; 1472; 1473*
	2022			-	20	129	69	1689; 1690; 1694; 1695; 1696; 1697; 1698*
	2023			-	19	61	29	1750 *; 1751 *; 1752; 1753; 1754
Jelgava MN	2010	22	33.684	2013; 2022	-	3	189	738; 739
	2011			2023	3	108	147	761; 762
	2014			2020	5	-	-	872 *
	2016			2020	23	-	-	931 *; 932 *; 933 *; 934 *
	2017			2020	45	-	-	967 *; 978 *
	2018			2020	89	-	-	962 *; 963 *
	2019			-	40	73	34	1409; 1410; 1411 *; 1412 *
	2020			-	56	-	-	1434 *; 1435 *; 1436 *
	2021			-	25	-	-	1474 *
	2022			-	-	40	-	1708
Kalsnava MN	2004	37	47.946	2012	-	20	-	236 **
	2007			2012; 2013	-	139	-	629; 630; 807
	2010.			2013; 2022	-	2	169	727; 733
	2011			2022	3	69	124	757; 758; 759; 760
	2014			2020	5	-	-	892 *
	2016			2020	20	-	-	929 *; 930 *
	2017			2020	51	-	-	974 *; 975 *
	2018			2020	90	-	-	964 *; 965 *
	2019			-	31	72	27	1386 *; 1387; 1388; 1389

<table>
<tr><th rowspan="2">Location of site</th><th rowspan="2">Year of establishment</th><th rowspan="2">Number of trials</th><th rowspan="2">Area, ha</th><th rowspan="2">Year of measurement</th><th colspan="3">Number of</th><th rowspan="2">No. of experiment</th></tr>
<tr><th>clones</th><th>families / provenances / average samples of seed orchard</th><th>crosses</th></tr>
<tr><td rowspan="4"></td><td>2020</td><td rowspan="4"></td><td rowspan="4"></td><td>-</td><td>53</td><td>-</td><td>-</td><td>1439 *; 1440 *; 1441 *; 1442 *</td></tr>
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<tr><td>2023</td><td>-</td><td>19</td><td>-</td><td>-</td><td>1762 *; 1763 *</td></tr>
<tr><td rowspan="9">Mežole MN</td><td>2004</td><td rowspan="9">26</td><td rowspan="9">52.51</td><td>-</td><td>-</td><td>14</td><td>-</td><td>333**</td></tr>
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<tr><td>2011</td><td>-</td><td>-</td><td>4</td><td>35</td><td>756</td></tr>
<tr><td>2019</td><td>-</td><td>-</td><td>60</td><td>34</td><td>1382; 1383</td></tr>
<tr><td>2020</td><td>-</td><td>51</td><td>-</td><td>-</td><td>1432 *; 1433 *</td></tr>
<tr><td>2021</td><td>-</td><td>24</td><td>-</td><td>-</td><td>1533 *</td></tr>
<tr><td>2022</td><td>-</td><td>36</td><td>129</td><td>69</td><td>1719; 1720; 1721; 1722; 1727; 1728; 1732; 1733; 1734 *; 1735 *; 1736</td></tr>
<tr><td>2023</td><td>-</td><td>9</td><td>61</td><td>29</td><td>1758; 1759; 1760; 1761 *</td></tr>
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<tr><td>2019</td><td>-</td><td>25</td><td>-</td><td>-</td><td>1378*</td></tr>
<tr><td rowspan="2">Rembate parish</td><td>1998</td><td rowspan="2">2</td><td rowspan="2">35.5</td><td>2007</td><td>-</td><td>15</td><td>-</td><td>53</td></tr>
<tr><td>1999</td><td>2007; 2008; 2011; 2012; 2019</td><td>-</td><td>637</td><td>-</td><td>54</td></tr>
<tr><td>Ukri parish</td><td>2000</td><td>1</td><td>10.5</td><td>2008; 2013; 2021</td><td>-</td><td>826</td><td>-</td><td>55</td></tr>
<tr><td>Taurene parish</td><td>2000</td><td>1</td><td>9.3</td><td>2008; 2012; 2021</td><td>-</td><td>621</td><td>-</td><td>589</td></tr>
<tr><td>Svente parish</td><td>2004</td><td>1</td><td>3.2</td><td>-</td><td>-</td><td>17</td><td>-</td><td>752 **</td></tr>
<tr><td>Vecumnieki parish</td><td>1975</td><td>1</td><td>0.5</td><td>-</td><td>-</td><td>16</td><td>-</td><td>769 **</td></tr>
<tr><td>Andrupene parish</td><td>1998</td><td>1</td><td>2.5</td><td>2011</td><td>-</td><td>15</td><td>-</td><td>792</td></tr>
<tr><td>Total</td><td>-</td><td>122</td><td>274.344</td><td>-</td><td>-</td><td>-</td><td>-</td><td>-</td></tr>
</table>

* Vegetatively propagated;
** Provenance trial, MN – district of the Forest Research Station.

1.3 Evaluation of silver birch progeny trials

The evaluation of progeny trials and ranking of families are carried out according to the **selection index**. For traits to be included in the index such aspects are essential:

a) the economic value;
b) high genetic determination (greater chances of altering it through breeding than through silviculture);
c) a sufficient genetically determined variation;
d) low (and/or negative from a practical point of view) correlation with other traits already present in the selection index (Burdon 1989).

The evaluation of stem diameter, tree height and stem quality is decisive for the selection of genotypes for the establishment of breeding populations and seed orchards. Moreover, selection on such basis also indirectly affects the traits of wood and fibres which are essential for chemical processing. For the implementation of selection work in practise it is important, also in greenhouse seed orchards, for trees to flower at an early age, often and abundantly, and that the juvenile growth of the selected clones is rapid and the clones can be vegetatively propagated (Stener & Jansson 2005). Stem straightness, apical dominance and desirable branching traits are the most important traits of stem quality which, together with dry matter (DM), are included in the selection index (Stener & Hedenberg 2003, Stener & Jansson 2005). The traits of the stem quality – straightness and apical dominance – are the most important from an economic point of view. The stem quality defects – forking and the formation of spike knots – are caused by frost, insects or fungi damage, or by a drought-induced replacement of the leading shoot (Stener & Jansson 2005).

For example, the relationship between growth rate, traits of stem and wood quality has been evaluated for 11-year-old micropropagated progenies of 30 clones in an experimental plantation in southern Sweden (Stener & Hedenberg 2003). The mean values of the evaluated traits and genetic parameters are shown in Table 1.5. Due to the fact that the genetic variation for stem straightness was near zero, then this trait was excluded from further analysis.

Table 1.5

Mean values, standard errors and genetic parameters for 30 micropropagated clones in southern Sweden

(Stener & Hedenberg 2003)

No.	Trait	Unit	H^2	SE (H^2)	CV_G, %
1	Tree height	dm	0.43	0.12	5.5
2	Diameter	mm	0.46	0.11	11.1
3	Stem volume	dm^3	0.43	0.12	22.7
4	Dry matter	kg	0.39	0.12	21.1
5	Stem taper	%	0.40	0.12	5.8

No.	Trait	Unit	H^2	SE (H^2)	CV_G, %
6	Apical dominance	points (1–5)	0.17	0.12	-
7	Branch thickness	points (1–5)	0.18	0.12	-
8	Branch number	points (1–5)	0.63	0.09	-
9	Branch angle	points (1–5)	0.10	0.12	-
10	Wood density	kg m^{-3}	0.73	0.08	4.7
11	Fibre length	mm	0.68	0.08	4.5
12	Fibre width	µm	0.66	0.09	3.5
13	Fibre roughness	mg m^{-1}	0.45	0.11	6.2

Abbreviations: H^2 – broad-sense heritability coefficient; SE (H^2) – Standard error of heritability coefficient; CV_G – genotypic coefficient of variation.

High values of broad-sense heritability coefficient (H^2 = 0.43–0.73) have been found for growth, wood and fibre traits, while low for stem and branch traits, except for the branch number. The highest genotypic coefficient of variation (CV_G) was for stem volume (22.7%) and DM (21.1%), high for stem diameter (11.1%), while for wood density, fibre length and roughness (4.5–6.2%), it was similar to tree height (5.5%). Compared to other studies, the CV_G of tree height in this study was lower. In the three clone trials in southern Sweden, where 78 clones were evaluated, including the 30 mentioned above, the CV_G of tree height ranged from 6.3% to 7.9% (Stener & Hedenberg 2003). On the other hand, the additive coefficient of variation (CV_A) determined by the additive genetic effect was 9.5% (Stener & Wennström 2000) when evaluating the progenies of 398 plus trees in a plantation in northern Sweden. As stem diameter has a more sensitive reaction to the increase in competition than tree height, then the significant difference found in this study (Stener & Hedenberg 2003) between the CV_G of tree height and stem diameter could be explained by the competition between the trees.

The genotypic correlation (r_g) between the wood density and growth traits, a significant correlation was found only for diameter (r_g = –0.53), other evaluated traits were negative (Table 1.6). The genetic correlations found between growth and wood fibre traits were close to zero. Predominantly negative and statistically irrelevant genetic correlations were between growth and stem quality traits. The correlation between the branch number and fibre length, as well as the correlation between fibre width and roughness, was positive and statistically significant; genetic correlations between fibre traits and wood density, between fibre traits and stem quality traits, between different wood fibre traits, have been identified as weak and insignificant. Other than growth traits, the phenotypic correlation between the traits was also weak.

It is common that in studies with tree species with diffusely dispersed wood vessels do not reveal a correlation between wood density and growth traits, as the most commonly evaluated traits are determined phenotypically. A weak phenotypic correlation (r_p = –0.23) between wood density and stem diameter was also found in this study.

Table 1.6

Genetic correlation (top right of table) and phenotypic correlation (bottom left) between traits

(Stener & Jansson 2005)

Trait	1	2	3	4	5	6	7	8	9	10	11	12	13
1. Height	-	0.57 *	0.71 *	0.75 *	0.65 *	–0.36	–0.13	0.30	0.83	–0.07	0.38	0.19	–0.11
2. Diameter at breast height	0.58	-	0.99 *	0.96 *	–0.08	–0.61	–0.58	–0.48	–0.01	–0.53 *	–0.14	–0.01	–0.13
3. Stem volume	0.69	0.97 *	-	0.98 *	0.09	–0.60	–0.43	–0.34	0.27	–0.48	–0.08	0.04	–0.15
4. Dry matter	0.69	0.95 *	0.98 *	-	0.18	–0.64	–0.42	–0.30	0.37	–0.30	–0.05	0.00	–0.17
5. Stem taper	0.23	–0.10	–0.05	–0.01	-	0.10	0.42	0.46 *	1.57	0.40	0.37	0.28	0.08
6. Apical dominance	–0.12	–0.28 *	–0.27 *	–0.27 *	0.22	-	0.39	0.63	0.71	–0.05	0.18	–0.21	–0.07
7. Branch thickness	–0.10	–0.33 *	–0.28 *	–0.30 *	–0.06	0.03	-	0.89 *	0.88	0.12	–0.05	–0.04	–0.28
8. Branch number	0.02	–0.40 *	–0.33 *	–0.31 *	0.29 *	0.18	0.34 *	-	1.16 *	0.30	0.41 *	0.04	–0.08
9. Branch angle	–0.05	–0.23	–0.19	–0.18	0.21	0.03	0.36 *	0.51 *	-	0.33	0.31	0.17	0.25
10. Wood density	0.01	–0.23	–0.20	–0.04	0.22	0.02	–0.04	0.14	0.11	-	0.14	–0.11	–0.05
11. Fibfe length	0.34	–0.05	–0.03	–0.01	0.25	0.06	–0.06	0.26	0.06	0.11	-	0.33	0.13
12. Fibre width	0.16	0.10	0.08	0.05	0.13	–0.10	0.03	–0.05	–0.06	–0.14	0.32 *	-	0.74 *
13. Fibre roughness	0.14	0.15	0.14	0.14	0.02	–0.09	–0.04	–0.05	–0.07	0.03	0.02	0.43 *	-

* $p < 0.05$.

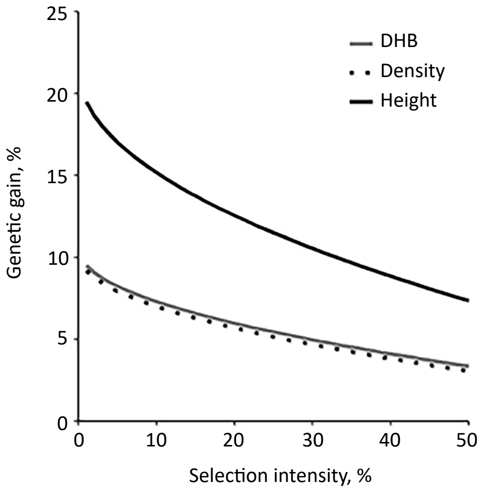

Figure 1.4 **Genetic gain for three traits, depending on the intensity of selection following the same traits**

(Stener & Hedenberg 2003), DBH – diameter at breast height

The observed genetic gain was similar when selection is made based on tree height or wood density, but approximately half as small as when selection is made based on stem diameter (Fig. 1.4).

In the selection carried out based on stem diameter, the stem volume and the dry wood mass were significantly increased, while reducing the wood density slightly – by 2.5% (12 kg m^{-3}). When selection is made by tree height, the decrease in wood density is insignificant, but the genetic gain for stem volume is less than when selected by stem diameter.

The growth of micropropagated birch plus tree clones (~55%) and open-pollinated progenies (~ 45%) under 10 years of age in 10 plantations (number of plus trees 39–83) in southern Sweden has been analysed by L.-G. Stener & G. Jansson (2005). Growth traits have been found to have high genetic control and significant genetic variation in most cases, as well as high genetic gain. The values of the heritability coefficient varied broadly, both between the types of experiments (progenies of clones or open-pollinated progenies) and between the experiments: in plantations, the H^2 of tree height varied from 0.07 to 0.56 for the progenies of clones and h^2 from 0.08 to 0.54 for the open-pollinated progenies. The values of heritability coefficient for tree branching traits were medium or high, while for stem straightness and apical dominance – generally low.

The wide variation of heritability coefficient for height and diameter can be largely attributed to the success of establishment of plantations. Birch, as a pronounced pioneer species, is particularly characterised by the environmental impact on the coefficient values and its growth is strongly influenced by the intensity of tending of the plantation during the first years after establishment. For example, in areas with strong competition and low survival, the values of heritability coefficient for growth traits were also very low, while in a plantation with regular tending during the first two years after establishment, a very high narrow-sense habitability coefficient was found. Areas rated as homogeneous, in a sense of environmental conditions, also have higher heritability coefficients. This leads to a conclusion that the values of habitability coefficient reflect the efficacy of the experiment and also the genetic determination of a trait. The values of broad-sense habitability coefficient H^2 should be higher than in the values of narrow-sense heritability coefficient h^2, which has not been found in this study – differences between H^2 and h^2 were not significant for any of the traits, it was expected because of the initially different height of micropropagated material and the low number of observations. On the other hand, the coefficients of genotypic variation CV_G and CV_A for height (7% and 9% respectively) were lower than for diameter (12% and 15% respectively); no significant differences were observed between progenies of clones and open-pollinated progenies. For comparison, the CV_A for height of open-pollinated progenies at the age of 9 in northern Sweden was 9.5% (Stener & Wennström 2000).

The age at which selection can be made is decisive for the effectiveness of selection. High genetic correlation of the traits of interest at the age of evaluation and target age enables successful early selection. Genetic correlation between the value of a trait at age 10 and 4 for tree height in the L.-G. Stener & G. Jansson (2005) study was 0.60, but at age 10 and 5 or 6 was 0.94. This suggests that it is possible to select clones with the best height as early as around the age of 6, when the approximate height is 4 m. It can be concluded that a short evaluation period may be applied for heritability trials in the selection of birch; however, it should be noted that if selection is performed at the age 4–6 instead of 10 years, the breeding efficiency (genetic gain per year) was 20–40% lower.

The estimated correlations between quality traits (r_g or r_a) were mostly weak and not significant. Straightness and apical dominance are mutually correlating traits, but the genetic determination of these traits is low due to relatively low values of heritability coefficient for both traits. Therefore, improving these traits with selection methods is more difficult than those characterized by moderate or high values of heritability coefficient, such as branch traits. The traits of growth and stem quality are genetically relatively independent because r_g values between them are low, as their genetic correlation analysis shows. However, there has been unwanted medium to strong correlation, from an economic point of view, between stem diameter and branch number, and in some plantations a desirable correlation between growth and branch angle. The study has shown mixed results on the relationship between growth and quality traits, so it is recommended that a general evaluation of stem quality (e.g. 5-point scale) is used to evaluate clones alongside the evaluation of growth traits (Stener & Jansson 2005).

Although there is currently no risk of autumn frost damage to birch in southern Sweden, if height is used as the sole selection criterion for selection, this risk could increase in the long term. For example, a positive correlation (r_G = 0.38) was found between height and additional increment (after August 8). Therefore, in addition, a criterion related to the cessation of the increment growth should be necessary if the breeding results are to be used in areas with frost risk. However, the genetic correlation between growth and growth cessation time in autumn was weak, from which it can be concluded that it is possible to select clones characterized by both growth superiority and early growth cessation. The results of the study show that the effect of genotype × environmental interaction is weak, as indicated by close genetic correlation for both growth and stem quality traits. Such relationship was found even in plantations with very different environmental conditions, such as forest and agricultural land, and in plantations with different climatic conditions. A stable clone ranking has maintained for micropropagated material (Stener & Jansson 2005).

Overall, the results show that traits of silver birch growth are characterised by high genetic conditionality, significant genetic variation, mostly low unwanted genetic relationship between growth and quality traits, and therefore high potential effect of breeding work. The development of birch breeding in Latvia is considered similar to other Baltic Sea region countries and has a significant base – a basic breeding population with 929 selected trees, as well as 34 provenances with a wide range of origin – for a complex analysis and obtaining results from the analysis. This base is used both for the development and updating of the selection index and for phenotypic delination of provenance regions and/or for the clarification of their boundaries.

2 PROPAGATION OF SILVER BIRCH

2.1 Birch seed orchards

First generation birch seed orchards have been established using grafts from phenotypically selected plus trees. In Latvia, the first silver birch (*Betula pendula* Roth) plantation with 22 plus tree clones was established in 1972 in Katvari, in Limbaži municipality, the clones were planted with 5 × 5 m spacing. Without a timely shape pruning, the canopy closure occurred already at the age of 15–20 years and the lower branches died, so it was not possible to harvest seeds in the plantation. The seed orchard is currently used as a clone plantation for evaluation of their growth rate.

The establishment of the next first-generation plantations was started in 1997 at the Forest Research Station, Kalsnava district (Table 2.1). Using the prepared material, in 2001 two birch seed orchards were established in greenhouses (each 0.08 ha) in Jaunkalsnava by JSC 'Latvia's State Forests' unit 'Seeds and plants'. Separate plantation blocks have been established for the northern (Kalsnava 1A) and western (Kalsnava 2R) seed production areas defined at the time. The first harvest was in 2003.

In 2007, silver birch seed orchards – clone archives "Vēžinieki R" and "Vēžinieki A" were established in Viesīte municipality, basing on the selection of clones selected in 1996–1998. In addition to this work, a set of clones "Kalsnava 3" was created in 2007 – 50 clones of the producing seed orchards "Kalsnava 1A" and "Vēžinieki A" were selected and reproduced. The set of clones created has been used in the "Kalsnava 3A" seed orchard, which was established in 2016, with ramets of clones being grown in containers.

Norupe is the first seed plantation to use the information and material from progeny trials (the best trees from the superior families), established in autumn 2009 in the Daugava forestry territory. After evaluating the 921 open-pollinated families in the progeny trials (No. 54, 55, 589), the best families were selected and phenotypically best trees were selected within them for the establishment of seed orchards suitable for the western (25 clones) and eastern (36 clones; Table 2.2, Fig. 2.1) provenance regions. After grafting in 2014, the new 3rd generation seed orchards "Kalsnava – 4R" and "Kalsnava – 5A" were established in 2016 and the first significant seed crop was already in 2019. Simultaneously with the selection of clones for seed orchards, eligible clones for a potential production of vegetatively propagated seedlings have also been selected for further *in vitro* testing.

In 2016, the tree nursery of Forest Research Station in Jaunkalsnava started setting up a clonal archive, where silver birch breeding material of 607 ramets from 188 clones (2019) are grown in pots (50 litres), grafted and propagated *in vitro* in 2013–2018, for the stimulation of flowering for controlled crossing. Flowering in

Table 2.1

Seed orchards of silver birch

Location	Manager	Plantation	Year of establish-ment	Initial spacing, m	Area, ha	Number of clones	Genera-tion of seed orchard	Category of FRM	Region of use for FRM	Seed har-vest
Limbažu county	LVM	Katvari	1972	5 × 5	5.0	22	1	-	-	not harvested
Kalsnava parish	LVM	Kalsnava – 1A	2001	3.4 × 3.7	0.08	55	1	qualified	N	2003–2014
	LVM	Kalsnava – 2R	2001	3.4 × 3.7	0.08	55			W	
Viesīte county	LVM	Vēžinieki A	2007	4 × 5	0.7	88	1	qualified	E; W	from 2012
	LVM	Vēžinieki R	2007	4 × 5	0.5	58			W	
Ogre county	RM	Norupe	2009	7 × 7	1.1	48	2	tested	E; W	from 2018
Kalsnava parish	LVM	Kalsnava –3A *	2016	-	0.015	50	1	qualified	E	from 2017
	LVM	Kalsnava – 4R	2016	3.4 × 3.7	0.08	25	3	tested	W	
	LVM	Kalsnava – 5A	2016	3.4 × 3.7	0.08	36		tested	E	
	MPS	Klonu arhīvs *	2016	-	-	97	3	tested	E; W	from 2018
	LVM	Kalsnava – 6A	2024	3.6 × 3.75	0.25	32	3	tested	W	-

Notes: * ramets of clones are grown in containers; LVM – JSC ‘Latvia’s State Forests’ RM – ‘Riga Forests’ Ltd., MPS – Forest Research Station.

Table 2.2

Place of origin of clones included in the silver birch seed orchards

No. of place of origin *	Place of origin **	Seed orchard										
		Katvari	Kalsnava – 1	Kalsnava – 2	Kalsnava – 3A	Kalsnava – 4	Kalsnava – 5	Kalsnava – 6A	Vēžinieki A	Vēžinieki R	Norupe	Klonu arhīvs
1	Aizpute VVM Aizpute VM	-	-	-	-	-	-	-	-	-	-	1
2	Aizpute VVM Kalvene VM	-	-	-	-	-	-	-	-	-	-	-
3	Alūksne VVM Mālupe VM	-	36	-	21	-	-	-	43	-	-	-
5	Bauska VVM Bauska VM	-	-	-	-	-	6	-	-	-	7	4
6	Bauska VVM Ceraukste VM	-	-	-	-	-	-	-	-	-	-	2
7	Cesvaine VVM Cesvaine VM	-	-	-	-	5	-	4	-	-	1	9
9	Daugavpils VVM Svente VM	-	-	-	-	3	-	3	-	-	2	5
10	Dobele VVM Īle VM	-	-	-	-	-	5	-	-	-	4	1
11	GNP Gauja VM	-	-	-	-	2	-	2	-	-	-	9
12	GNP Medņi VM	-	-	-	-	3	-	5	-	-	7	9
13	Gulbene VVM Dauksti VM	-	-	-	-	4	-	3	1	-	3	6
14	Jelgava VVM Garoza VM	-	-	-	-	-	-	-	-	-	-	2
15	Jēkabpils VVM Ābeles VM	-	-	-	19	6	-	4	22	-	6	5
17	Koknese VVM Koknese VM	-	-	-	-	1	-	1	-	-	1	1
19	Kuldīga VVM Kuldīga VM	-	-	-	-	-	-	-	-	-	-	2
21	Liepāja VVM Priekule VM	-	-	-	-	-	9	-	-	-	3	6
22	Limbaži VVM Limbaži sēklu plant.	21	-	-	-	1	-	1	-	-	2	1
23	LLU MPMS Šķēde VM	-	-	-	-	-	-	-	-	-	-	5
24	Ludza VVM Zilupe VM	-	-	-	-	1	-	1	-	-	-	1

No. of place of origin *	Place of origin **	Seed orchard										
		Katvari	Kalsnava – 1	Kalsnava – 2	Kalsnava – 3A	Kalsnava – 4	Kalsnava – 5	Kalsnava – 6A	Vēžinieki A	Vēžinieki R	Norupe	Klonu arhīvs
25	MPS Kalsnava VM	1	-	-	-	-	-	-	-	-	-	-
26	Ogre VVM Suntaži VM	-	-	-	-	8	-	7	-	-	11	7
27	Rēzekne VVM Gaigalava VM	-	-	-	-	-	-	-	-	-	-	2
28	Rēzekne VVM Viļāni VM	-	-	-	-	2	-	1	-	-	-	2
30	Strenči VVM Strenči VM	-	-	-	-	-	-	-	-	-	-	-
31	Talsi VVM Andumi VM	-	-	-	-	-	5	-	-	-	-	4
32	Valmiera VVM Daliņi VM	-	-	-	-	-	-	-	-	-	-	-
33	Valmiera VVM Naukšēni VM	-	-	-	-	-	-	-	-	-	-	7
34	Valmiera VVM Rūjupe VM	-	-	-	-	-	-	-	-	-	-	1
35	Alūksne VVM Liepna VM	-	19	-	10	-	-	-	22	-	-	-
36	Tukums VVM Kaive VM	-	-	55	-	-	-	-	-	58	-	-
	Other	-	-	-	-	-	-	-	-	-	-	5
	Clones in total	22	55	55	50	36	25	32	88	58	47	97

Notes: * the number in the table corresponds to the marks on the map in Figure 2.1; ** names of names of regional forestries (VVM) and districts within (VM) according to the division in the year of harvesting.

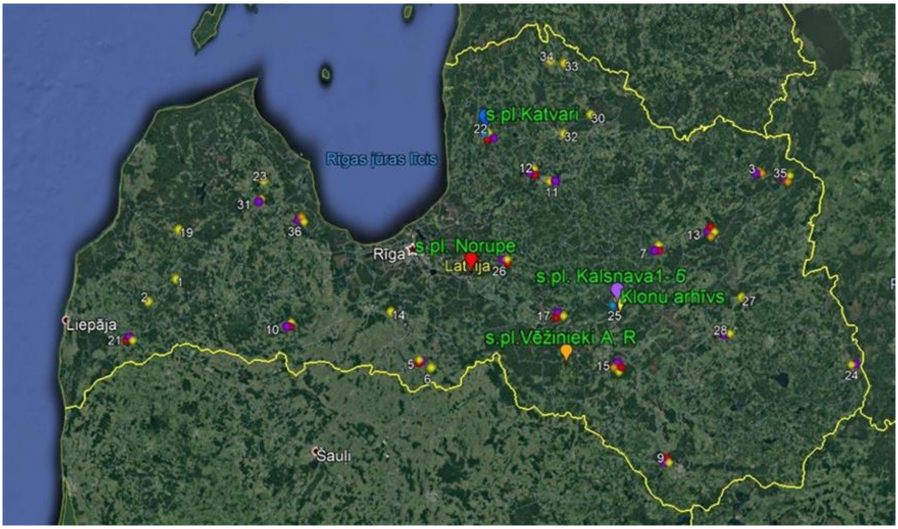

Figure 2.1 **Locations of silver birch seed orchards, clone archives and origin of clones, included in them**

The number corresponds to the place of origin as listed in Table 2.2 and colour corresponds to the origin of the clones for the respective seed orchard (s.pl.) or clone archive (klonu arhīvs)

2018, 2019, 2020 provided the opportunity for controlled crossing for the next breeding cycle. After it, part of the clone collection is no longer maintained, currently containing 344 ramets from 97 clones.

The number of clones is changing because plants are periodically restored, some of the original clones are no longer maintained.

In June 2024, the newest 3rd generation greenhouse-type birch seed orchard "Kalsnava 6A" (Fig. 2.2) with 32 clones (65% propagated *in vitro*, 35% grafted) has been put into service in the tree nursery 'Mežvidi' of JSC 'Latvia's State Forests' in Jaunkalsnava. These clones, phenotypically selected best trees from the best families in the progeny trials, currently are considered the most suitable for eastern provenance region.

Figure 2.2 **3rd generation birch seed orchard "Kalsnava 6A"**
(Photo: Ā. Jansons)

Establishment of birch seed orchards ensures that the results of forest selection can be used in practice by using the category "qualified" and "tested" plants in forest regeneration and afforestation.

2.2 Vegetative propagation of silver birch

Vegetative propagation gives an opportunity to implement in practice all of the genetic gain achieved by using only a small number of best genotypes. This approach also makes it possible to shorten the time between the acquisition of results of the breeding work (selected sets of genotypes with the desired traits) and the practical use of these results for forest regeneration, as there is no need to wait until the start of production of seed orchard. However, this benefit is small for birch compared to spruce, for example, because the first seed crops in a purposefully managed plantation can be obtained from significantly younger ramets. The most significant benefit of vegetative propagation for forest tree breeding is higher accuracy of progeny tests (reducing the impact of local variations and evaluation of genetic parameters) and shorter time of implementation. The highest genetic gain can be achieved by using a larger number of candidates after controlled crossing from each sib family and testing each with a small (6–10) number of ramets at each of the 3–4 sites (Danusevicius & Lindgren 2002a, b, 2004, Isik et al. 2003, 2004, 2005, Dieters et al. 2004, Stener & Jansson 2005).

The large-scale production of seedlings from vegetatively propagated crosses of superior families or individuals characterized by a set of economically desirable traits (ideotypes) has been compelling since the creation of micropropagation technology (Naujoks et al. 2002). The main methods of mass vegetative propagation of birches are organogenesis and somatic embryogenesis. In the organogenesis process, the induction of new plants comes from organs of a plant – buds, shoots, leaves, parts of the flower. The process requires two different hormonal signals to trigger the development of shoot organs and roots. The somatic embryogenesis is the development of plant embryos by differentiation of somatic cells. Somatic embryo contains both shoot and root meristems, so initiation requires one hormonal signal. With the use of somatic embryogenesis, it is possible to obtain a large number of genetically identical embryos and to create artificial seeds the cost of which would be comparable to natural seeds. Growth-enhancing rhizobacteria, minerals and pesticides could be incorporated into the artificial seed coatings. The method has potential, but has so far not been developed so far as to be applicable in the practical production of forest seedlings (Rihan et al. 2017).

The micropropagation process consists of organogenesis of plants in artificial medium under sterile conditions. The research on micropropagation of woody plants has been taking place since the 20th century. Birch trees are among the first micropropagated trees (Jacquiot 1955 cited by McCown 1989). In Scandinavian countries and elsewhere in Europe, studies of birch micropropagation began in the 1980-ies with the aim to learn methods for propagating the selected genotype for afforestation purposes and accelerating the breeding process (Welander 1988). The acquisition of birch micropropagation possibilities was started in 2006 in the Laboratory of plant physiology of LSFRI 'Silava'. There are currently more than 150 specially selected birch genotypes in the *in vitro* collection of birch.

Micropropagation begins by harvesting material from the selected trees (genotypes) and initiation it into an artificial (laboratory) environment – in a medium that contains all the minerals, carbohydrates, vitamins, amino acids, phytohormones needed for the plant. As juvenile parts of plants as possible are collected for the genotypes selected for the initiation of tissue culture. An important factor for initiation of culture is the time of extraction of the explants, the age and the physiological state of the mother plant. The initial development of culture depends on the choice of an appropriate medium. Growth regulators, mainly cytokinins and auxins, are the most important. Cytokinins contribute to cell division and slows down their aging, but auxins promote cell development. Growth regulators also perform specific regulatory functions. They can affect enzyme function, gene expression and alter even the characteristics of cell membranes.

After the stabilisation of *in vitro* culture, the next stage of micropropagation – micropropagation itself – can be initiated. For its purposes, the plants are placed in proliferation media that stimulates plant's lateral bud burst and dormant buds to form, as well as provides the optimal temperature and light regimes. In order to ensure the efficiency of this method in the production of seedlings, maximum length growth of the main and lateral shoots of the plants and an increase in the number of lateral shoots should be achieved (Fig. 2.3). This ensures that several plants are produced after a certain period of time (4–5 weeks for birch), dividing plant by shoots and planting each shoot separately. For the breeding process to be effective, the number of new plants to be extracted should be at least five.

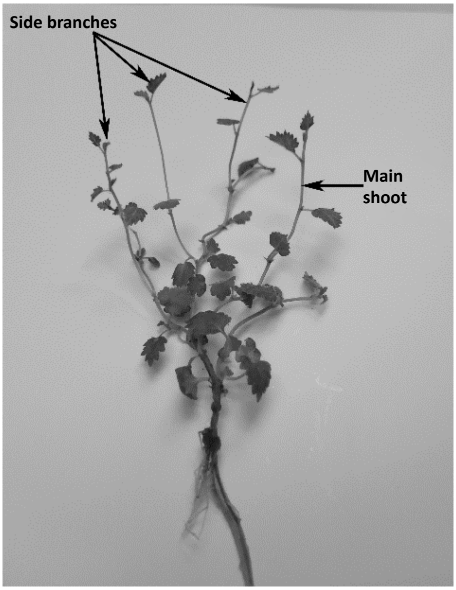

Figure 2.3 **Micropropagated silver birch**

The defined minimum number (propagation coefficient) will depend on the cost of production and the market value of the plants.

Clone (genotype) is an important factor influencing multiplication rate (Koski & Rousi 2005), so not all genotypes with desired properties will be able to be efficiently propagated vegetatively. It has also been found that for different clones better results can be achieved in different proliferation media – therefore, an experimental work is needed and carried out to find the most suitable media for the specific most productive and qualitative clones.

The final phase of this vegetative propagation method is the acclimatisation of plants for growth in non-sterile environments. They are planted in a peat substrate, initially in a greenhouse with a fogging system, ensuring high (> 80%) humidity and precisely controlling the plant cultivation regime, later the plants are transplanted in larger size containers and moved to an outdoor environment.

The micropropagation method also has its flaws. It is expensive because it takes a long manual work in sterile conditions and qualified staff. In some cases, growth regulators added to the media may cause somaclonal mutations. However, this can be avoided by limiting the duration of culture *in vitro* conditions, as changes accumulate over time.

The growth of vegetatively propagated trees in forest is not different from generatively propagated individuals with corresponding genetic gain, as demonstrated by extensive and long-term studies (Meier-Dinkel 1992, Viherä-Aarnio 1994). The result to be obtained is more predictable – with less variation – and with the possibility of achieving a higher genetic gain in practice. The widest practical use of micropropagated seedlings has taken place in Finland, as part of cooperation between several companies, starting in 1989, when 30,000 seedlings were produced from 30 different clones (Viherä-Aarnio & Ryynänen 1994). In early 1990, more than one million seedlings were produced, but larger-scale micropropagation was stopped in 1994 (Viherä-Aarnio & Velling 2001). There were several reasons for such a decision. Labour costs increased relatively rapidly, increasing the cost of planting material; similarly, the browsing damage by ungulates in young birch stands increased rapidly, reducing interest (and meaning) in planting this tree species. But the most important reason was the propagated material – the clones used in the project were not characterized by positive genetic gain. Finnish researchers point out that the selection of clones for the propagation programme did not result in a correct selection in the progeny trials; often the work was carried out by persons without adequate knowledge (Viherä-Aarnio & Velling 2001). In ten progeny trials with total area of 17 ha in southern Finland, a total of 29,000 trees were compared between 6–7-year-old micropropagated progenies of 11 clones and seedlings of 10 families. It was concluded that the type of planting material does not have a significant impact on survival, height increment and biotic risk factors (damages by rodents and ungulates, cancer, etc.), but significant differences for these traits were found between clones. Selection of carefully tested best clones for large scale micropropagation is recommended (Viherä-Aarnio & Ryynänen 1994, Viherä-Aarnio & Velling 2001).

In Sweden, micropropagation is not yet used to produce seedlings. The breeding programme has carried out the propagation of plus trees in plant tissue cultures, but it has not been possible to propagate a large part of the clones in this way. An example of individual private company initiatives is the research and technological development company 'SweTree technologies', which develops automated vegetative propagation technologies. A study by this company evaluated the cultivation of *Betula pendula* explants in a new temporary immersion bioreactor system, demonstrating the potential to expand and automate micropropagation for commercial use (Businge et al. 2017).

Studies are also being carried out in Russia for the production of high-quality birch container seedlings with the micropropagation of clones, developing methods for ensuring acclimatisation of seedlings. This would avoid the costs associated with artificial fogging equipment and at the same time ensure the survival of 90–95% of the seedlings from *in vitro* cultures when transplanting them *ex vitro*. Planting and evaluation are carried out in high density (660–900 seedlings m^{-2}) mini cells (20 ml), which reduces costs (Lebedev et al. 2017). In Lithuania, the initiation and maintenance of cultures of explant *in vitro* has been evaluated in order to prepare practical recommendations for further use of micropropagation in the production of seedlings (Vaičiukynė et al. 2017).

Member States of the European Union are allowed to regulate the production and application of vegetatively propagated forest reproductive material in forest regeneration or afforestation. As such material in the Baltic and Fennoscandian regions is generally produced and used a little, detailed restrictions are rarely applied. In Latvia, the only restriction – for clones registered to produce FRM "qualified", the maximum number of progenies (ramets) obtained by vegetative propagation method is one million grown saplings. For clones registered to produce category "tested", the maximum number of progenies (ramets) to be obtained is not restricted (Regulation of the Cabinet of Ministers No. 159 "On forest reproductive material").

Overall, it can be concluded that micropropagation of birch for forest regeneration is currently not practised in Latvia or in neighbouring countries, however, its principles are clear. The development of technology, including clone-specific, tailored nutrient media, is important for practical application.

2.3 Regeneration and afforestation of birch stands

Breeding provides a practical contribution to the economy only if the results of it are used for forest regeneration and afforestation. On average, 15.3 thousand ha of birch stands are felled per year in final fellings (statistics of State Forest Service from 2013-2023), most of which (74– 100%) are regenerated with birch. However, in both state and the rest of the forests, regeneration of birch stands is dominated by natural regeneration (Fig. 2.4). This situation is linked both to lower regeneration costs and to the lack of birch seedlings.

In the Register of basic material (sources of forest reproductive material – FRM) of State Forest Service, from registered 134 silver birch sources, 100 are in

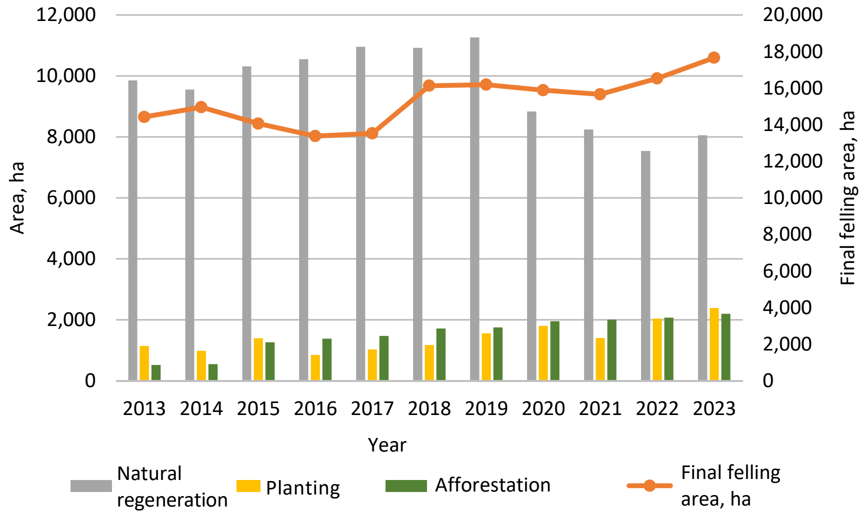

Figure 2.4 **Final felling of birch and forest regeneration with birch in all forests in total**

(Data: State Forest Service)

the lowest category "place of provenance known", one – in category "selected", 30 in category "qualified" (5 seed orchards, 7 clones and parents of 18 families) and 3 seed orchards in category "tested" (data of State Forest Service until 2023). Between 2013 and 2023, birch is dominated by the production of FRM of the lowest category – growing seedlings from seeds collected in forest stands (Fig. 2.5), the production of FRM category "qualified" has halved, while seed material of the

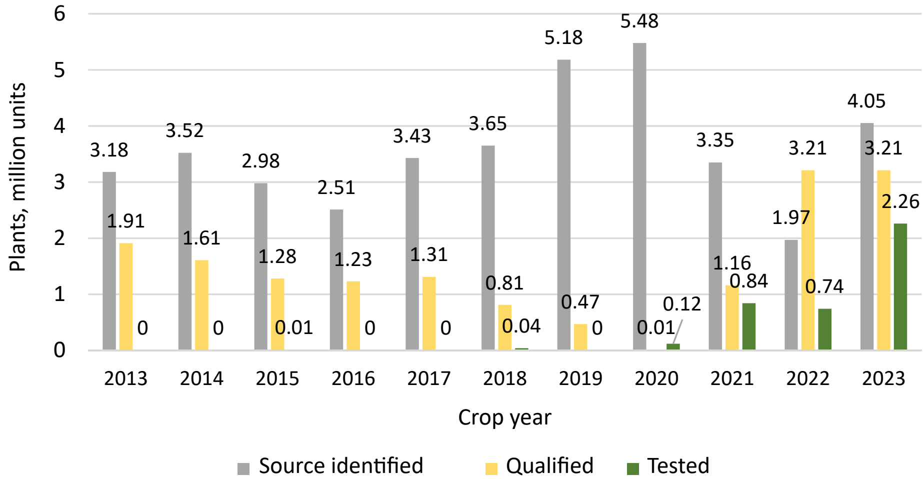

Figure 2.5 **Production of forest reproductive material of silver birch by categories**

(Data: State Forest Service)

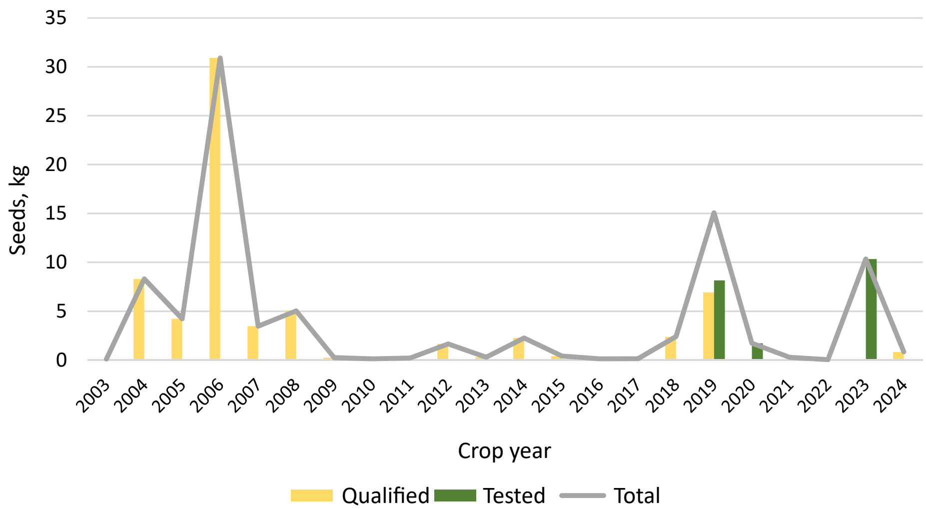

Figure 2.6 **Seed volume produced in seed orchards of JSC 'Latvia's State Forests'**
(Data: JSC 'Latvia's State Forests' unit 'Seeds and plants')

category "tested" has become available in recent years and the amount of produced FRM is small.

As with all tree species, for silver birch as well, seed crop varies year after year both in forest stands and seed orchards (Fig. 2.6). Greenhouse-type orchards have the potential to stimulate flowering, for example, by using CO_2, which can increase seed yields and therefore make birch seeds of the highest category more accessible in the production of seedlings.

In recent years (2019, 2020 and 2023) newly producing 3rd generation silver birch seed orchards "Kalsnava – 4" and "Kalsnava – 5" of the JSC 'Latvia's State Forests' have the potential to increase production and provide nurseries with high-quality category "tested" seeds (Fig. 2.6).

The transfer of breeding results to forest regeneration is highly restricted, mainly due to challenges of seed production, but not to the availability of the breeding results themselves (clones with specific tested traits).

3 FINANCIAL BENEFIT OF BREEDING AND ITS EFFECT ON GENETIC DIVERSITY

3.1 Financial benefit

Comparing the material from seed orchards and using unimproved progenies of forest stands as control, the impact of genetic factors on stem quality and growth traits in birch aged 8–12 has been studied in progeny trials established on former agricultural land in southern Finland. The superiority of progenies of seed orchards has been established in terms of both productivity and stem quality. The realised genetic gain at age 8–12 for progenies of seed orchards reached 26.3–29.3% for stem volume, 9.7–13.6% for stem taper and 6.1–10.1% for relative branch diameter; relative differences are projected to persist until at least the age of 30 years (Hagqvist & Hahl 1998). The evaluation of progenies of open-pollinated families at the age of 13 in southern Finland showed 20–30% better growth and stem quality for the best genotypes compared to the mean values of plantations (Raulo & Koski 1977, Koski & Rousi 2005). The range of growth differences between the same families remained at the age of 32, with the stem volume and yield of the best families being above the mean values of plantations by 13–28 and 24–28%, respectively. Whereas, the yield of open-pollinated families per ha at 32 was 12–16% higher than that of the progenies of forest stands (Viherä-Aarnio & Velling 1999). It should be noted that in Finland, where birch breeding was started already in 1961, the improved birch has the highest proportion in the production of planting material (almost 100%; Jansson et al. 2017). In Finland, the profitability of seed orchards has also been analysed using the net present value (NPV; Ahtikoski 2000) as an indicator. The calculated NPV was positive at the discount rate of 4% and the predicted genetic gain of 20% in southern Finland and 14% in central Finland.

The realised genetic gain has been evaluated for 19 progenies of seed orchards in 34 progeny trials in southern and central Finland at the age of 9–24. Progenies of seed orchards showed an improvement in all the traits evaluated compared to control material from naturally regenerated forest stands, but the results varied significantly by seed orchards, with the younger ones showing better performance. The realised genetic gain for height, diameter and stem volume was 1.6–12.1%, 0.6–9.4% and 1.0–31.1%, respectively. The improved trees had 6.8% (up to 26.7%) less spike knots on average and 16.2% (up to 57.6%) fewer double leaders than controls (Haapanen 2024).

In southern Sweden, the realised genetic gain for clones aged 9 compared to the slowest growing genotype was on average 22% for height and 16% for diameter; at the age of 26, the gain reached 32% for basal area and 56% for yield (Liziniewicz et al. 2022).

The best birch families from Finnish and Swedish breeding programmes in Norway showed a 10% superiority in height over material of local provenances (Kohmann 1998). In Norway, in trials of diallel crosses of nine open-pollinated families on agricultural land at the age of 37 (after two thinnings), the standing volume was 308 m^3 ha^{-1}, and at the family level a very different proportion of the total standing volume was assessed – the standing volume of progenies of the most productive family was three times higher than for the crosses representing the slowest growing family (Skrøppa & Solvin 2019). In this progeny trial, the high correlations between the height and diameter measurements of families at the age of six and 37 also confirm that selection of the best families is possible at an early age when the trees have reached a height of 2.5 m to 3 m.

Six-year-old progenies of 100 open-pollinated families of local origin have been analysed in Lithuania and their genetic gain has been evaluated by selecting 30% of the best families by survival, height, diameter, stem straightness and branch thickness (a coefficient of 1.5 applied to height; Baliuckiené 2009). The genetic gain of tree survival reached close to 60%; for height and diameter it ranged from 20% to 40%; the improvement for stem straightness reached 10%. The genetic gain of branch thickness was small (up to 5%) or non-significantly negative, depending on the breeding zone.

Silver birch is included in forest tree breeding programmes in Lithuania, Sweden and Finland, and as an additional species of lesser importance in Norway.

It should be noted that the realised genetic gain is determined not only by the selection process itself, but also by the way in which this genetic gain is carried forward in practice. For example, a greenhouse-type birch seed orchard is more effective than an open-pollinated seed orchard, where the background pollen can reduce the gain by two times (Ruotsalainen 2014).

It is generally assumed that the genetic gain is realised over a longer period of time after planting – during thinnings and final felling. However, there is an immediate benefit from the use of improved planting material as it allows the initial planting density to be reduced due to higher stem quality, thus reducing the initial investments (Ruotsalainen 2014).

Along with the breeding goal to increase productivity and improve the result of high-quality assortments, an increase in carbon sequestration of about 10–20% (Ameray et al. 2021) can also be achieved. Selection, intensive management and an appropriate rotation period for production of long-lasting wood products – together are important tools for increasing carbon removals. For example, *Pinus taeda* plantations in the south of the United States estimate that improved pine trees of this species can be characterised by 17% higher standing volume and 13% higher carbon removals than unimproved trees (Aspinwall et al. 2012). By sequestring carbon, planted stands will play a major role in the carbon market, boosting the forest owner's income. A study in Finland estimates that if the aim of forest management is both wood production and carbon storage then the financial benefits in improved stands are higher than if the only goal is wood production (Ahtikoski et al. 2020).

Forest management for carbon sequestration requires adaptation actions (adaptive forestry) in the changing climate. The changing climate threatens forests' ability to sequestrate carbon as temperatures rise and rainfall seasonality changes, as well as natural disturbances such as drought, wind or forest pest damage increases in frequency and severity (Seidl et al. 2017, Ontl et al. 2020). The cessation of forest management with an aim to maximising the amount of carbon in the ecosystem is considered unrealistic in regions such as the Baltic and Nordic countries, where forestry plays an important role in the economy, and adaptive forestry such as productive planted stands with improved reproductive material and with lower initial stand density to enhance their stability can therefore increase resistance to, for example, the risk of wind damage and thus reduce the risk of carbon loss in the long term (Jandl et al. 2015). Given that the improved planting material is usually used on the most suitable soils for the species (highest site index), where its additional growth benefits are best reflected (Zeltiņš et al. 2024), the interaction of the genetic gain with other forestry activities is important in risk mitigation. Namely, the use of improved seedlings, lower initial stand density and timely thinning both increase the stability of the stand and reduce the duration of rotation to the target diameter, thus reducing the time when trees are subjected to the risks of wind and other damages while improving the financial benefit (Donis et al. 2020, Samariks et al. 2020).

So far, there is a lack of evaluation of the financial benefit from birch breeding in commercial thinnings, which allows the forest owner to determine the benefits even before the age of the final felling. Similarly, there is relatively little evaluation of the benefits of breeding at the age of the final felling, as well as for the entire breeding cycle as a whole.

3.2 Genetic diversity

In the context of a wider use of breeding population and vegetatively propagated material, it is essential to take into account the genetic diversity (GD), which is the basis for biodiversity at both species and ecosystem level (Koskela et al. 2007, de Vries et al. 2015). The GD ensures the conservation and evolution of living organisms, including trees, in a changing environment.

GD in the breeding population is important as it:

a) provides possibilities for changing the breeding objectives in the future;
b) prevents (reduce) gene drift and inbreeding and the adverse effects related to them;
c) improves the adaptive potential of the improved material, which is particularly significant in a rapidly changing environment.

GD is also variable in tree populations (parts of populations) not altered by humans, making it difficult to define any numerical indicator values that would characterise high or sufficient size. A comparison with not improved autochthonous material provides the most accurate picture of GD conservation in the breeding population. Several authors indicate at least 95% of the number of alleles found in populations unaffected by forest management (in parts of them, such as old stands that have not been planted or sown with improved materials) as a target for GD conservation in breeding population, spending the lowest possible resources on it (Thomas et al. 2014).

Only a small proportion of the breeding population is used for propagation – for the production and planting of seedlings in forest: genotypes selected based on a specific set of traits in the selection index. It is important for GD to be sufficient to maintain the diversity of a particular species in the forest landscape in the long term. Seed orchards often use an effective number of clones (N_e) to characterise this level of GD – the number of individuals in an ideal population (at Hardy-Weinberg Equilibrium), which has the same inbreeding coefficient (or variance) as the given population (Falconer & Mackay 1996). N_e affects both the number of clones and their relatedness to each other and their different representation in the progeny cluster of seed orchard due to differences in flowering phenology, differences in flowering intensity and sex ratio, differences in total seed crop and its quality (Charlesworth 2009). Together with mutation frequency, N_e determinates the level of genetic diversity (mostly neutral diversity which has little or no impact on natural selection). It is customary that the effects of gene drift (accidental loss of any allele or alleles from the population through change of generations and death of an individual who alone has a particular allele or alleles) are not significant, if $N_e > 25$. This value, or even a significantly lower value ($N_e = 10–16$), is recommended for use in a seed orchard (review: Jansons 2008). Lower value is largely attributed to the fact that seed orchards are producing for a relatively short period of time (after which the clones are replaced) and the progenies of the plantations are not expected to cross only with each other in future generations. Crossing with adjacent stand trees will increase the number of effective clones and prevent GD loss. The same arguments are also valid when assessing the use of vegetatively propagated material (clones) for forest regeneration.

Vegetative propagation and the use of clones is relatively low in the Baltic Sea region (Högberg & Varis 2016), so the link between clones and genetic diversity can be analysed in theory or using examples from other regions where it is used more widely. For example, about half of the eucalyptus groves in Brazil are clone plantations (Wu 2019). It is also possible to evaluate stands that regenerate with root and/or stump suckers. Such naturally regenerated stands show significant phenotypic differences in trees determined by heterogeneous environmental conditions, even if they are only 3–5 clone ramets (Bradshaw et al. 2019), so external environmental factors that negatively affect a clone ramet will not have such effect on another. Thus, stands with a small number of clones can exist for a very long time. Paleoecological studies have concluded that part of Europe has had a long period with such stands of clones of black alder and small-leaved lime established in early Holocene (Giesecke et al. 2017). This period has been interrupted by anthropogenic effects with significant livestock damage, which limited further regeneration with coppice and destroyed clones that may have been several thousand years old. The age of such clones is also indicated by Cook (1985). The oldest known Norway spruce (Old Tjikko, > 9,000 years) found in Sweden has also existed as a clone, with its surface part periodically regenerating (Öberg & Kullman 2011).

When evaluating information on the distribution of genetic diversity of 45 plant species, including woody plants, it has been found that many of their genotypes are apparently restricted to only one population in which more than 25 genotypes are rarely found (Widén et al. 1994). For Eurasian aspen (*Populus tremula* L.), the average number of clones per ha calculated in a study in Latvia ranged from 6.1 to 26.8, the average distance between ramets was 48 ± 9.5 m, and the maximum mean distance was 85.6 m (Zeps et al. 2017). Finland has similar results (Suvanto & Latva-Karjanmaa 2005). Intense competition between each other as well as external factors (e.g. browsing damage) significantly reduce the number of genotypes in the stand during the first years of growth (Krasny & Johnson 1992, Watkinson & Powell 1993, Edenius & Ericsson 2007).

In nature, the loss of genetic diversity is often associated with some regional and/or historical impact of major environmental changes. For example, an ice age in which conifers survived only in very small areas in Scandinavia (Parducci et al. 2012). At the same time, research shows that these ancient populations have contributed very little to the genetic diversity of modern spruce trees in Fennoscandia (Tollefsrud et al. 2008, Öberg & Kullman 2011, Parducci et al. 2012), with the species mostly coming from other areas after the ice age. Natural spruce populations in Sweden and Norway are with the lowest genetic variability in Europe, but with high phenotypic plasticity (Bradshaw et al. 2019) and with an ability to survive under both harsh and changing environmental conditions. This reaffirms that genetic diversity and adaptability are not the same thing.

The prevalence of clones in natural populations indicates that under harsh conditions it is a natural survival strategy, so that the use of suitable clones in the context of climate change should be considered to be a kind of imitation of natural processes. Whereas, the limited number of genotypes in natural populations characterised by vegetative reproduction indicates that a large number of clones may not be required at stand level.

The **effect of use of clones on genetic diversity** is determined by (Ingvarsson & Dahlberg 2019):

1) the extent to which a given breeding population represents the existing genetic diversity of the species in a given area (i.e. from which group the most suitable genotypes are selected);
2) how many clones and how many ramets of these clones will be used;
3) total area planted with (specific) clonal material.

Risks associated with potential degradation of diversity can be managed by:

1) the selection index for the selection of clones includes resilience-defining traits (the determination of which may require more extensive testing under more varied conditions and/or longer-term testing);

2) ensuring against unknown (potential) future risks, preserving the species gene pool for long-term breeding, for example in clone archives and forest stands of genetic resources (Hoban & Schlarbaum 2014, Hoban et al. 2018, Rosvall et al. 2019, Proschowsky et al. 2020).

The impact of clones on genetic diversity (and other levels of diversity) is assessed at two spatial levels: individual stands (plantations) and landscapes (forest landscape).

The impact of the use of clones **at stand level** will depend on:

1) the number of clones used;
2) the specific characteristics of these clones;
3) forestry practices in these stands.

When evaluating the number of clones used and expressing the loss of heterozygosity or adaptive genetic variability, as a function of the effective number of population specimens, the $N_e \approx 10$ in the first generation provides approximately 95% of the initial genetic variability in the population (Roberds et al. 1990). A study of a third-generation tea tree breeding population in Australia found no differences in heterozygosity between sets of different numbers of clones (10, 15 and 20 individuals were re-selected (10 times) from 114 tree breeding populations). However, a set of 10 clones found reduced heterozygosity compared to a set of 20 individuals and a breeding population. The inbreeding coefficient for a set of 20 clones is substantially less than for 10 clones. As expected, the size of the set greatly influences the number of alleles included, with the smaller sample size containing fewer rare alleles. However, the diversity of alleles for all sets is the equivalent by selecting 7 individuals from all populations (Voelker & Shepherd 2020).

In the context of genetic variability, it is also important to distinguish between genetic diversity and genotypic diversity. Genetic diversity refers to genetic variability in the population and depends on the number and frequency of different alleles. Genotypic diversity refers to the unique genotypes that are present. For example, 10 unique clones provide equivalent genetic diversity to all of their potential progenies that come from using these trees as parents. However, the genetic diversity of these 10 clones is lower than planting the progenies resulted from randomly crossing among them. In this case, the repeated combination associated with meiosis ensures that all progenies will have unique genotypes, even if they are coming from such a limited number of parents. Once a sufficient number of clones are used in forest regeneration, the loss of genetic diversity will be minimal. However, genotypic diversity is significantly reduced even when a large number of unique clones are used (Ingvarsson & Dahlberg 2019).

Lindgren (2009) recommends for Norway spruce, under Swedish conditions, the use of a mix of 25 clones with minimum gene diversity, expressed as a status number $N_s = 4$. This equates to gene diversity in two infinitely large sib families with four unrelated parents or one large semi-sib family, i.e. one mother tree and an infinitely large number of father trees. In the long run, such clonal mixture with $N_s = 4$ provides 87.5% of the original gene diversity (Wu 2019). In eucalyptus plantations 5–14 clones are used, which is a sufficient efficient number to provide the required GD (Rosvall et al. 2019). In Europe, 10–20 clones are often used for species (Lelu-Walter et al. 2013). When assessing the probability of loss of clone plantation, differences between risk levels are very small when 13–25 clones are used (Roberds et al. 1990, Roberds & Bishir 1997). When modelling the situation with complex resistance (defined by many genes) to known and unknown pests in the future, the results largely confirm this trend – around 18 genotypes are an optimum to reduce future unknown risks, although the differences between 6, 18 and 30 genotypes are very small (Yanchuk et al. 2006). These results can be generalised and attributed to boreal forest's tree species with a long lifecycle (Wu 2019).

All approaches to determining the minimum number of clones indicate the same trend: increasing the number of genotypes above a certain threshold has little impact on the probability of GD decline: 5–30 clones provide as high "safety" against expected future risks as an infinitely large population, and the optimum level of diversity exists in a population of 18 genotypes (Wu 2019). In practice, little more clones are worth using in the clonal mixture, incorporating more clones from the superior (by selection index) families (Weng et al. 2012). Regulating the proportion of clones in a mixture can improve both productivity and stability in space and time, thereby mitigating risks (Weng et al. 2013). When planting a clonal mixture, it is recommended to mix all clones together to reduce the spatial association of ramets of one clone (Prospero & Cleary 2017). When assessing objections to a modified (reduced) GD, which is argued for increased effects of pathogens and dendrophagous insects (Aitken et al. 2008), it should be recalled that these factors can also have a significant impact on areas with high genetic diversity and genetic variability between the stands (Jump et al. 2009, Prospero & Cleary 2017), with a cardinally reduced number of individuals not only at a stands level of the species concerned (e.g. single spruce stand) but also at a forest landscape level or even at a regional level (examples: elm and ash in Europe). The relative risk changes should therefore be analysed.

Clones are not only used in intensive forestry. It can be part of a combined regeneration, in line with a close-to-nature forestry approach. For example, selected genotypes with small branches can be planted in lower initial density, reaching the desired dimensions without thinnings and creating more open conditions for richer undergrowth vegetation and greater diversity of its species.

Criticism of the use of clones, like any other genetically improved forest reproductive material, is also linked to "genetic contamination" in surrounding forest stands with the pollen or seeds of the plantation. However, there is no real impact in this respect as long as the reproductive material used in the plantation is not genetically modified and is derived from a breeding population sustaining extensive genetic diversity of tree species that are suitable for local conditions and/or are of local origin (Bradshaw et al. 2019).

The actions to be taken to ensure structures relevant to the diversity of species (such as dead wood, legacy trees, etc.) are independent of the type of propagation of the planting material or the number of clones (Ratcliffe & Peterken 1995, Felton et al. 2010). However, usually in studies of species diversity or the occurrence of individual species, a "plantation" – understood as clonal plantation, usually in a large, homogenous area – is analysed as a single set without distinguishing between the effects of genetics (clones) and forestry. Such "plantations" usually show reduced or the same diversity and density of species (in general or of a particular group) as in naturally regenerated stands (Peterken & Game 1984, Humphrey et al. 2002, Plue et al. 2017).

Homogeneous growth conditions and intensive, standardized forestry are factors that lead to uniformity in clone plantations and therefore to a small number of habitats and species diversity associated with these habitats (Bradshaw et al. 2019). However, the negative impact on diversity can be mitigated or completely eliminated by a formation of small (2–20 ha) plantations located in the forest landscape between different tree species and stands of different forestry purposes. Such approach would be very appropriate in Latvia, where larger homogeneous (pure, singe species and age) managed forest patches are very rare anyway.

In general, there are two approaches to the location of plantation in **forest landscape**:

1) concentration in a large, homogeneous area. This approach ensures high forestry efficiency, job mechanisation and even automation. Moreover, it is possible to obtain all the required amount of wood in a relatively small part of the total forest area. For example, in New Zealand, which is a regional producer and exporter of wood and its products, the absolute majority of wood (> 99%) comes from plantations covering around 7% of its area (New Zealand Forest ... 2023). The rest of the forest area can therefore be used for other purposes and forestry objectives have no significant impact on forest biodiversity in the country. Similarly, in the southern United States, which is a region with the world's largest areas of forest plantations, large part of wood comes from stands naturally regenerated (Bettinger et al. 2009): so there are very large areas of such forests as well. This approach is appropriate and applied in areas where large continuous areas suitable for the creation of plantation forests are available and where the climate is characteristic for a short rotation cycle (6–26 years);
2) dispersed placement in a wider territory. Heterogeneity at landscape level is maintained by genetic variability between the stands, i.e. different clone mixes are used in different stands at landscape level (Lindgren 1993), as well as adjacent naturally regenerated stands and clone plantations. Even a small number of clones per plantation, if the proportion of such plantations remains low (2 clones up to ~ 10%, 10 clones up to ~ 35%), makes it possible to maintain the same genetic diversity at the forest landscape level as if there were no such plantations (Fig. 3.1). As can also be seen from this approach (dispersed placement of plantations), the ecological impact depends heavily on the area (proportion) devoted to intensive or clonal forestry (Bettinger et

al. 2009, Bradshaw et al. 2019). Studies in Sweden have estimated that even under the most intensive management scenario, half of the spruce population will regenerate by self-seeding (Rosvall 2019) and provide opportunities to apply clone plantations in the rest of the territory while maintaining GD (Ingvarsson & Dahlberg 2019). It should also be noted that in the landscape the same clone mixes are not used for a long period of time – new, better (according to the value of the selection index) clones replacing previous ones are selected in each breeding cycle or even more often. The overall genetic diversity of the species is also maintained by forest stands of genetic resources involved in the conservation of rare alleles and the transfer of such alleles to the breeding population, providing potential for selection of suitable (productive) genotypes also under very variable or harsh conditions (Maxted et al. 2007, Trethowan & Mujeeb-Kazi 2008, Khoury et al. 2010, Hanso & Drenkhan 2012, McCouch et al. 2012). Analysis shows that the conservation of self-seeded stands or planted (progenies of seed orchards) forest stands in the forest landscape is important for the expansion of large-scale clonal forestry (Wu 2019).

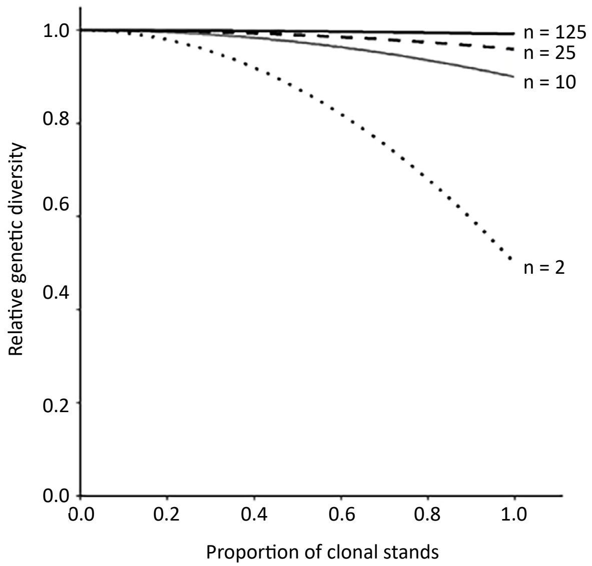

Figure 3.1 **Relative genetic diversity versus a situation where clones are not used**

It is assumed that there are 2,000 trees in the stand and 125, 25, 10 and 2 clones were used to regenerate it. It is assumed that different stands are planted using different sets of clones from a breeding population large and constant in time (by Ingvarsson & Dahlberg 2019)

The results of the analysis show that in boreal conditions characterised by abundant natural regeneration of birch, spruce and other tree species and the free outcrossing of these species also between remote stands, clone plantations have relatively little impact on the overall gene pool, until these plantations do not form the majority of the stands in the landscape and as long as they contain diverse sets of genotypes (Rosvall 2019). Most of the alleles found in the population in other forest stands will also be in the mix of clones, only in varying frequencies. The mix of clones can include a vast gene pool even with a limited number of genotypes (Ingvarsson & Dahlberg 2019).

Under Latvian conditions, modelling the proportions of planted improved silver birch stands (open-pollinated progenies of first generation seed orchard) at the forest landscape level and the impact of the number of families used (5 to 30 families) in the production of planting material on genetic diversity, it has been assessed that indicators of genetic diversity (Shannon-Wiener Diversity Index and the expected heterozygosity) are highest when 50 to 55% of the stands are regenerated by planting and using at least 20 families (Fig. 3.2). Whereas, using selected top 5 families, the genetic diversity is comparable to that found in natural regeneration when the proportion of planted stands in the landscape does not exceed 55% (Bāders et al. 2024).

It can be concluded that studies support the use of a limited number (5) of best genotypes in intensive forestry, provided that the proportion of such planted stands between naturally regenerated forest stands in the landscape do not exceed approximately 55%. This approach ensures a balance between productivity and maintaining genetic diversity in managed forest ecosystems.

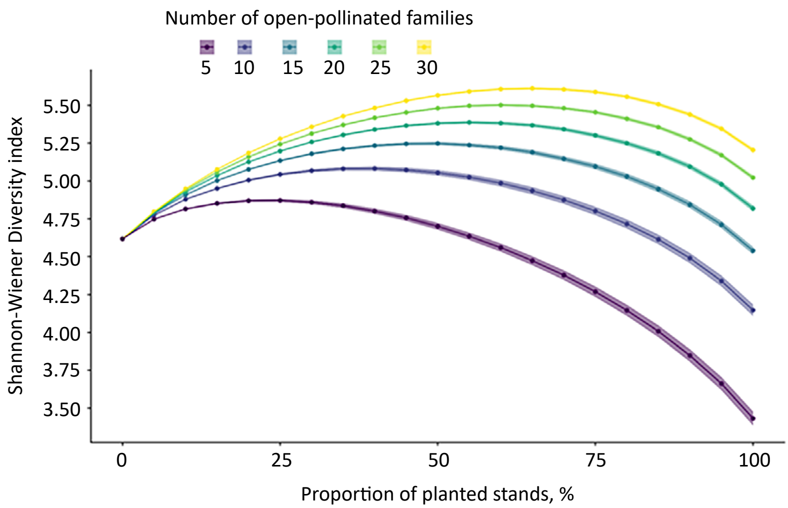

Figure 3.2 **The effect of the proportion of planted stands and the number of families used for producing planting stock within them on genetic diversity at landscape level**

(Bāders et al. 2024)

Summary

In Latvia, as in other Baltic Sea region countries, extensive progeny trials have been established, reaching an age where a previously lacking detailed evaluation and analysis can now be conducted to derive well-grounded conclusions. It is essential to assess the genetic determination of economically important traits and their genotypic correlations, which may vary across different populations.

Progeny trials serve as a basis for selecting clones not only for seed orchard establishment but also for vegetative propagation. Genotypes suitable for sapling production can be identified through further in vitro testing. Genotype plays a crucial role in the successful micropropagation of birch, making it essential to develop technology with media compositions tailored to specific clones for practical application. For the justified use of vegetatively propagated planting stock in practice – where practical experience already exists, for example, in Finland – a comprehensive evaluation of the entire growth cycle is necessary. This assessment should include plantations that have reached target diameters.

The profitability of breeding is determined by the additional productivity achieved (including improved resilience to various environmental risks), higher stem quality to increase the proportion of high-quality assortments in final harvesting, and the positive impact of shortening the rotation cycle. However, the financial gains from commercial thinning operations remain under-evaluated.

4 MATERIALS AND METHODS

4.1 Evaluation of progeny trials (I, II and III publication)

The dissertation analyses data from a total of 122 birch breeding trials, covering an area of 274.3 hectares since their establishment began in 1975 (Table 1.4). The climatic conditions at the trial sites vary slightly, with continentality increasing from the Baltic Sea coast toward inland areas (Laiviņš & Melecis 2003). According to the Latvian Environment, Geology, and Meteorology Centre, the average annual air temperature in Latvia over recent decades has been +6.4°C, ranging from +5.2–+5.3°C in inland highlands to +6.8–+7.4°C along the Baltic Sea coast. July is the warmest month, with an average air temperature of +17.4°C and an average maximum temperature of +22.3°C. February is the coldest month, with an average air temperature of –3.7°C and an average minimum temperature of –6.6°C. The average annual precipitation in Latvia is 692 mm. The rainiest months are July and August, with 76–77 mm of precipitation, while April is the driest month, receiving only 34 mm.

4.1.1 Data collection

A provenance trial was established in central Latvia on mesotrophic soil with a normal moisture regime and an initial planting density of 4,200 trees ha^{-1} (planting scheme 2 × 1.2 m). The trial included 16 provenances: 8 from Latvia, 4 from Finland, and 4 from Poland, spanning a latitude range of 51°–61° N. The experiment was set up as a completely randomized block design with 24-tree block plots in six replicates. Measurements were conducted at the age of 37 years, with no thinning performed before the assessment. Height (H) and diameter at breast height (DBH) were measured for each tree, and occurrences of spike knots and double leaders were recorded. A subsample of 10 trees, representing the range of DBH, was felled, and data on branch and stem biomass were obtained by sectioning the stem into 1-meter segments. These data were used to calculate the height of the tree's center of mass.

The seeds for the largest open-pollinated progeny trials analyzed in this study were collected during 1995–1998 from plus trees in 26 forest stands across Latvia. The trials were established on abandoned agricultural land in Taurene (57°06′ N, 25°38′ E), Ukri (56°22′ N, 23°07′ E), and Rembate (56°46′ N, 24°48′ E), on mesotrophic soils with normal moisture regimes. The experimental design in Ukri and Taurene consisted of randomized block layouts with single-tree plots, replicated 10–93 and 10–77 times, respectively, and a planting distance of 2 × 2.5 m. In Rembate, a completely randomized block design was used, with 32-tree block plots per family replicated three to five times and a planting distance of 2 × 2 m. The Rembate trial was established in the spring of 1999, while the trials in Ukri and Taurene were established in the spring of 2000, using one-year-old container seedlings. Differences in the establishment year were accounted for during measurements to ensure that all trials were assessed at the same tree age, allowing data from all three sites to be included in a unified analysis.

In all three open-pollinated progeny trials, evaluation was done at the age of 10 and 14 years. For the first evaluation, measurements from 68,256 trees were available for analysis (9,643, 11,917, and 46,696 trees in Ukri, Taurene and Rembate, respectively). For the second evaluation, 82,367 trees were measured (18,371, 10,964, and 53,032 trees in Ukri, Taurene and Rembate respectively). During the first evaluation, for each individual (a) tree height (H), (b) diameter of the largest branch until the stem height of 2 m (BrD), and (c) mean branch angle (BrA) was measured. Occurrence of spike knots (SpKn), double leaders (Doubl) and lost top (LostTop) were recorded as binary variables (1 – present, 0 – absent), and ordinal scores using 3-point-scale of stem straightness (StStr; bent, slightly bent, and straight) and overall stem quality (StQual; poor, intermediate, and good) were assessed. At the age of 14 years, H and diameter at breast height (DBH) were measured (except for Rembate, where H was not measured). Afterwards, stem volume (V) was calculated according to Liepa (1996). In trial Rembate, BrA was measured, but in Ukri and Taurene it was assessed using 3-point ordinal score (1 – from 65° to 90°; 2 – from 45° to 60°; 3 – from 0° to 40°). Occurrence of SpKn, Doubl, LostTop, and ordinal scores of StStr and StQual were assessed as described above.

4.1.2 Statistical analysis

In the provenance trial, characteristics such as stem volume, basal area, and stand volume per hectare were calculated, along with the significance of their differences and the expected values at the time when they reach the target diameter (25 cm). This time was determined using the growth model developed by LSFRI 'Silava' (Donis et al. 2024).

For **the open-pollinated families in the studied progeny trials**, variance and covariance components for continuous traits were estimated using SAS MIXED procedure with the restricted maximum likelihood approach (REML; Littell et al. 2006). Diagnostic plots were used to verify for normal distribution of residuals. For the binomial variables, a generalised linear mixed model applying binomial residual distribution and a *logit* link function was fitted. For the ordinal variables, ordinal logistic regression was fitted. The binary/categorical traits were analysed using the Generalized Linear Mixed (GLIMMIX) procedure (Littell et al. 2006). Standard errors were calculated using Dickerson's approximation (Dickerson 1969). For a combined-site analysis of Ukri and Taurene, which had similar experimental design and set of families, the following mixed model was used:

$$y_{ijkl} = \mu + S_i + B_j + F_k + SF_{ik} + \varepsilon_{ijkl} \ , \tag{4.1}$$

where:

y_{ijk} – the observation on the *l*th tree from the *k*th family in the *j*th block within the *i*th site;

μ – the overall mean;
S_i and B_j – the fixed effects of the ith site and the jth block within the ith site, respectively.

The F_k and SF_{ik} are the random effects of the kth family and interaction of the ith site and the kth family, respectively, and ε_{ijkl} is the random residual effect. Preliminary analyses indicated significant effect for the provenance-by-site interaction for studied traits.

For an individual site analysis of Ukri and Taurene, following model was used:

$$y_{jkl} = \mu + B_j + F_k + \varepsilon_{jkl} \ , \tag{4.2}$$

where:
y_{jkl} – the observation on the lth tree from the kth family in the jth block.

For individual site analysis of Rembate, the model was complemented with an effect of the block and family interaction (a multiple-tree plot effect):

$$y_{jkl} = \mu + B_j + F_k + BF_{jk} + \varepsilon_{jkl} \ , \tag{4.3}$$

where:
BF_{jk} – a random interactive effect of the jth block and the kth family.

The estimates of narrow-sense individual-tree heritability (h^2) were obtained for each trait using the variance components from the individual and joint-site analysis described above (Falconer & Mackay 1996). The individual-tree narrow-sense heritability in the joint-site analysis of Ukri and Taurene was calculated as:

$$h^2 = \frac{4 \cdot \hat{\sigma}_f^2}{\hat{\sigma}_f^2 + \hat{\sigma}_{fs}^2 + \hat{\sigma}_\varepsilon^2} \ , \tag{4.4}$$

where:
h^2 – narrow-sense heritability;
$\hat{\sigma}_f^2$, $\hat{\sigma}_{fs}^2$, and $\hat{\sigma}_\varepsilon^2$ – the estimated variance components of family, family × site interaction and residual, respectively.

For an individual single-tree plot site, following formula was used:

$$h^2 = \frac{4 \cdot \hat{\sigma}_f^2}{\hat{\sigma}_f^2 + \hat{\sigma}_\varepsilon^2} \tag{4.5}$$

For a multiple-tree-plot design in Rembate, following formula was used:

$$h^2 = \frac{4 \cdot \hat{\sigma}_f^2}{\hat{\sigma}_f^2 + \hat{\sigma}_{fb}^2 + \hat{\sigma}_\varepsilon^2} \ , \tag{4.6}$$

where:
$\hat{\sigma}_{fb}^2$ – the estimated variance component of site × block interaction.

Additive genetic coefficient of variation (CV_a) describing the extent of genetic variability for the quantitative traits in each site (Falconer & Mackay 1996), was calculated as:

$$CV_a = \sqrt{4\hat{\sigma}_f^2} \cdot \frac{100}{\bar{x}} \ , \tag{4.7}$$

where:
$\bar{x}$ – the phenotypic mean.

Genetic correlations (type-A) between traits and age-age genetic correlations for each trait were estimated using formula:

$$r_G = \frac{\widehat{Cov}_{(xy)}}{\sqrt{\hat{\sigma}^2_{(x)} \cdot \hat{\sigma}^2_{(y)}}} \ , \tag{4.8}$$

where:
$\hat{\sigma}^2_{(x)}$ un $\hat{\sigma}^2_{(y)}$ – a) the estimated genotypic variances for traits *x* and *y*, or b) the same trait variances at two different ages;
$\hat{Cov}_{(xy)}$ – the estimated genotypic covariance between traits *x* and *y* or between two measurements of the same trait.

The genotype × environment interaction (G × E) for studied traits was evaluated by estimating type-B genetic correlations (r_B) between two experiments (Bourdon 1977). Considering similar experimental design and set of the same families, the type-B genetic correlation between Ukri and Taurene was calculated as (Lu & Charrette 2008):

$$r_B = \frac{\widehat{Cov}_{(a1a2)}}{\sqrt{\hat{\sigma}^2_{(a1)} \cdot \hat{\sigma}^2_{(a2)}}} \ , \tag{4.9}$$

where:
$\hat{Cov}_{(a1a2)}$ – the covariance between genotypic effects of the same traits in different sites;
$\hat{\sigma}^2_{(a1)}$ and $\hat{\sigma}^2_{(a2)}$ – genotypic variances for the same traits in each of the trails, respectively.

Both r_G and r_B with their standard errors were estimated by multivariate REML using the MIXED procedure of SAS (Piepho & Möhring 2011) extending univariate mixed models described above.

Breeding values were estimated for each trait to evaluate gain from selection of the best families. We obtain general combining ability (GCA) values of parents by a Best Linear Unbiased Predictors (BLUP) procedure in SAS using the analytical models defined above. Since parent can only transmit half of its genes to its progeny (Falconer & Mackay 1996), breeding values (BV) of families were calculated as double BLUPs. Since the linear predictors for the binary traits from the generalized mixed models were calculated on a *logit* scale, predicted probabilities of stem defects for families were estimated by applying the inverse of the link function (Littell et al. 1996). Genetic gains, assuming the selection intensity of 10% (as commonly used in tree breeding practice in Latvia), were estimated from BV as the percentage over the trial means.

Principal Component Analysis (PCA) was conducted for the combined Ukri and Taurene trials to evaluate the variation in standardized phenotypic traits of birch provenances (Fig. 1.2) and to link this variation to their geographic origin. The evaluated mean values for provenances were obtained using mixed-effects models:

$$y_{ijklm} = \mu + P_i + F_j + S_k + b_l + sf_{jk} + \varepsilon_{ijklm} \ , \tag{4.10}$$

where:
y_{ijklm} – the observation;
μ – the overall mean;

P_i, F_j and S_k – the fixed effects of provenance, family, and site, respectively;
b_l and sf_{jk} – random effects of the block and the site × family interaction;
ε_{ijklm} – the random residual effect.

The significance of the principal components (PCs) was determined using a Monte Carlo (randomization) test with 1,000 iterations. Pearson correlation analysis was used to assess the relationships between the studied traits and latitude/longitude with the first two principal components. For each provenance region identified by PCA, variance components for the evaluated traits were calculated using Equation 4.1 and heritability (h^2) and additive coefficient of variation (CV_a) were estimated.

4.2 Vegetative propagation of silver birch and its potential for mass propagation (IV and V publication)

4.2.1 Data collection

The studied material for **silver birch culture initiation *in vitro* and testing genotype determined differences in micropropagation** was collected from a 15-year-old progeny trial in Rembate, described in the section 4.1.1). To assess the effect of the mother-tree age on shoot initiation *in vitro*, the explants from clone 54–95 in Rembate were compared with the explants from one-year-old grafted scions (one year after grafting on two-year-old rootstock) of the same clone in Kalsnava (56°40′ N, 25°58′ E), and all samples were collected in March. To assess the effect of the time of the explant collection, twigs of clone 54–95 from Rembate were collected from the lowest part of the canopy four times per year: in March and April (spring), and in June (mid-summer) and September (autumn). In total, 100 twig segments per each ontogenetic age and collection time were initiated in vitro. In laboratory, stem segments containing one bud were excised and gently washed with a toothbrush and dish soap under running tap water, and rinsed toughly. Stem segments were sterilised for 10 min in 0.1% $HgCl_2$ with a few drops of Tween 20, and rinsed three times with distilled water. The stem segments were inserted into glass test tubes (18 × 180 mm, with a metal cap) containing 3 mL of woody plant medium (WPM; Lloyd, McCown 1980) supplemented with WPM micronutrients, WPM vitamins, 1.0 mg L^{-1} of 6-benzylaminopurine (BAP), 0.05 mg L^{-1} of naphthaleneacetic acid, 20 g L^{-1} of sucrose, and 6 g L^{-1} of agar. The pH of the medium was adjusted to 5.8, and the tubes were autoclaved for 15 min (110 kPa, 121°C). The culture was incubated at 25 ± 3°C under a 16-hour photoperiod of cool-white fluorescent light (photosynthetically active radiation with photon flux density at 140 to 160 µmol m^{-2} s^{-1}). After 30 days, the proportion of initiated shoots was evaluated.

The multiplication rate and the growth of shoots between 50 genotypes in Rembate were assessed using a stabilised *in vitro* culture. Ten shoots per each clone were inserted into test tubes (one explant per tube) containing 3 mL of Murashige and Skoog (MS) basal media (Murashige & Skoog 1962), supplemented with

MS micronutrients, 0.2 mg L^{-1} of zeatin, MS vitamins, 20 g L^{-1} of sucrose, and 6 g L^{1} of agar. The pH of the medium and the cultivation conditions were set as described for the culture initiation. After 30 days, 500 shoots were assessed. The main shoot was measured. The lateral shoots ≥ 0.5 cm were counted, and the multiplication rate of each shoot was determined by the number of 1.5-cm-long shoot fragments (hyperhydrated shoots were not counted) that could be obtained from one plant. The total multiplication rate and occurrence of hyperhydrated shoots were noted. According to the growth parameters, the clones were divided into four groups to assess the effect of the macronutrient media and plant growth regulators. Group divisions were based on the multiplication rate and ability to proliferate. Group 1 has a multiplication rate of 3.4 to 6.8. Group 2 has a multiplication rate of 1.7 to 3.3. Group 3 has a multiplication rate of 0 to 1.6 with proliferation, and Group 4 has a multiplication rate of 0 to 1.6 without proliferation.

Three clones from each group (24 shoots per clone in each treatment) were randomly selected to test the effect of the multiplication medium and cytokinin type and concentration in the following combinations: (1) WPM, zeatin 0.1 mg L^{-1}; (2) WPM, zeatin 0.5 mg L^{-1}; (3) MS, zeatin 0.1 mg L^{-1}; (4) MS, zeatin 0.5 mg L^{-1}; (5) MS, zeatin 1.0 mg L^{-1}; (6) MS, BAP 0.5 mg L^{-1}; and (7) MS, BAP 1.0 mg L^{-1}. The pH of the medium and the cultivation conditions were set as described for the culture initiation. After 30 days, 2,016 shoots were assessed. The main and lateral shoots were measured. The lateral shoots ≥ 0.5 cm were counted. The multiplication rate of each shoot was determined by the number of 1.5-cm-long shoot fragments (hyperhydrated shoots were not counted) that could be obtained from one plant. Finally, the total multiplication rate and occurrence of the hyperhydrated shoots were noted.

Genetic parameters of growth traits and stem quality of vegetatively propagated silver birch clones were examined in a low-density plantation located in the central part of Latvia (57°32′ N, 24°44′ E). The topography was flat (elevation < 100 m above sea level). The mean annual temperature was 6.2°C; the mean monthly temperature ranged from 4.6°C to 17.5°C in February and July, respectively. The mean annual precipitation was ca. 690 mm.

The trial was established in 1972 on agricultural land, equivalent to *Oxalidosa* stand type with mesotrophic loamy soil. One year after grafting, clones of 22 birch plus-trees from the central part of Latvia (56°37′–57°28′ N, 24°50′–26°24′ E) were planted in a 5 × 5 m grid (400 trees ha^{-1}) as single-tree plots in 13–56 randomly distributed replications. Clones were randomized spatially all over the planting site. Initially, the plantation was intended as a seed orchard, but abandoned soon thereafter; hence no management, except some initial cleaning, was performed. The area of the plantation was 1.8 ha (720 planting spots). At the age of 40 years in 2012, for each tree (1) DBH, (2) H, (3) height of the lowest living branch (m), (4) BrA, (5) mean projection of crown (MPC, m), (6) occurrence of SpKn, (7) Doubl, and (8) stem cracks (present/absent), and arbitrary scores using 6-point-scales of (9) StStr, and (10) branchiness were measured.

4.2.2 Data analysis

For **silver birch *in vitro* study**, the chi-square (χ^2) test was used to assess the distribution of the initiated shoots between the time of explant collection and the age of the mother-tree. The analysis of variance and Tukey's honestly significant difference test were used to assess the differences in the length of the main shoots, the length and number of lateral shoots, the multiplication rate, and proportion of the hyperhydrated shoots between the clones and groups of clones. Generalised linear models with a Poisson distribution were used to assess the relationship between the length of the main shoot and the number of the lateral shoots, as well as to evaluate the effect that the length of the main shoot, number of lateral shoots, length of lateral shoots, and total multiplication rate had on the number of hyperhydrated shoots. Linear model was used to assess relationship between the length of the main shoot and the length of the lateral shoots. The regression coefficients ± standard errors are shown. All calculations were done in R 3.5.1. (R Core Team 2018). In addition, all tests were performed at $\alpha = 0.05$.

For each tree **in the low-density clonal silver birch plantation**, stemwood volume was calculated according to the local model (Liepa 1996). The assortment outcome from each harvested tree was calculated using the model developed by R. Ozoliņš (Ozolins 2002) and modified by J. Donis (Donis et al. 2024). Wood defects and stem quality traits were considered when determining the structure of stemwood assortment (according to the practices of commercial forestry in Latvia). According to the estimated volume of assortments, the monetary value of stem wood (MV) of each sampled tree was calculated as an integrative parameter. Prices of different assortments according to top diameter, as used in the calculation of MV, were 20, 26, 45, 60, and 70 EUR m^{-3} for firewood (< 13 cm), pulpwood (< 13 cm), logs 14–18 cm, logs 19–25 cm, and logs > 26 cm, respectively.

Heritability coefficients H^2 (broad-sense individual-tree heritability) for the studied variables were calculated (Falconer & Mackay 1996):

$$H^2 = \frac{\sigma_G^2}{\sigma_P^2} \ , \tag{4.11}$$

where:
σ_G^2 – genotypic variance;
σ_P^2 – phenotypic variance constituted of genotypic and environmental variance.

Genetic gain was estimated according to formula (Falconer & Mackay 1996):

$$R = S \cdot H^2 \ , \tag{4.12}$$

where:
S – selection differential, which is the mean phenotypic value of the selected clones expressed as a deviation from the trial mean.

For each variable, superiority of the top three clones against trial mean was assessed.

Genotypic and phenotypic clone mean Pearson correlations were estimated for the studied variables (Falconer & Mackay 1996). Genotypic correlations between the traits were calculated using the Equation 4.8. Standard errors for the genotypic correlation estimates were obtained with the delta method (Lynch, Walsh 1998).

Genotypic coefficients of variation (CV_g), describing the extent of genetic variability of a variable in relation to the mean of trial, were calculated as:

$$CV_g = \sqrt{\sigma_G^2} \cdot \frac{100}{\bar{x}} \ , \tag{4.13}$$

where:

$\bar{x}$ – the phenotypic mean.

The corresponding components of genotypic and environmental variance were extracted using a random model:

$$y_{ij} = \mu + c_i + \varepsilon_{ij} \ , \tag{4.14}$$

where:

y_{ij} – observation of each trait of the *ij*th tree;

μ – the overall mean;

c_i – the random clone effect.

For the quantitative variables (e.g., DBH, H), a linear mixed model was used. For the binomial variables (e.g., survival, probability of cracks, etc.), a generalized linear mixed model applying binomial residual distribution and *logit* link function was fitted. For both models, R package lme4 was used (Bates et al. 2014). For StStr and branchiness, ordinal logistic regression was applied (Long 1997) using R package ordinal (Christensen 2015). The environmental variance of the link functions was determined as $\pi^2/3$, or 3.29. Genetic covariance $\sigma_{G(x,y)}$ between any two traits *x* and *y* was estimated using function *varcomp* in package "lme4". Data analysis was conducted in program R, v. 3.3. (R Development Core Team 2016).

4.3 Profitability of utilizing genetically improved silver birch (VI and VII publication)

4.3.1 Data collection

Profitability of silver birch breeding in Latvia was examined, considering whole breading population. All available breeding material of silver birch in Latvia can be divided in 2 groups:

1) open-pollinated progenies of 921 phenotypically selected plus tree or superior stand tree (Section 4.1.1);
2) progenies of 360 controlled crosses of 100 untested (phenotypically selected) clones in seed orchard that have not reached the age for evaluation.

Both groups of available material can be integrated at the end of the second breeding cycle of the first group; therefore, it is chosen as a time horizon for the analysis.

For the bulk of material (first group) it is planned to establish two breeding populations, based on delineated provenance regions (eastern and western), and using altogether 150 trees – phenotypically selected progenies from the most productive and qualitative open-pollinated families, since the mother trees are not available any more. Among the members of the breeding population, double-pair mating are performed. For further activities 3 different alternatives are compared: (1) phenotypic (FEN) selection of the best individuals within a family, (2) clonally (VEG – vegetative) testing, where the selection of candidates within a family and their vegetative propagation is performed, followed by the establishment of clonal progeny trials and backward selection of the two best candidates from each family, (3) progeny (GEN – generative) testing, where phenotypic selection of candidates within a family and their flowering stimulation to obtain seeds is done, followed by the establishment of open-pollinated progeny trials and backward selection of the two best candidates from each family.

Effect of breeding on income at first commercial thinning in silver birch was studied in the trial Rembate (characterized in Section 4.1.1). For the particular study, only families represented in at least 3 replications (524 in total) were assessed. In 2014, at the age of 14 years, DBH and H were measured for each living tree before the harvest and removed trees noted after the harvest. In total, 84% of the initially planted trees had survived until harvesting; each replication (block-plot) contained from 24 to 32 trees. The harvesting was performed by chain saws (motor-manual) to reduce damage to the remaining trees; timber was transported by a forwarder. Thinning from below was performed; basal area was reduced from 14.62 to 7.52 m^2 ha^{-1}.

4.3.2 Data analysis

For **profitability analysis of silver birch breeding**, planned activities, that are not explicitly analysed in the study, but costs are added to each of the alternatives:

1) for the first group of material, before the beginning of the second breeding cycle: repeated measuring of part of the trials, selection of individual trees within superior families;
2) for the second group of material: tending work in progeny trials, measurements, selection of individual trees within superior families.

The comparison of alternatives is based and differential approach is used, i.e., only positions of benefits and costs, which differ between 2 regeneration methods – natural and planting of selected material – are considered (Ahtikoski 2000). In the analysis, differential costs are based on prices of the year 2010 and represented by:

1) costs of tree breeding activities, obtained from practical experience in the Latvian State Forest Research Institute ‘Silava’ according to activities needed to carry out each of the alternatives (FEN, VEG, GEN);
2) costs of seed orchard establishment and maintenance, obtained from the JSC ‘Latvia’s State Forests’, that owns the productive birch seed orchards in Latvia;
3) costs of regeneration: plants, soil preparation, planting, and two extra cleanings, information from the results of the tenders of the JSC ‘Latvia’s State Forests’.

The differential benefit is represented by additional yield and shorter rotation time (cutting by target diameter, if possible) of the stands regenerated by the selected reproductive material. Values of genetic gain for each of alternatives, scale and timing of tree breeding works were partly assessed using the 'Breeding Cycle Analyser' (Danusevicius & Lindgren 2002a, b) with genetic gain per unit of time as the target to be maximized (Table 4.1). Genetic gain of an improved stand expressed relative to diameter and height growth of an unimproved stand was calculated based on constant proportional advantage approach (Ahtikoski 2000).

Growth models for traditional (high initial density, delayed, low intensity thinnings) and targeted (aimed to maximize the mean diameter and total volume of trees at the final felling age, and characterized by low initial stand density) silvicultural systems and thinning regimes, the same for naturally regenerated and planted (improved) stand were chosen, based on recommendation of P. Zālītis and J. Jansons (2009). The assortment structure in thinning and final felling was calculated; the assortment prices for the years 2006–2010 were obtained from Central Statistical Bureau and JSC 'Latvia's State Forests'. Assortments were set as follows: first grade logs (top diameter exceeds 25.9 cm, length 4.9 m), second grade (18– 25.9 cm, 4.9 m), third grade (14–17.9 cm, 4.9 m), pulpwood (6–13.9 cm, 3 m), firewood (3.0–5.9 cm, 2 m).

Area of seed orchard was based on minimal number of clones to ensure genetic diversity as well as predicted seed needs, assuming that all birch stands on fertile soils would be clear-felled and replanted with improved material. Selected set of clones is set to be used for 24 years, since none of the alternatives could switch to new set of clones of higher genetic quality faster than that.

Table 4.1

Scale and timing of tree breeding works based on different alternatives used in analysis

Size of breeding material and duration of different phases		Tree breeding alternative		
		FEN	VEG	GEN
Duration of activity, years	Recombination	6	6	6
	Time before	2	4	2
	Testing of progenies	25	12	14
	Time after	-	-	5
	Time before	-	-	2
	Testing of candidates	-	-	12
	Total time	33	22	41
Size of breeding material	Number of families	150	150	150
	Number of trees per family	300	100	120
	Number of candidates	-	40	25
	Number of progenies/ramets per candidate	-	40	35

To ensure unbiased comparison between regeneration methods and breeding alternatives, net present value (NPV) was calculated with the interest rate 3%.

For **evaluating effect of breeding on income at first commercial thinning in silver birch plantation**, stemwood volume and assortment outcome from each harvested tree was calculated). To demonstrate the influence of market fluctuations on the income, low (in 2014) and high (2018) timber prices were used (Table 4.2).

Table 4.2

Assortment classes by diameter at the top end and monetary value with low and high timber prices

Assortment	Length, m	Diameter at the top end, cm	Price, EUR m^{-3}		Proportion of the harvested volume, %
			low (in 2014)	high (in 2018)	
Sawlogs	3.0	12.0	47	56	1.3
Firewood	3.0	10.0	37	50	14.3
Pulpwood	3.0	6.0	35	54	59.3
Energy-wood	3.0	3.0	22.5	30	25.1

Genetic parameters were calculated using three largest (by DBH) trees per family and replication. To assess the heritability of the traits (DBH, stemwood value, and proportion of industrial timber), variance and covariance components (σ) were estimated using the mixed model analysis with the restricted maximum likelihood approach in SAS (Version 9, SAS Institute, Cary, NC, USA; Littell et al. 2006) according to Equation 4.3. Considering the randomized block design of the trial, heritability (h^2) was estimated as in Equation 4.6. The coefficient of additive genetic variation (CV_a) describing the extent of genetic variability for the quantitative traits (Falconer & Mackay 1996), was calculated as in Equation 4.7. Genetic gain (GG) was calculated using a 10% selection intensity (i; Falconer & Mackay 1996). The net wood value (NWV), net present value (NPV) and internal rate of return (IRR) were calculated as the economic indicators for the harvested timber. To assess the economic effect of breeding, the indicators were calculated for the trial mean, as well as for the top and bottom 10% of the families, ranked by the GG of DBH.

For each tree, sawlog income was calculated as:

$$NWV = I_{income} - H_{costs} \ , \tag{4.15}$$

where

I_{income} – income from harvesting, and

H_{costs} – is the harvesting costs (Central Statistical Bureau of Latvia 2016).

Income and costs were included in the analysis by calculating NPV, which was calculated as the discounted value of the future expected net cash flow.

$$NPV = \frac{NWV - E_{costs}}{(1+r)^n} \ , \tag{4.16}$$

where

E_{costs} – the establishment costs (low and high prices),

r – the discount rate (3% and 5%), and

n – the number of years (14).

The establishment costs were acquired from the Central Statistical Bureau of Latvia.

To estimate the profitability of the potential investment, the IRR was calculated using the following equation:

$$NPV = \frac{NWV - E_{costs}}{(1+r)^n} \quad , \tag{4.17}$$

where

r_a – the lower discount rate (3%),
r_b – the higher discount rate (5%),
NPV_a – NPV at r_a, and
NPV_b – NPV at r_b discount rate.

5 RESULTS AND DISCUSSION

5.1 Evaluation of progeny trials (I, II and III publication)

In the provenance tests, origin was a significant factor affecting survival; for specific provenances survival ranged from 11% to 63% and it was lowest for birched from Finland (on average 16%), higher for birches from Poland (42%) and highest from local birches (50%). Provenance was also a significant factor, affecting height (Fig. 5.1), breast height diameter and, consequently, stem volume of birches, yet the occurrence of spike knots did not show significant differences among origins.

Correlation between mean height of the provenances at the age of 5 years (earlier measurements) and 37 years was statistically significant (r = 0.78).

Provenance specific standing volume ranged from 24 m^3 ha^{-1} to 405 m^3 ha^{-1} and was on average 204 m^3 ha^{-1}. Calculations estimating even survival for all provenances reveal similar trend than based on actual survival – largest standing volume was for local (Latvian) birch, lower – for birch from Poland, and lowest – from Finland. Top-ranking provenances based both on H (Table 5.1, Fig. 5.2) and DBH were from Latvia; however, there was large variation in the traits and potential to select some birches from Poland, that could reach similar growth than the local provenances. Thus, the material from similar stage of breeding (seed orchard progenies or clones) could be further tested to find genotypes with superior performance in

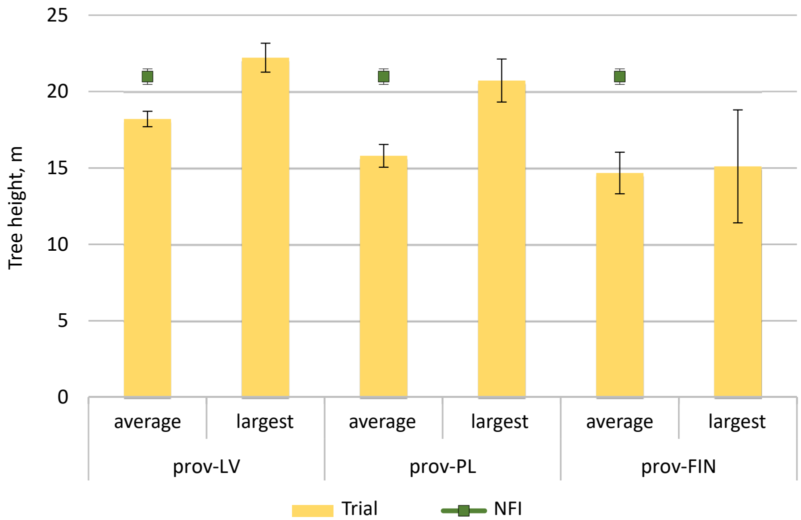

Figure 5.1 **Height for the groups of provenances in trial in comparison to the parameters in birch stands in Latvia on average**

(whiskers denote 96% confidence intervals; data: National Forest Inventory (NFI)) current (in Latvia) and slightly warmer (as currently in Poland) conditions. Birches from Finland were heavily outperformed and testing only for superior genotypes (e.g. very fast-growing clone) could be justified.

Table 5.1

Forest inventory parameters of provenance groups from different countries

Provenance group	Mean			Highest		
	density, trees ha^{-1}	height, m	diameter at breast height, cm	density, trees ha^{-1}	height, m	diameter at breast height, cm
Latvia (LV)	2,064	17.9	13.0	521	22.2	17.0
Finland (FIN)	669	14.2	9.5	521	15.1	10.0
Poland (PL)	1,691	15.4	10.0	521	20.7	15.0

Abbreviations: Mean – measured forest inventory parameters; highest – parameters for the tallest trees corresponding to the specified stand density (521 trees per hectare).

Rather small differences in the H and DBH at the measurement age corresponds to large differences in time, when the target diameter can be reached (Table 5.2). In sparser stand (521 trees ha^{-1}) assuming the best growth and good conditions for silver birch in Latvia (age 27, highest), this diameter can be reached as early as at the age of 48 years. It is close to the values actually found in Latvia in sparse clonal plantation of birch (**IV**), where the mean diameter exceeded 28 cm at the age of 40 years, yet the density was lower (initial: 400 trees ha^{-1}). Polish birch provenances would reach the target diameter at the age of 57 years and have a similar yield than the Latvian provenances 10 years earlier (272 m^3 ha^{-1} and 263 m^3 ha^{-1}, respectively) under similar input parameters in the model. Thus, the

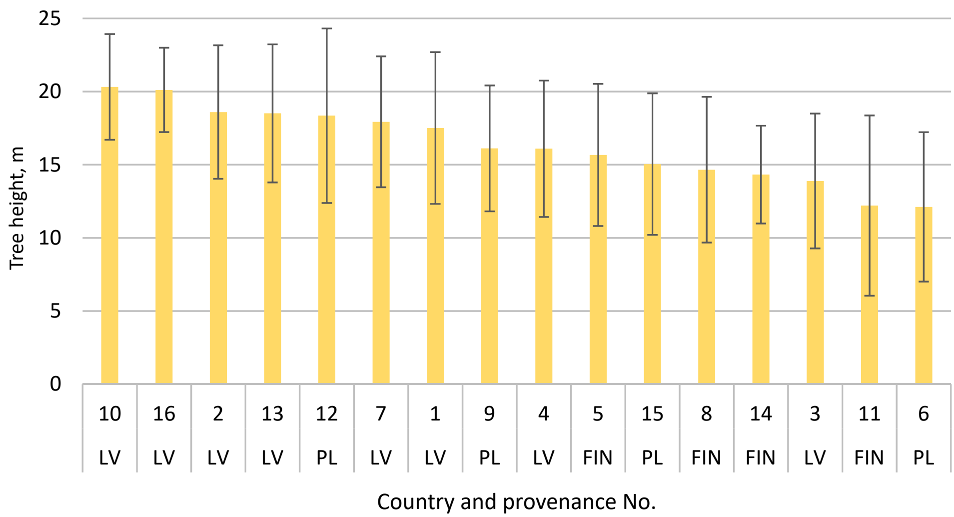

Figure 5.2 **Mean height of the provenances in trial**

Provenance No. corresponds to the number in the Figure 2.1

potential growth for birches from Poland is slightly lower than that of local provenances. Birches from Finland in any of the analysed combination of the parameters cannot reach the target diameter earlier than at the age of 100 years that is significantly later than the cutting age set in legislation in Latvia (71 year). In the actual conditions, target diameter cannot be reached before the cutting age; assuming better growing conditions and actual stand data – only local provenance, where in case thinning is carried out, can reach the intended target diameter at the age of 67 years.

Table 5.2

Age when target diameter (25 cm) is reached for different groups of provenances

Group of provenances from	Data	Age	
		27	37
Latvia (LV)	actual	91	127
Latvia (LV)	actual *	67	94
Finland (FIN)	actual	111	157
Poland (PL)	actual	127	167
Latvia (LV)	highest	48	67
Finland (FIN)	highest	100	143
Poland (PL)	highest	57	81

* commercial thinning carried out; other abbreviations in accordance to Table 2.1.

Commercial thinning had significant impact, boosting diameter increment in the provenance trial in accordance to the model (Fig. 5.3). However, it might be overestimated due to high density and thus reduced length of green crown in the stand. Birch provenances from Poland and Finland did not reach the basal area required for commercial thinning, thus it was not planned.

Mass centre was higher for provenances from Latvia due to faster tree growth, since its relative height in relation to tree height was quite stable. It can lead to higher wind damage risk for Latvian birch due to similar rotation periods for provenances from different countries (except for modelled growth on good growing conditions for birch). Further studies need to be carried out for detailed evaluate this effect.

In the studied **open-pollinated silver birch progeny tests**, the survival was high at both measurement times in Rembate (> 80%) and Ukri (> 90%), yet lower in Taurene (> 60%), which was most likely affected by the insufficient moisture in dry summer after the establishment due to the fine textured soil in the trial (Sutinen et al. 2002). However, first years after planting, necessary weed control was applied sufficiently to eliminate further mortality induced by weed competition (Ferm et al. 1994, Hynynen et al. 2010). At the age of 10 years, the means for H in Taurene and Ukri were the same (6.7 m), and other measured traits and proportion of trees with stem defects were similar. In Rembate, H was lower (5.5 m), and proportion of trees with SpKn was ca. three times lower than in the both other trials. At the age of 14 years, mean H was somewhat advanced ahead for Ukri comparing to Taurene (12.3 m and 11.5 m, respectively), yet other traits were stably alike. In Rembate,

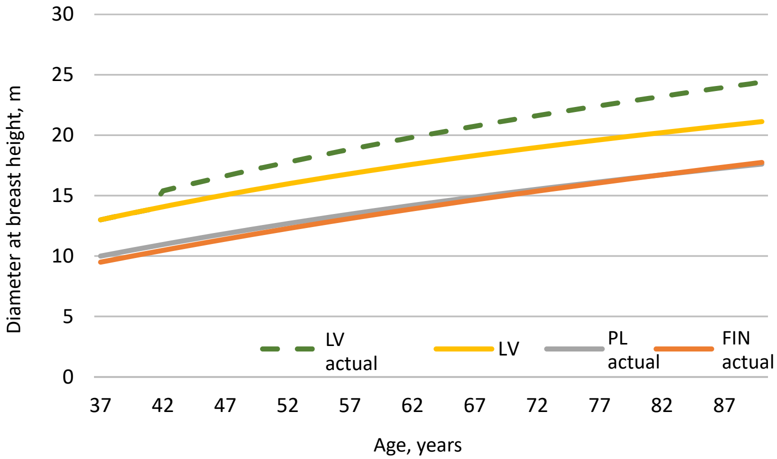

Figure 5.3 **Modelled development of breast height diameter for different provenances**

Dotted line – of commercial thinning implemented;
other abbreviations in accordance to Table 2.1

proportion of trees with SpKn had increased and was high (ca. 60%) and similar to both other trials. In all trials, proportion of trees with SpKn and LostTop was rather high (> 50%), while only 6–12% of trees had Doubl, seemingly not affected by different continentality of the studied trials (Laiviņš & Melecis 2003). Viherä-Aarnio and Velling (1999) reported 13% of trees with SpKn. Similar to Viherä-Aarnio and Velling (1999), most of the trees had at least a light stem sweep.

In the Baltic Sea region, heritability for growth and stem quality of common forest tree species Scots pine and Norway spruce reported to vary from 0.05 to 0.25 (Velling 1982, Haapanen et al. 1997, Hannrup et al. 1998, Olsson & Ericsson 2002, Jansons et al. 2006). In our study, the estimated narrow-sense heritability (h^2) varied among the variables, generally being higher for growth traits than stem quality (Table 5.3), supported by earlier findings in Latvia (Zeltiņš et al. 2018). The highest h^2 was estimated for H, DBH, V (0.30–0.64), except low value (0.12) for DBH in Rembate. Similarly, high h^2 had StStr (0.35–0.45), while StQual, BrD, and Doubl had generally lower values (0.04–0.35). Heritability for BrA varied considerably (0.25–0.83) depending on site and year, but LostTop showed the overall lowest values (0.02–0.12). Rather high CV_a was estimated for V, ranging from 25.3 to 40.3% in Rembate and Ukri, respectively. Branch angle showed low degree of genetic variation in all trials (3.7–6.4%; Table 5.4). The estimates of r_G among growth traits were similar and high in all studied trials (0.90–0.99; Table 5.5), yet having mainly low to moderate genetic correlations with stem quality traits ($-0.10 < r_G < 0.40$). Branch angle had moderate to strong negative correlations with StStr and StQual ($-0.67 < r_G < -0.45$), which both strongly correlated with each other (0.83–0.84). Rather high positive correlations between SpKn and Doubl (0.60–0.74) were found.

Table 5.3

Narrow sense heritabilities (h^2) and type-B genetic correlations (r_B) with standard errors (SE)

(all r_B are significant $p < 0.01$)

Trial	$h^2 \pm$ SE								$r_B \pm$ SE
	Taurene		Ukri		Rembate		Ukri & Taurene together		
Age, years	10	14	10	14	10	14	10	14	14
H	0.37 ± 0.03	0.45 ± 0.04	0.47 ± 0.04	0.64 ± 0.04	0.30 ± 0.07	na	0.37 ± 0.03	0.52 ± 0.03	0.94 ± 0.02
DBH	nd	0.45 ± 0.04	nd	0.52 ± 0.03	nd	0.12 ± 0.02	nd	0.42 ± 0.03	0.89 ± 0.03
V	nd	0.41 ± 0.03	nd	0.53 ± 0.03	nd	nd	nd	0.41 ± 0.03	0.97 ± 0.03
BrD	0.24 ± 0.03	nd	0.20 ± 0.03	nd	0.10 ± 0.03	nd	0.17 ± 0.02	nd	nd
BrA	0.33 ± 0.03	0.83 ± 0.19	0.27 ± 0.03	0.61 ± 0.07	0.30 ± 0.03	0.31 ± 0.03	0.25 ± 0.02	0.37 ± 0.1	0.78 ± 0.12
SpKn	0.07 ± 0.02	0.08 ± 0.02	0.06 ± 0.02	0.05 ± 0.01	0.04 ± 0.03	0.07 ± 0.02	0.07 ± nd	0.06 ± 0.02	nd
Doubl	0.29 ± 0.07	0.05 ± 0.06	0.04 ± 0.03	0.19 ± 0.04	0.08 ± 0.04	0.27 ± 0.05	0.1 ± nd	nd	nd
LostTop	0.09 ± 0.03	0.04 ± 0.02	0.06 ± 0.03	0.05 ± 0.01	0.12 ± 0.03	0.06 ± 0.02	0.05 ± 0.04	0.02 ± 0.01	nd
StStr	0.45 ± 0.05	0.35 ± 0.05	0.41 ± 0.05	0.45 ± 0.05	0.32 ± 0.05	0.39 ± 0.05	0.40 ± 0.06	0.4 ± 0.05	0.97 ± 0.05
StQual	0.15 ± 0.03	0.35 ± 0.05	0.11 ± 0.03	0.21 ± 0.03	0.14 ± 0.03	0.26 ± 0.04	0.10 ± 0.03	0.23 ± 0.03	0.89 ± 0.08

Abbreviations: H – height, DBH – diameter at breast height, V – stem volume, SpKn – spike knots, Doubl – double leaders, LostTop – lost top, StStr – stem straightness, BrD – branch diameter, BrA – branch angle, StQual – stem quality, nd – no data.

Still, stem quality traits generally had low to moderate genetic correlations with each other (Table 5.5).

Table 5.4

Genetic coefficients of variation for quantitative traits (CV_a) in the studied open-pollinated *Betula pendula* progeny trials at the age of 10 and 14 years

Trial	Taurene		Ukri		Rembate	
Age, years	10	14	10	14	10	14
H	10.4	8.5	11.4	5.5	7.5	nd
DBH	nd	18.7	nd	10.3	nd	4.7
V	nd	32.5	nd	20.1	nd	nd
BrD	16.2	nd	12.6	nd	4.3	nd
BrA	4.4	nd	4.7	nd	3.2	1.9

Abbreviations: H –height, DBH – diameter at breast height, V – stem volume, BrD – branch diameter, BrA – branch angle, nd – no data.

Considering that the genes controlling each of growth traits might be strongly correlated (Searle 1961), selection may be based on tree height, which possessed the highest h^2. In earlier studies, estimated h^2 and broad-sense heritability H^2 of corresponding traits for silver birch reported to vary widely from low to high (Nepveu & Velling 1983, Malcolm & Worrell 2001, Stener & Jansson 2005, Zeltiņš et al. 2018). In Norway, h^2 of six-years-old open-pollinated families estimated to be rather low, i.e. 0.09 and 0.17 for H and DBH, respectively (Skrøppa & Solvin 2019). In the present study, high heritability values and low variety among trails for growth traits might correspond to relatively homogenous growing conditions on agricultural land sufficiently maintained after establishment. Thus, genetically determined differences were better revealed comparing to forestland (Haapanen 1996, Hannrup et al. 2004). Although h^2 values from individual-site analysis are commonly overestimated and higher comparing to joint-site estimates (Hodge & White 1992, Haapanen 2001, Wu et al. 2008), our estimates of Ukri and Taurene together were close to heritability in separate sites. In contrast, insufficient maintenance, subsequent uneven survival and heterogeneous growth conditions commonly reported to result in low heritability indices with low accuracy, reducing benefits from tree breeding (Haapanen 1996, Mäkinen 1996, Talbot 1997, Nummi 1999, Olsson & Ericsson 2002, Koski & Rousi 2005). Nevertheless, mainly low h^2 for such stem defects as SpKn, Doubl and LostTop coincides with earlier findings (Stener & Hedenberg 2003, Zeltiņš et al. 2018), suggesting relatively weak genetic control and strong prevailing effect of such environmental factors as drought, frost or biotic damage (Malcolm & Worrell 2001, Stener & Hedenberg 2003). Stener and Jansson (2005) reported low h^2 and H^2 values (0.09–0.27) for StStr in a series of up to 10 years old silver birch clonal and progeny trials. Although StQual had low h^2 values (0.10–0.15) at the age of 10 years, moderate to high heritability (0.21–0.45) and rather weak genetic correlations (Table 5.5) with growth traits for both StStr and StQual implied substantial improvement for wood quality in our study.

Table 5.5

Genetic correlations (standard errors in brackets) in combined Ukri and Taurene (the upper diagonal part) and in Rembate (the lower diagonal part) open-pollinated *Betula pendula* progeny trials at the age of 14 years

Trial	DBH	V	SpKn	Doubl	LostTop	StStr	BrA	StQual
H	0.92 (0.01)	0.94 (0.01)	0.43 (0.07)	0.23 (0.07)	0.05 (0.09)	–0.10 (0.05)	0.26 (0.06)	0.16 (0.06)
DBH	-	0.99 (0.00)	0.39 (0.07)	0.20 (0.07)	0.10 (0.09)	–0.06 (0.05)	0.22 (0.06)	0.17 (0.06)
V	nd	-	0.39 (0.07)	0.23 (0.07)	0.06 (0.09)	–0.06 (0.05)	0.23 (0.06)	0.17 (0.06)
SpKn	0.13 (0.13)	nd	-	0.60 (0.11)	0.08 (0.20)	–0.29 (0.08)	–0.02 (0.09)	–0.51 (0.07)
Doubl	–0.10 (0.11)	nd	0.74 (0.11)	-	–0.51 (0.11)	0.03 (0.08)	–0.12 (0.09)	–0.16 (0.08)
LostTop	0.10 (0.13)	nd	–0.06 (0.14)	–0.49 (0.11)	-	–0.69 (0.09)	0.52 (0.11)	–0.58 (0.09)
StStr	0.02 (0.09)	nd	–0.39 (0.10)	–0.08 (0.09)	–0.71 (0.09)	-	–0.67 (0.05)	0.83 (0.03)
BrA	0.00 (0.25)	nd	–0.01 (0.10)	0.09 (0.09)	0.28 (0.10)	–0.57 (0.06)	-	–0.45 (0.07)
StQual	0.40 (0.24)	nd	–0.67 (0.09)	–0.28 (0.08)	–0.62 (0.08)	0.84 (0.04)	–0.48 (0.07)	-

Abbreviations: H –height, DBH – diameter at breast height, V – stem volume, SpKn – spike knots, Doubl – double leaders, LostTop – lost top, StStr – stem straightness, BrA – branch angle, StQual – stem quality, nd – no data.

In addition, generally moderate negative correlations between StQual and stem defects suggests that selection based on inclusive ordinal score of stem quality traits might reduce occurrence of stem defects despite low heritability of them, thus improving timber quality and increasing amount of merchantable wood (Agestam et al. 1998, Möttönen 2005). Mainly weak genetic correlations reported among quality traits as well as between growth and quality traits, likely related to rather low genetic variance of the latter ones (Koski & Rousi 2005, Stener & Jansson 2005). In Scotland, straight stems found to be associated with superior volume growth (Malcolm & Worrell 2001), yet not observed in our study. Similar to previous findings in Sweden and Latvia (Stener & Jansson 2005, Zeltiņš et al. 2018), BrD and BrA possessed high heritability. However, the substantial negative correlations between BrA and StStr might result in enlarged knot size for straighter logs, thus reducing technical quality (Niemistö 1995a). Larger BrD had been commonly reported as negative effect for fast growing silver birch (Niemistö 1995b, Stener & Jansson 2005), suggested to be mitigated with sufficient planting density of at least 1,600 trees ha^{-1} for smaller knot size and improved wood strength (Niemistö 1995a, Dunham et al. 1999). Nevertheless, study in 40-years old low-density clonal silver birch plantation in Latvia showed possibility to obtain high-quality plywood applying wide (5 × 5 m) initial spacing (Zeltiņš et al. 2018). Besides heritability, considerable CV_a (20.1–32.5%) suggested potential of breeding to improve V. Lower CV_a values for stem quality traits comparing to growth traits coincide with results in Lithuania, where CV_a for StStr and BrA was ca. 13% (Baliuckienė & Baliuckas 2006). In a recent study of low-density clonal plantation, estimated CV_g for H was almost three times lower (3.2%) than CV_a in the present study (on average, ca. 8%; Zeltiņš et al. 2018). It might be partly explained with remarkable differences in initial spacing (5 × 5 and 2 × 2.5 m in clonal plantation and our study sites, respectively), since genetic variance can be higher in closer spacing (Franklin 1979, Euler et al. 1992). Nevertheless, similar CV_a for H reported in north Sweden (Stener & Jansson 2005). Generally higher estimated CV_a values for DBH as for H were similar to results in Swedish progeny tests (14 and 8% for DBH and height, respectively; Stener & Jansson 2005).

For growth traits, selection of top 10% families resulted in GG% of 9.6–26.6% for H and DBH, while reaching 25.3–61.6% for V. Similar to h^2 values, GG% were generally lower for stem quality traits: 8.6–21.2% for StStr, 5.5–10.3% for StQual, 6.9–18.2% for BrD, 1.6–9.1% for BrA. Estimated GG% for the stem defects (Doubl and LostTop) varied notably among the trials and years, ranging from 5.2 to 58.3%. Estimated GG% confirmed general trends for h^2 and CV_a discussed above, reaching the highest values for V (25.3–61.6%), while being overall lower for stem quality (1.6–21.2%). Such estimates are over the means of trials instead of general population due to the lack of control plots, and thereby gains over forest stands might be higher (Malcolm & Worrel 2001). Nevertheless, selection of genotypes should compromise improved productivity with sufficient quality as well as improved performance in different growth conditions (Matheson & Cotterill 1990), especially when the aim is to produce high-quality silver birch timber for plywood industry

(Hynynen et al. 2010). As indicated by single-trait gains, CV_a values (Table 5.4) and mainly weak r_G between growth and quality traits (Table 5.5), further development of index for simultaneous selection of both growth and stem quality traits may be possible.

The studied traits showed low G × E interaction, indicated by strong type-B correlations for all studied traits ($r_B \geq 0.78$) between trials Ukri and Taurene (Table 5.3). Contradictory results have been reported previously: from strong and significant correlations between trials even in rather different environments (Stener & Hedenberg 2003, Stener & Jansson 2005) to substantial genotype by site interaction (Baliuckienė 2009). However, the accuracy of r_B might not be high (Bourdon 1977, Haapanen 1996), often related to inappropriate design of progeny trials, which has insufficient number of replications not following natural patterns of growing conditions (Haapanen 1996). Still, high type-B correlations with rather low standard errors for growth traits and low variation of h^2 for the same trait among trails discussed above indicated stability of performance over different environments, as well as appropriate experimental design.

Another relevant question regarding experimental design is the use of single-tree- or multiple-tree (block) plots. In general, single-tree plots in Ukri and Taurene had higher estimated heritabilities for growth traits and BrA than block-plots in Rembate (Table 5.3). Single-tree plots in many replications allow assessing genetic differences in statistically effective way (White et al. 2007), since progenies of plus-trees are represented in possibly wide range of competition and growing conditions within a trial (Haapenen 1992, 1995). However, inter-tree competition among different genotypes may exaggerate estimated genetic variance for growth traits promoting initially fast-growing families (Malcolm & Worrell 2001, Vergara et al. 2004, Gould & Marshall 2010). In the present study, growth traits might be somewhat affected by competition in the single-tree-plot trials Ukri and Taurene, since estimates from the block plots in Rembate were slightly lower. Still, estimates from more trials would be needed for generalized conclusions.

L.-G. Stener and Ö. Hedenberg (2003) stressed general lack of information about age-age correlations for silver birch. In our study, the genetic age-age correlations for traits measured at the age of 10 and 14 years were mainly strong (> 0.78) in all trials, implying as accurate selection for the respective traits at the first measurement time as at the second inventory. Nevertheless, strong correlations between so close ages are not very informative about long-term trends. Still, strong age-age correlations have been indicated for V for up to three decades in southern Finland (Hagqvist & Hahl 1998). There have been reported correlations ranging from 0.75 to 0.86 between the ages of 9 and 26 years; correlation of 0.94 between the ages of 5 and 10 years, and 0.84 between the age of 11 and 18 years for tree height (Stener & Hedenberg 2003). L.-G. Stener and G. Jansson (2005) found moderate to strong age-age correlations (0.60–0.99) for H and quality traits.

Phenotypic plasticity and local (genetic) specialization are key factors influencing trees' adaptability to a changing climate and are therefore critical elements of climate-adapted forest management strategies (Aitken & Bemmels 2016, Moran et al. 2017). An analysis of families at the provenance level in Ukri and Taurene revealed pronounced local specialization, particularly in growth traits. Birch from inland regions demonstrated superior growth. The distinct coastal-inland gradient and varying intensity of genetic control aligned with the climatic zoning of the region (Laiviņš, Melecis 2003, Reitalu et al. 2013). Using PCA (Principal Component Analysis) to group phenotypic traits of provenances, the first two principal components (PCs) were statistically significant ($p < 0.001$), capturing 57.6% of the total variation in the studied traits. The first PC was strongly associated with growth traits, indicating regional differences in productivity. The second PC was linked to quality traits, suggesting separate sources of variation for growth and quality. The third PC accounted for 19.8% of the variation and was associated with stem defects. Provenances formed a single group in the ordination space, indicating a continuous gradient of trait variation. However, the first PC significantly correlated with geographic longitude (r = 0.46, $p = 0.01$), reflecting growth differences between coastal and inland areas, while the second PC showed no correlation (r = 0.02, $p = 0.92$).

Correlations between the PCs and latitude were weak ($|r| < 0.22$, $p > 0.24$), indicating an absence of a north-south gradient. Based on the relationship between the first PC and geographic origin, two regions can be delineated in Latvia (Fig. 5.4). The coastal region includes the western and northern parts of the country, while the inland region covers the central and eastern areas (Fig. 5.4). The inland region exhibited significantly higher ($p < 0.01$) values for height (h), diameter at breast height (d), and stem volume (V). However, average stem straightness, overall stem quality, and live crown ratio (BrA) did not differ between the regions.

Moderate to high heritability ($h^2 > 0.20$) was observed for the studied traits in both regions, except for stem defects ($h^2 < 0.15$). The intensity of genetic control for traits varied geographically: the heritability of height (H) in the inland region was more than twice as high as in the coastal region (0.61 ± 0.061 vs. 0.28 ± 0.037, respectively), while heritability differences for volume (StVol) and diameter at breast height (DBH) reached 31.3–41.4%. In the coastal region, high heritability ($h^2 \geq 0.45$) was observed for stem straightness and branch angle, whereas these traits showed moderate heritability in the inland region ($0.26 \leq h^2 \leq 0.30$). Furthermore, the calculated additive genetic coefficient of variation (CV_a) was slightly higher (by 0.97–4.06%) in the inland region compared to the coastal region, indicating minor differences in plasticity. The capacity to respond to natural selection, as characterized by CV_a, was approximately three times higher for StVol compared to h in both regions.

Genetic specialization was more pronounced in the continental climate of the inland region, resulting in higher heterogeneity and explaining the greater h^2 and CV_a values for growth traits compared to the coastal region. High heritability likely indicated greater differences among genotypes from different provenances relative to within-genotype variation caused by environmental conditions (Griffiths et al. 2000). The calculated h^2 for growth traits was higher in the inland

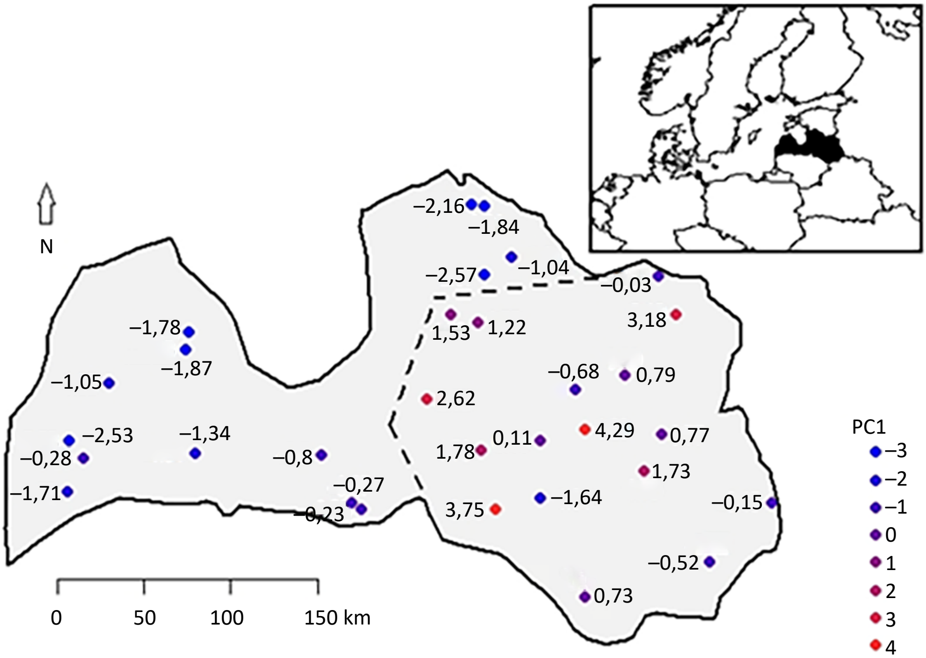

Figure 5.4 **The PC1 values of phenotypic traits for the assessed birch progeny at the provenance level**

The dashed line indicates the boundary between the two identified regions of silver birch provenances: the coastal (western) region and the inland (eastern)

region and lower for coastal provenances compared to the entire breeding population (h^2 = 0.41–0.52), suggesting greater selection efficiency in the inland region.

5.2 Vegetative propagation of silver birch and its potential for mass propagation (IV and V publication)

Culture initiation *in vitro* is the most important stage in micropropagation because the outcome determines further operation possibilities. However, it is also the most problematic stage in the micropropagation of perennial plants. Recalcitrance (i.e. the inability of plant cells, tissues, and organs to respond to *in vitro* manipulations) could be a major limiting factor in the application of *in vitro* propagation (Benson 2000). Several factors, such as the collection time, age of the stock plant, bud position in the mother-tree crown, genotype, pre-treatment storage time, conditions, and medium content (Welander 1988, 1993, McCown 2000, Vaičiukynė et al. 2017), affect the responsiveness of the plant material. In our study (**IV**), the age of the mother-tree and explant collection time had a significant effect (both $p < 0.001$) on the shoot initiation *in vitro* (Fig. 5.5).

Plants have complex life cycles, associated with reproduction, vegetative development, and morphogenesis. Temperate species undergo cycles of dorman-

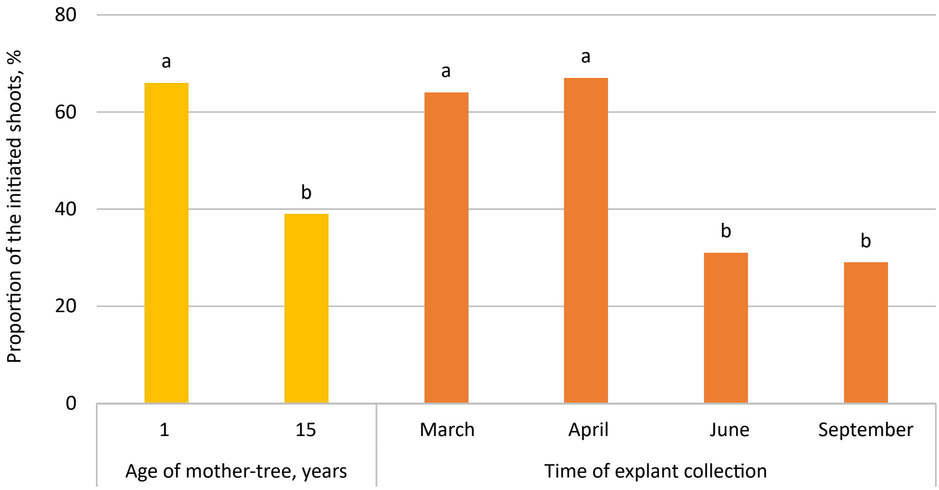

Figure 5.5 **The proportion of initiated shoots according to the age of the mother-tree and explant collection time**

Statistically significant differences between groups of age and between groups of collection time are denoted with different letters (both $p \leq 0.001$)

cy that determine periods of active shoot growth and cell division. Consequently, plants exhibit seasonal differences in their responses to tissue culture, depending on the time of the year when the explants are procured (Benson 2000). The explant collected from the one-year-old trees had 66% initiated shoots, and the explant collected from the 15-year-old trees had 39% of initiated shoots. The explants collected in spring developed a higher proportion of initiated shoots (64% in March and 67% in April) than explants collected in June and September (31% and 29% of shoots initiated, respectively; Fig. 5.5). This result corresponds well with the general pattern that cultures are most easily initiated from the explants collected in spring to early summer after a break of dormancy (George et al. 2008a).

A similar trend had been observed for other temperate tree species. *Populus tremula* L. had the highest survival rates of buds collected in late February and early March, while buds collected earlier had less intensive callus formation and plantlet development, and buds collected later had intense decay and infections (Peternel et al. 2009). For *Quercus robur* L., the most responsive explants were collected later, from May to July (Civínová & Sladský 1990), which is probably related to their later bud burst in comparison to the aspen and birch (Linkosalo 2000, Lange et al. 2016). In contrast, others have found that the initiation of the silver birch culture was more successful from explants collected in autumn and winter (Jokinen & Törmälä 1991), and bud treatment that induces dormancy resulted in a higher proportion of buds developed into shoots (Welander 1993), suggesting that factors other than the growing season might be more significant for culture initiation.

Plant growth regulators applied during the initiation affect the induction of the shoot formation (Magnusson et al. 2009). Seasonal cycles of perennial plants determine the dynamics of the endogenous levels of growth regulators, which are responsible for the induction of dormancy or inhibit growth and further development. For instance, a low concentration of applied BAP (0.2 mg L^{-1}) resulted in a higher shoot number in *Q. robur* explants collected in February and March but with an increased BAP concentration (1 and 2 mg L^{-1}) better results were obtained from buds collected from May to July (Civínová, Sladský 1990). Moreover, buds collected from May to July had a higher regeneration capacity than those from February to April, but higher BAP concentrations were needed to stimulate their meristematic activity (Civínová & Sladský 1990).

Higher initiation success in spring might be related to the seasonally determined occurrence of microbes within the buds. For mature *B. lenta* L., dormant buds demonstrated lower contamination than buds collected in spring (Rathwell et al. 2016). Similar results were obtained for *Platanus occidentalis* L., and the contamination rate gradually increased from 14% in January to 48% in July (Tao et al. 2007). Spring was the most appropriate time for bud collection to reduce contamination in *Ulmus americana* L., whereas almost all were contaminated among dormant buds (Shukla et al. 2012). In contrast, low contamination from May to October and significantly higher contamination from December to April were found for *Pinus sylvestris* L., which is assumed to be related to better resistance of the tissue against pathogens during the active period (Hohtola 1988).

Trees exhibit developmental changes as plants progress from the juvenile to adult phases leading to a decline in their potential for micropropagation (von Aderkas & Bonga 2000). Juvenile seedling tissue is generally more responsive to culture initiation *in vitro* than that of mature trees. Juvenile seedlings are more easily initiated and grow and proliferate at a more rapid rate than adult material (George et al. 2008a). Cultures from mature trees are more problematic due to higher contamination rates, the browning of tissues, and recalcitrance (George et al. 2008a). One of the methods to obtain juvenile material is grafting, which can lead to a partial rejuvenation of the donor plant and can overcome recalcitrance in mature trees (Benson 2000). No assessment of true rejuvenation or reinvigoration of the scion (Wendling et al. 2014) was done in our study, yet, explants from the grafted one-year-old tree had a significantly higher proportion of initiated shoots than the explants from the 15-year-old tree (Fig. 5.5). Similarly, a high bud initiation (80%) was achieved using three-year-old plants of *B. lenta*, whereas the explants from mature trees did not develop into shoots (Rathwell et al. 2016). However, most *Betula* species can be propagated from adult material without major difficulties (Welander 1993), and several studies found success using buds from mature birch trees (Ryynänen & Ryynänen 1986, Jones et al. 1996, Aubakirova & Kalashnikova 2011).

Our results are limited by using only one genotype (clone 54–95) to assess the effect of the explant collection time and age of the mother-tree. The initiation success is more affected by the genotype than the aforementioned factors (Jokinen & Törmälä 1991), but the genotype response is affected by the physiological heterogeneity of the ramets and buds of the same ramet (Civínová & Sladský

1990). However, these limiting factors could be overcome if the genotype is generally competent for growing *in vitro* (Jokinen & Törmälä 1991).

Once the culture is fully stabilised, biologically responsive tissues show little seasonality and progression through phase states (McCown 2000). In the stabilised culture, the growth parameters greatly differed between the clones. The multiplication rate varied from 1.0 (no multiplication) to 6.8 shoots per explant (Fig. 5.6), and the lengths of the main shoots varied from 1.3 to 7.8 cm (Fig. 5.7). The number of lateral shoots varied from 0 to 3.8 per explant. Close results (a multiplication rate between 1.6 and 7.4) were found among 10 genotypes selected in Sweden, Finland, and Germany (Ewald et al. 2002). Large variations but higher multiplication rates (from 2 to 20) were observed between 100 genotypes by K. Jokinen and T. Törmälä (1991).

Clones exhibited different growth patterns. Several genotypes had a large main shoot but a low number of lateral shoots (e.g. clone L 29, Fig. 5.7(a)), whereas others had a short main stem but a high number of lateral shoots (e.g. clone Bau 40-13, Fig. 5.7(a)). A high multiplication rate was achieved by both of these patterns and by the intermedium between them. Regardless of the large variation, the number of lateral shoots showed a negative relationship to the length of the main stem ($p < 0.01$, regression coefficient -0.11 ± 0.04). Almost a quarter of the

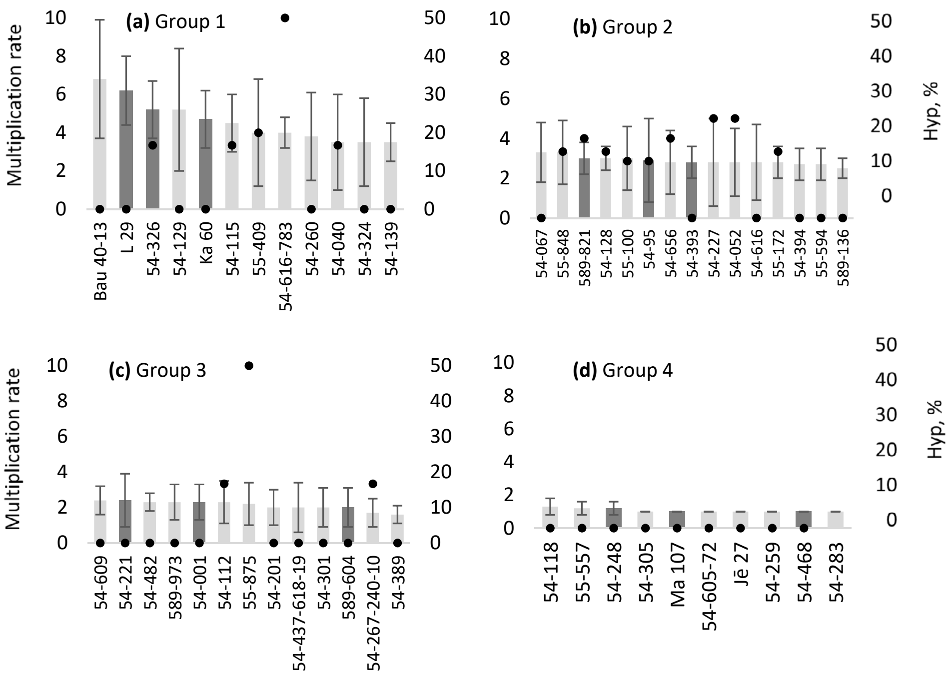

Figure 5.6 **The multiplication rate (bars; ± standard error) and proportion of hyperhydrated shoots (Hyp%; bullets) among the clones in (a) Group 1, (b) Group 2, (c) Group 3, and (d) Group 4**

Clones that were selected to test the effect of different treatments are dark grey

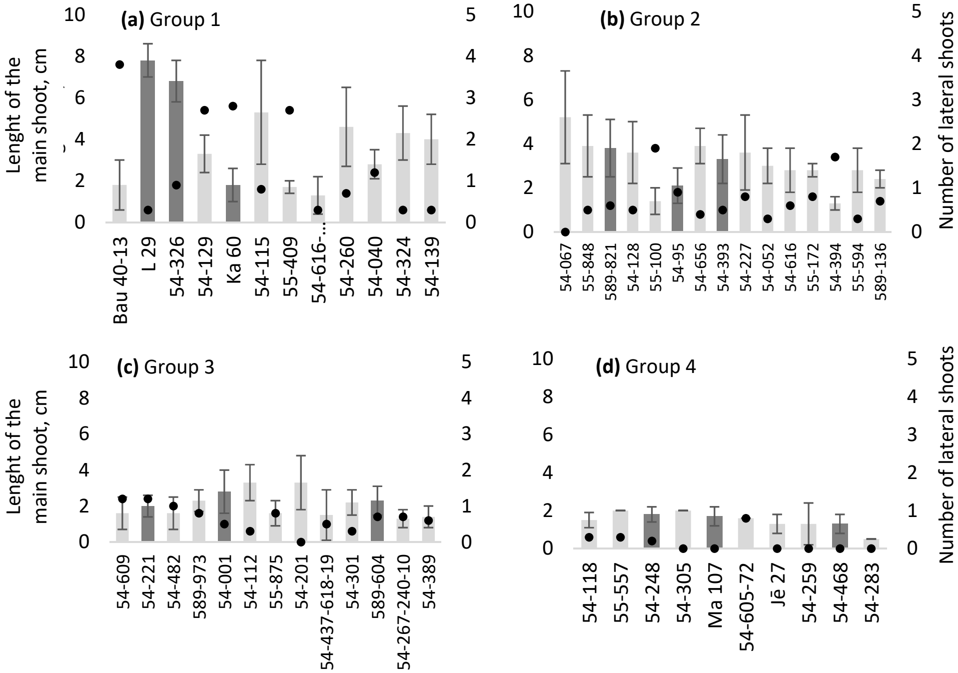

Figure 5.7 **Length of the main shoot (bars; ± standard error) and the number of lateral shoots (bullets) among the clones in (a) Group 1, (b) Group 2, (c) Group 3, and (d) Group 4**

Clones that were selected to test the effect of different treatments are dark grey

clones had a low multiplication rate; 12 clones had a mean multiplication rate lower than two, and seven clones did not multiply. This might be related to the limited time of the study because four to ten weeks are required for bud induction in birch, depending on the explant type, age, and physiological conditions of the mother-tree and genotype (Welander 1993).

Moreover, the applied medium and plant growth regulators affect genotype performance. The optimal media composition is species – and genotype-specific, and while a number of plants exhibit decent growth in the range of media, others may have considerable differences in their performance (McCown & Sellmer 1987). Therefore, the number of genotypes that are possible to micropropagate could be increased by modifying the composition of the medium and applying different types and concentrations of cytokinins (Jokinen & Törmälä 1991). For optimal shoot growth *in vitro*, the optimal amount of minerals should be provided. The most commonly used basal media in micropropagation of birch are the MS and WPM basal media, although others are also used (Ewald et al. 2000, Iliev et al. 2003). The mean multiplication rate between the treatments varied from 1.8 to 6.7 (mean 3.9). Within all groups, the culture on the MS medium exhibited a higher multiplication rate (Fig. 5.8) and a longer length of the main stem than the culture on the WPM. For these two parameters, the difference between the media type was most pronounced for Group 1 (Fig. 5.8(a)) and gradually decreased for Group 4 (Fig. 5.8(d)). However, the culture on the WPM had a substantially lower proportion of hyperhydrated shoots than the culture on the MS medium, and it ranged from 0 to 6.3 (mean 2.9) for WPM and from 0 to 38.0 (mean 13.2) for the MS medium. The number and length of the lateral shoots had no clear relation to the media type.

Similarly, poorer growth on the WPM was shown for *B. lenta*. The shoots on WPM cultures had red pigmentation, were significantly shorter, and had fewer nodes compared to the MS cultures, although the multiplication rate was not significantly lower (Rathwell et al. 2016). They associated this response to ionic strength (i.e. salt concentration) in the basal salt mixture, as the amount of ammonium nitrate is about a quarter lower in the WPM than in the MS medium. A limiting effect of low nitrogen was revealed for a given genotype of *Populus* hybrid. At first, the cultures on the WPM had poor growth, whereas these cultures on the MS medium were maintainable indefinitely. However, after an increase in NH_4NO_3 on the WPM to the level of MS, growth improved substantially, and was similar to that observed

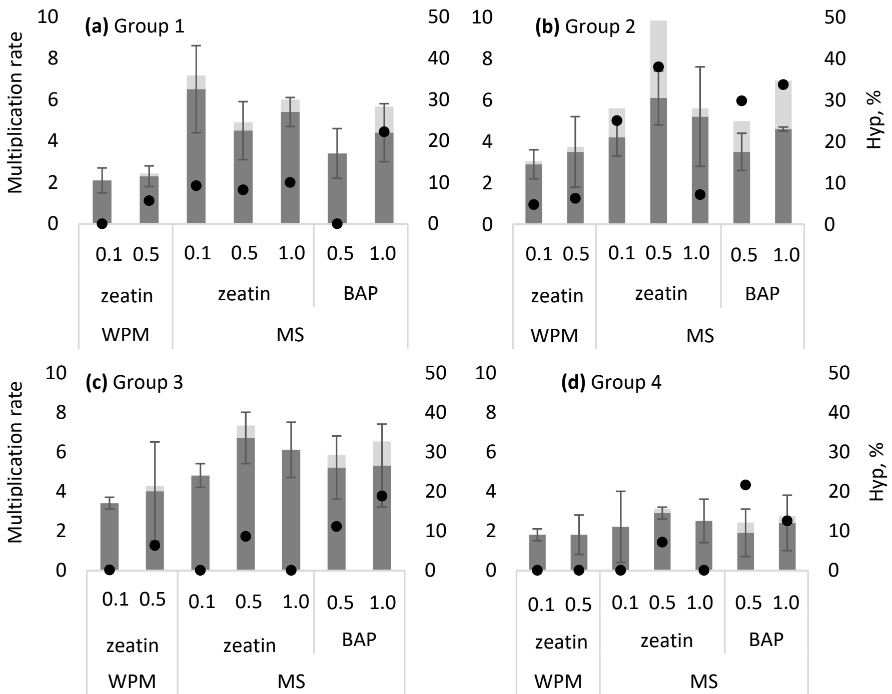

Figure 5.8 **Stacked multiplication rate (dark grey; ± standard error) and number of hyperhydrated shoots (light grey), and proportion of hyperhydrated shoots (Hyp%, bullets) according to the media content in (a) Group 1, (b) Group 2, (c) Group 3, and (d) Group 4**

WPM – woody plat medium, MS – Murashige and Skoog basal media, BAP – 6-benzylaminopurine for the MS medium (McCown & Sellmer 1987). In contrast, four genotypes of *Betula platyphylla* Sukatchev var. *japonica* (Miq.) Hara × *B. pendula* had a constantly higher multiplication rate on the WPM than on the MS medium, with the mean long-term multiplication rate on these media at 3.7 and 2.8, respectively (Meier-Dinkel 1992).

Plant growth regulators have the most important role in birch *in vitro* shoot initiation and cultivation. Among them, cytokinins are highly effective in stimulating cell division and the control of morphogenesis (George et al. 2008b). For shoot multiplication, the most commonly used cytokinins are single BAP or zeatin at concentrations of 0.2 to 5.0 mg L^{-1} and 1.0 to 5.0 mg L^{-1}, respectively, or BAP concentrations of 0.7 to 2.0 mg L^{-1} in combination with a low concentration of auxin (Meier-Dinkel 1992). Within the studies, the same cytokinin is used under two names – BA (6-benzyladenine) and BAP (6-benzylaminopurine; Teixeira da Silva 2012), and for more clarity, we consistently use BAP throughout study even if the authors in the original papers used BA.

The effect of the particular cytokinin should be assessed experimentally, and the response is determined by the particular compound used, type of culture, genotype, and ontogenetic stage of the tissue (George et al. 2008b). For instance, two *B. pendula* genotypes demonstrated a distinct response to supplementation with cytokinin. One of them had a significant decrease in the shoot length and an increase in the number of shoots per explant, whereas the other did not affect these parameters. Simultaneously, the latter genotype had a higher number of shoots per explant in both the control medium and the medium supplemented with BAP (Vaičiukynė et al. 2017). For several *Betula* species, the absence of cytokinins resulted in the poor growth of new shoots (Cheng et al. 2000) or no shoot development and explant death (Magnusson et al. 2009, Rathwell et al. 2016, Girgžde & Samsone 2017). Yet, typically, a narrow range of concentration achieves the best results. The effect of the cytokinin type and concentration on the growth parameters was assessed separately on the WPM and MS medium. On the MS medium, regardless of the concentration, zeatin exhibited better results on the multiplication rate and length of the main stem than BAP for all groups (Fig. 5.8). Within the groups, the mean difference between the zeatin and BAP treatments was 11% to 29% for the multiplication rate and 21% to 29% for the length of the main stem. Among the MS and zeatin treatments, the highest multiplication rate was obtained with a concentration of 0.5 mg L^{-1} in total, and for all groups except Group 1 (Fig. 5.8). This concentration also resulted in the highest mean length of the main stem within all groups. On treatments supplemented with BAP, a higher concentration of cytokinin resulted in a somewhat higher multiplication rate than a lower concentration. The observed tendencies remained non-significant due to the large variation, although these tendencies were nearly constant between the groups of clones.

On the WPM, the zeatin at a concentration of 0.5 mg L^{-1} had an equal or slightly higher multiplication rate and a longer length of shoots than zeatin at a concentration of 0.1 mg L^{-1}, but these differences were more negligible than on the MS medium. The number of lateral shoots between the different treatments varied from 0.1 to 1.2 (mean 0.6). No specific relation between the length and number of lateral shoots and cytokinin type was observed.

Several studies have tested optimal concentrations of cytokinins on *Betula* genotypes. The effect of the BAP concentration was tested on a cultivar of *B. platyphylla*. The concentration at 2.2 µM of BAP (rounded 0.5 mg L^{-1}) resulted in about a four-times higher number of new shoots than a concentration at 1.1 µM, and in a twice higher number of new shoots than the concentration at 4.4 µM (Cheng et al. 2000). For the *B. pendula* genotype, the main shoots on 1.0 mg L^{-1} of BAP had a similar length to those on treatments containing zeatin (0.5–1.0 mg L^{-1}). Yet, 1.0 mg L^{-1} of BAP had more than a two-fold higher number of lateral shoots and hence achieved a significantly higher multiplication rate than the other treatments (Girgžde & Samsone 2017). In addition, a study of *B. lenta* revealed a significantly higher result of shoot growth with BAP treatment compared to the supplementation of 2-isopentenyladenine (2-IP) and thidiazuron (TDZ), and the highest multiplication rate was achieved at a BAP concentration of 5.0 µM (rounded to 1.1 mg L^{-1}; Rathwell et al. 2016). For *B. platyphylla* and *B. papyrifera* Marsh, the BAP at a concentration of 10 to 20 µM (rounded to 2.3–4.5 mg L^{-1}) and TDZ at a concentration of 4 to 8 µM proliferated more shoots than other treatments (Magnusson et al. 2009). Different intensities of response to cytokinins might be related to the dynamics of the endogenous levels of growth regulators over the seasons, and thus could be related to the explant collection time. B. Civínová and Z. Sladský (1990) found that *Q. robur* explants collected from May to July needed a higher concentration (2 mg L^{-1}) of BAP than those collected from February to April (0.5 mg L^{-1}) to achieve the highest regeneration capacity.

The length of the main shoot showed a significant relation to the length of the lateral shoots ($p < 0.001$, regression coefficient 1.68 ± 0.24) and the number of lateral shoots ($p < 0.01$, regression coefficient 0.23 ± 0.06). The length of the main shoot had a consistent ranking between the groups of clones (Fig. 5.9(a)). However, the number of lateral shoots highly fluctuated between treatments (Fig. 5.9(b)), affecting the ranking of the multiplication rate (Fig. 5.9(c)). Regardless of the media and cytokinin type, both the multiplication rate and length of the main stem were the highest in Group 3, followed by Group 2 and then Group 1. As expected, Group 4 contained clones with the poorest growth among the genotypes and had the poorest results for all growth parameters (Figs. 5.8 and 5.9). Groups of clones had reversed ranking in the multiplication rate in comparison to the first subculture (assessment of different genotypes, Figs. 5.8 and 5.9), although, typically, the multiplication rate remains stable during several subcultures (Jokinen & Törmälä 1991). The difference in the performance of the groups between subcultures indicates the importance of the careful selection of the media content.

A higher cytokinin concentration is beneficial until a certain study-specific threshold is reached, and afterwards, shoot abnormalities appear. The explant might form many small shoots that fail to elongate, and the leaves might have an unusual shape (George et al. 2008b). For instance, a high concentration of zeatin

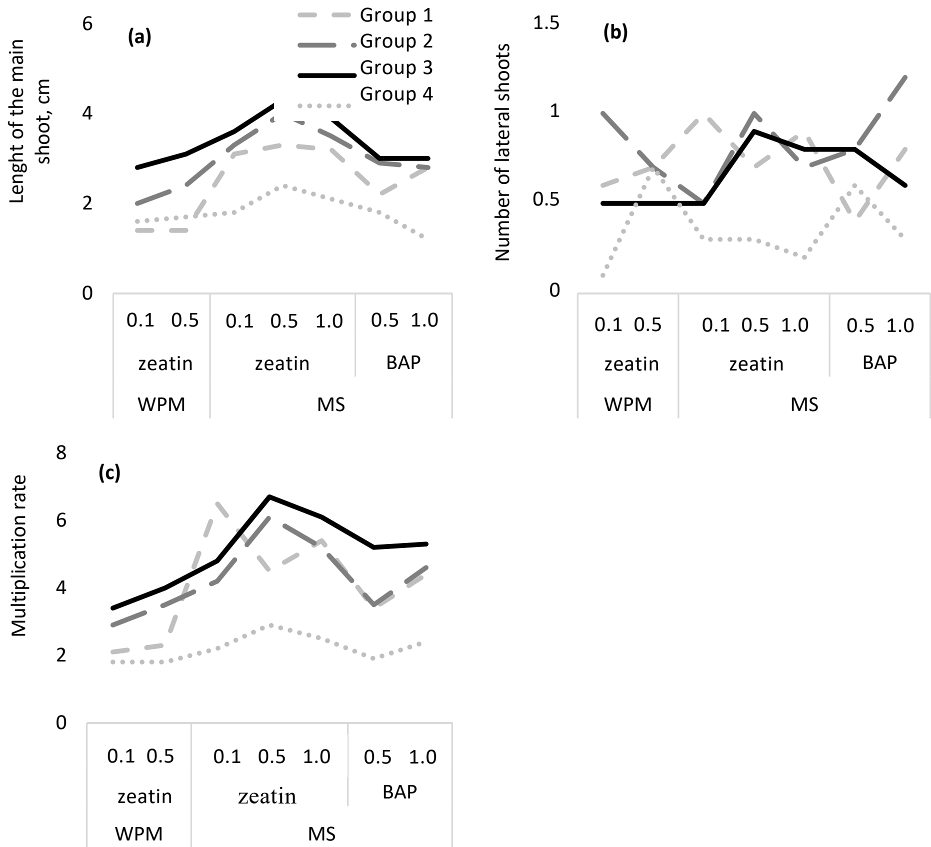

Figure 5.9 **Group mean (a) length of the main shoot, (b) number of lateral shoots, and (c) multiplication rate according to the media content**

WPM – woody plat medium, MS – Murashige and Skoog basal media,
BAP – 6- benzylaminopurine

induced the spontaneous appearance of abnormal shoots in *B. pendula*. A concentration of 5 mg L^{-1} resulted in 3.4% fasciated shoots, and 10 mg L^{-1} resulted in 4.2% fasciated shoots, whereas all shoots appeared anatomically normal in the absence of or at a low concentration (2 mg L^{-1}; Iliev et al. 2003). In another study, at the highest tested BAP concentration (5.3 µM; rounded to 1.2 mg L^{-1}), the shoots had variable sizes and appeared hyperhydrated and chlorotic (Cheng et al. 2000). Hyperhydricity (previously called "vitrification") characterises frequently observed malformations during vegetative propagation *in vitro*, where the plants appear turgid and watery at their surface and are hypolignified (Gaspar 1991, Debergh et al. 1992). Their shoots have broad and thick stems; short internodes; and thick, frequently very elongated, wrinkled, curled, and brittle leaves (Franck et al. 1995).

In the present study, 34% of the clones had hyperhydrated shoots (Fig. 5.6), ranging from none to 50% of the shoots. On clonal level, high proportion (50%)

of hyperhydrated shoots was present for two clones, one among the clones with a high multiplication rate (clone 54-616-783; Fig. 5.6(a)) and the other with a low multiplication rate (clone 55-875; Fig. 5.7). A moderate proportion (14%–25%) of the hyperhydrated shoots was present for 15 out of 50 clones. At clonal level, the number of hyperhydrated shoots demonstrated no relationship (both $p > 0.05$) to the length of the main stem and number of lateral shoots. However, a positive relationship ($p < 0.001$, regression coefficient 0.56 ± 0.04) exists between the number of hyperhydrated shoots and the total multiplication rate. When examining different media contents, the number of hyperhydrated shoots showed a positive relation with all shoot growth parameters: the length of the main stem ($p < 0.001$, regression coefficient 0.77 ± 0.07), the number ($p < 0.001$, regression coefficient 3.11 ± 0.07), and length of the lateral shoots ($p < 0.001$, regression coefficient 0.98 ± 0.21). Consequently, a significant relation ($p < 0.001$, regression coefficient 0.44 ± 0.02) between the number of hyperhydrated shoots and the total multiplication rate exists. These results agree with the study conducted by Gaspar (1991), who reported that hyperhydricity is related to intensive multiplication, i.e. frequent subcultures with a high rate of regeneration, but is not affected by the physiological conditions of the mother-tree at the time of the explant collection.

Hyperhydricity is related to the particular conditions of the *in vitro* culture and results from the inability of the shoots to adapt normally to the reactions caused by stress factors, e.g. wounding, high ionic strength, and inappropriate lighting and temperature (Kevers et al. 2004). Within all studied groups, the treatments with zeatin had a lower mean proportion of hyperhydrated shoots (ranging from 2.4%–23.4%) than the treatment with BAP (ranging from 11.1%–31.8%). Still, a high proportion of hyperhydrated shoots was also present for zeatin at a concentration of 0.5 mg L^{-1}, i.e. for treatment that resulted in the highest multiplication rate.

The studied low-density silver birch clonal plantation had 84.4% survival at the age of 40 years. The mean (± standard deviation) height and DBH of trees was 26.2 ± 2.2 m and 27.7 ± 5.6 cm, respectively. The total standing stemwood volume of the plantation was 210 m^3 ha^{-1}, and the mean annual stemwood increment was 5.25 m^3 ha^{-1} $year^{-1}$. Accordingly, MV was estimated ca. 9,600 EUR ha^{-1}, mainly contributed by the logs of smaller, medium, and large dimensions (44%, 25%, and 21%, respectively).

The estimated H^2 and CV_g differed among the variables (Table 5.6). The highest heritability was estimated for branch angle, mean projection of crown (MPC), branchiness, and stem straightness ($0.40 \leq H^2 \leq 0.29$, respectively), while the lowest heritability was estimated for survival, probability of spike knots and cracks (< 0.08). Intermediate $H^2 = 0.16$ for MV was similar to commonly reported tree height, height of the lowest living branch, and DBH (0.14, 0.14, and 0.21. respectively). The CV_g of the quantitative variables ranged from 3.2% to 21.8% for tree height and MV, respectively (Table 5.6). For DBH and height of the lowest living branch, intermediate genotypic variation (ca. 9%) around the phenotypic mean was estimated, while it was higher for branch angle and MPC at 14.8% and 19.2%, respectively.

Table 5.6

Statistics, coefficients of heritability (H^2), and genotypic variation (CV_g, %) of the morphometric variables (traits), and monetary value of 40-year-old grafted birch plus-trees from the low-density plantation

The monetary value of stemwood was calculated considering stem quality

Indicator	Mean	Min	Max	Standard deviation	Heritability coefficient H^2 ± Standard error	Genotypic coefficient of variation CV_g ± Standard error, %
Quantitative variables						
Stem diameter at breast height, cm	27.7	14.2	45.8	5.6	0.21 ± 0.06	9.5 ± 1.5
Tree height, m	26.2	15.3	31.6	2.2	0.14 ± 0.05	3.2 ± 0.5
Height of the lowest living branch, m	11.2	1.8	18.0	2.7	0.14 ± 0.05	9.3 ± 1.4
Branch angle, °	43.2	15.0	80.0	10.4	0.40 ± 0.08	14.8 ± 2.3
Mean projection of crown, m	2.9	1.1	6.3	0.8	0.39 ± 0.08	19.2 ± 3.0
Monetary value of stemwood, Euro	28.2	3.7	95.4	14.6	0.16 ± 0.05	21.8 ± 3.4
Qualitative variables						
Survival, % of trees *	84.4	59.6	100.0	-	0.08 ± 0.03	-
Spike knot, % of trees *	23.2	5.2	42.8	-	0.02 ± 0.02	-
Double tops, % of trees *	34.9	6.0	75.1	-	0.14 ± 0.05	-
Stem straightness, score *	3.2	2.5	4.7	-	0.29 ± 0.07	-
Branchiness, score *	3.3	2.5	5.3	-	0.33 ± 0.08	-
Stem cracks, % of trees *	24.9	0.0	50.3	-	0.08 ± 0.03	-

* Mean values for clones.

Table 5.7

Genotypic correlations (standard errors by delta method in brackets) in the upper diagonal part and phenotypic clone mean Pearson correlations (significant correlations with $p \leq 0.05$ in bold) in the lower diagonal part

Indicator	Tree height	Stem diameter at breast height	Stem cracks	Height of the lowest living branch	Branch angle	Double tops	Spike knots	Stem straightness	Branchiness	Mean projection of crown	Monetary value of stemwood
Tree height	**1**	0.65 (0.16)	0.02 (0.30)	0.14 (0.27)	0.43 (0.21)	0.03 (0.27)	0.17 (0.45)	−0.16 (0.25)	0.16 (0.25)	0.35 (0.22)	0.79 (0.11)
Stem diameter at breast height	0.63	**1**	0.11 (0.29)	−0.56 (0.19)	0.23 (0.23)	0.35 (0.23)	−0.23 (0.43)	0.44 (0.20)	0.79 (0.10)	0.86 (0.07)	0.93 (0.03)
Stem cracks	0.03	0.10	**1**	−0.11 (*)	0.08 (0.02)	−0.68 (0.20)	0.38 (0.44)	−0.60 (0.21)	−0.30 (0.27)	−0.20 (0.27)	0.47 (*)
Height of the lowest living branch	0.17	**−0.51**	0.07	**1**	0.29 (0.23)	−0.75 (0.13)	0.90 (0.37)	−0.76 (0.12)	−0.85 (0.24)	−0.77 (0.11)	−0.32 (0.25)
Branch angle	0.36	0.22	0.15	0.25	**1**	−0.37 (0.22)	0.67 (0.31)	−0.09 (0.23)	−0.25 (0.07)	0.27 (0.22)	0.29 (0.23)
Double tops	0.05	0.35	**−0.51**	**−0.69**	−0.34	**1**	−1.19 (0.35)	0.78 (0.12)	0.74 (0.13)	0.60 (0.17)	−0.10 (*)
Spike knot	0.06	−0.07	0.29	0.40	**0.46**	**−0.68**	**1**	−0.47 (0.43)	−0.64 (0.40)	−0.35 (0.22)	0.06 (0.48)
Stem straightness	−0.15	**0.42**	−0.41	**−0.71**	−0.08	**0.70**	−0.15	**1**	0.87 (0.07)	0.60 (0.14)	0.12 (0.25)
Branchiness	0.19	**0.79**	−0.22	**−0.78**	−0.05	**0.67**	−0.26	**0.82**	**1**	0.93 (0.03)	0.28 (0.28)
Mean projection of crown	0.36	**0.86**	−0.15	**−0.71**	0.26	**0.56**	−0.16	**0.70**	**0.93**	**1**	0.65 (0.14)
Monetary value of stemwood	0.74	**0.93**	0.32	−0.30	0.28	0.14	0.03	0.14	**0.54**	**0.66**	**1**

* Calculation stopped due to infinite likelihood.

The calculated H^2 (Table 5.6) implied potential for substantial improvement of productivity and stem quality, hence yields of birch plantations by tree breeding (Stener & Hedenberg 2003). Nevertheless, H^2 of the variables differed (Table 5.6), implying unequal potential for the improvement of the traits (Falconer 1996). Branch angle, branchiness, projection of crown, and stem straightness, which largely influence timber quality (Savill et al. 1997), were highly heritable and had intermediate CV_g (Table 5.6), implying potential for considerable improvement (Falconer 1996). High CV_g for MV (21.8%), indicated potential financial benefits from breeding.

The estimated genotypic correlations among the studied variables were similar to phenotypic clone mean Pearson correlations (Table 5.7); the latter are described. Correlations among tree height, DBH, and MV were high ($r > 0.63$); nevertheless, DBH and MV ($r > 0.66$) correlated with MPC. Branchiness correlated with DBH ($r = 0.79$), yet not with tree height (p- value = 0.41). Moderate to strong ($0.30 < |r| < 0.78$) negative correlations were observed between height of the lowest living branch and DBH, double tops, stem straightness, branchiness, and MPC. Occurrence of double tops showed moderate to strong correlations with stem straightness, branchiness, and MPC ($r = 0.70$, 0.67, and 0.56, respectively), but a negative correlation ($r = -0.68$) with occurrence of spike knots. Mostly, weak and non-significant correlations were observed between the occurrence of stem cracks as well as branch angle and other variables.

The strong correlation between branchiness and DBH, MPC, and stem straightness indicated possible negative effects on stem quality when selecting fast growing trees with straight stems (Table 5.7). Additionally, height of the lowest living branch had significant negative correlations with the same variables, supporting the abovementioned consideration. Earlier studies reported a significant moderate correlation between DBH and number of branches (Stener & Hedenberg 2003, Stener & Jansson 2005). Significant negative genotypic correlation between productivity traits and stem straightness (r_G ranging from −0.45 to −0.72) was noticed in Sweden (Stener & Jansson 2005). However, other stem quality traits such as spike knots, stem cracks, and double tops did not show significant relation to productivity traits and MV, suggesting the possibility for simultaneous improvement (Viherä-Aarnio & Velling 1999, Stener & Jansson 2005).

The heritability of survival was low (Table 5.6), suggesting the prevailing effect of the micro-site conditions, as shown by L.-G. Stener and G.Jansson (2005) for birch in Sweden. Environmental factors can strongly affect performance of the species, masking the genetic effect and resulting in low heritability parameters (Koski & Rousi 2005). The estimated genetic parameters (Table 5.6) might have been already affected by the pre-selection of planting material (plus-trees) with improved branching and stem properties, as a seed orchard was initially intended. Although the utilization of grafted silver birch is not a common practice in commercial forestry, the trial provided information about genetic parameters at middle age that has not been previously published. This might have caused some imprecisions in genetic parameters due to uncontrolled rootstock × scion effect.

Although the issue has been scarcely studied for forest trees (Jayawickrama et al. 1991), for loblolly pine, the rootstock × scion effect has been negligible compared to the effects of clone and site factors (Jayawickrama et al. 1997). This was also supported by good survival of grafts indicating compatibility between rootstock and scions. The negative effect of cyclophysis due to different biological ages of rootstock and scion (Olesen 1978, Greenwood & Hutchison 1993, Viherä-Aarnio & Ryynänen 1994, Wendling et al. 2014) appeared insubstantial, as indicated by the productivity of the plantation. Similarly, a weak effect of cyclophysis on growth and survival of vegetatively propagated silver birch has been shown in boreal conditions (Jones et al. 1996, Viherä-Aarnio & Velling 2001). Still, grafts might have lower branchiness and branch thickness (Viherä-Aarnio & Ryynänen 1995).

The single-tree-plot design of the plantation might have also affected genetic parameters of the traits, as the measurements from such plots are influenced by competition among different genotypes (Vergara et al. 2004). However, low planting density likely had postponed the onset of inter-tree competition, therefore reducing exaggeration of the genotypic variance of growth traits (Malcolm & Worrell 2001, Stener & Hedenberg 2003, Stener & Jansson 2005). Hence, the estimated H^2 and CV_g were somewhat lower than reported in earlier studies, in which H^2 ranged 0.07–0.56 for tree height, and 0.11–0.59 for DBH, while CV_g for the respective traits has been reported to range between 5 and 14, and between 9 and 21, respectively (Malcolm & Worrell 2001, Stener & Hedenberg 2003, Stener & Jansson 2005). Still, heritability of height and DBH varies widely among different trials (Stener & Jansson 2005). Considering varying genetic control of the studied traits, H^2 and CV_g of MV were intermediate (0.16 and 21.8), as similarly observed in Sweden (Stener & Hedenberg 2003).

For silver birch, genetic gains of around 10% for height and 20% for DBH of the top 10% clones at the age of 7–11 years are reported (Stener & Hedenberg 2003, Stener & Jansson 2005), while corresponding realized gains in our study site at the moment of possible final-harvest was around 17 and 5 times lower, respectively. For each variable, selection of top three clones resulted in 3.8%, 0.6%, and 2.7% genetic gain for DBH, tree height, and MV, respectively. This may imply weak age-age correlations, as well as reflect lower heritability and high variability due to strong environmental effects. However, earlier measurements from the studied trial were not available for comparison.

The studied plantation appeared ready for the final harvest already at the age of 40 years. Higher productivity (up to 8.90 m^3 ha^{-1} $year^{-1}$ (Oikarinen 1983) vs. 5.25 m^3 ha^{-1} $year^{-1}$ in studied trial) and good stem quality might be achieved in conventional plantations with higher planting densities (Niemistö 1995a), although increasing planting distance does not influence the height growth (Niemistö 1995b). Nevertheless, decreased competition and application of the pre-selected planting material apparently improved the assortment structure of the studied birch, shifting its distribution towards the higher value, thus suggesting efficiency of the low-density clonal plantation for the production of solid wood and possible further economic improvement in a low-density short-rotation plantation. Together with selected planting material, reduced establishment costs with wider spacing might be a strong driving factor for choosing lower planting densities. Increased value does not only result from increases in volume production, but also from improved stem quality leading to more valuable logs (Moore et al. 2018). Besides, breeding effect on productivity might not fully express in dense stands, since birch maintain vigorous growth when presented with low within-stand competition (Hynynen et al. 2010).

For practical application of using superior vegetatively propagated clones, there is no specific regulation in Latvia. Planting of clones or mixtures of clones is allowed without specific restrictions. Vegetative propagation is regulated, similar to most EU countries. Only forest reproductive material from categories "selected", "qualified" and "tested" shall be allowed to be vegetatively propagated. For clones and mixture of clones in the category "qualified", the maximum amount of propagation (number of offspring or ramets) is 1 million grown plants. Material of the category "tested" has no restrictions on the amount of propagation.

5.3 Profitability of utilizing genetically improved silver birch (VI and VII publication)

Results **of silver birch breeding profitability analysis** reveal that NPV of tree breeding costs are highest in VEG alternative, followed by GEN (60% of VEG costs) and FEN (40%). Genetic gain of FEN alternative is approximately 79% of the other alternatives that is according to theory (Falconer & Mackay 2004) and reflects increased precision of selection, based on progeny testing. In the current situation (prices and costs of the year 2010, on average a bit below 500 ha year^{-1} birch planting used, predictions of genetic gain for height and diameter 14% for FEN and 18% for VEG and GEN, targeted and traditional silviculture applied in equal proportions of area) highest differential benefit is achieved with VEG alternative, followed by GEN and FEN (Fig. 5.10).

Results reveal that superiority of selection based on clonal testing (VEG) remains across the range of genetic gain levels, that exceed 10%, and is increasing in absolute value, as higher the genetic gain is. It is in line with conclusions of Stener and Jansson (2005) that also noted superiority of vegetative (clonal) testing.

Figures of genetic gain used in this study are in line with other published estimates: at the age of 10 years, 10% gain in height and 18% in diameter has been found for silver birch (Stener & Jansson 2005). Other studies report no notable difference in genetic gain at the age of 10 and 20–36 years, the absolute value being 29% for yield (Hagqvist & Hahl 1998) that would roughly correspond with 14% increase in height and diameter. Genetic gain 10–25% at age 21–32 years are estimated (for height) and 20% predicted for yield at mature age for Scots pine (Ståhl & Jansson 2002, Andersson et al. 2006, Jansson 2007) for the first breeding cycle. Considerable decrease in genetic variation have been found between wild population and selected plus trees, but the next steps of selection, based on progeny testing corresponds to only marginal changes in genetic variation (Bouffier et al. 2008).

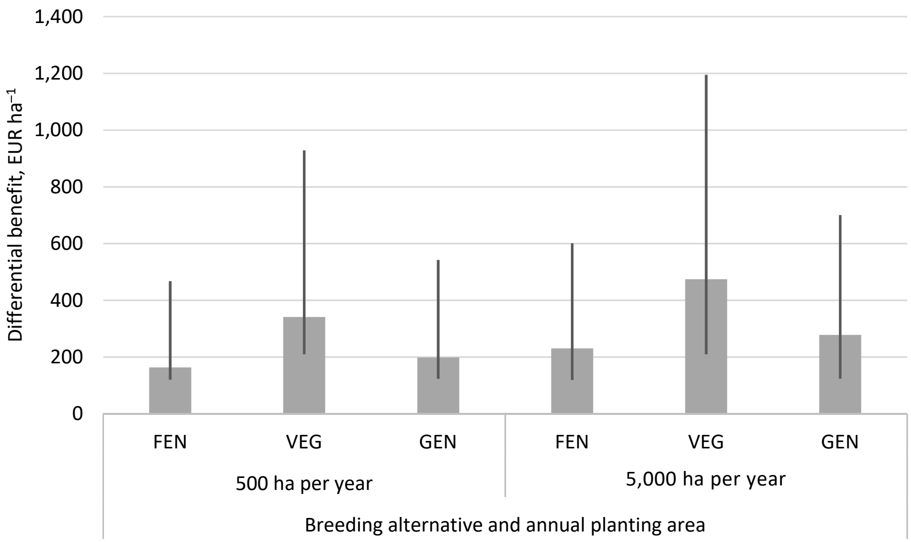

Figure 5.10 **Comparison of differential benefits for breeding alternatives in EUR, adjusted to the 2023 price index**

Bars indicate values based on the average roundwood assortment price; whiskers represent the minimum and maximum roundwood assortment prices during the evaluated period (2006– 2010). Breeding effects for height and diameter were 14% for the FEN alternative and 18% for the VEG and GEN alternatives, assuming targeted and traditional forestry were applied in equal proportions of the area

Therefore, it can be assumed that the possibility of further improvement in next breeding cycle remains the same as in the first one.

Value of differential benefits is influenced not only by genetic gain, but also by annual planting area and fluctuation in assortment prices (Figs. 5.11 and 5.12).

Annual planting area has a profound effect on value of differential benefits: as it increases from 500 ha year^{-1}, planted during the last decade on average, up to 5,000 ha year^{-1} the differential benefits increases by 60% on average, ranging from 25% to more than doubling. It is related to constant costs involved in equation – the more the area increases, the lower are the costs of seed orchard establishment and maintenance per one hectare planted with material grown from selected seeds. Tight link between economic value of tree breeding process and the size of the area, where selected forest reproductive material is utilized, is also noted by other authors (Ledig & Porterfield 1982).

Fluctuation of wood prices has remarkable influence on the value of differential benefits: difference between the lowest and highest estimate for the same alternative and annual area of planting varies 2.4–5.0 times. That indicates the importance of selection of proper final harvest time, based on market conditions in order to reap highest benefits from the use of selected material in forest regeneration. Results also demonstrate that rather conservative genetic gain estimate ensures positive differential benefits from tree breeding and use of selected

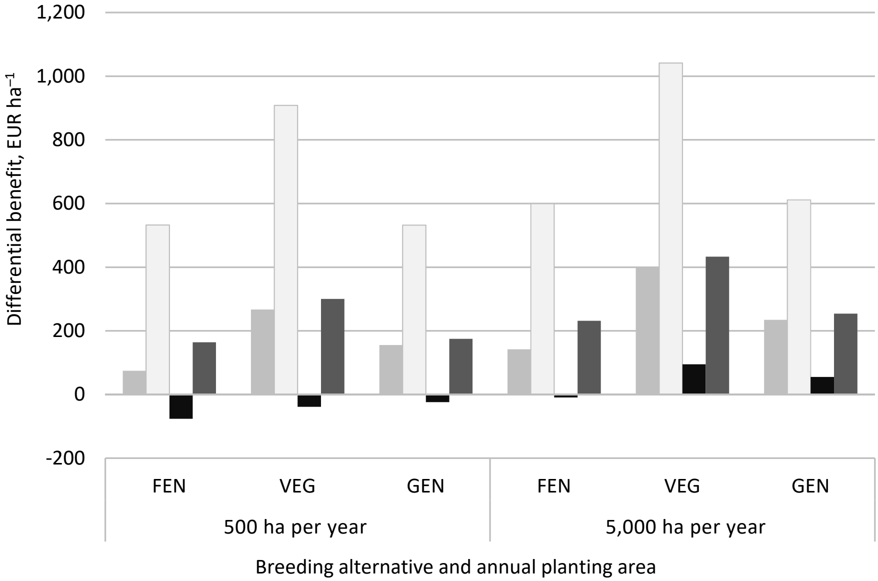

Figure 5.11 **Influence of silvicultural system applied on the differential benefits from forestry in the year of high (2007) and low (2009) wood prices, in EUR, adjusted to the 2023 price index:**

2007 traditional 2007 targeted 2009 traditional 2009 targeted

Genetic gain for height and diameter 14% for FEN and 18% for VEG and GEN alternatives

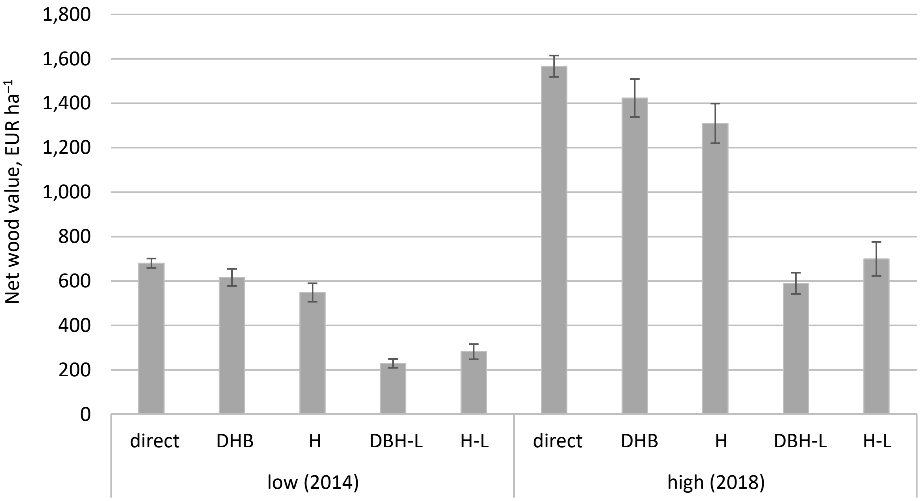

Figure 5.12 **Net wood value of the thinning at the age of 14 years, based on low or high timber prices and selection of 10% best or worst (-L) families either directly (by value) or indirectly (by DBH or by height at the age of 10 years)**

material, even with the least beneficial alternative and in years with the lowest wood prices.

Silvicultural system has a notable influence on stand parameters. Results demonstrate that stands with “targeted” management regime, involving only one commercial thinning ensures notably higher differential benefits than stands with “traditional” one regardless of selection alternative or wood price conditions (Fig. 5.11). Main cause of it is faster diameter increment in “targeted” management, providing opportunity to shorten rotation period as well as to obtain higher proportion of most valuable assortments. In the study we were not able to address aspects of genotype-silvicultural system (like initial spacing, intensity of pre-commercial thinning etc.). Only few studies of this aspect have been carried out in the region based on very limited Scots pine material. They indicate that genotype – initial spacing interaction might have a practical importance (Persson 1994, Roth et al. 2007). Selection of assortments in our study is based only on dimensions, and quality is not considered. However, studies demonstrate that up to 90% of proportion of veneer logs from tree is determined by branch quality (Hagqvist 2001). Genetics is even more important than the silviculture in determining quality traits of birch, like natural pruning (Zālītis & Zālītis 2002), branch diameter and angle (Hagqvist & Hahl 1998), wood quality (Koski & Rousi 2005). Genetics has significant effect even on slenderness of trees (Kroon et al. 2008). Therefore, increased quality and proportion of the most valuable assortments could be an important part of differential benefit from use of selected material and shall be addressed in further studies, as soon as there is sufficient data from National Forest Inventory and older birch trials. Average proportion of elite-grade logs could be determined also by equations, developed by P. Zālītis and colleagues (Zālītis et al. 2002), but it does not allow to consider the additional gain from quality improvement. Constant proportional advantage, adding the genetic gain to parameters of unimproved stand at any age, is used in our study. However, genetic gain could be different at different age, and thinning regime could be optimized to reap highest benefits from the use of selected material.

Considering the above mentioned – thinning regime not optimized, quality traits not estimated and elite veneer assortment not assessed – as well as probability, that no extra cleanings might be needed for planted stand in comparison to naturally regenerated. It can be stated that the results of our study are close to the lowest limit of estimates of differential benefits from the use of selected material.

Interest rate used in the study – 3% – might seem rather low, but it is in line with values usually used in economic analysis in forestry (Pesonen & Hirvelä 1992, Pentinten 1999).

In the trial, studied **for effect of breeding on income at first commercial thinning**, the mean DBH and tree height (± confidence interval) at the age of 14 years was 9.1 ± 0.2 cm and 13.4 ± 0.2 m, respectively; standing volume (yield) was 91 ± 1.9 m^3 ha^{-1}. Heritability for timber value and for the usual trait of selection (DBH) was very similar (Table 5.8). However, the proportion of industrial timber (sawlogs and pulpwood) was less heritable. Genetic gain values had a similar trend as the CV_a. There were negligible differences in genetic gain from direct selection or selection by DBH.

The estimated heritability (Table 5.8) implies a high potential for improvement of DBH and timber value (Stener & Hedenberg 2003) by breeding. It was higher than observed for birch in Norway (0.23; Skrøppa & Solvin, 2019) and in Sweden (0.32; Stenner & Jansson 2005). The increased values of higher genetic gain might be related to diverse population structures of birch in Latvia (Gailis et al. 2012), which is a result of the post-glacial recolonization of vegetation in northern Europe. Accordingly, a higher genetic diversity allowed obtaining a broader spectrum of phenotypes, hence the intensive selection of the material was efficient (Palmé et al. 2002).

Table 5.8

Coefficients of heritability (h^2), genetic variation (CV_a) and genetic gain (GG_10%) of progenies of plus-trees of silver birch plantation at the age of 14 years

Trait	Heritability coefficients h^2 ± Standard errors	Coefficients of additive genetic variation CV_a, %	Genetic gain GG_10% direct	Genetic gain GG_10% DBH
DBH	0.49 ± 0.08	8.4	8.9	8.9
Proportion of industrial timber	0.18 ± 0.07	3.7	1.7	1.6
Timber value (low prices)	0.49 ± 0.08	22.7	26.9	26.3
Timber value (high prices)	0.50 ± 0.075	20.0	22.9	22.5

The coefficients of additive genetic variation (CV_a) ranged from 3.7% to 22.7% for the proportion of industrial timber and timber value, respectively (Table 5.8). The CV_a for DBH was relatively low, which might be explained by the effect of stand competition (Stenner & Jansson 2005, Egbäck et al. 2018, Zeltiņš et al. 2018), but the higher coefficients for the timber value might be explained by the cumulative effect of DBH and tree height. Nevertheless, the estimated genetic gain from the 10% top-performing families had a similar trend as the CV_a and was similar to other studies. For instance, Stener and Jansson (2005) and Hagqvist and Hahl (1988) found 18% and 11% gains for DBH when first-generation seeds were compared with ordinary seed material at the age of 7 to 12 years. Such genetic gains from improved material supports the reliability of genotypic selection and the effect of breeding (Zeltiņš et al. 2018).

For the trees subjected to thinning, the DBH and height were 8.0 ± 0.3 cm and 13.0 ± 0.4 m, respectively. The remaining trees had a mean DBH of 10.0 ± 0.3 cm and height of 10.0 ± 0.4 m. The volume of harvested industrial timber on average was 28.0 ± 0.8 m^3 ha^{-1}.

Income from the thinning differed greatly with fluctuations of timber market: with low timber prices, it was 1,275 ± 29 EUR ha^{-1} on average; with high, 1,863 ± 33 EUR ha^{-1} (Table 5.9). Similar differences were observed with NWV (Fig. 5.12): the top-performing families reached 1,424 ± 86 EUR ha^{-1} with high timber prices, and 616 ± 39 EUR ha^{-1} with low prices; corresponding mean figures in an open-pollinated plus-tree progeny trial were statistically significantly lower: 1,030 ± 25 EUR ha^{-1} and 426 ± 11 EUR ha^{-1}, respectively. Selected (best performing) families had a positive NPVs (with a 3% discount rate) from 370 to 741 EUR ha^{-1}. Moreover, for the best-performing families, NPVs at a high timber price and low discount rate were 50% higher compared with the trial mean; at a low timber price, the improvements were 35%. This could, at least in part, be attributed to low establishment costs: good quality planting material ensured a need for only one tending. Compared to conventional stands of Scots pine in Sweden (Ahtikoski et al. 2018), the estimated NPV of the top-performing families of silver birch at the age of 14 was high: 2,305 and 1,488 EUR ha^{-1}, with high and low timber prices, respectively. It indicates high potential for the application of improved reproductive material of birch in commercial forestry with the possibility of early return on investments. Simonsen et al. (2010) and Jansson et al. (2017) indicates that genetically improved material significantly increases tree growth with lower investment costs. However, Jansson et al. (2017) indicated that, with 5.3% IRR, the income is still low due to increasing establishment and harvesting costs, which might not be met by the improved growth rates.

Table 5.9

The economic indicators of the selected trees of the silver birch trial at the first thinning at the age of 14 years

Timber price	Trial mean				Top 10% families			Bottom 10% families		
	WV, EUR ha^{-1}	NPV		IRR, %	NPV		IRR, %	NPV		IRR, %
		3%	5%		3%	5%		3%	5%	
High (2018)	1,863 ± 33	741	451	8.1	1,484	1,018	9.4	106	–33	4.5
Low (2014)	1,275 ± 29	370	171	6.7	780	484	8.3	–7	–117	2.9

Abbreviations: WV – total value of the harvested timber.

In Latvia, the establishment and management costs would not increase as fast as in Sweden, due to the parity of the costs. Estimated IRR for the mean and top-performing families resulted in good profitability even when timber price is low; the values ranged from 6.7% to 8.3% (Table 5.9), thus exceeding those of naturally regenerating stands (Jansson et al. 2017). IRR for the worst-performing families reached 2.9% in an unfavourable timber market, and 4.5% in a favourable one. Overall, these values might be lower if lower planting density is used, due to smaller harvested volume. Similarly, the value would be reduced with an even earlier thinning, aiming to improve the growth of the remaining birch. Thus, additional calculations using growth models would be useful to optimize the planting density. The main value of this study is to demonstrate the practical gain obtained from an actual, large (23.1 ha) thinning area at an early age, and the actual value added by the tree breeding.

CONCLUSIONS AND RECOMMENDATIONS

Conclusions

1) The efficient selection of high-value and climate-adapted birch genotypes can be achieved in the designated Eastern provenance region, characterized by higher genetic variability (heritability) for evaluated phenotypic traits and higher productivity. Maintaining the delineated birch provenance regions is advisable, as progeny test analysis confirms differences in growth-related traits between these regions.
2) Birch breeding can significantly enhance growth rate and stem quality, as evidenced by high heritability coefficients for tree height, diameter, and stem volume (mean $h^2 = 0.43$), as well as for traits characterizing branching and stem straightness (mean $h^2 = 0.32$) in young stands. Similar results were observed for traits corresponding to final harvest criteria (mean $H^2 = 0.18$ and $H^2 = 0.31$, respectively). Low genotype × environment interaction effects and high genetic correlations among trials for most traits indicate the generalizability of these results.
3) It is possible to achieve high breeding efficiency for both growth and stem quality (branching) traits simultaneously, supported by relatively high genetic variation (mean CV_a = 13.0% and CV_a = 6.8% in young stands and CV_g = 6.4% and CV_g = 14.3% in older stands, respectively) and weak genetic correlation between these trait groups.
4) Selecting the top 10% of families using various breeding indices at the first thinning stage results in a 27%–60% higher value of obtainable timber and, depending on wood price, an increase in the internal rate of return on investments in stand establishment and management by 16–23 percentage points. Birch genetic traits significantly influence the financial value of birch stands, both at the first thinning and final harvest stages.
5) The success of propagating specific clones is influenced by the composition of the growth medium.
6) The differential benefit of implementing the second cycle of birch breeding is positive if a 3% real interest rate is applied to investments in breeding, seed orchard management, and forest planting. This benefit increases proportionally with the practical implementation of breeding outcomes, i.e., the annual area planted.

Recommendations

It is recommended to increase the proportion of purposefully regenerated silver birch stands, particularly in areas with growth conditions suitable for high-yielding forest stands. This approach ensures higher financial returns on investments in forest breeding and more efficient use of forest land. In addition to enhancing stand productivity, it is advisable to use vegetatively propagated planting material from the forest reproductive material category “tested”.

The implementation of the second breeding cycle should follow a family-clonal selection scheme, with the final evaluation of progeny tests conducted at the age of 10 years. To enable accurate assessment of traits affecting stem quality, the trials should be established under the most homogeneous conditions possible.

It is recommended to include a higher proportion of genotypes from the Eastern provenance region in the breeding population and to incorporate birch genotypes from northern Poland (53–54° N latitude) to improve adaptive traits. The use of birch reproductive material originating north of Latvia or south of 53° N latitude for forest regeneration is not permissible without specific trials evaluating the growth and quality of the material under local conditions.

The plus trees (61) selected from progeny trials within this doctoral thesis are recommended for use as clones in seed orchards to produce “tested” forest reproductive material.

It is further recommended to utilize the vegetative propagation technology developed in this doctoral thesis, along with the selected silver birch clones, for producing planting material.

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ASSESSMENT OF SILVER BIRCH (*BETULA PENDULA* ROTH.) GEOGRAPHICAL PROVENANCES IN LATVIA

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ABSTRACT

Plant production and planting of silver birch is gradually increasing in Latvia. It comes with the recognition on the potential to improve the growth and quality of next generation of birch stands while using the improved (selected) material (seeds for plant production mainly from seed orchard). In very fertile sites with fast over-growth of clear-cut with dense vegetation, planting also helps to ensure successful and fast forest regeneration. Planting is a significant investment, thus forest owners are interested to maximize the profit from it. It includes both ensuring the highest possible productivity as well as minimizing the risks, mainly – wind damage probability. Therefore aim of our study is to assess the transferred silver birch provenances for potential use in tree breeding.

Trial, established in central part of Latvia (56°N), includes provenances from region north and south of our country: Finland and Poland, respectively, latitudes 51°to 61°N. Initial spacing 2x1.2m, no thinning carried out before the measurement at the age of 37 years. Material from altogether 16 provenances planted in 24 tree block plots in 6 replications.

Statistically significant influence of provenance on tree height, yield and height of the mass point were detected. Largest height was reached by birch provenances from Latvia (18.2±0.5m), slightly lower- from Poland (15.8±0.7m) and lowest – from Finland (14.7±1.4m). Differences in yield between provenances from these countries followed the same trend both when the actual survival was considered as well as when 90% survival was assumed. Mass centre was higher for provenances from Latvia, however, the actual wind damage risk might be lower, since faster growth ensured shorter period until the final harvest, set by target diameter.

Key words: productivity, growth model, mass point, risk

INTRODUCTION

Birch (mostly silver birch) is increasingly more common in forests of northern Europe, mainly due to is natural regeneration after the clear-cuts with absence other management and/or changes in agricultural practice, leading to abandonment of marginal farmlands and following afforestation. This afforestation had happened in rather large scale, e.g. in Latvia alone during the last two decades forest land area had increase by c.a. 1% [1]. Birch is used for pulp and energy production, however, the assortment generating high income forest owner is plywood. If logs of such quality are ensured, owner generate higher profit from its birch stand than from other broadleaved tree stands in comparable situation or than from birch stands with management targeted for lower quality, but higher volume birch wood production [12]. Share of saw-logs can be increased to 17-25% already at the second commercial thinning, if stands are planted with selected (improved) plants [6]. Notable, genetically determined differences in stem monetary value has been found also at the stage of final harvest (set by target diameter at the age of 40 years) in clonal birch trial in Latvia. It demonstrates in practice the opportunity for the owner to minimize risks (due to shorter rotation period) as well as increase the income while applying tree breeding results [14]. In turn, breeding of birch had been proven as income generating activity (both from the owner and at the state perspective) if its results are sufficiently used: 30-40% of the annual clearcut areas in birch stands regenerated by planting of selected material [5]. Currently, this is not the case in Latvia or other neighbouring countries, thus information (like publications) in the genetically determined differences between provenances, families or clones are important to educate the forest owners. Provenance level differences might be of importance in consideration of regeneration (or afforestation) method. The greatest (or most visible) of them are in quality traits: most common defect of birch being crooked stems (11%-14% of trees, as reported in the study in Finland) and forking (13%- 23% of trees) [11]. Large within-stand genetic variation, commonly found in the studies of wind-pollinated forest trees [15], does not exclude the pronounced stem quality differences even within so comparatively small area as Latvia. Genetically determined differences were also found in the occurrence of damages, caused by biotic factors at young age [13]. Repeated browsing damages of top-shoot can substantially reduce tree growth [10]. Such impact is becoming present also in birch stands in areas with notably increasing browsing pressure and can't be reduced with selection of provenances. Similarly, impact of forest fires that are linked to management activities even in rather remote sites [7] depends on meteorology and trees age, rather than genetics. Other traits, like drought resistance, have shown a notable differences among far distant provenances, thus the improvement is possible. Altered precipitation regime, as predicted in Baltic States due to climate change in future, might have a negative impact on growth of birch on fertile mineral soils [8]. Effect is not so pronounced, however, would not allow birch stands to achieve highest possible productivity, unless the proper genotypes are selected. Selection needs to be combined with the appropriate silviculture. In Finland, in order to achieve high outcome of sawlogs, comparably low initial density of the stands are recommended (ensuring long green crown) and rather intensive thinnings: first, when dominant height reaches 13-15 m, leaving 700-800 trees ha^{-1} and second c.a. 15 years later, leaving 350-400 trees ha^{-1} [4, 2]. Such approach would also higher individual tree wind stability, important, when the stands exceed roughly 10 m height [9]. However, even higher stability can be achieved with sparser initial density and no commercial thinning, minimizing the time to achieve target diameter of trees for final harvest [14, 3]. High productivity of birch stands are important also to ensure steady flow of timber supply for the wood processing industry. According to data of National forest inventory, there is a notable gap in areas of birch stand after 30-40 years in Latvia. This impact can be minimized with intensive silviculture, leading to fast-growing stands, that includes also selection and use of appropriate reproductive material. Therefore aim of our study is to assess the transferred silver birch provenances for potential use in tree breeding.

MATERIAL AND METHODS

Provenance trial had been established in central part of Latvia with initial spacing 2x1.2m and measured at the age of 37 years. Altogether 16 provenances (Fig.1) from the neighbouring areas (latitude 51°-61°) were used, experimental design – 24 tree block plots in 6 replications. No thinning carried out before the measurements. Height and DBH was measured for every tree and used to calculate stem volume, basal area and yield. Presence of spike knots or double tops (counted as one stem defect) was assessed. The growth in trial overall was rather poor due to unfertile mineral soil, with low site index for birch. It corresponded to that at the age of 27 years on average in birch stands in Latvia in accordance to National forest inventory data. Due to this and lack of thinning, growth model, developed at LSFRI Silava by J. Donis and G Šņepsts was used to assess the development of the stands, formed by groups of provenances from different countries (input data – Table 1). Age to reach a target diameter (25 cm) was assessed.

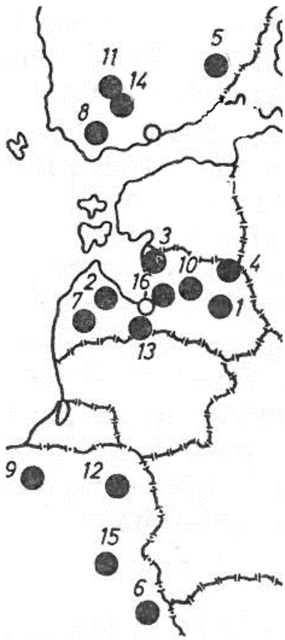


Figure 1. Provenances (dots) represented in the trial in central part of Latvia (open circle)

Table 1. Forest inventory parameters of the groups of birch provenances from different countries

Group of provenances from	Actual			Highest (max)		
	density, trees ha^{-1}	height, m	diameter, cm	density, trees ha^{-1}	height, m	diameter, cm
Latvia (LV)	2064	17.9	13.0	521	22.2	17.0
Finland (FIN)	669	14.2	9.5	521	15.1	10.0
Poland (PL)	1691	15.4	10.0	521	20.7	15.0

Actual – measured forest inventory parameters; highest – parameters of the highest trees, corresponding to given stand density (521 trees ha^{-1}). Diameter – diameter at breast height.

Ten sample trees, representing the range of breast height diameters in the site, were cut, and data on branch and stem biomass obtained by 1m section. These data were used to calculate the height of the mass centre of the trees.

RESULTS AND DISSCUSION

Provenance was a significant factor affecting survival; for specific provenances survival ranged from 11% to 63% and it was lowest for birched from Finland (on average 16%), higher for birches from Poland (42%) and highest from local birches (50%). Provenance was also a significant factor, affecting height (Fig. 2), breast height diameter and, consequently, stem volume of birches. Correlation between mean height of the provenances at the age of 5 years (earlier measurements) and 37 years was statistically significant (r=0.78).

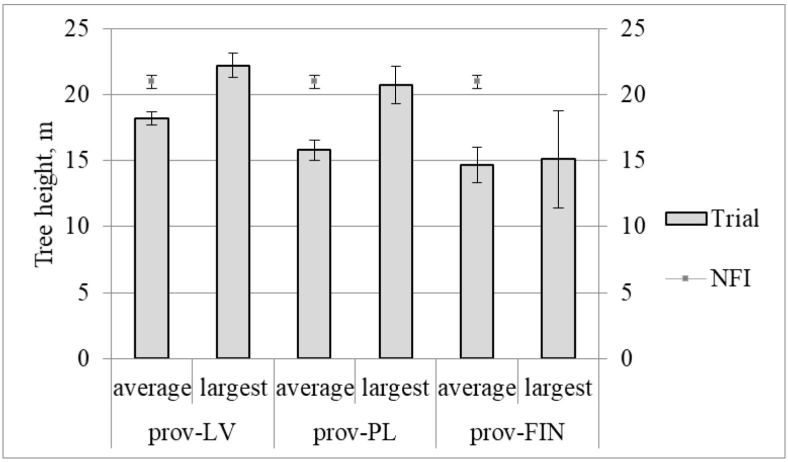
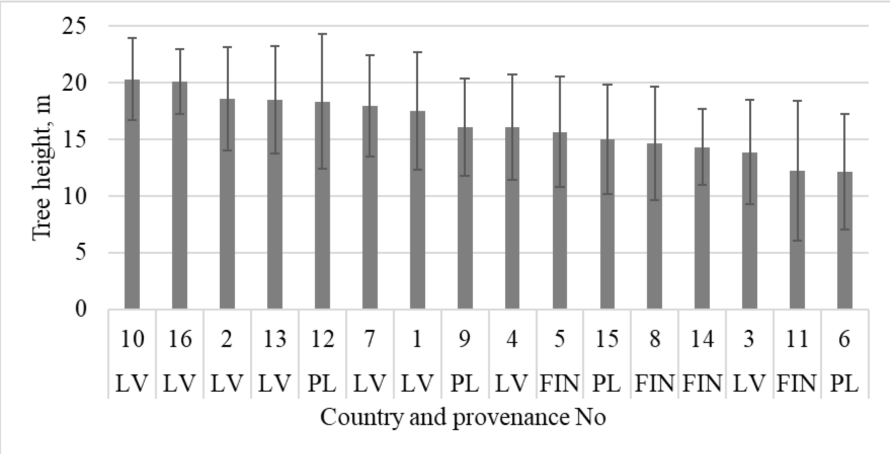


Figure 2. Height for the groups of provenances in trial in comparison to the parameters in birch stands in Latvia on average (National forest inventory – NFI – data)

Standing volume ranged from 24 m^3ha^{-1} to 405 m^3ha^{-1} and was on average 204 m^3ha^{-1}. Calculations estimating even survival for all provenances reveal similar trend, than based on actual survival – largest standing volume was for local (Latvian) birch, lower – for birch from Poland, and lowest – from Finland. Top-ranking provenances based both on height (Fig. 3) and breast height diameter were from Latvia, however, there was large variation in the traits and potential to select some birches from Poland, that could reach similar growth, than the local provenances. Thus the material from similar stage of breeding (seed orchard progenies or clones) could be further tested to find genotypes with superior performance in current (in Latvia) and slightly warmer (as currently in Poland) conditions. Birches from Finland were heavily outperformed and testing only for superior genotypes (e.g. very fast growing clone) could be justified.



Provenance No corresponds to the number in the Figure 1

Figure 3. Mean height of the provenances in trial

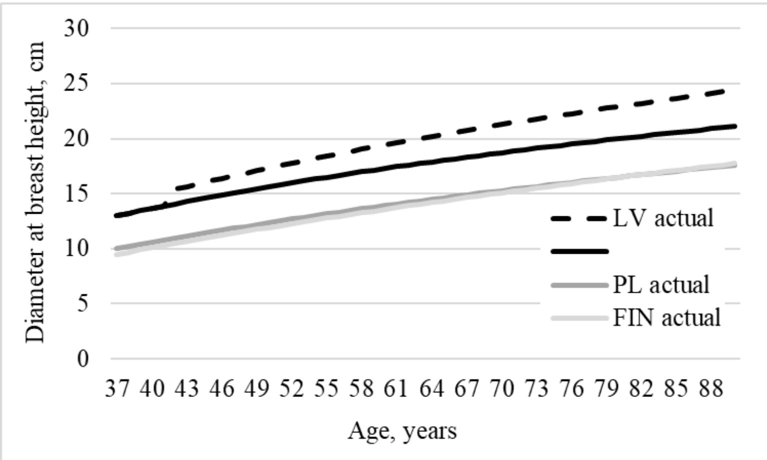
Rather small differences in the height and diameter at the measurement age corresponds to large differences in time, when the target diameter can be reached (Tab. 2). In sparser stand (521 trees ha^{-1}) assuming the best growth and good conditions for silver birch in Latvia (age 27, highest), this diameter can be reached as early as at the age of 48 years. It is close to the values actually found in Latvia in sparse clonal plantation of birch [14], where the mean diameter exceeded 28 cm at the age of 40 years, but also the density was lower (initial: 400 trees ha^{-1}). Under similar input parameters in the model Polish birch provenances would reach the target diameter at the age of 57 years and have a similar yield than the Latvian provenances 10 years earlier (272 m^3ha^{-1} and 263 m^3ha^{-1}, respectively). Thus, the potential growth for birches from Poland is slightly lower than that of local provenances. Birches from Finland in any of the analysed combination of the parameters cannot reach the target diameter earlier than at the age of 100 years that is significantly later than the cutting age set in legislation in Latvia (71 year). In the actual conditions target diameter cannot be reached before the cutting age; assuming better growing conditions and actual stand data – only local provenance, where in case thinning is carried out, can reach the intended target diameter at the age of 67 years.

Commercial thinning had significant impact, boosting diameter increment in the trial in accordance to the model (Fig. 1). However it might be overestimated due to high density and thus reduced length of green crown in the stand. Birch provenances from Poland and Finland did not reach the basal area required for commercial thinning, thus it was not planned.

Table 2. Age when target diameter (25 cm) will reached for different groups of provenances

Group of provenances from	Data	Age	
		27	37
Latvia (LV)	actual	91	127
Latvia (LV)	actual*	67	94
Finland (FIN)	actual	111	157
Poland (PL)	actual	127	167
Latvia (LV)	highest	48	67
Finland (FIN)	highest	100	143
Poland (PL)	highest	57	81

*commercial thinning carried out; other abbreviations in accordance to Table 1



Dotted line – of commercial thinning implemented; other abbreviations in accordance to Table 1

Figure 3. Modelled development of breast height diameter for different provenances

Mass centre was higher for provenances from Latvia due to faster tree growth, since its relative height in relation to tree height was quite stable. It can lead to higher wind damage risk for Latvian birch due to similar rotation periods for provenances from different countries (except for modelled growth on good growing conditions for birch). Further studies needs to be carried out for detailed evaluate this effect.

Provenance was not a significant factor affecting the occurrence of spike knots.

CONCLUSION

Provenance trials are important source of information on long-term performance of transferred forest reproductive material. Ongoing climate change increases the importance to evaluate growth of the genotypes form conditions wormer than currently in the location of interest to assess, if material, growing well in the current and predicted future conditions could be selected. Such selection can be for direct use or inclusion in controlled crossings in tree breeding program.

Provenances from Finland demonstrated inferior growth and thus could not be recommended for further evaluation and potential use in Latvia. Provenances from Northern part of Poland (latitude 53-54°N) demonstrated slower growth than the best performing Latvian provenances but exceeded worst local provenances; thus material from this region can be used in further testing and potential inclusion in tree breeding program, if better adaptation to the climatic conditions predicted in Latvia in future can be found.

Target diameter of 25 cm can be reached as early as at the age of 48 years in sparser stand assuming the best growth and good conditions for silver birch in Latvia. Under similar scenario Polish birch provenances would reach the target diameter at the age of 57 years and have a similar yield than the Latvian provenances 10 years earlier (272 m^3ha^{-1} and 263 m^3ha^{-1}, respectively). Thus, the potential growth for birches from Poland is slightly lower than that of local provenances. Birches from Finland in any of the analysed combination of the parameters cannot reach the target diameter earlier than at the age of 100 years that is significantly later than the cutting age set in legislation in Latvia (71 year). In the actual conditions target diameter cannot be reached before the cutting age; this prolongs the time, when relative faster growing trees (local provenances) can be affected by the wind-storm.

ACKNOWLEDGMENT

Study carried out in JSC Latvijas valsts meži research project “Tree breeding for selection of genetically valuable forest reproductive material” and Latvian Council of Science project “Reduction of wind storm damage risk in private forest management”, No lzp-2018/2-0349

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Silva Fennica vol. 54 no. 2 article id 10220
Category: research article
https://doi.org/10.14214/sf.10220

Silva Fennica

http://www.silvafennica.fi

ISSN-L 0037-5330 | ISSN 2242-4075 (Online)
The Finnish Society of Forest Science

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Genetic parameters of growth and quality traits in open-pollinated silver birch progeny tests

Gailis A., Zeltiņš P., Purviņš A., Augustovs J., Vīndedzis V., Zariņa I., Jansons Ā. (2020). Genetic parameters of growth and quality traits in open-pollinated silver birch progeny tests. Silva Fennica vol. 54 no. 2 article id 10220. 14 p. https://doi.org/10.14214/sf.10220

Highlights

- Growth and stem quality traits were under strong genetic control.
- Weak genetic correlations between tree growth and stem quality were found.
- Strong age-age and type-B correlations suggest robust improvement over time and different environments.
- Simultaneous improvement of growth and stem quality might be applicable.

Abstract

Genetic parameters of growth and stem quality traits were estimated for open-pollinated silver birch *Betula pendula* Roth progenies in Latvia at the age of 10 and 14 years. Tree height and stem volume were found to be under strong genetic control at both inventories (narrow-sense heritabilities varied from 0.41 to 0.66). Mainly low heritabilities were found for stem defects, yet genetic control of branch diameter, stem straightness and overall stem quality varied from low to high depending on study site. High additive genetic coefficient of variation was found for stem volume (25.3–32.5%). Genetic correlations among growth traits were strong and positive (0.90–0.99). Mainly weak genetic correlations between growth and quality traits implied simultaneous improvement. Still, strong negative correlations between branch angle and stem straightness might result in enlarged knot size for straighter logs. The genetic age-age correlations were strong. Weak genotype by environment interaction and stability of best genotypes over different sites was indicated by strong genetic correlations between trials. Each growth or quality trait alone showed substantial improvement in terms of estimated genetic gain (up to 62% over trial mean for stem volume). Therefore, selection index combining both growth and stem quality may be developed.

Keywords *Betula pendula*; genetic gain; genetic parameters; tree breeding
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Received 27 June 2019 **Revised** 28 February 2020 **Accepted** 3 March 2020

1 Introduction

In Latvia, comprehensive breeding of silver birch *Betula pendula* Roth was initiated in the middle of 1990s. For basic breeding material, 921 plus-trees and superior stand trees were phenotypically selected in 26 natural stands thorough the country, and their progeny tests were established in 1999 and 2000. Although breeding of coniferous species (Scots pine *Pinus sylvestris* L. and Norway spruce *Picea abies* (L.) H. Karst.) has longer history in Latvia, silver birch as a commercially important tree species is yet included in the long-term breeding program, aiming to develop seed production and raise the financial value of forests (Jansons 2008).

In the Eastern Baltic region, breeding activities in combination with appropriate silviculture (e.g. planting density) can result in highly productive silver birch stands for valuable plywood production (Stener and Hedenberg 2003), as confirmed by a clonal birch plantation in Central Latvia ready for harvest at the age of 40 years (Zeltiņš et al. 2018). The selection of genotypes must be based on the growth traits and stem quality traits such as stem straightness, desirable branch properties, and apical dominance (Stener and Hedenberg 2003). As indicated by mainly negligible genetic correlations between both types of traits (Koski and Rousi 2005; Stener and Jansson 2005), such simultaneous selection may be applicable. For plywood production, logs with no stem defects such as crooks, forking, and with knots as few as possible are required (Donaldson and Turner 2001; Heräjärvi 2001). For silver birch, growth traits have been reported to be mostly under strong genetic control (Stener and Hedenberg 2003; Stener and Jansson 2005), yet rapid growth not having strong negative effect on wood and stem properties (Dunham et al. 1999; Heräjärvi 2001; Heräjärvi 2004a and 2004b; Baliuckienė and Baliuckas 2006). In Scandinavia, heritability for growth traits found to vary considerably from 0.07 to 0.56 up to the age of 10 years, largely depending on planting site (Stener and Jansson 2005; Skrøppa and Solvin 2019). Moderate h^2 (cf. Falconer and Mackay 1996) for growth traits (0.20–0.39) reported in Scottish and Lithuanian studies (Malcolm and Worrell 2001; Baliuckienė and Baliuckas 2006). Genetic coefficients of variation (CV_a and CV_g), indicating level of genetic variability, reported to range from 4.6 to 20.5% for growth and from 9.8 to 15.1% for stem quality traits (Stener and Jansson 2005; Baliuckienė and Baliuckas 2006). Early selection has been justified by moderate to strong age-age genetic correlations for periods up to 17 years (Hagqvist and Hahl 1998; Stener and Hedenberg 2003; Stener and Jansson 2005), yet general information about long-term time trends for genetic control is limited (Stener and Hedenberg 2003).

In Fennoscandia, the silver birch breeding programs have resulted in substantial improvements of productivity and stem quality, genetic gains reaching 5–30% (Hagqvist and Hahl 1998; Rosvall et al. 2001; Jansson et al. 2017). In Latvia, the use of silver birch in plywood production, accounting for ca. 9% of total forest sector export value (Central Statistical Bureau of Latvia 2016) and being one of the leading branches of the wood processing industry (Liepins and Rieksts-Riekstins 2013) indicates the importance of birch breeding for the production of fast growing planting stock with desirable quality traits. However, comprehensive analysis of silver birch quantitative genetic parameters and potential genetic gains in the Eastern Baltic region is still lacking. Therefore, the aim of the study was to estimate genetic parameters for growth and stem quality traits in open-pollinated silver birch progeny trials at the age of 10 and 14 years.

Table 1. Description of the studied open-pollinated *Betula pendula* progeny trails.

Name	Latitude	Longitude	Altitude (m)	Planting year	No. of open-pollinated families assessed		No. of measured trees		No. of replications
					age 10	age 14	age 10	age 14	
Rembate	56°46´N	24°48´E	50	1999	637	637	46696	53032	3–5
Ukri	56°22´N	23°07´E	75	2000	639	657	9643	18371	10–93
Taurene	57°06´N	25°38´E	215	2000	612	621	11917	10964	10–77

2 Material and methods

For the progeny testing, the seeds were collected in years 1995–1998 from the plus-trees in 26 forest stands thorough the country (55°40´–58°05´N, 20°58´–28°14´E). Data were collected from three extensive silver birch open-pollinated progeny trials Taurene (57°06´N, 25°38´E), Ukri (56°22´N, 23°07´E), and Rembate (56°46´N, 24°48´E) (Table 1). In Ukri and Taurene, the field design was randomized blocks with single-tree plots in 10–93 and 10–77 replications, respectively, with spacing 2 × 2.5 m. Rembate was planted in a randomized complete block design with 32-tree four-row plots for each family in three to five replications with 2 × 2 m spacing (Table 1). The trial Rembate was established in spring 1999, but the trails Ukri and Taurene – in spring 2000 on former agricultural land with one-year-old containerized seedlings. All trials were characterized with dry silty soils and mesotrophic conditions comparable to *Oxalidosa* according to the Latvian forest typology (Bušs 1981).

The mildest climate was in Ukri, where the mean annual temperature (MAT) was 6.4 °C, the mean monthly temperature ranged from –4.4 °C to +17.4 °C in January and July, respectively; the mean annual precipitation (PRECIP) was ca. 630 mm (Harris et al. 2014). In Rembate, the MAT was 6.1 °C, the mean monthly temperature ranged from –5.0 °C to +17.4 °C; the PRECIP was 618 mm. Taurene trial was located in more continental climate of eastern Latvia (Laiviņš and Melecis 2003), where MAT was 5.1 °C, mean monthly temperature ranged from –6.3 °C to +16.9 °C; PRECIP was 670 mm (Harris et al. 2014).

2.1 Data collection

In all trials, evaluation was done at the age of 10 and 14 years. For the first evaluation, measurements from 68 256 trees were available for analysis (9643, 11 917, and 46 696 trees in Ukri, Taurene and Rembate, respectively). For the second evaluation, 82 367 trees were measured (18 371, 10 964, and 53 032 trees in Ukri, Taurene and Rembate respectively) (Table 1). During the first evaluation, for each individual a) tree height (H), b) diameter of the largest branch until the stem height of 2 m (BrD), and c) mean branch angle (BrA) was measured. Occurrence of spike knots (SpKn), double leaders (Doubl) and lost top (LostTop) were recorded as binary variables (1 – present, 0 – absent), and ordinal scores using 3-point-scale of stem straightness (StStr; bent, slightly bent, and straight) and overall stem quality (StQual; poor, intermediate, and good) were assessed. At the age of 14 years, H and diameter at breast height (DBH) were measured (except for Rembate, where H was not measured). Afterwards, stem volume (V) was calculated according to Liepa (1996). In trial Rembate, BrA was measured, but in Ukri and Taurene it was assessed using 3-point ordinal score (1 – from 65° to 90°; 2 – from 45° to 60°; 3 – from 0° to 40°). Occurrence of SpKn, Doubl, LostTop, and ordinal scores of StStr and StQual were assessed as described above.

2.2 Statistical analysis

Variance and covariance components for continuous traits were estimated using SAS MIXED procedure with the restricted maximum likelihood approach (REML) (Littel et al. 2006). Diagnostic plots were used to verify for normal distribution of residuals. For the binomial variables, a generalised linear mixed models applying binomial residual distribution and a "logit" link function were fitted. For the ordinal variables, ordinal logistic regression was fitted. The binary/categorical traits were analysed using the Generalized Linear Mixed (GLIMMIX) procedure (Littell et al. 2006). Standard errors were calculated using Dickerson's approximation (Dickerson 1969). For a combined-site analysis of Ukri and Taurene, which had similar experimental design and set of families, the following mixed model was used:

$$y_{ijkl} = \mu + S_i + B_j + F_k + SF_{ij} + \varepsilon_{ijkl}, \qquad (1)$$

where y_{ijk} is the observation on the lth tree from the kth family in the jth block within the ith site; μ is the overall mean; S_i and B_j are the fixed effects of the ith site and the jth block within the ith site, respectively. The F_k and SF_{ik} are the random effects of the kth family and interaction of the ith site and the kth family, respectively, and ε_{ijkl} is the random residual effect. Preliminary analyses indicated significant effect for the family-by-site interaction for studied traits.

For an individual site analysis of Ukri and Taurene, following model was used:

$$y_{jkl} = \mu + B_j + F_k + \varepsilon_{jkl}, \qquad (2)$$

where y_{jk} is the observation on the lth tree from the kth family in the jth block. For individual site analysis of Rembate, the model was complemented with an effect of the block and family interaction (a multiple-tree plot effect):

$$y_{jkl} = \mu + B_j + F_k + BF_{jk} + \varepsilon_{jkl}, \qquad (3)$$

where BF_{jk} is a random interactive effect of the jth block and the kth family.

The estimates of narrow-sense individual-tree heritability (h^2) were obtained for each trait using the variance components from the individual and joint-site analysis described above (Falconer and Mackay 1996). The individual-tree narrow-sense heritability in the joint-site analysis of Ukri and Taurene was calculated as:

$$h^2 = \frac{4 \times \hat{\sigma}_f^2}{\hat{\sigma}_f^2 + \hat{\sigma}_{fs}^2 + \hat{\sigma}_\varepsilon^2}, \qquad (4)$$

where h^2 is narrow-sense heritability, and $\hat{\sigma}_f^2, \hat{\sigma}_{fs}^2$ and $\hat{\sigma}_\varepsilon^2$ are the estimated variance components of family, family × site interaction and residual, respectively.

For an individual single-tree plot site, following formula was used:

$$h^2 = \frac{4 \times \hat{\sigma}_f^2}{\hat{\sigma}_f^2 + \hat{\sigma}_\varepsilon^2}. \qquad (5)$$

For a multiple-tree-plot design in Rembate, following formula was used:

$$h^2 = \frac{4 \times \hat{\sigma}_f^2}{\hat{\sigma}_f^2 + \hat{\sigma}_{fb}^2 + \hat{\sigma}_\varepsilon^2}, \quad (6)$$

where $\hat{\sigma}_{fb}^2$ is the estimated variance component of site × block interaction.

Additive genetic coefficient of variation (CV_a) describing the extent of genetic variability for the quantitative traits in each site (Falconer and Mackay 1996), was calculated as:

$$CV_a = \sqrt{4\hat{\sigma}_f^2} \cdot \frac{100}{\bar{x}}, \quad (7)$$

where $\bar{x}$ is the phenotypic mean.

Genetic correlations (type-A) between traits and age-age genetic correlations for each trait were estimated using formula:

$$r_G = \frac{\widehat{Cov}_{(xy)}}{\sqrt{\hat{\sigma}_{(x)}^2 \times \hat{\sigma}_{(y)}^2}}, \quad (8)$$

where $\hat{\sigma}_{(x)}^2$ and $\hat{\sigma}_{(y)}^2$ are a) the estimated genotypic variances for traits x and y, or b) the same trait variances at two different ages; and $\widehat{Cov}_{(xy)}$ is the estimated genotypic covariance between traits x and y or between two measurements of the same trait.

The genotype × environment interaction (G × E) for studied traits was evaluated by estimating type-B genetic correlations (r_B) between two experiments (Bourdon 1977). Considering similar experimental design and set of the same families, the type-B genetic correlation between Ukri and Taurene was calculated as (Lu and Charrette 2008):

$$r_B = \frac{\widehat{Cov}_{(a1a2)}}{\sqrt{\hat{\sigma}_{(a1)}^2 \times \hat{\sigma}_{(a2)}^2}}, \quad (9)$$

where $\widehat{Cov}_{(a1a2)}$ is the covariance between genotypic effects of the same traits in different sites, and $\hat{\sigma}_{(a1)}^2$ and $\hat{\sigma}_{(a2)}^2$ are genotypic variances for the same traits in each of the trails, respectively. Both r_G and r_B with their standard errors were estimated by multivariate REML using the MIXED procedure of SAS (Piepho and Möhring 2011) extending univariate mixed models described above.

Breeding values were estimated for each trait to evaluate gain from selection of the best families. We obtained general combining ability (GCA) values of parents by a Best Linear Unbiased Predictors (BLUP) procedure in SAS using the analytical models defined above. Since parent can only transmit half of its genes to its progeny (Falconer and Mackay 1996), breeding values (BV) of families were calculated as double BLUPs. Since the linear predictors for the binary traits from the generalized mixed models were calculated on a logit scale, predicted probabilities of stem defects for families were estimated by applying the inverse of the link function (Littell et al. 1996). Genetic gains, assuming the selection intensity of 10% (as commonly used in tree breeding practice in Latvia), were estimated from BV as the percentage over the trial means.

Table 2. Narrow sense heritabilities (h^2) and type-B genetic correlations (r_B) with standard errors (SE) (all r_B are significant $p < 0.01$) in the studied open-pollinated *Betula pendula* progeny trials at the age of 10 and 14 years.

	$h^2 \pm$ SE								$r_B \pm$ SE
Trial	Taurene		Ukri		Rembate		Ukri & Taurene together		
Age (years)	10	14	10	14	10	14	10	14	14
H	0.37 ± 0.03	0.45 ± 0.04	0.47 ± 0.04	0.64 ± 0.04	0.30 ± 0.07	na	0.37 ± 0.03	0.52 ± 0.03	0.94 ± 0.02
DBH	na	0.45 ± 0.04	na	0.52 ± 0.03	na	0.12 ± 0.02	na	0.42 ± 0.03	0.89 ± 0.03
V	na	0.41 ± 0.03	na	0.53 ± 0.03	na	na	na	0.41 ± 0.03	0.97 ± 0.03
BrD	0.24 ± 0.03	na	0.20 ± 0.03	na	0.10 ± 0.03	na	0.17 ± 0.02	na	na
BrA	0.33 ± 0.03	0.83 ± 0.19	0.27 ± 0.03	0.61 ± 0.07	0.30 ± 0.03	0.31 ± 0.03	0.25 ± 0.02	0.37 ± 0.1	0.78 ± 0.12
SpKn	0.07 ± 0.02	0.08 ± 0.02	0.06 ± 0.02	0.05 ± 0.01	0.04 ± 0.03	0.07 ± 0.02	0.07 ± na	0.06 ± 0.02	na
Doubl	0.29 ± 0.07	0.05 ± 0.06	0.04 ± 0.03	0.19 ± 0.04	0.08 ± 0.04	0.27 ± 0.05	0.1 ± na	na	na
LostTop	0.09 ± 0.03	0.04 ± 0.02	0.06 ± 0.03	0.05 ± 0.01	0.12 ± 0.03	0.06 ± 0.02	0.05 ± 0.04	0.02 ± 0.01	na
StStr	0.45 ± 0.05	0.35 ± 0.05	0.41 ± 0.05	0.45 ± 0.05	0.32 ± 0.05	0.39 ± 0.05	0.40 ± 0.06	0.4 ± 0.05	0.97 ± 0.05
StQual	0.15 ± 0.03	0.35 ± 0.05	0.11 ± 0.03	0.21 ± 0.03	0.14 ± 0.03	0.26 ± 0.04	0.10 ± 0.03	0.23 ± 0.03	0.89 ± 0.08

H – height, DBH – diameter at breast height, V – stem volume, SpKn – spike knots, Doubl – double leaders, LostTop – lost top, StStr – stem straightness, BrD – branch diameter, BrA – branch angle, StQual – stem quality.

3 Results

The survival was high at both measurement times in Rembate (>80%) and Ukri (>90%), yet lower in Taurene (>60%). At the age of 10 years, the means for H in Taurene and Ukri were the same (6.7 m), and other measured traits and proportion of trees with stem defects were similar. In Rembate, H was lower (5.5 m), and proportion of trees with SpKn was ca. three times lower than in the both other trials. At the age of 14 years, mean H was somewhat advanced ahead for Ukri comparing to Taurene (12.3 m and 11.5 m, respectively), yet other traits were stably alike. In Rembate, proportion of trees with SpKn had increased and was high (ca. 60%) and similar to both other trials. In all trials, proportion of trees with SpKn and LostTop was rather high (>50%), while only 6–12% of trees had Doubl.

The estimated narrow-sense heritability (h^2) varied among the variables, generally being higher for growth traits than stem quality (Table 2). The highest h^2 was estimated for H, DBH, V (0.30–0.64), except low value (0.12) for DBH in Rembate. Similarly high h^2 had StStr (0.35–0.45), while StQual, BrD, and Doubl had generally lower values (0.04–0.35). Heritability for BrA varied considerably (0.25–0.83) depending on site and year, but LostTop showed the overall lowest values (0.02–0.12). The genetic coefficient of variation CV_a for H ranged between 8.5 and 15.0% at age of 10 years, while DBH showed ca. two times higher genetic variation in Ukri and Taurene (20.6 and 18.7%, respectively), yet being around the same in Rembate (9.3%) (Table 3). Rather high CV_a was estimated for V, ranging from 25.3 to 40.3% in Rembate and Ukri, respectively. Branch angle showed low degree of genetic variation in all trials (3.7–6.4%) (Table 3).

The estimates of r_G among growth traits were similar and high in all studied trials (0.90–0.99) (Table 4), yet having mainly low to moderate genetic correlations with stem quality traits ($-0.10 < r_G < 0.40$). Branch angle had moderate to strong negative correlations with StStr and StQual ($-0.67 < r_G < -0.45$), which both strongly correlated with each other (0.83–0.84). Rather high positive correlations between SpKn and Doubl (0.60–0.74) were found. Still, stem quality traits generally had low to moderate genetic correlations with each other (Table 4). Genetic age-age correlations for traits measured at both inventories were mostly strong (>0.78) in all trials. Estimated type-B genetic correlations between Ukri and Taurene were high (0.78–0.97) for both growth and stem quality traits (Table 2). Considering low h^2 values, age-age and type-B correlations for SpKn, Doubl, and LostTop were not estimated.

For growth traits, selection of top 10% families resulted in GG% of 9.6–26.6% for H and DBH, while reaching 25.3–61.6% for V. Similar to h^2 values, GG% were generally lower for stem quality traits: 8.6–21.2% for StStr, 5.5–10.3% for StQual, 6.9–18.2% for BrD, 1.6–9.1% for BrA. Estimated GG% for the stem defects (Doubl and LostTop) varied notably among the trials and years, ranging from 5.2 to 58.3%.

Table 3. Genetic coefficients of variation for quantitative traits (CV_a) in the studied open-pollinated *Betula pendula* progeny trials at the age of 10 and 14 years.

Trial	Taurene		Ukri		Rembate	
Age (years)	10	14	10	14	10	14
H	10.4	8.5	11.4	5.5	7.5	na
DBH	na	18.7	na	10.3	na	4.7
V	na	32.5	na	20.1	na	na
BrD	16.2	na	12.6	na	4.3	na
BrA	4.4	na	4.7	na	3.2	1.9

H – height, DBH – diameter at breast height, V – stem volume, BrD – branch diameter, BrA – branch angle.

Table 4. Genetic correlations (standard errors in brackets) in combined Ukri and Taurene (the upper diagonal part) and in Rembate (the lower diagonal part) open-pollinated *Betula pendula* progeny trials at the age of 14 years.

	DBH	V	SpKn	Doubl	LostTop	StStr	BrA	StQual
H	0.92 (0.01)	0.94 (0.01)	0.43 (0.07)	0.23 (0.07)	0.05 (0.09)	–0.10 (0.05)	0.26 (0.06)	0.16 (0.06)
DBH		0.99 (0.00)	0.39 (0.07)	0.20 (0.07)	0.10 (0.09)	–0.06 (0.05)	0.22 (0.06)	0.17 (0.06)
V	na		0.39 (0.07)	0.23 (0.07)	0.06 (0.09)	–0.06 (0.05)	0.23 (0.06)	0.17 (0.06)
SpKn	0.13 (0.13)	na		0.60 (0.11)	0.08 (0.20)	–0.29 (0.08)	–0.02 (0.09)	–0.51 (0.07)
Doubl	–0.10 (0.11)	na	0.74 (0.11)		–0.51 (0.11)	0.03 (0.08)	–0.12 (0.09)	–0.16 (0.08)
LostTop	0.10 (0.13)	na	–0.06 (0.14)	–0.49 (0.11)		–0.69 (0.09)	0.52 (0.11)	–0.58 (0.09)
StStr	0.02 (0.09)	na	–0.39 (0.10)	–0.08 (0.09)	–0.71 (0.09)		–0.67 (0.05)	0.83 (0.03)
BrA	0.00 (0.25)	na	–0.01 (0.10)	0.09 (0.09)	0.28 (0.10)	–0.57 (0.06)		–0.45 (0.07)
StQual	0.40 (0.24)	na	–0.67 (0.09)	–0.28 (0.08)	–0.62 (0.08)	0.84 (0.04)	–0.48 (0.07)	

H – height, DBH – diameter at breast height, V – stem volume, SpKn – spike knots, Doubl – double leaders, LostTop – lost top, StStr – stem straightness, BrA – branch angle, StQual – stem quality.

4 Discussion

The survival was high in Rembate and Ukri (>80%), yet lower in Taurene (>60%), which was most likely affected by the insufficient moisture in dry summer after the establishment due to the fine textured soil in the trial (Sutinen et al. 2002). However, first years after planting, necessary weed control was applied sufficiently to eliminate further mortality induced by weed competition (Ferm et al. 1994; Hynynen et al. 2010). In all trials, proportion of trees with SpKn and LostTop was rather high (>50%), while only 6–12% of trees had Doubl, seemingly not affected by different continentality of the studied trials (Laiviņš and Melecis 2003). Viherä-Aarnio and Velling (1999) reported 13% of trees with SpKn. Similar to Viherä-Aarnio and Velling (1999), most of the trees had at least a light stem sweep.

4.1 Genetic parameters

In the Baltic sea region, heritabilities for growth and stem quality of common forest tree species Scots pine and Norway spruce reported to vary from 0.05 to 0.25 (Velling 1982; Haapanen et al. 1997; Hannrup et al. 1998; Olsson and Ericsson 2002; Jansons et al. 2006). In our study, h^2 for growth traits were mainly moderate to high, and genetic correlation among them were strong, supported by earlier findings in Latvia (Zeltiņš et al. 2018). Considering that the genes controlling each of growth traits might be strongly correlated (Searle 1961), selection may be based on tree height, which possessed the highest h^2. In earlier studies, estimated h^2 and broad-sense heritability H^2 of corresponding traits for silver birch reported to vary widely from low to high (Nepveu and Velling 1983; Malcolm and Worrell 2001; Stener and Jansson 2005; Zeltiņš et al. 2018). In Norway, narrow-sense heritability h^2 of six-years-old open-pollinated families estimated to be rather low, i.e. 0.09 and 0.17 for H and DBH, respectively (Skrøppa and Solvin 2019). In the present study, high heritability values and low variety among trails for growth traits might correspond to relatively homogenous growing conditions on agricultural land sufficiently maintained after establishment. Thus, genetically determined differences were better revealed comparing to forestland (Haapanen 1996; Hannrup et al. 2004). Although h^2 values from individual-site analysis are commonly over-estimated and higher comparing to joint-site estimates (Hodge and White 1992; Haapanen 2001; Wu et al. 2008), our estimates of Ukri and Taurene together were close to heritabilities in separate sites. In contrast, insufficient maintenance, subsequent uneven survival and heterogeneous growth conditions commonly reported to result in low heritability indices with low accuracy, reducing benefits from tree breeding (Haapanen 1996; Mäkinen 1996; Talbot 1997; Nummi 1999; Olsson and Ericsson 2002; Koski and Rousi 2005). Nevertheless, mainly low h^2 for such stem defects as SpKn, Doubl and LostTop (0.04–0.29) coincides with earlier findings (Stener and Hedenberg 2003; Zeltiņš et al. 2018), suggesting relatively weak genetic control and strong prevailing effect of such environmental factors as drought, frost or biotic damage (Malcolm and Worrell 2001; Stener and Hedenberg 2003).

Stener and Jansson (2005) reported low h^2 and H^2 values (0.09–0.27) for StStr in a series of up to 10 years old silver birch clonal and progeny trials. Although StQual had low h^2 values (0.10–0.15) at the age of 10 years (Table 2), moderate to high heritabilities (0.21–0.45) and rather weak genetic correlations (Table 4) with growth traits for both StStr and StQual implied substantial improvement for wood quality in our study. In addition, generally moderate negative correlations between StQual and stem defects suggests that selection based on inclusive ordinal score of stem quality traits might reduce occurrence of stem defects despite low heritabilities of them, thus improving timber quality and increasing amount of merchantable wood (Agestam et al. 1998; Möttönen 2005). Mainly weak genetic correlations reported among quality traits as well as between growth and quality traits, likely related to rather low genetic variance of the latter ones (Koski and Rousi 2005; Stener and Jansson 2005). In Scotland, straight stems found to be associated with superior volume growth (Malcolm and Worrell 2001), yet not observed in our study. Similar to previous findings in Sweden and Latvia (Stener and Jansson 2005; Zeltiņš et al. 2018), BrD and BrA possessed high heritabilities. However, the substantial negative correlations between BrA and StStr might result in enlarged knot size for straighter logs, thus reducing technical quality (Niemistö 1995a). Larger BrD had been commonly reported as negative effect for fast growing silver birch (Niemistö 1995b, Stener and Jansson 2005), suggested to be mitigated with sufficient planting density of at least 1600 trees ha^{-1} for smaller knot size and improved wood strength (Niemistö 1995a; Dunham et al. 1999). Nevertheless, study in 40-years old low-density clonal silver birch plantation in Latvia showed possibility to obtain high-quality plywood applying wide (5 × 5 m) initial spacing (Zeltiņš et al. 2018).

Besides heritability, considerable CV_a (20.1–32.5%) suggested potential of breeding to improve V (Table 3). Lower CV_a values for stem quality traits comparing to growth traits coincide with results in Lithuania, where CV_a for StStr and BrA was ca. 13% (Baliuckienė and Baliuckas 2006). In a recent study of low-density clonal plantation, estimated CV_g for H was almost three times lower (3.2%) than CV_a in the present study (on average, ca. 8%) (Zeltiņš et al. 2018). It might be partly explained with remarkable differences in initial spacing (5 × 5 and 2 × 2.5 m in clonal plantation and our study sites, respectively), since genetic variance can be higher in closer spacing (Franklin 1979; Euler et al. 1992). Nevertheless, similar CV_a for H reported in north Sweden (Stener and Jansson 2005). Generally higher estimated CV_a values for DBH as for H were similar to results in Swedish progeny tests (14 and 8% for DBH and height, respectively) (Stener and Jansson 2005).

Estimated GG% confirmed general trends for h^2 and CV_a discussed above, reaching the highest values for V (25.3–61.6%), while being overall lower for stem quality (1.6–21.2%). Such estimates are over the means of trials instead of general population due to the lack of control plots, and thereby gains over forest stands might be higher (Malcolm and Worrel 2001). Nevertheless, selection of genotypes should compromise improved productivity with sufficient quality as well as improved performance in different growth conditions (Matheson and Cotterill 1990), especially when the aim is to produce high-quality silver birch timber for plywood industry (Hynynen et al. 2010). As indicated by single-trait gains, CV_a values (Table 3) and mainly weak r_G between growth and quality traits (Table 4), further development of index for simultaneous selection of both growth and stem quality traits may be possible.

4.2 Genotype by environment interaction

The studied traits showed low G × E interaction, indicated by strong type-B correlations for all studied traits ($r_B \geq 0.78$) between trials Ukri and Taurene (Table 2). Contradictory results have been reported previously: from strong and significant correlations between trials even in rather different environments (Stener and Hedenberg 2003; Stener and Jansson 2005) to substantial genotype by site interaction (Baliuckienė 2009). However, the accuracy of r_B might not be high (Bourdon 1977; Haapanen 1996), often related to inappropriate design of progeny trials, which has insufficient number of replications not following natural patterns of growing conditions (Haapanen 1996). Still, high type-B correlations with rather low standard errors for growth traits and low variation of h^2 for the same trait among trails discussed above indicated stability of performance over different environments, as well as appropriate experimental design.

Another relevant question regarding experimental design is the use of single-tree- or multiple-tree (block) plots. In general, single-tree plots in Ukri and Taurene had higher estimated heritabilities for growth traits and BrA than block-plots in Rembate (Table 2). Single-tree plots in many replications allow assessing genetic differences in statistically effective way (White et al. 2007), since progenies of plus-trees are represented in possibly wide range of competition and growing conditions within a trial (Haapenen 1992; Haapanen 1995). However, inter-tree competition among different genotypes may exaggerate estimated genetic variance for growth traits promoting initially fast growing families (Malcolm and Worrell 2001; Vergara et al. 2004; Gould and Marshall 2010). In the present study, growth traits might be somewhat affected by competition in the single-tree-plot trials Ukri and Taurene, since estimates from the block plots in Rembate were lightly lower. Still, estimates from more trials would be needed for generalized conclusions.

Stener and Hedenberg (2003) stressed general lack of information about age-age correlations for silver birch. In our study, the genetic age-age correlations for traits measured at the age of 10 and 14 years were mainly strong, implying as accurate selection for the respective traits at the first measurement time as at the second inventory. Nevertheless, strong correlations between so close ages are not very informative about long-term trends. Still, strong age-age correlations have been indicated for V for up to three decades in southern Finland (Hagqvist and Hahl 1998). There have been reported correlations ranging from 0.75 to 0.86 between the ages of 9 and 26 years; correlation of 0.94 between the ages of 5 and 10 years, and 0.84 between the age of 11 and 18 years for tree height (Stener and Hedenberg 2003). Stener and Jansson (2005) found moderate to strong age-age correlations (0.60–0.99) for H and quality traits.

5 Conclusions

Growth and stem quality traits were mostly under strong genetic control, yet occurrence of stem defects – spike knots, double tops and lost top – were more affected by environmental factors. Weak positive genetic correlations between growth traits and inclusive stem quality score indicated potential for improved productivity and wood quality simultaneously. Still, improvement for stem straightness might increase stem knottiness. Strong genetic correlations between different study trials, as well as strong age-age correlations indicated stability for improvements of silver birch planted on former agricultural land. Considerable single-trait gains, additive genetic coefficient of variation values, and mainly weak genetic correlations between growth and quality traits suggest further development of selection index for simultaneous improvement of both growth and stem quality.

Acknowledgements

The study was funded by the research project "Forest tree breeding to select genetically high value forest reproductive material" of JSC "Latvia's State Forests". We thank the anonymous reviewers for their constructive comments.

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Silva Fennica vol. 55 no. 2 article id 10524
Category: research note
https://doi.org/10.14214/sf.10524

SILVA FENNICA

http://www.silvafennica.fi
ISSN-L 0037-5330 | ISSN 2242-4075 (Online)
The Finnish Society of Forest Science

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Local adaptation of phenotypic stem traits distinguishes two provenance regions of silver birch in Latvia

Gailis A., Zeltiņš P., Matisons R., Purviņš A., Augustovs J., Vīndedzis V., Jansons Ā. (2021). Local adaptation of phenotypic stem traits distinguishes two provenance regions of silver birch in Latvia. Silva Fennica vol. 55 no. 2 article id 10524. 12 p. https://doi.org/10.14214/sf.10524

Highlights

- Two provenance subregions in Latvia – coastal and inland – were distinguished.
- Silver birch populations in inland region possessed better growth, higher heritability, and phenotypic plasticity.
- Moderate to high heritability for stem quality was estimated in both regions.
- Silver birch from inland region possesses higher potential for improvement of adaptability.

Abstract

Populations of tree species with a wide geographic range, such as silver birch (*Betula pendula* Roth), show genetic specialization to native environments, while maintaining high phenotypical plasticity. Accordingly, assessment of local specialization is essential for adaptive management. The aim of the study was to detect geographic patterns of local adaptation of growth and stem quality based on two open-pollinated progeny trials in Latvia testing local material. Two provenance regions differing by continentality were distinguished, which also differed in genetic control of growth traits, likely originating from the post-glacial recolonization of vegetation and subsequent natural adaptation. Heritability of the traits was estimated for each of the distinguished regions, indicating differing patterns of genetic adaptation and potential for future selection. Trees from the more continental inland showed superior growth and possessed higher heritability. The coastal provenance region showed slower growth and intermediate heritability of the respective traits. Moderate to high heritability for stem quality traits was estimated irrespectively of region. Overall, better growth and higher heritability suggests that anthropogenic selection within the best inland provenances may constitute better performing and adaptable breeding population compared to the coastal one. Still, overlapping phenotypical variation and heritability of quality traits implies improved stemwood quality for plywood regardless of the provenance region. High adaptive capacity of silver birch genotypes suggests ability to cope with climatic changes, highlighting its potential for climate-smart forestry.

Keywords *Betula pendula*; population genetics; phenotypic traits; genetic parameters; climate-smart forestry
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Received 8 February 2021 **Revised** 29 April 2021 **Accepted** 30 April 2021

1 Introduction

Populations of tree species with wide geographic range, such as silver birch (*Betula pendula* Roth), show genetic specialization to native environments, while maintaining high phenotypical plasticity (Sultan 1987; Gapare et al. 2008). Silver birch has high genetic diversity, yet low population genetic differentiation (Hamrick et al. 1992; Palmé et al. 2003; Wesselink et al. 2018); e.g., 97% variation within the populations, and only up to 3% among them in the Eastern Baltic region (Zhuk et al. 2009). Nonetheless, explicit differentiation in phenotypic traits might be present due to strong local adaptation, and such genetic specialization is the precondition for successful breeding (Savolainen et al. 2007; Sork et al. 2013). In the Eastern Baltic region, silver birch is a highly important forest resource, especially for plywood industry (Hynynen et al. 2010; Liepins and Rieksts-Riekstins 2013). Accordingly, breeding programs are implemented throughout the region (Donaldson and Turner 2001; Heräjärvi 2001; Stener and Hedenberg 2003; Gailis et al. 2020).

Phenotypic traits have shown considerable genotypic variation in the Latvian silver birch breeding population (Gailis et al. 2020), yet the potential sub-regional differences have not been accounted. The species shows substantial ecological plasticity shaped by environmental contrasts (Koski and Rousi 2005; Savolainen et al. 2007), hence assessment of regional and sub-regional phenotypic differences (Falconer and Mackay 1996; Griffiths et al. 2000) is essential to improve efficiency of breeding (Malcolm and Worrell 2001). Bio-climatic zonation is commonly used to distinguish regional differences in tree growth, for example in classification of seed zones (Laiviņš and Melecis 2003; Hamann et al. 2011; Stakenas et al. 2012; Ge et al. 2013; Reitalu et al. 2013). However, the climatic zones might be different from the actual distribution of metapopulations of tree species. Different environmental conditions and the post-glacial history of vegetation interactively can result in spatially varying selection pressure, hence distinct phenotypic differences and genetic variance (Palmé et al. 2003; Väliranta et al. 2011; Tenkanen et al. 2020). Thus, assessment of the differences in phenotypes and specialization among forest provenances are still essential for clarification of provenance regions, which might not be detected by molecular markers (Karhu et al. 1996; Reed and Frankham 2001; O'brien et al. 2007; Wesselink et al. 2018).

Furthermore, the rapid pace of climate change rises concerns about the adaptative capacity of tree populations in the future (Aitken et al. 2008; Fady et al. 2020). Improved forest reproductive material enhances forest adaptation (Lefèvre et al. 2014) as a component of pro-active adaptive forest management (Bolte et al. 2009; Nabuurs et al. 2018). Considering the opportunistic (ruderal) nature of silver birch (Brzeziecki and Kienast 1994), fast growth and tolerance to weather fluctuation in the Eastern Baltic region (Liepiņš 2011; Jansons et al. 2016), a conservative climate-smart management approach may utilize improved local genotypes to enhance adaptability (Ahrens et al. 2020). Therefore, information about genetic variation and phenotypic plasticity reflecting adaptability of local seed sources (Lamy et al. 2011), is advantageous for more efficient breeding. The aim of the study was to distinguish sub-regional differences in strength of local adaptation in terms of growth and stem quality traits. We hypothesized that local bio-climate had an explicit effect on local adaptation, and two silver birch provenance regions could be delineated.

2 Material and methods

2.1 Trials and measurements

The study material consisted of the open-pollinated progenies of silver birch plus-trees from 31 forest provenances across Latvia (55°40′–58°05′N, 20°58′–28°14′E). The studied two parallel silver birch trials Taurene (57°06′N, 25°38′E) and Ukri (56°22′N, 23°07′E) contained progenies of the same sets of provenances and 533 half-sib families within them. The trials were established in 2000 on agricultural land with one-year-old containerized seedlings. The experimental design was complete randomized blocks of single-tree plots in 10 to 93 replications with 2 × 2.5 m initial spacing. Both trials were growing in mesotrophic conditions on dry silty soils. Climate was milder in the Ukri trial; the mean annual temperature was 6.4 °C, and the mean monthly temperature ranged from –4.4 °C to +17.4 °C in January and July, respectively; the mean annual precipitation was ca. 630 mm (Harris et al. 2020). In Taurene, the mean annual temperature was 5.1 °C, and the mean monthly temperature ranged from –6.3°C to +16.9 °C. The mean annual precipitation was ca. 670 mm (Harris et al. 2020).

At the age of 14 years, measurements of height (H) and diameter at breast height (DBH) were available for 11 657 and 18 804 trees in Taurene and Ukri trails, respectively. The occurrence of spike knots (SpKn), double leaders (Doubl), and lost top (LostTop) was recorded as binary variables. Stem straightness (StStr), overall stem quality (StQual), and branch angle (BrA) were assessed visually, using a 3-point ordinal scale (Gailis et al. 2020). Stem volume (StVol) was calculated according to a local equation (Liepa 1996).

2.2 Statistical analysis

We performed Principal Component Analysis to assess the main patterns in variation of scaled phenotypic traits of the studied silver birch provenances, and to associate them with the location of origin. Estimated marginal provenance means were obtained from mixed effects models:

$$y_{ijklm} = \mu + P_i + F_j + S_k + b_l + sf_{jk} + \varepsilon_{ijklm} \qquad (1)$$

, where y_{ijk} is the response variable, μ is the overall mean; P_i, F_j and S_k are the fixed effects of the provenance, the family, and the site, respectively. The b_l and sf_{jk} are the random effects of block and site × family interaction, respectively, and ε_{ijklm} is the random residual effect. The significance of principal components (PC) was determined by the Monte Carlo (randomization) test performing 1000 iterations. Relationships of the studied traits and latitude/longitude with the first two PC were assessed by Pearson correlation analysis.

The phenotypic differences in the studied traits among the distinguished provenance regions were assessed using mixed models:

$$y_{ijklm} = \mu + R_i + S_j + b_k + \varepsilon_{ijkl} \qquad (2)$$

, where y_{ijk} is the response variable, R_i is the fixed effect of the provenance region, s_j is the fixed effect of site, b_k is the random effect of a block within a site, and ε_{ijk} is the error.

To estimate the extent of genetic adaptation and genetically determined plasticity for each of the determined provenance regions, the variance components were estimated from the combined data from both trials, and narrow-sense heritability (h^2) and additive genetic coefficient of variation (CV_a) were calculated according to Falconer and Mackay (1996).

For the continuous quantitative variables (H, DBH, StVol), linear mixed effects models were used. For the binomial variables (SpKn, Doubl, LostTop), generalised linear mixed models applying binomial residual distribution and a "logit" link function were fitted. For the ordinal variables (StStr, StQual, BrA), ordinal logistic regression was applied (Long 1997). Data analysis was conducted in SAS v. 9.3 using the procedures PROC MIXED, PROC GLIMMIX, and PROC CORR (Littel et al. 2006; Piepho and Möhring 2011).

3 Results

Distinct clustering of phenotypic traits was observed. The first two PCs were significant (p-value $<$ 0.001) and corresponded for 57.6% of the total variance of the studied traits (Fig. 1). The third PC covered 19.8% of the variance and was related to stem defects – Lost and Doubl. The first PC was strongly related to the growth traits indicating regional differences in productivity (Fig. 1). The second PC was related to the quality traits, suggesting diverse sources of variation for growth and quality. In the ordination space, the provenances formed single group indicating continuous gradient in variation of the studied traits. Nevertheless, the first PC was significantly correlated with the longitude of origin of the provenances ($r = 0.46$, $p = 0.01$), suggesting growth differences between the coastal and inland parts of the country, while the second PC did not ($r = 0.02$, $p = 0.92$).

Correlations of the PCs with latitude of origin were weak ($|r| < 0.22$, p-value $>$ 0.24), indicating absence of north-south gradient. Based on the scores of the first PC of provenances, which were overlain on their geographic locations, two regions of Latvia were arbitrarily distinguished (Fig. 2). The coastal region included the western and the very northern part of the country, while the inland region covered the central and eastern parts (Fig. 2). The inland region showed significantly (p-value $<$ 0.01) higher H, DBH, and StVol (Table 1). The mean StStr, StQual, and BrA had no differences between regions. High occurrence of SpKn and LostTop was observed in both regions (49.2–59.1%), while trees with Doubl were less frequent, lacking practically meaningful differences between regions (Table 1).

The studied silver birch populations possessed substantial additive genetic variance in growth and stem quality (Supplementary file S1, available at https://doi.org/10.14214/sf.10524). Moderate to high heritability ($h^2 > 0.20$) was estimated for the studied traits in both regions except for stem defects ($h^2 < 0.15$) (Table 1). Geographically varying strength of genetic control of the traits was observed: h^2 of H was more than twice higher in the inland than in the coastal region (0.61 ± 0.061 and 0.28 ± 0.037, respectively), while for StVol and DBH differences in h^2 reached 31.3–41.4%. In the coastal region, high ($h^2 \geq 0.45$) heritability was estimated for StStr and BrA, while these traits showed intermediate heritability ($0.26 \leq h^2 \leq 0.30$) in the inland. Also, the estimated CV_a was slightly (0.97–4.06%) higher for the inland comparing to the coastal region implying slight differences in plasticity. The ability to respond to natural selection, indicated by CV_a, was ca. three times higher for StVol comparing to H in both regions (Table 1).

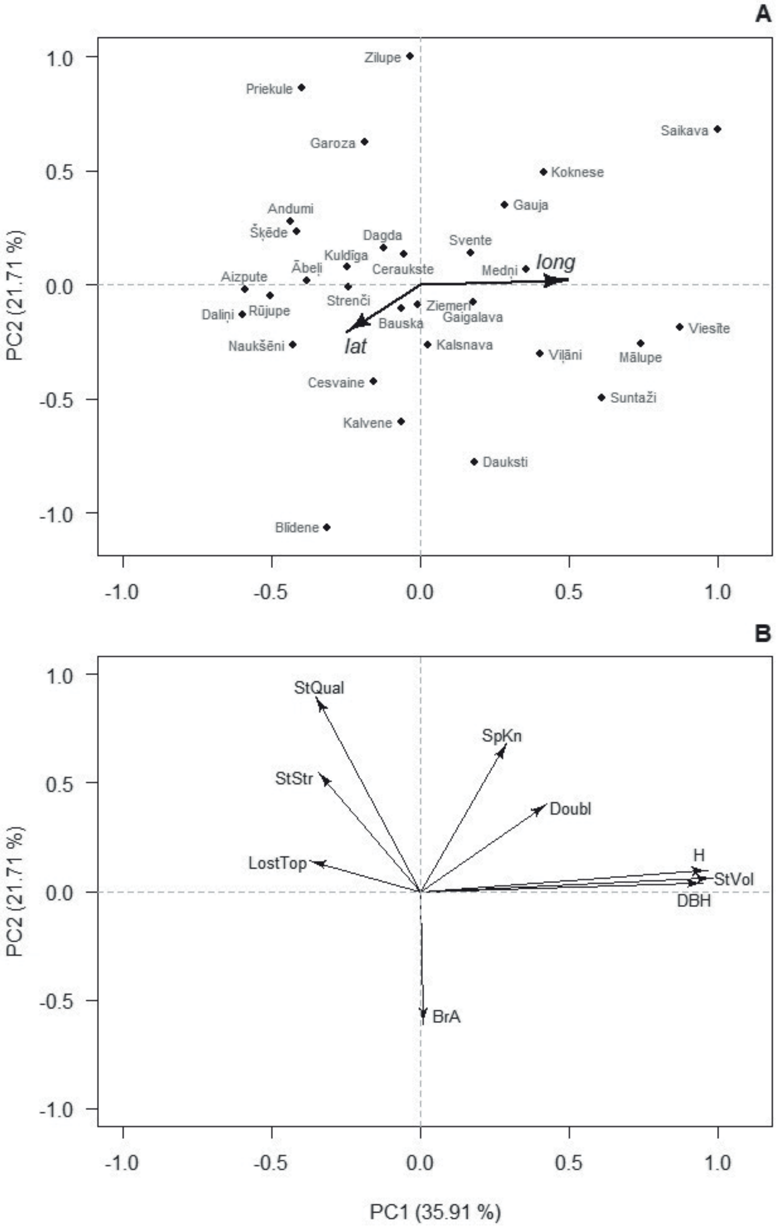

Fig. 1. Ordination of the studied provenances (A) and studied traits (B) of 14-years-old silver birch in Latvia according to the first two principal components (PC) of their variation. In A, axes are rescaled for clarity; and arrows indicate correlation with latitude (lat) and longitude (lon) of origin of the provenances. Numbers in brackets indicate the amount of explained variation. Abbreviations: H – height, DBH – diameter at breast height, StVol – stem volume, Doubl –probability of double leaders, SpKn – spike knots, StQual – overall stem quality, StStr – stem straightness, LostTop – lost top, BrA – branch angle.

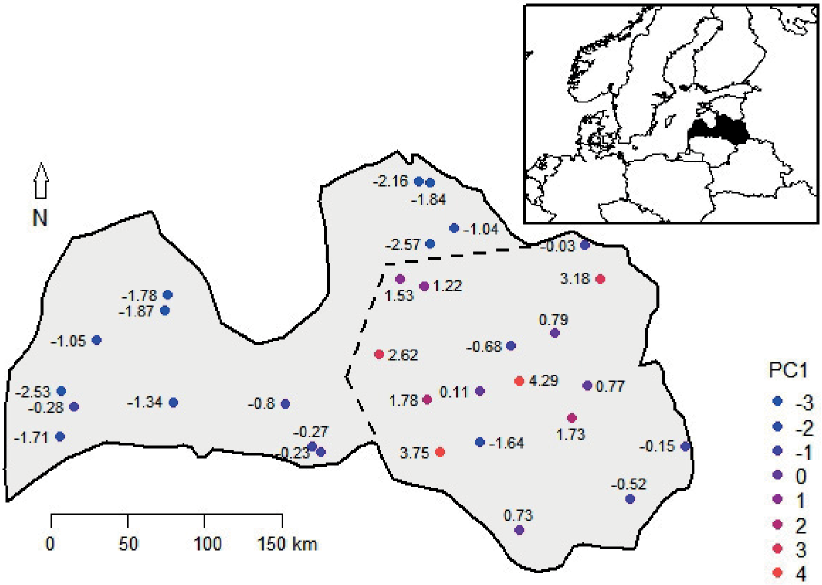

Fig. 2. The scores of the first principal component (PC1) of studied phenotypic traits of 14-years-old silver birch progenies overlain on their geographic locations in Latvia. The dotted line indicates border of two arbitrarily distinguished silver birch provenance regions – the coastal (western) and the inland (eastern) region.

Table 1. Regional means, minimum and maximum provenance means, narrow sense individual tree heritability and additive genetic coefficient of variation of the studied traits in the phenotypically distinguished provenance regions of silver birch in Latvia. Letters in uppercase denote significant differences ($p \leq 0.05$) between provenance regions for each trait.

Trait	Regional mean ± standard deviation		Minimum provenance mean		Maximum provenance mean		Individual tree heritability h^2 ± standard error (additive genetic coefficient of variation CV_a, %)	
	Coastal	Inland	Coastal	Inland	Coastal	Inland	Coastal	Inland
Height (m)	11.8^A ± 1.90	12.3^B ± 1.89	11.2	11.7	12.0	12.5	0.28 ± 0.037 (7.16)	0.61 ± 0.061 (10.11)
Diameter at breast height (cm)	9.06^A ± 2.81	9.8^B ± 2.84	8.5	8.7	10.0	10.7	0.32 ± 0.037 (16.56)	0.42 ± 0.048 (17.53)
Stem volume (dm^3)	45.2^A ± 26.56	53.2^B ± 29.87	39.3	43.2	49.2	62.1	0.29 ± 0.035 (29.35)	0.41 ± 0.048 (33.41)
Spike knots (% of trees)	57.3^A	59.1^B	42.1	53.6	60.8	65.4	0.05 ± 0.017	0.07 ± 0.020
Double leaders (% of trees)	9.7^A	11.4^B	2.8	5.00	10.4	13.9	0.15 ± 0.041	0.16 ± 0.014
Lost top (% of trees)	52.3^A	49.2^B	50.7	46.2	65.6	62.4	0.03 ± 0.017	0.01 ± 0.017
Stem straightness score	2.2^A	2.2^A	2.1	2.1	2.2	2.2	0.45 ± 0.060	0.26 ± 0.060
Overall stem quality score	2.8^A	2.8^A	2.7	2.7	2.8	2.9	0.24 ± 0.040	0.28 ± 0.061
Branch angle score	2.0^A	2.0^A	2.0	2.0	2.0	2.0	0.51 ± 0.110	0.30 ± 0.118

4 Discussion

Phenotypic plasticity and local (genetic) specialization are key factors affecting adaptability of trees to changing climate, hence crucial for climate-smart forest management (Aitken and Bemmels 2016; Moran et al. 2017). Distinct local specialization of silver birch was observed, particularly for the growth traits (Table 1). Silver birch of the inland region possessed better growth (Table 1, Fig. 1). The explicit coastal-inland gradient (Fig. 1) and differing strength of genetic control (Table 1) followed general spatial pattern of the climatic zonation within the region (Laiviņš and Melecis 2003; Reitalu et al. 2013).

The distribution of silver birch provenance regions showed some specifics in growth traits and their genotypic variation (Fig. 2, Table 1), which might be explained by the post-glacial recolonization routes from different refugees (Palmé et al. 2003; Kapeller et al. 2017; Tsuda et al. 2017; Tenkanen et al. 2020). Also, this might be due to continentality of climate (White et al. 2007; Hoffmann and Sgrò 2011), as determined by westerlies and proximity of the Baltic Sea (Laiviņš and Melecis 2003); hence differing strength of environmental forcing of adaptation (Suppl. file S2).

Population genetic studies have shown persistence of silver birch in relatively high latitudes during last glacial maximum, as a scattered dispersal nuclei enabling rapid post-glacial recolonization in different directions (Stewart and Lister 2001; Binney et al. 2009; Väliranta et al. 2011; Kapeller et al. 2017; Tsuda et al. 2017). The inland region appeared to be westwards extension of a source population located east from Latvia. Still, such dispersal nuclei are difficult to locate (Amon et al. 2014), and wider regional scale study would be necessary to clarify this issue. However, natural selection after the post-glacial recolonization has likely been the main driver determining geographic variation of studied traits (Fig. 2) as observed in the region (Collignon et al. 2002; Kremer et al. 2002; Savolainen et al. 2007; Väliranta et al. 2011).

Although high within- and low between-population genetic diversity has been observed for silver birch in Northern and Eastern Europe (Hamrick et al. 1992; Palmé et al. 2003; Rusanen et al. 2003; Maliouchenko et al. 2007; Zhuk et al. 2009), the former has apparently favoured strong specialization to local conditions, hence explicit phenotypical differences (White et al. 2007; Hoffmann and Sgrò 2011). Considerably higher CV_a for StVol (29.35–33.41%) comparing to H and DBH (7.16–17.43%) corresponded to a common trend in forest trees (Cornelius 1994). The heritability is affected by the history of the region (Falconer and Mackay 1996; Griffiths et al. 2000), and can vary greatly for phenotypic traits of forest tree species (Cornelius 1994). Higher genetic specialization was more evident under more continental climate in the inland region (Fig. 2), resulting in higher heterogeneity of field performance (Fig. 1), and explained higher h^2 and CV_a of growth traits, compared to the coastal region (Table 1). High heritability likely indicated larger differences between genotypes from different forest provenances comparing to the environmental variation within genotypes (Griffiths et al. 2000). Estimated h^2 for growth traits was higher in the inland and lower in the coastal provenances comparing to the whole breeding population ($h^2 = 0.41$–0.52) (Gailis et al. 2020), indicating better response to selection in the first. One commonly acknowledged risk of intensive breeding within certain populations can be reduced genetic diversity, yet threats to silver birch are unlikely, considering the highly-connected populations with extensive gene flow (Hoban and Schlarbaum 2014).

Indistinct phenotypic differences and similar moderate to high heritability for stem quality (Table 1) might have been set by uniform natural selection in both regions despite climatic differences (Lamy et al. 2011). Still, moderate genetic control of StStr, previously reported for various trees species (Cornelius 1994), indicated potential improvement of selection. Meanwhile weak genetic control of stem defects (Table 1) correspond to the earlier findings, likely shaped by prevailing environmental factors, such as frost, insect damage or browsing (Malcolm and Worrell 2001; Stener and Jansson 2005; Zeltiņš et al. 2018).

Heritability and CV_a reflect pre-existing standing genetic variation, which is essential to adapt to a broad spectrum of future climate via natural selection (Alberto et al. 2013; Ahrens et al. 2020). Although low genetic variance not necessarily means poor selection response (Walsh and Blows 2009; Hoffmann and Sgrò 2011), lower h^2 of growth traits in coastal region (Table 1) could indicate weaker adaptability to ongoing climate change (Hoffmann and Sgrò 2011). Still, it is unclear, whether populations currently possessing weaker local adaptation could show better fitness in the future (Fady et al. 2020). Coastal provenances could benefit from projected milder winters and increased precipitation intensity thorough the country, yet more frequent extreme events (e.g. summer drought) may suppress positive effect (Avotniece et al. 2010). Use of robust superior seed sources from more continental inland climate may imply potentially higher capacity to adapt to changing conditions (Sork et al. 2013), facilitating resilience of future stands (Aitken and Bemmels 2016). Still, the indistinct phenotypical and genetic variation for stem quality traits suggested potential for improvement of breeding for plywood production also combining material, with higher preference from the inland region.

5 Conclusions

Delineation of two provenance regions – coastal and inland – for silver birch in Latvia with respect to growth performance and genotypic variation, justified earlier climatic zonation. Overall, better growth and higher heritability suggests that selection and breeding within the best provenances in more continental inland region possessing higher genotypic variation may constitute better performing and adaptable breeding population for climate-smart management comparing to the coastal region. Still, uniformity and estimated heritability of quality traits implies improved stem-wood quality for plywood production regardless of the distinguished region. A wider regional scale study, however, would be necessary to clarify differences in phenotypic and genotypic variation as a proxy for adaptation capacity to changing climate.

Supplementary files

S1.pdf; Variance components from mixed-models for estimating heritability of phenotypic traits in the two delineated silver birch provenance regions according to local adaptation to bio-climate in Latvia,
S2.pdf; Mean annual precipitation sum and mean annual temperature in Latvia for the period 1901–2018. The extrapolation is based on the CRU TS monthly high-resolution gridded multivariate climate dataset (available at https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_4.05/),

available at https://doi.org/10.14214/sf.10524.

Declaration of openness of research materials, data, and code

The data that support the findings of this study are available from the corresponding author, PZ, upon reasonable request.

Authors' contributions

AG and ĀJ developed design of the work, conceptualized research question, and revised the work. PZ and RM conducted data analysis and revised the work. AP, JA and VV were responsible for data acquisition. All authors contributed to scientific writing of the work.

Funding

The study was funded by 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".

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Total of 62 references.

New Forests (2021) 52:791–806
https://doi.org/10.1007/s11056-020-09828-9

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Silver birch (*Betula pendula* Roth.) culture initiation in vitro and genotype determined differences in micropropagation

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Received: 27 June 2020 / Accepted: 11 December 2020 / Published online: 4 January 2021

Abstract
Micropropagation has several advantages over conventional vegetative propagation methods, but it is limited by genotype responsiveness. We assessed the effect of age of the mother-tree and the time of explant collection on culture initiation, as well as the multiplication ability and effect of different nutrient media and plant growth regulators on silver birch genotypes. Explants collected from 1-year-old trees (66%) and explants collected in spring (64–67%) developed a significantly (both $p<0.001$) higher proportion of shoots than those from 15-year-old trees (39%) and those collected in mid-summer (31%) and autumn (29%), respectively. In a stabilised culture, the length of the main shoot varied from 1.3 to 7.8 cm between genotypes, and the multiplication rate ranged from 1.0 to 6.8 shoots per explant. Hyperhydrated shoots were present in 17 out of 50 clones, and, among the clones, ranged from 14 to 50%. Cultures on the Murashige and Skoog basal medium had a higher multiplication rate than cultures on a Woody Plant Medium, and the application of zeatin provided better results than 6-benzylaminopurine. The difference between cytokinin types was 11–29% for the multiplication rate and 21–29% for the length of the main stem. The highest multiplication rate was obtained using a zeatin concentration of 0.5 mg L^{-1}. However, better shoot growth and proliferation had a significant positive relation to shoot hyperhydration (all $p<0.001$). Therefore, a medium with an optimal balance between the multiplication rate and the number of hyperhydrated shoots should be carefully selected.

Keywords *Betula pendula* · Genotype · Micropropagation · Culture initiation · Cytokinin

Introduction

Wood is the most versatile renewable material that is used to substitute for fossil resources from construction wood and packaging boards to textiles and biochemical production. The growth of population and middle-class income, as well as bioeconomic development have steadily increased the global demand for wood and wood-based products: wood demand is forecasted to increase more than twice from 2010 to 2030, and more than thrice from 2010

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to 2050 (WWF 2012), while roundwood production under the continuous trend is forecasted to increase by 16% from 2018 to 2050 (Hetemäki et al. 2020). The increase in the productivity of native species and the establishment of fast-growing species and genotypes plantations are strategies to ensure a sufficient wood supply (Mola-Yudego et al. 2017). In both respects, silver birch (*Betula pendula* Roth) has potential in the Northern European and Baltic states (Rytter et al. 2013). Here, birch is one of the most abundant tree species (Brus et al. 2012) and is highly productive both in forest sites and on abandoned agricultural land (Uri et al. 2012; Lutter et al. 2015). It has several advantages over other fast-growing species that are suitable for the region, especially concerning environmental risks, due to its high tolerance and adaptation capacity to a large variety of climates and soils (Dubois et al. 2020). In contrast, spruce (*Picea abies* (L.) Karst.) is prone to wind, drought, and bark beetles (Mezei et al. 2017). Moreover, these disturbances are increasing in frequency (Seidl et al. 2017). *Populus* species and their hybrids are preferred by herbivores. In addition, due to their non-native origin (except for *P. tremula*), these species might be damaged by abiotic factors, such as early autumn frost (Lazdiņa et al. 2016; Šēnhofa et al. 2016). The *Salix* species or genotypes may suffer from frost- and bacteria-induced dieback (Cambours et al. 2005). Moreover, this species has limited wood-processing possibilities due to stem size.

Size and external quality traits, including the absence of defects (cracks) in the stem, have a substantial effect on the financial return for birch (Kilpeläinen et al. 2011; Viherä-Aarnio and Velling 2017). High-quality timber is a valuable resource for plywood, sawnwood, and wood-based panel production, whereas lower-grade timber is used as pulpwood, and the residue is utilised for bioenergy. Planting is the preferred stand establishment method for the intended management of a high-quality plantation (Hynynen et al. 2010). However, birch is primarily established via natural regeneration. For instance, in Latvia, only 11% of the area regenerated with birch is planted (Valsts meža dienests 2019). Although planting requires a higher initial investment, artificial seedlings have more vigorous growth in comparison to naturally regenerated seedlings; thus, they are more competitive with ground vegetation and require less intensive management, i.e. less frequent tending, in young stands (Hynynen et al. 2010). Moreover, planting allows the use of genotypes with enhanced desired characteristics because the seedlings originate from improved material, i.e. seeds collected from seed orchards (Gailis et al. 2012).

Silver birch has considerable ecological adaptability and climatic differentiation, which are related to its wide distribution (Koski and Rousi 2005; Rousi et al. 2011), thus providing a good basis for breeding. To improve the stem quality, the phenotypic selection of plus-trees is based on stem straightness, apical dominance, and desirable branch properties, including good natural pruning (Koski and Rousi 2005; Stener and Jansson 2005), yet breeding aims to balance between increased growth, timber quality, and resistance to biotic and abiotic factors. Several studies have affirmed the economic gain from the use of improved regeneration material (Jansson et al. 2017). In Latvia, the breeding of birch trees started in 1995 and has substantially improved the yield and stem quality (Jansons et al. 2011; Zeltiņš et al. 2018). The selection of the top 10% of families in the progeny trials at the age of 14 years resulted in a genetic gain of 10–27% for height and diameter at breast height, accounting for 26–62% of the stem volume. The gain in the overall stem quality was 6–10%, with improved straightness by 9–21% and branch diameter and angle by 2–18% (Gailis et al. 2020a). Furthermore, the occurrence of stem defects, such as spike knots, double tops, and lost tops, were more affected by environmental factors than genetic control, and low-to-moderate genetic correlations between growth and stem quality traits indicated the potential to improve productivity and wood quality simultaneously. As a result, the use of improved planting material significantly increased the economic gain from commercial thinning (Gailis et al. 2020b).

Breeding is performed in repeated cycles of selection of the best-performing genotypes and their recombination using controlled pollination and progeny testing (Ruotsalainen 2014). The establishment of clonal collections and seed orchards can be accelerated when vegetative propagation is used. Moreover, vegetative propagation allows the maintenance of all inherent traits of the mother-tree (Ryynänen and Aronen 2005) and produces uniform-sized plantlets (Jones et al. 1996). Such trees reach the target diameter for final felling sooner (Zeltiņš et al. 2018), and any time-related damage is lower (Donis et al. 2020): as the vegetative propagation ensures a way to propagate the best-growing genotypes, time (and, consequently, the probability of damages) to reach similar dimensions of conventionally propagated trees can be reduced. However, using conventional vegetative propagation methods on mature birch has not been successful. Cuttings can be rooted only up to the age of five years, and grafting is limited by the incompatibility of rootstock and scion and delayed graft failure (Ryynänen and Ryynänen 1986; Welander 1993; Mikola 2009). Therefore, micropropagation can be used as an alternative method with several advantages: numerous pathogen-free plantlets can be obtained in a short period and propagation can be done throughout the year regardless of the season (Jones et al. 1996; McCown 2000; Ryynänen and Aronen 2005).

Yet, micropropagation per se does not infer a general advantage over seed-born plants, and careful selection of clones to be multiplied has crucial importance on breeding gain (Viherä-Aarnio and Velling 2001). Micropropagation is a laborious process that involves skilful manual work in an aseptic laboratory and therefore results in higher costs than conventional nursery practice (Koski and Rousi 2005). The success of culture initiation depends on the explant type and its position on the stock plant, the age of the stock plant, the tree species, and variations among trees of the same species (Welander 1993). Not all genotypes multiply with equal success (Koski and Rousi, 2005), but multiplication is largely dependent on the applied nutrient media and plant growth regulators (Jokinen and Törmälä 1991), which must be determined experimentally.

This study aimed to assess the effect of the mother-tree age and the time of the explant collection on the culture initiation in vitro. This is followed by an assessment of the reproduction capacity of different genotypes and the optimal medium content.

Materials and methods

The study material was collected from a 15-year-old progeny trial in Rembate (56°44′ N, 24°49′ E) that was established using open-pollinated (half-sib) families of silver birch (*Betula pendula* Roth) plus-trees phenotypically selected across forests in Latvia (55°40′–58°05′ N, 20°58′–28°14′ E). The trial was established on former agricultural land with mesotrophic, mesic, and silty soil, corresponding to the forest site type *Oxalidosa* (according to the classification by Bušs (1997)). One-year-old containerised seedlings were planted in a randomised complete block design with four-row plots of 32 trees per row for each family in three to five replications at initial density of 2500 trees ha^{-1} (2×2 m).

To assess the effect of the mother-tree age on shoot initiation in vitro, the explants from clone 54–95 in Rembate were compared with the explants from one-year-old grafted scions (one year after grafting on two-year-old rootstock) of the same clone in Kalsnava (56°40′ N, 25°58′ E), and all samples were collected in March. To assess the effect of the time of the explant collection, twigs of clone 54-95 from Rembate were collected from the lowest part of the canopy four times per year: in March and April (spring), and in June (mid-summer) and September (autumn). In total, 100 stem segments per each ontogenetic age and collection time were initiated in vitro.

In laboratory, stem segments containing one bud were excised and gently washed with a toothbrush and dish soap under running tap water, and rinsed toughly. Stem segments were sterilised for 10 min in 0.1% $HgCl_2$ with a few drops of Tween 20, and rinsed three times with distilled water. The stem segments were inserted into glass test tubes (18 × 180 mm, with a metal cap) containing 3 mL of woody plant medium (WPM; Lloyd and McCown 1980) supplemented with WPM micronutrients, WPM vitamins, 1.0 mg L^{-1} of 6-benzylaminopurine (BAP), 0.05 mg L^{-1} of naphthaleneacetic acid, 20 g L^{-1} of sucrose, and 6 g L^{-1} of agar. The pH of the medium was adjusted to 5.8, and the tubes were autoclaved for 15 min (110 kPa, 121 °C). The culture was incubated at 25 ± 3 °C under a 16-h photoperiod of cool-white fluorescent light (photosynthetically active radiation with photon flux density at 140–160 µmol m^{-2} s^{-1}). After 30 days, the proportion of initiated shoots was evaluated.

The multiplication rate and the growth of shoots between 50 genotypes in Rembate were assessed using a stabilised in vitro culture. Ten shoots per each clone were inserted into test tubes (one explant per tube) containing 3 mL of Murashige and Skoog (MS) basal media (Murashige and Skoog 1962), supplemented with MS micronutrients, 0.2 mg L^{-1} of zeatin, MS vitamins, 20 g L^{-1} of sucrose, and 6 g L^{-1} of agar. The pH of the medium and the cultivation conditions were set as described for the culture initiation. After 30 days, 500 shoots were assessed. The main shoot was measured. The lateral shoots ≥ 0.5 cm were counted, and the multiplication rate of each shoot was determined by the number of 1.5-cm-long shoot fragments (hyperhydrated shoots were not counted) that could be obtained from one plant. The total multiplication rate and occurrence of hyperhydrated shoots were noted. According to the growth parameters, the clones were divided into four groups to assess the effect of the macronutrient media and plant growth regulators. Group divisions were based on the multiplication rate and ability to proliferate. Group 1 has a multiplication rate of 3.4–6.8. Group 2 has a multiplication rate of 1.7–3.3. Group 3 has a multiplication rate of 0–1.6 with proliferation, and Group 4 has a multiplication rate of 0–1.6 without proliferation.

Three clones from each group (24 shoots per clone in each treatment) were randomly selected to test the effect of the multiplication medium and cytokinin type and concentration in the following combinations: (1) WPM, zeatin 0.1 mg L^{-1}, (2) WPM, zeatin 0.5 mg L^{-1}, (3) MS, zeatin 0.1 mg L^{-1}, (4) MS, zeatin 0.5 mg L^{-1}, (5) MS, zeatin 1.0 mg L^{-1}, (6) MS, BAP 0.5 mg L^{-1}, and (7) MS, BAP 1.0 mg L^{-1}. The pH of the medium and the cultivation conditions were set as described for the culture initiation. After 30 days, 2016 shoots were assessed. The main and lateral shoots were measured. The lateral shoots ≥ 0.5 cm were counted. The multiplication rate of each shoot was determined by the number of 1.5-cm-long shoot fragments (hyperhydrated shoots were not counted) that could be obtained from one plant. Finally, the total multiplication rate and occurrence of the hyperhydrated shoots were noted.

We used the chi-square (χ^2) test to assess the distribution of the initiated shoots between the time of explant collection and the age of the mother-tree. The analysis of variance and Tukey's honestly significant difference test were used to assess the differences in the length of the main shoots, the length and number of lateral shoots, the multiplication rate, and proportion of the hyperhydrated shoots between the clones and groups of clones. We used generalised linear models with a Poisson distribution to assess the relationship between the length of the main shoot and the number of the lateral shoots, as well as to evaluate the effect that the length of the main shoot, number of lateral shoots, length of lateral shoots, and total multiplication rate had on the number of hyperhydrated shoots. Linear model was used to assess relationship between the length of the main shoot and the length of the lateral shoots. The regression coefficients ± standard error are shown. All calculations were done in R 3.5.1. (R core team 2018). In addition, all tests were performed at $\alpha = 0.05$.

Results

The age of the mother-tree and explant collection time had a significant effect (both $p < 0.001$) on the shoot initiation in vitro (Fig. 1). The explant collected from the one-year-old trees had 66% initiated shoots, and the explant collected from the 15-year-old trees had 39% of initiated shoots. The explants collected in spring developed a higher proportion of initiated shoots (64% in March and 67% in April) than explants collected in June and September (31% and 29% of shoots initiated, respectively).

In the stabilised culture, the growth parameters greatly differed between the clones. The multiplication rate varied from 1.0 (no multiplication) to 6.8 shoots per explant (Fig. 2), and the lengths of the main shoots varied from 1.3 to 7.8 cm (Fig. 3). Moreover, the number of lateral shoots varied from 0 to 3.8 per explant.

Clones exhibited different growth patterns. Several genotypes had a large main shoot but a low number of lateral shoots (e.g. clone L 29, Fig. 3a), whereas others had a short main stem but a high number of lateral shoots (e.g. clone Bau 40-13, Fig. 3a). A high multiplication rate was achieved by both of these patterns and by the intermedium between them. Regardless of the large variation, the number of lateral shoots showed a negative relationship to the length of the main stem ($p < 0.01$, regression coefficient -0.11 ± 0.04). Almost a quarter of the clones had a low multiplication rate; 12 clones had a mean multiplication rate lower than two, and seven clones did not multiply.

A high proportion (50%) of hyperhydrated shoots was present for two clones, one among the clones with a high multiplication rate (clone 54-616-783, Fig. 2a) and the other

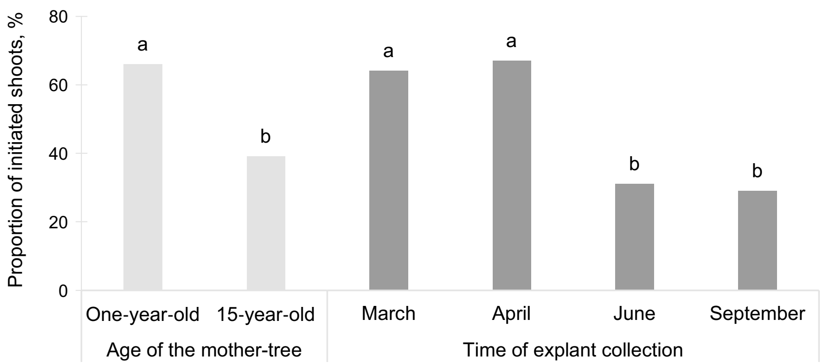

Fig. 1 The proportion of initiated shoots according to the age of the mother-tree and explant collection time. Statistically significant differences between groups of age and between groups of collection time are denoted with different letters (both $p \leq 0.001$)

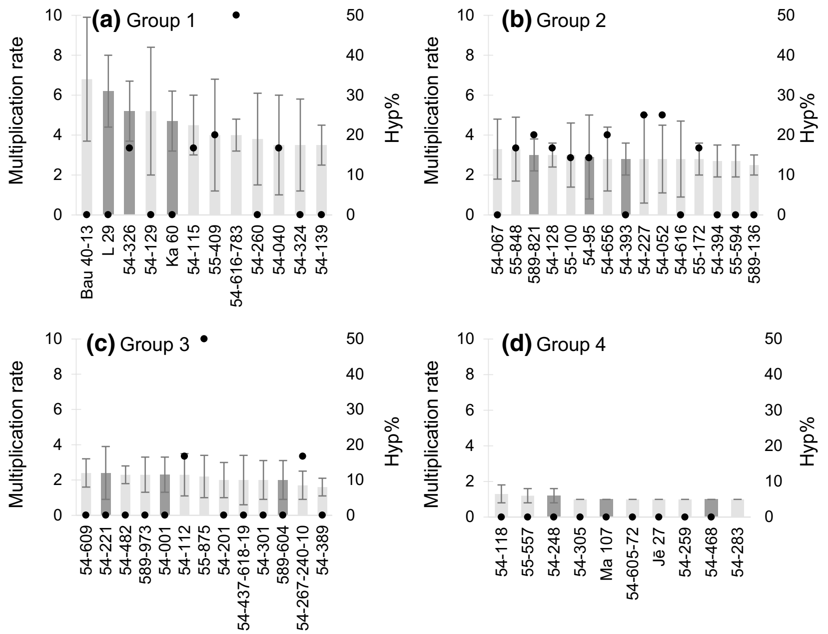

Fig. 2 The multiplication rate (bars; ± standard error) and proportion of hyperhydrated shoots (Hyp%; bullets) among the clones in (**a**) Group 1, (**b**) Group 2, (**c**) Group 3, and (**d**) Group 4. Clones that were selected to test the effect of different treatments are dark grey

with a low multiplication rate (clone 55-875, Fig. 3). A moderate proportion (14–25%) of the hyperhydrated shoots was present for 15 out of 50 clones. The number of hyperhydrated shoots demonstrated no relationship (both $p > 0.05$) to the length of the main stem and number of lateral shoots. However, a positive relationship ($p < 0.001$, regression coefficient 0.56 ± 0.04) exists between the number of hyperhydrated shoots and the total multiplication rate.

The mean multiplication rate between the treatments varied from 1.8 to 6.7 (mean 3.9). Within all groups, the culture on the MS medium exhibited a higher multiplication rate (Fig. 4) and a longer length of the main stem than the culture on the WPM. For these two parameters, the difference between the media type was most pronounced for Group 1 (Fig. 4a) and gradually decreased for Group 4 (Fig. 4d). However, the culture on the WPM had a substantially lower proportion of hyperhydrated shoots than the culture on the MS medium, and it ranged from 0 to 6.3 (mean 2.9) for WPM and from 0 to 38.0 (mean 13.2) for the MS medium. The number and length of the lateral shoots had no clear relation to the media type.

The length of the main shoot showed a significant relation to the length of the lateral shoots ($p < 0.001$, regression coefficient 1.68 ± 0.24) and the number of lateral shoots ($p < 0.01$, regression coefficient 0.23 ± 0.06). The length of the main shoot had a consistent ranking between the groups of clones (Fig. 5a). However, the number of lateral shoots highly fluctuated between treatments (Fig. 5b), affecting the ranking of the multiplication rate (Fig. 5c). Regardless of the media and cytokinin type, both the

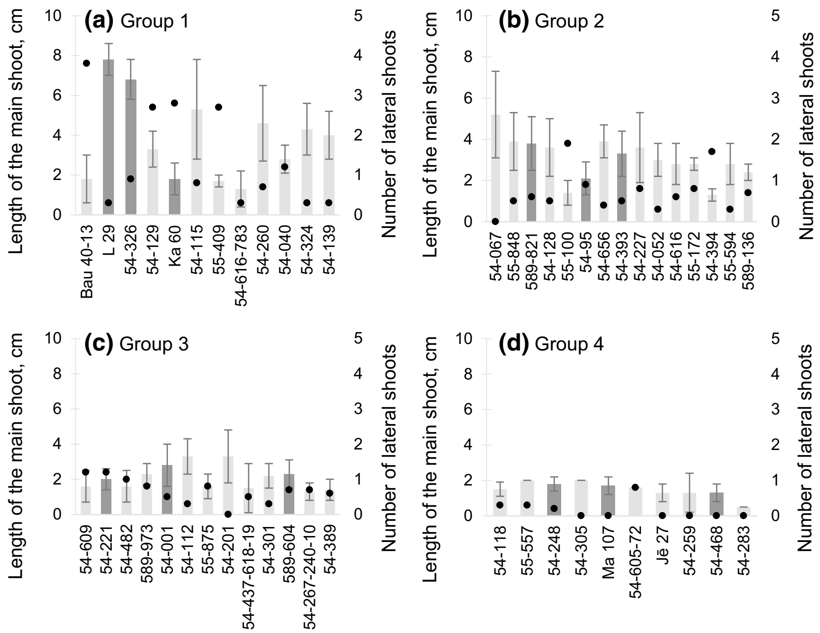

Fig. 3 Length of the main shoot (bars; ± standard error) and the number of lateral shoots (bullets) among the clones in (**a**) Group 1, (**b**) Group 2, (**c**) Group 3, and (**d**) Group 4. Clones that were selected to test the effect of different treatments are dark grey

multiplication rate and length of the main stem were the highest in Group 3, followed by Group 2 and then Group 1. As expected, Group 4 contained clones with the poorest growth among the genotypes and had the poorest results for all growth parameters (Figs. 4 and 5). The number of hyperhydrated shoots showed a positive relation with all shoot growth parameters: the length of the main stem ($p < 0.001$, regression coefficient 0.77 ± 0.07), the number ($p < 0.001$, regression coefficient 3.11 ± 0.07), and length of the lateral shoots ($p < 0.001$, regression coefficient 0.98 ± 0.21). Consequently, a significant relation ($p < 0.001$, regression coefficient 0.44 ± 0.02) between the number of hyperhydrated shoots and the total multiplication rate exists.

The effect of the cytokinin type and concentration on the growth parameters was assessed separately on the WPM and MS medium. On the MS medium, regardless of the concentration, zeatin exhibited better results on the multiplication rate and length of the main stem than BAP for all groups (Fig. 4). Within the groups, the mean difference between the zeatin and BAP treatments was 11–29% for the multiplication rate and 21–29% for the length of the main stem. Moreover, within all groups, the treatments with zeatin had a lower mean proportion of hyperhydrated shoots (ranging from 2.4 to 23.4%) than the treatment with BAP (ranging from 11.1 to 31.8%). Among the MS and zeatin treatments, the highest multiplication rate was obtained with a concentration of 0.5 mg L^{-1} in total, and for all groups except Group 1 (Fig. 4). This concentration also resulted in the highest mean length of the main stem within all groups.

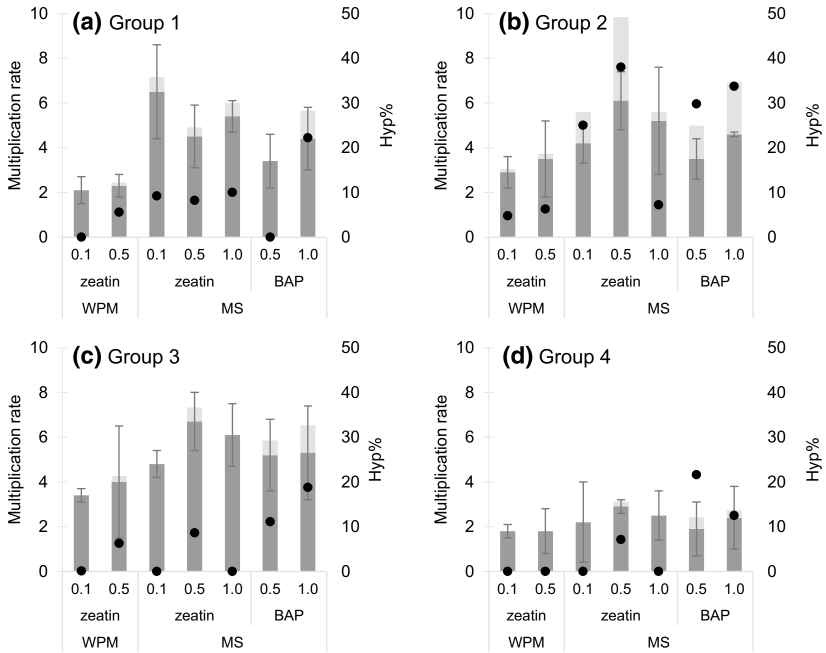

Fig. 4 Stacked multiplication rate (dark grey; ± standard error) and number of hyperhydrated shoots (light grey), and proportion of hyperhydrated shoots (Hyp%, bullets) according to the media content in (**a**) Group 1, (**b**) Group 2, (**c**) Group 3, and (**d**) Group 4. WPM, woody plat medium; MS, Murashige and Skoog basal media; BAP, 6-benzylaminopurine

On the WPM, the zeatin at a concentration of 0.5 mg L^{-1} had an equal or slightly higher multiplication rate and a longer length of shoots than zeatin at a concentration of 0.1 mg L^{-1}, but these differences were more negligible than on the MS medium. The number of lateral shoots between the different treatments varied from 0.1 to 1.2 (mean 0.6). No specific relation between the length and number of lateral shoots and cytokinin type was observed.

Discussion

Culture initiation in vitro is the most important stage in micropropagation because the outcome determines further operation possibilities. However, it is also the most problematic stage in the micropropagation of perennial plants. Recalcitrance (i.e. the inability of plant cells, tissues, and organs to respond to in vitro manipulations) could be a major limiting factor in the application of in vitro propagation (Benson 2000). Several factors, such as the collection time, age of the stock plant, bud position in the mother-tree crown, genotype, pre-treatment storage time, conditions, and medium content (Welander 1993, 1988; McCown 2000; Vaičiukynė et al. 2017), affect the responsiveness of the plant material.

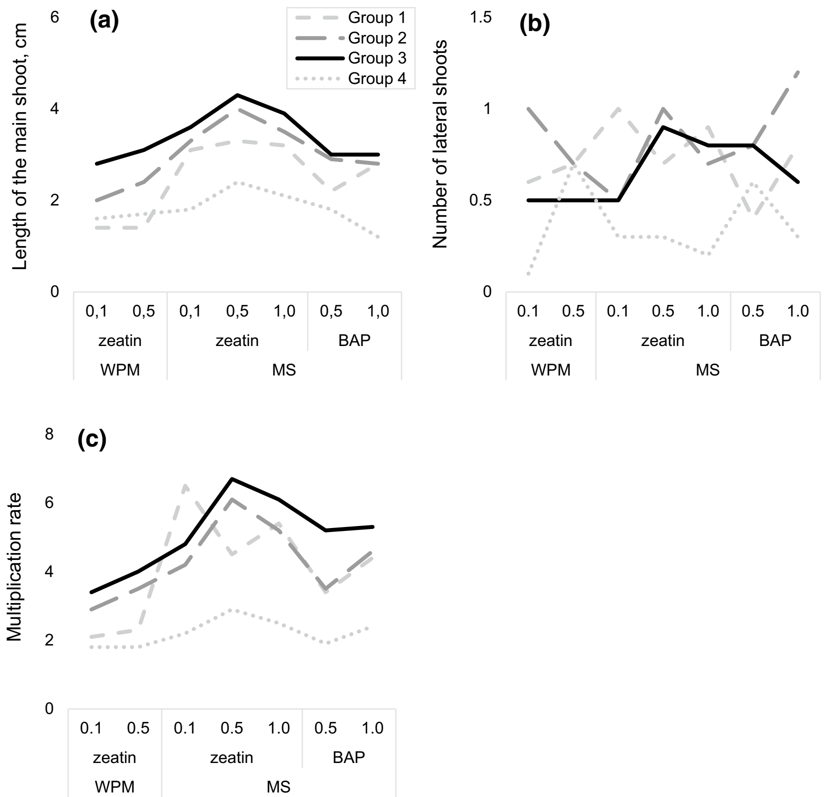

Fig. 5 Group mean (**a**) length of the main shoot, (**b**) number of lateral shoots, and (**c**) multiplication rate according to the media content. WPM, woody plat medium; MS, Murashige and Skoog basal media; BAP, 6-benzylaminopurine

Plants have complex life cycles, associated with reproduction, vegetative development, and morphogenesis. Temperate species undergo cycles of dormancy that determine periods of active shoot growth and cell division. Consequently, plants exhibit seasonal differences in their responses to tissue culture, depending on the time of the year when the explants are procured (Benson 2000). We obtained the highest proportion (about 65%) of initiated shoots from the explants collected in spring (Fig. 1). About one-third of the explants collected in mid-summer and autumn developed shoots, although the initiation rate was significantly lower than that in spring. This result corresponds well with the general pattern that cultures are most easily initiated from the explants collected in spring to early summer after a break of dormancy (George et al. 2008a).

A similar trend had been observed for other temperate tree species. *Populus tremula* L. had the highest survival rates of buds collected in late February and early March, while buds collected earlier had less intensive callus formation and plantlet development, and buds collected later had intense decay and infections (Peternel et al. 2009). For *Quercus robur* L., the most responsive explants were collected later, from May to

July (Civínová and Sladský 1990), which is probably related to their later bud burst in comparison to the aspen and birch (Linkosalo 2000; Lange et al. 2016). In contrast, others have found that the initiation of the silver birch culture was more successful from explants collected in autumn and winter (Jokinen and Törmälä 1991), and bud treatment that induces dormancy resulted in a higher proportion of buds developed into shoots (Welander 1993), suggesting that factors other than the growing season might be more significant for culture initiation.

Plant growth regulators applied during the initiation affect the induction of the shoot formation (Magnusson et al. 2009). Seasonal cycles of perennial plants determine the dynamics of the endogenous levels of growth regulators, which are responsible for the induction of dormancy or inhibit growth and further development. For instance, a low concentration of applied BAP (0.2 mg L^{-1}) resulted in a higher shoot number in *Q. robur* explants collected in February and March but with an increased BAP concentration (1 and 2 mg L^{-1}) better results were obtained from buds collected from May to July (Civínová and Sladský 1990). Moreover, buds collected from May to July had a higher regeneration capacity than those from February to April, but higher BAP concentrations were needed to stimulate their meristematic activity (Civínová and Sladský 1990).

Higher initiation success in spring might be related to the seasonally determined occurrence of microbes within the buds. For mature *B. lenta* L., dormant buds demonstrated lower contamination than buds collected in spring (Rathwell et al. 2016). Similar results were obtained for *Platanus occidentalis* L., and the contamination rate gradually increased from 14% in January to 48% in July (Tao et al. 2007). Spring was the most appropriate time for bud collection to reduce contamination in *Ulmus americana* L., whereas almost all were contaminated among dormant buds (Shukla et al. 2012). In contrast, low contamination from May to October and significantly higher contamination from December to April were found for *Pinus sylvestris* L., which is assumed to be related to better resistance of the tissue against pathogens during the active period (Hohtola 1988).

Trees exhibit developmental changes as plants progress from the juvenile to adult phases leading to a decline in their potential for micropropagation (von Aderkas and Bonga 2000). Juvenile seedling tissue is generally more responsive to culture initiation in vitro than that of mature trees. Juvenile seedlings are more easily initiated and grow and proliferate at a more rapid rate than adult material (George et al. 2008a). Cultures from mature trees are more problematic due to higher contamination rates, the browning of tissues, and recalcitrance (George et al. 2008a). One of the methods to obtain juvenile material is grafting, which can lead to a partial rejuvenation of the donor plant and can overcome recalcitrance in mature trees (Benson 2000). No assessment of true rejuvenation or reinvigoration of the scion (Wendling et al. 2014) was done in our study, yet, explants from the grafted one-year-old tree had a significantly higher proportion of initiated shoots than the explants from the 15-year-old tree (Fig. 1). Similarly, a high bud initiation (80%) was achieved using 3-year-old plants of *B. lenta*, whereas the explants from mature trees did not develop into shoots (Rathwell et al. 2016). However, most *Betula* species can be propagated from adult material without major difficulties (Welander 1993), and several studies found success using buds from mature birch trees (Ryynänen and Ryynänen 1986; Jones et al. 1996; Aubakirova and Kalashnikova 2011).

Our results are limited by using only one genotype (clone 54–95) to assess the effect of the explant collection time and age of the mother-tree. The initiation success is more affected by the genotype than the aforementioned factors (Jokinen and Törmälä 1991), but the genotype response is affected by the physiological heterogeneity of the ramets and buds of the same ramet (Civínová and Sladský 1990). However, these limiting factors could be overcome if the genotype is generally competent for growing in vitro (Jokinen and Törmälä 1991).

Once the culture is fully stabilised, biologically responsive tissues show little seasonality and progression through phase states (McCown 2000). We observed large variations in the multiplication rate between and within genotypes (Fig. 3), ranging from 1.0 to 6.8 among the clones. Close results (a multiplication rate between 1.6 and 7.4) were found among 10 genotypes selected in Sweden, Finland, and Germany (Ewald et al. 2002). Large variations but higher multiplication rates (from 2 to 20) were observed between 100 genotypes by Jokinen and Törmälä (1991). Among our tested genotypes, 12 clones had a mean multiplication rate lower than two, and seven clones did not multiply. This might be related to the limited time of the study because four to ten weeks are required for bud induction in birch, depending on the explant type, age, and physiological conditions of the mother-tree and genotype (Welander 1993). Moreover, the applied medium and plant growth regulators affect genotype performance.

The optimal media composition is species- and genotype-specific, and while a number of plants exhibit decent growth in the range of media, others may have considerable differences in their performance (McCown and Sellmer 1987). Therefore, the number of genotypes that are possible to micropropagate could be increased by modifying the composition of the medium and applying different types and concentrations of cytokinins (Jokinen and Törmälä 1991). For optimal shoot growth in vitro, the optimal amount of minerals should be provided. The most commonly used basal media in micropropagation of birch are the MS and WPM basal media, although others are also used (Ewald et al. 2000; Iliev et al. 2003). We observed a slightly higher multiplication rate (Fig. 4) and longer length of the main stem for cultures on the MS medium than those on the WPM. Similarly, poorer growth on the WPM was shown for *B. lenta*. The shoots on WPM cultures had red pigmentation, were significantly shorter, and had fewer nodes compared to the MS cultures, although the multiplication rate was not significantly lower (Rathwell et al. 2016). They associated this response to ionic strength (i.e. salt concentration) in the basal salt mixture, as the amount of ammonium nitrate is about a quarter lower in the WPM than in the MS medium. A limiting effect of low nitrogen was revealed for a given genotype of *Populus* hybrid. At first, the cultures on the WPM had poor growth, whereas these cultures on the MS medium were maintainable indefinitely. However, after an increase in NH_4NO_2 on the WPM to the level of MS, growth improved substantially, and was similar to that observed for the MS medium (McCown and Sellmer 1987). In contrast, four genotypes of *Betula platyphylla* Sukatchev var. *japonica* (Miq.) Hara × *B. pendula* had a constantly higher multiplication rate on the WPM than on the MS medium, with the mean long-term multiplication rate on these media at 3.7 and 2.8, respectively (Meier-Dinkel 1992).

Plant growth regulators have the most important role in birch in vitro shoot initiation and cultivation. Among them, cytokinins are highly effective in stimulating cell division and the control of morphogenesis (George et al. 2008b). For shoot multiplication, the most commonly used cytokinins are single BAP or zeatin at concentrations of 0.2–5.0 mg L^{-1} and 1.0–5.0 mg L^{-1}, respectively, or BAP concentrations of 0.7–2.0 mg L^{-1} in combination with a low concentration of auxin (Meier-Dinkel 1992).

The effect of the particular cytokinin should be assessed experimentally, and the response is determined by the particular compound used, type of culture, genotype, and ontogenetic stage of the tissue (George et al. 2008b). For instance, two *B. pendula* genotypes demonstrated a distinct response to supplementation with cytokinin. One of them had a significant decrease in the shoot length and an increase in the number of shoots per explant, whereas the other did not affect these parameters. Simultaneously, the latter genotype had a higher number of shoots per explant in both the control medium and the medium supplemented with BAP (Vaičiukynė et al. 2017). For several *Betula* species, the absence of cytokinins resulted in the poor growth of new shoots (Cheng et al. 2000) or no shoot development and explant death (Magnusson et al. 2009; Rathwell et al. 2016; Girgžde and Samsone 2017). Yet, typically, a narrow range of concentration achieves the best results. We observed slightly better results for the multiplication rate and length of the main stem on the media supplemented with zeatin instead of BAP. On the MS medium supplemented with zeatin, a concentration of 0.5 mg L^{-1} resulted in the highest mean length of the main stem within all groups and in the highest multiplication rate for three out of four groups (Fig. 4). On treatments supplemented with BAP, a higher concentration of cytokinin resulted in a somewhat higher multiplication rate than a lower concentration. The observed tendencies remained non-significant due to the large variation, although these tendencies were nearly constant between the groups of clones.

Several studies have tested optimal concentrations of cytokinins on *Betula* genotypes. The effect of the BAP concentration was tested on a cultivar of *B. platyphylla.* The concentration at 2.2 µM of BAP (rounded 0.5 mg L^{-1}) resulted in about a four-times higher number of new shoots than a concentration at 1.1 µM, and in a twice higher number of new shoots than the concentration at 4.4 µM (Cheng et al. 2000). For the *B. pendula* genotype, the main shoots on 1.0 mg L^{-1} of BAP had a similar length to those on treatments containing zeatin (0.5–1.0 mg L^{-1}). Yet, 1.0 mg L^{-1} of BAP had more than a two-fold higher number of lateral shoots and hence achieved a significantly higher multiplication rate than the other treatments (Girgžde and Samsone 2017). In addition, a study of *B. lenta* revealed a significantly higher result of shoot growth with BAP treatment compared to the supplementation of 2-isopentenyladenine (2-IP) and thidiazuron (TDZ), and the highest multiplication rate was achieved at a BAP concentration of 5.0 µM (rounded to 1.1 mg L^{-1}; Rathwell et al. 2016). For *B. platyphylla* and *B. papyrifera* Marsh, the BAP at a concentration of 10–20 µM (rounded to 2.3–4.5 mg L^{-1}) and TDZ at a concentration of 4–8 µM proliferated more shoots than other treatments (Magnusson et al. 2009). Different intensities of response to cytokinins might be related to the dynamics of the endogenous levels of growth regulators over the seasons, and thus could be related to the explant collection time. Civínová and Sladský (1990) found that *Q. robur* explants collected from May to July needed a higher concentration (2 mg L^{-1}) of BAP than those collected from February to April (0.5 mg L^{-1}) to achieve the highest regeneration capacity.

Within the tested media composition, groups of clones had a generally consistent ranking for the length of the main shoots (Fig. 5), but the number of lateral shoots fluctuated with the treatments, hence affecting the ranking of the multiplication rate. Moreover, groups of clones had reversed ranking in the multiplication rate in comparison to the first subculture (assessment of different genotypes, Figs. 2 and 3), although, typically, the multiplication rate remains stable during several subcultures (Jokinen and Törmälä 1991). The difference in the performance of the groups between subcultures indicates the importance of the careful selection of the media content.

A higher cytokinin concentration is beneficial until a certain study-specific threshold is reached, and afterwards, shoot abnormalities appear. The explant might form many small shoots that fail to elongate, and the leaves might have an unusual shape (George et al. 2008b). For instance, a high concentration of zeatin induced the spontaneous appearance of abnormal shoots in *B. pendula*. A concentration of 5 mg L^{-1} resulted in 3.4% fasciated shoots, and 10 mg L^{-1} resulted in 4.2% fasciated shoots, whereas all shoots appeared anatomically normal in the absence of or at a low concentration (2 mg L^{-1}; Iliev et al. 2003). In another study, at the highest tested BAP concentration (5.3 µM; rounded to 1.2 mg L^{-1}), the shoots had variable sizes and appeared hyperhydrated and chlorotic (Cheng et al. 2000). Hyperhydricity (previously called 'vitrification') characterises frequently observed malformations during vegetative propagation in vitro*,* where the plants appear turgid and watery at their surface and are hypolignified (Gaspar 1991; Debergh et al. 1992). Their shoots have broad and thick stems; short internodes; and thick, frequently very elongated, wrinkled, curled, and brittle leaves (Franck et al. 1995).

In our study, 34% of the clones had hyperhydrated shoots (Fig. 3), ranging from none to 50% of the shoots. Hyperhydricity is related to the particular conditions of the in vitro culture and results from the inability of the shoots to adapt normally to the reactions caused by stress factors, e.g. wounding, high ionic strength, and inappropriate lighting and temperature (Kevers et al. 2004). In our study, BAP promoted more hyperhydration. A high proportion of hyperhydrated shoots was also present for zeatin at a concentration of 0.5 mg L^{-1}, i.e. for treatment that resulted in the highest multiplication rate. Overall, the number of hyperhydrated shoots was positively related to better shoot growth and proliferation. These results agree with the study conducted by Gaspar (1991), who reported that hyperhydricity is related to intensive multiplication, i.e. frequent subcultures with a high rate of regeneration, but is not affected by the physiological conditions of the mother-tree at the time of the explant collection.

Conclusions

We aimed to assess the effect of the mother-tree age and explant collection time on the culture initiation in vitro, as well as to assess the multiplication capacity of different genotypes and the optimal media content on stabilised cultures. For initiation, explants from ontogenetic younger trees, and explants collected in spring had a substantially higher proportion of developed shoots. The genotype performance on the stabilised culture had substantial variation with several growth patterns. Clones had a consistent response in terms of the length of the main shoot among different media content. Our results suggest hyperhydration as a key limiting factor for the in vitro propagation of silver birch genotypes. The media with an optimal balance between multiplication and hyperhydration should be carefully selected to reduce the waste of resources. Yet, economic implications should be addressed with caution because even small differences in the multiplication rate between genotypes within a subculture result in the expansion in the number of produced seedlings per genotype in a year. Moreover, the multiplication capability should be viewed in the context of the rooting and acclimatisation of the seedlings and the field performance of the given genotypes.

Funding The study was conducted in the Forest Competence Centre (ERDF) project "Technologies for efficient transfer of genetic gain in plant production and forestry" (No. 1.2.1.1/18/A/004).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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Genetic Parameters of Growth Traits and Stem Quality of Silver Birch in a Low-Density Clonal Plantation

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Received: 4 December 2017; Accepted: 22 January 2018; Published: 23 January 2018

Abstract: Silver birch (*Betula pendula* Roth) is productive on abandoned agriculture land, and thus might be considered as an option for profitable plantation forestry. Application of the most productive genotypes is essential. However, information about genetic gains in low-density plantations is still lacking. A 40-year-old low-density (400 trees ha^{-1}) plantation of 22 grafted silver birch plus-tree clones growing on former agricultural land in the central Latvia was studied. Although grafted plantations are not common in commercial forestry, the trial provided an opportunity to assess genetic parameters of middle-aged birch. The plantation that had reached the target diameter for final harvest (DBH (diameter at breast height) = 27.7 ± 5.5 cm) had an 85% survival rate, and stemwood productivity was 5.25 m^3 ha^{-1}year^{-1}. Still, rootstock × scion interaction and cyclophysis might have caused some biases. Broad-sense heritability (H^2) ranged from 0.02 for probability of spike knots to 0.40 for branch angle. Estimated H^2 for monetary value of stemwood was 0.16. In general, the correlations between growth and stem quality traits were weak, implying independent genetic control, though branchiness strongly correlated with diameter at breast height. The monetary value of stemwood strongly correlated with productivity traits. The observed correlations suggested that productivity and stem quality of birch might be improved simultaneously by genetic selection.

Keywords: mature *Betula pendula*; clonal forestry; tree breeding; target diameter

1. Introduction

The economic importance of plantation forestry on abandoned agricultural land is increasing [1]. Application of the most productive genotypes is essential for profitability of such plantations [2]. In the Baltics, hybrids of *Populus* L. are highly productive, yet they are strongly damaged by wildlife and require continuous protection [3]. Silver birch (*Betula pendula* Roth) has substantially lower environmental risks, yet is productive on agricultural land [4], and might be considered as an alternative. When appropriately cultivated (e.g., in a low-density plantation), birch can rapidly reach target diameter, reducing rotation time and increasing profitability of a plantation [4]. However, information about very low-density plantations is lacking.

Many traits including productivity and branchiness are highly heritable, emphasizing the potential to improve growth and stem quality [5,6]. Nevertheless, some traits can have common genetic control [7], which might differ regionally [4,6]. Furthermore, genetic parameters, such as heritability or genotypic coefficients of variation at final-harvest age, are unknown for silver birch. Genetic gains can be estimated theoretically from young trials, but the information about actual realization of these gains at mature age is available for tropical tree species [8,9], although is still lacking for silver birch.

The aim of this study was to estimate genetic parameters at the final-harvest age for stem quality and growth traits of silver birch clones planted in a low-density (400 trees ha^{-1}) plantation on former agricultural land. We hypothesized that the gain of productivity and stem quality of silver birch in a low-density plantation can be substantially improved by tree breeding.

2. Materials and Methods

The study site was located in the central part of Latvia (57°32′ N, 24°44′ E). The topography was flat (elevation < 100 m above sea level). The mean annual temperature was 6.2 °C; the mean monthly temperature ranged from 4.6 °C to 17.5 °C in February and July, respectively. The mean annual precipitation was ca. 690 mm.

The trial was established in 1972 on agricultural land, equivalent to *Oxalidosa* stand type with mesotrophic loamy soil. One year after grafting, clones of 22 birch plus-trees from the central part of Latvia (56°37′–57°28′ N; 24°50′–26°24′ E) were planted in a 5 × 5 m grid (400 trees ha^{-1}) as single-tree plots in 13–56 randomly distributed replications. Clones were randomized spatially all over the planting site. Initially, the plantation was intended as a seed orchard, but abandoned soon thereafter; hence no management, except some initial cleaning, was performed. The area of the plantation was 1.8 ha (720 planting spots).

At the age of 40 years in 2012, for each tree (1) diameter at breast height (DBH; cm); (2) height (m); (3) height of the lowest living branch (m); (4) mean branch angle (°); (5) mean projection of crown (MPC; m); (6) occurrence of spike knots; (7) double tops; and (8) stem cracks (present/absent), and arbitrary scores using 6-point-scales of (9) stem straightness and (10) branchiness were measured.

Data analysis was conducted in program R, v. 3.3. [10]. For each tree, the volume of stemwood assortments was calculated according to the model by Ozolins [11]. Wood defects and stem quality traits were considered when determining the structure of stemwood assortment (according to the practices of commercial forestry in Latvia). According to the estimated volume of assortments, the monetary value of stemwood (MV) of each sampled tree was calculated as an integrative parameter. Prices of different assortments according to top diameter, as used in the calculation of MV, were 20, 26, 45, 60, and 70 euro m^{-3} for firewood (<13 cm), pulpwood (<13 cm), logs 14–18 cm, logs 19–25 cm, and logs >26 cm, respectively.

Heritability coefficients H^2 (broad-sense individual-tree heritability) for the studied variables were calculated [7]:

$$H^2 = \sigma_G^2 / \sigma_P^2, \tag{1}$$

where σ_G^2 is genotypic variance and σ_P^2 is phenotypic variance constituted of genotypic and environmental variance.

Genetic gain was estimated according to formula [7]:

$$R = S \cdot H^2, \tag{2}$$

where ***S*** is selection differential, which is the mean phenotypic value of the selected clones expressed as a deviation from the trial mean. For each variable, superiority of the top three clones against trial mean was assessed.

Genotypic and phenotypic clone mean Pearson correlations were estimated for the studied variables [7]. Genotypic correlations between the traits were calculated using the formula:

$$r_G = \frac{\sigma_{G(x,y)}}{\sqrt{\sigma_{G(x)}^2 \sigma_{G(y)}^2}}, \tag{3}$$

where $\sigma_{G(x,y)}$ is the genetic covariance between traits x and y; $\sigma_{G(x)}^2$ and $\sigma_{G(y)}^2$ are the genotypic components of variance estimated for the traits. Standard errors for the genotypic correlation estimates were obtained with the delta method [12].

Genotypic coefficients of variation (CVg), describing the extent of genetic variability of a variable in relation to the mean of trial, were calculated as:

$$CVg = \sqrt{\sigma_G^2} \cdot 100/\overline{x}, \tag{4}$$

where $\overline{x}$ is the phenotypic mean.

The corresponding components of genotypic and environmental variance were extracted using a random model:

$$y_{ij} = \mu + c_i + \varepsilon_{ij}, \tag{5}$$

where y_{ij} is observation of each trait of the ijth tree, μ is the overall mean, and c_i isthe random clone effect. For the quantitative variables (e.g., DBH, tree height), a linear mixed model was used. For the binomial variables (e.g., survival, probability of cracks, etc.), a generalized linear mixed model applying binomial residual distribution and "logit" link function was fitted. For both models, R package lme4 was used [13]. For stem straightness and branchiness, ordinal logistic regression was applied [14] using R package ordinal [15]. The environmental variance of the link functions was determined as $\pi^2/3$, or 3.29. Genetic covariance $\sigma_{G(x,y)}$ between any two traits x and y was estimated using function varcomp in package lme4.

3. Results

The studied planation had 84.4% survival at the age of 40 years. The mean (±standard deviation) height and DBH of trees was 26.2 ± 2.2 m and 27.7 ± 5.6 cm, respectively. The total standing stemwood volume of the plantation was 210 m^3 ha^{-1}, and the mean annual stemwood increment was 5.25 m^3 ha^{-1} $year^{-1}$. Accordingly, MV was estimated ca. 9600 euro ha^{-1}, mainly contributed by the logs of smaller, medium, and large dimensions (44%, 25%, and 21%, respectively).

The estimated H^2 and CVg differed among the variables (Table 1). The highest heritability was estimated for branch angle, mean projection of crown (MPC), branchiness, and stem straightness ($0.40 \leq H^2 \leq 0.29$, respectively), while the lowest heritability was estimated for survival, probability of spike knots and cracks (<0.08). Intermediate H^2 = 0.16 for MV was similar to commonly reported tree height, height of the lowest living branch, and DBH (0.14, 0.14, and 0.21. respectively). The CVg of the quantitative variables ranged from 3.2% to 21.8% for tree height and MV, respectively (Table 1). For DBH and height of the lowest living branch, intermediate genotypic variation (ca. 9%) around the phenotypic mean was estimated, while it was higher for branch angle and MPC at −14.8% and 19.2%, respectively. For each variable, selection of top three clones resulted in 3.8%, 0.6%, and 2.7% genetic gain for DBH, tree height, and MV, respectively (Table 2).

The estimated genotypic correlations among the studied variables were similar to phenotypic clone mean Pearson correlations (Table 3); the latter are described. Correlations among tree height, DBH, and MV were high (r > 0.63); nevertheless, DBH and MV (r > 0.66) correlated with MPC. Branchiness correlated with DBH (r = 0.79), yet not with tree height (p-value = 0.41). Moderate to strong ($0.30 < |r| < 0.78$) negative correlations were observed between height of the lowest living branch and DBH, double tops, stem straightness, branchiness, and MPC. Occurrence of double tops showed moderate to strong correlations with stem straightness, branchiness, and MPC (r = 0.70, 0.67, and 0.56, respectively), but a negative correlation (r = −0.68) with occurrence of spike knots. Mostly, weak and non-significant correlations were observed between the occurrence of stem cracks as well as branch angle and other variables.

Table 1. Statistics, coefficients of heritability (H^2), and genotypic variation (CVg, %) of the morphometric variables (traits), and monetary value of 40-year-old grafted birch plus-trees from the low-density plantation. The monetary value of stemwood was calculated considering stem quality.

	Mean	Min	Max	StandardDeviation	Heritability Coefficient $H^2 \pm$ Standard Error	Genotypic Coefficient of Variation $CV_g \pm$ Standard Error (%)
Quantitative variables						
Stem diameter at breast height, cm	27.7	14.2	45.8	5.6	0.21 ± 0.06	9.5 ± 1.5
Tree height, m	26.2	15.3	31.6	2.2	0.14 ± 0.05	3.2 ± 0.5
Height of the lowest living branch, m	11.2	1.8	18.0	2.7	0.14 ± 0.05	9.3 ± 1.4
Branch angle, °	43.2	15.0	80.0	10.4	0.40 ± 0.08	14.8 ± 2.3
Mean projection of crown, m	2.9	1.1	6.3	0.8	0.39 ± 0.08	19.2 ± 3.0
Monetary value of stemwood, euro	28.2	3.7	95.4	14.6	0.16 ± 0.05	21.8 ± 3.4
Qualitative variables						
Survival, % of trees *	84.4	59.6	100.0	-	0.08 ± 0.03	-
Spike knot, % of trees *	23.2	5.2	42.8	-	0.02 ± 0.02	-
Double tops, % of trees *	34.9	6.0	75.1	-	0.14 ± 0.05	-
Stem straightness, score *	3.2	2.5	4.7	-	0.29 ± 0.07	-
Branchiness, score *	3.3	2.5	5.3	-	0.33 ± 0.08	-
Stem cracks, % of trees *	24.9	0.0	50.3	-	0.08 ± 0.03	-

* Mean values for clones.

Table 2. Clone means with standard errors (SEs) for studied traits.

Clone	Number of Trees	Survival, %	Diameter at Breast Height, cm		Height, m		Height of the Lowest Living Branch, m		Branch Angle, °		Mean Projection of Crown, m		Monetary Value of Stemwood, Euro		Stem Straightness, Score		Branchiness, Score		Double Tops, % of Trees	Spike Knots, % of Trees	Stem Cracks, % of Trees
			Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE			
1	36	79.4	26.6	0.7	25.7	0.3	11.5	0.4	38.8	0.6	2.7	0.1	22.6	1.4	3.1	0.1	3.3	0.1	16.7	27.8	41.7
2	36	86.9	29.9	0.7	27.1	0.3	11.6	0.3	40.4	0.9	2.9	0.1	34.5	2.2	3.0	0.1	3.2	0.1	11.1	36.1	33.3
3	21	78.2	31.6	1.2	26.0	0.5	8.8	0.6	38.6	1.5	3.8	0.2	36.2	2.6	4.3	0.2	4.5	0.3	66.7	19.0	4.8
4	20	83.3	33.2	0.9	25.7	0.4	8.3	0.3	41.8	1.3	4.5	0.2	36.4	2.1	4.7	0.2	5.3	0.2	75.0	5.0	5.0
5	16	92.3	30.9	1.2	27.1	0.5	11.5	0.8	49.7	1.9	3.5	0.2	35.3	3.7	3.4	0.2	3.9	0.3	37.5	25.0	18.8
6	28	91.9	29.1	1.0	26.5	0.5	10.6	0.5	42.9	1.7	3.3	0.2	31.8	3.1	3.8	0.2	3.7	0.2	53.6	21.4	21.4
7	41	90.8	27.5	0.9	27.4	0.3	11.8	0.4	43.3	1.2	3.1	0.1	28.4	2.3	3.3	0.1	3.3	0.1	56.1	24.4	0.0
8	24	81.8	22.2	1.0	24.3	0.4	11.9	0.6	44.8	1.8	2.3	0.1	16.5	2.5	3.2	0.2	2.5	0.1	20.8	37.5	8.3
9	16	91.4	28.6	2.0	26.1	0.5	9.5	0.6	38.1	2.1	3.3	0.3	27.4	3.5	3.8	0.2	3.8	0.4	62.5	12.5	12.5
10	16	68.1	23.9	1.1	23.7	0.9	10.7	0.7	38.8	1.6	2.3	0.1	18.7	2.5	3.3	0.2	2.8	0.2	25.0	18.8	43.8

Table 2. *Cont.*

Clone	Number of Trees	Survival, %	Diameter at Breast Height, cm		Height, m		Height of the Lowest Living Branch, m		Branch Angle, °		Mean Projection of Crown, m		Monetary Value of Stemwood, Euro		Stem Straightness, Score		Branchiness, Score		Double Tops, % of Trees	Spike Knots, % of Trees	Stem Cracks, % of Trees
			Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE			
11	35	88.7	25.7	0.6	25.7	0.4	11.2	0.4	38.0	1.8	2.6	0.1	22.0	1.3	3.3	0.2	3.4	0.1	57.1	14.3	14.3
12	39	88.3	24.2	0.7	24.9	0.3	11.7	0.4	38.5	1.0	2.6	0.1	19.6	1.7	3.4	0.2	3.1	0.1	41.0	15.4	20.5
13	18	90.2	23.9	1.3	26.3	0.8	12.2	0.6	37.8	1.0	2.2	0.2	20.7	3.4	2.8	0.2	2.7	0.2	33.3	11.1	16.7
14	12	89.2	27.8	1.4	25.5	0.7	10.3	0.6	48.8	3.1	3.0	0.2	27.3	4.4	3.8	0.3	3.4	0.2	33.3	41.7	41.7
15	29	100.0	30.4	0.6	26.7	0.3	9.3	0.5	37.6	1.0	3.3	0.1	34.5	2.1	2.7	0.1	3.5	0.1	55.2	6.9	48.3
16	23	59.6	28.8	1.4	27.0	0.5	11.9	0.5	41.1	1.9	2.6	0.1	32.8	3.5	2.9	0.2	3.0	0.2	43.5	13.0	30.4
17	33	69.0	28.6	0.6	26.8	0.2	11.7	0.4	61.5	2.0	3.4	0.1	30.8	1.7	2.6	0.1	3.1	0.1	6.1	33.3	30.3
18	46	82.7	28.4	0.8	27.2	0.2	12.3	0.5	57.8	1.5	2.8	0.1	31.7	2.4	3.0	0.1	2.8	0.1	26.1	23.9	28.3
19	36	87.3	28.2	1.0	26.0	0.3	11.1	0.4	41.4	1.0	2.6	0.1	30.8	2.8	2.5	0.1	2.9	0.1	16.7	22.2	41.7
20	28	81.1	24.8	0.7	26.0	0.4	10.9	0.6	41.1	0.9	2.5	0.1	21.2	2.0	3.3	0.2	3.0	0.1	28.6	28.6	25.0
21	31	94.4	26.6	0.8	26.1	0.3	12.8	0.4	36.5	1.3	2.2	0.1	26.2	2.2	2.5	0.2	2.7	0.2	9.7	32.3	19.4
Ka1	14	82.9	33.3	2.0	27.4	0.5	11.0	0.6	49.3	2.5	3.8	0.3	42.0	6.8	3.6	0.2	4.1	0.3	28.6	42.9	50.0
Total	598	84.4	27.7	0.2	26.2	0.1	11.2	0.1	43.2	0.4	2.9	0.0	28.2	0.6	3.2	0.0	3.3	0.0	34.9	23.2	24.9

Table 3. Genotypic correlations (standard errors by delta method in brackets) in the upper diagonal part and phenotypic clone mean Pearson correlations (significant correlations with $p \leq 0.05$ in bold) in the lower diagonal part (*—calculation stopped due to infinite likelihood).

	Tree Height	Stem Diameter at Breast Height	Stem Cracks	Height of the Lowest Living Branch	Branch Angle	Double Tops	Spike Knots	Stem Straightness	Branchiness	Mean Projection of Crown	Monetary Value of Stemwood
Tree height	**1**	0.65 (0.16)	0.02 (0.30)	0.14 (0.27)	0.43 (0.21)	0.03 (0.27)	0.17 (0.45)	−0.16 (0.25)	0.16 (0.25)	0.35 (0.22)	0.79 (0.11)
Stem diameter at breast height	0.63	**1**	0.11 (0.29)	−0.56 (0.19)	0.23 (0.23)	0.35 (0.23)	−0.23 (0.43)	0.44 (0.20)	0.79 (0.10)	0.86 (0.07)	0.93 (0.03)
Stem cracks	0.03	0.10	**1**	−0.11 (*)	0.08 (0.02)	−0.68 (0.20)	0.38 (0.44)	−0.60 (0.21)	−0.30 (0.27)	−0.20 (0.27)	0.47 (*)
Height of the lowest living branch	0.17	**−0.51**	0.07	**1**	0.29 (0.23)	−0.75 (0.13)	0.90 (0.37)	−0.76 (0.12)	−0.85 (0.24)	−0.77 (0.11)	−0.32 (0.25)
Branch angle	0.36	0.22	0.15	0.25	**1**	−0.37 (0.22)	0.67 (0.31)	−0.09 (0.23)	−0.25 (0.07)	0.27 (0.22)	0.29 (0.23)
Double tops	0.05	0.35	**−0.51**	**−0.69**	−0.34	1	−1.19 (0.35)	0.78 (0.12)	0.74 (0.13)	0.60 (0.17)	−0.10 (*)
Spike knot	0.06	−0.07	0.29	0.40	**0.46**	**−0.68**	**1**	−0.47 (0.43)	−0.64 (0.40)	−0.35 (0.22)	0.06 (0.48)
Stem straightness	−0.15	**0.42**	−0.41	**−0.71**	−0.08	**0.70**	−0.15	**1**	0.87 (0.07)	0.60 (0.14)	0.12 (0.25)
Branchiness	0.19	**0.79**	−0.22	**−0.78**	−0.05	**0.67**	−0.26	**0.82**	**1**	0.93 (0.03)	0.28 (0.28)
Mean projection of crown	0.36	**0.86**	−0.15	**−0.71**	0.26	**0.56**	*−0.16*	**0.70**	**0.93**	**1**	0.65 (0.14)
Monetary value of stemwood	**0.74**	**0.93**	0.32	−0.30	0.28	0.14	0.03	0.14	**0.54**	**0.66**	**1**

4. Discussion

The calculated H^2 (Table 1) implied potential for substantial improvement of productivity and stem quality, hence yields of birch plantations by tree breeding [5]. Nevertheless, H^2 of the variables differed (Table 1), implying unequal potential for the improvement of the traits [7]. Branch angle, branchiness, projection of crown, and stem straightness, which largely influence timber quality [2], were highly heritable and had intermediate CVg (Table 1), implying potential for considerable improvement [7]. High CVg was also observed for MV (21.8), indicating potential financial benefits from breeding. Nevertheless, strong correlation between branchiness and DBH, MPC, and stem straightness indicated possible negative effects on stem quality when selecting fast growing trees with straight stems (Table 3). Additionally, height of the lowest living branch had significant negative correlations with the same variables, supporting the abovementioned consideration. Earlier studies reported a significant moderate correlation between DBH and number of branches [5,16]. Significant negative genotypic correlation between productivity traits and stem straightness (r_G ranging from -0.45 to -0.72) was noticed in Sweden [16]. However, other stem quality traits such as spike knots, stem cracks, and double tops did not show significant relation to productivity traits and MV, suggesting the possibility for simultaneous improvement [16,17].

The heritability of survival was low (Table 1), suggesting the prevailing effect of the micro-site conditions, as shown by Stener and Jansson [16] for birch in Sweden. Environmental factors can strongly affect performance of the species, masking the genetic effect and resulting in low heritability parameters [6]. The estimated genetic parameters (Table 1) might have been already affected by the pre-selection of planting material (plus-trees) with improved branching and stem properties, as a seed orchard was initially intended. Although the utilization of grafted silver birch is not a common practice in commercial forestry, the trial provided information about genetic parameters at middle age that has not been previously published. This might have caused some imprecisions in genetic parameters due to uncontrolled rootstock × scion effect. Although the issue has been scarcely studied for forest trees [18], for loblolly pine, the rootstock × scion effect has been negligible compared to the effects of clone and site factors [19]. This was also supported by good survival of grafts indicating compatibility between rootstock and scions. The negative effect of cyclophysis due to different biological ages of rootstock and scion [20–23] appeared insubstantial, as indicated by the productivity of the plantation. Similarly, a weak effect of cyclophysis on growth and survival of vegetatively propagated silver birch has been shown in boreal conditions [24,25]. Still, grafts might have lower branchiness and branch thickness [26].

The single-tree-plot design of the plantation might have also affected genetic parameters of the traits, as the measurements from such plots are influenced by competition among different genotypes [27]. However, low planting density likely had postponed the onset of inter-tree competition, therefore reducing exaggeration of the genotypic variance of growth traits [5,16,28]. Hence, the estimated H^2 and CVg were somewhat lower than reported in earlier studies, in which H^2 ranged 0.07–0.56 for tree height, and 0.11–0.59 for DBH, while CVg for the respective traits has been reported to range between 5 and 14, and between 9 and 21, respectively [5,16,28]. Still, heritability of height and DBH varies widely among different trials [16]. Considering varying genetic control of the studied traits, H^2 and CVg of MV were intermediate (0.16 and 21.8), as similarly observed in Sweden [5].

For silver birch, genetic gains of around 10% for height and 20% for DBH of the top 10% clones at the age of 7–11 years are reported [5,16], while corresponding realized gains in our study site at the moment of possible final-harvest was around 17 and 5 times lower, respectively. This may imply weak age-age correlations, as well as reflect lower heritability and high variability due to strong environmental effects (Table 2). However, earlier measurements from the studied trial were not available for comparison.

The studied plantation appeared ready for the final harvest already at the age of 40 years. Higher productivity (up to 8.90 m^3 ha^{-1} $year^{-1}$ [29] vs. 5.25 m^3 ha^{-1} $year^{-1}$ in studied trial) and good stem quality might be achieved in conventional plantations with higher planting densities [30,31], although increasing planting distance does not influence the height growth [31]. Nevertheless, decreased competition and application of the pre-selected planting material apparently improved the assortment structure of the studied birch, shifting its distribution towards the higher value, thus suggesting efficiency of the low-density clonal plantation for the production of solid wood and possible further economic improvement in a low-density short-rotation plantation. Together with selected planting material, reduced establishment costs with wider spacing might be a strong driving factor for choosing lower planting densities. Increased value does not only result from increases in volume production, but also from improved stem quality leading to more valuable logs [9]. Besides, breeding effect on productivity might not fully express in dense stands, since birch maintain vigorous growth when presented with low within-stand competition [4].

5. Conclusions

Although the utilization of grafted silver birch is not a common practice in commercial forestry, the studied forty-year-old, low-density grafted clonal plantation appeared efficient for the production of solid wood. Considering heritability and genetic gains of the studied traits, the gain of birch plantations might be substantially improved by breeding. The non-significant correlations between stem quality and dimensions of trees suggested that the traits could be improved simultaneously. However, the strong correlation between branchiness and DBH implied that stem quality would be reduced when selecting for productivity. Still, rootstock × scion interaction and cyclophysis effects are uncertain and might be potentially significant. Considering the potential for strong environmental effects on the performance of birch, verification of the results in diverse growing conditions is required.

Acknowledgments: The study was carried out in accordance to contract No. 1.2.1.1/16/A/009 between "Forest Sector Competence Centre" Ltd. and the Central Finance and Contracting Agency, funded by the European Regional Development Fund (ERDF) within the framework of the project "Forest Sector Competence Centre". We acknowledge JSC "Latvijas valsts meži" for information about standing stock of the conventional stands. Jānis Donis and Virgilijus Baliuckas helped with data analysis.

Author Contributions: Ā.J. conceived the original research idea. All authors contributed to the experimental design. J.K. and J.J. were responsible for data collection. Ā.J., R.M., and P.Z. analyzed the data. A.G., Ā.J., R.M., and P.Z. wrote the paper.

Conflicts of Interest: The authors declare no conflict of interest.

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PROFITABILITY OF SILVER BIRCH (*BETULA PENDULA* ROTH.) BREEDING IN LATVIA

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Abstract

Economic importance of Silver birch in Latvia has been increasing in last decade, triggering scientific research, dedicated to improvement of this species, including tree breeding. Bulk of progeny trials will reach the evaluation time in next few years; therefore, decisions for further tree breeding activities have to be made. The aim of our study is to evaluate profitability of silver birch breeding, based on current situation in the year 2010 and circumstances in Latvia and assess the factors that might notably influence the result. Analysis considers all available breeding material and links between tree breeding, seed orchards and end product – forest stand, regenerated with improved plants in order to evaluate profitability of different alternatives based on differential approach. Results reveal that differential benefits from forest regeneration with selected birch material in comparison to natural regeneration, in areas with highest site indexes (Ia-II) with 3% interest rate and at least part of the stands managed in order to maximize yield of large diameter trees at age of final felling, are positive. The highest profitability can be reached if selection of best individuals is done based on clonal testing, genetic gain is maximized and combined with proper silvicultural praxis and annual planting area (utilization of seeds from selected trees) are maximized.

Key words: differential benefits, birch improvement, selection.

Introduction

Silver birch is one of the birch species (*Betula pendula* Roth. and *Betula pubescens* Ehrh.) that in forest inventories are not distinguished from each other and together occupy 28.2% of forest area, being the second most widespread after Scots pine (Anonymous, 2008). During the 20th century birch in most of the forest areas was treated as a species of secondary importance that needs to be removed in thinnings in favor of coniferous trees. Economic value of birch has not been fully recognized until few decades ago. Birch is used now in plywood production that accounts for more than 10% of total export value of forest sector products (Anonymous, 2008) and also plays an important role in furniture production. Birch wood is used also in production of sown goods, ship boards.

After the collapse of the Soviet Union, large areas of agricultural lands are abandoned. Natural afforestation of these lands mainly is with birch. Birch is used also as one of the main species (38% of area) for afforestation of former agricultural lands. That has triggered plant production (nursery industry): in recent years on average around 4 million birch seedlings are produced annually and only minor portion of it (30%) used in forest regeneration on forest lands.

The advancement in recognition of birch value and use has triggered significant research activity in fields of plant production and afforestation technique (Liepiņš, 2003, 2004), thinning of birch stands (Zālītis and Zālītis, 2002) and tree breeding activities of this species. A large number of forest stands has been inventoried across Latvia, plus trees and phenotypically valuable trees selected altogether in 37 stands. Seeds from trees of theses stands have been used to establish open-pollinated progeny trials in 3 contracting sites in Latvia, altogether occupying 60 ha. This material forms a basis for further tree breeding activities.

As the demand for birch plants was growing, plus-trees were phenotypically selected and joint-stock company (JSC) 'Latvia's State Forests' established birch seed orchard in plastic greenhouse for production of improved seed material. That, in turn, triggered further interest in selection of new set of clones with even higher genetic value that would serve as a parent trees for new generation of planted forest stands. Bulk of the birch progeny tests is close to the evaluation and selection age i.e. close to the point of beginning of the second breeding cycle. Therefore, it is important to analyze the alternatives for further breeding activities in order to select the most economically efficient one.

Numerous theoretical studies have addressed the issue of the efficiency of and comparison among the breeding strategies (Danusevicius and Lindgren, 2002a, b, 2005) recently. Excel-based calculation tools have been developed to optimize the necessary amount of breeding material at different stages, scale the genetic diversity vs. genetic gain and compare breeding strategies (Danusevicius and Lindgren, 2002a, b). However, the studies have not been used for practical analysis in Latvia and have a number of limitations (like – no considerations of genotype-environment interaction, very limited available knowledge in values of some of the parameters etc.) for stand-alone practical application. Theoretical approaches of economic evaluation of profitability of tree breeding have been analysed by A. Ahtikoski (2000). It also included practical analysis of Scots pine and Silver birch seed orchards in Finland; however, the basis for optimization of tree breeding activities was not presented.

In order to maximize the gain from use of selected material, a detailed economic analysis for relative weights of different traits in selection index has been carried out mainly with species used in short rotation plantations (Lowe et al., 1999; Dinus and Welt, 1995), but recently also for Scots pine in Sweden (Berlin et al., 2009). This approach, however, requires detailed data on genetic parameters of traits and their importance in particular production process that are not available in our case.

The aim of the study is to evaluate profitability of silver birch breeding based on current situation and circumstances in Latvia and assess the factors that might notably influence the result.

Materials and Methods

All available breeding material of silver birch in Latvia can be divided in 2 groups:

1) open-pollinated progenies of 921 phenotypically selected plus tree or superior stand tree that have reached the age of 10 years in 2010 when this study was done;
2) progenies of 360 controlled crosses of 100 untested (phenotypically selected) clones in seed orchard that have reached the age of 4 years.

Both groups of available material can be integrated at the end of the second breeding cycle of the first group; therefore, it is chosen as a time horizon for the analysis.

For the bulk of material (first group) it is planned to establish 2 breeding populations, based on delineated provenance regions (eastern and western), and using altogether 150 trees – phenotypically selected progenies from the most productive and qualitative open-pollinated families, since the mother trees are not available any more. Among the members of the breeding population, double-pair mating will be performed. For further activities 3 different alternatives are compared: 1) phenotypic (FEN) selection of the best individuals within a family; 2) clonally (VEG - vegetative) testing, where the selection of candidates within a family and their vegetative propagation is performed, followed by the establishment of clonal progeny trials and backward selection of the two best candidates from each family; 3) progeny (GEN - generative) testing, where phenotypic selection of candidates within a family and their flowering stimulation to obtain seeds is done, followed by the establishment of open-pollinated progeny trials and backward selection of the two best candidates from each family. Planned activities, that are not explicitly analyzed in the study, but costs are added to each of the alternatives:

1) for the first group of material, before the beginning of the second breeding cycle: repeated measuring of part of the trials, selection of individual trees within superior families;
2) for the second group of material: tending work in progeny trials, measurements, selection of individual trees within superior families.

The comparison of alternatives is based and differential approach is used, i.e., only positions of benefits and costs, which differ between 2 regeneration methods – natural and planting of selected material – are considered (Ahtikoski, 2000). In the analysis differential costs are based on prices of the year 2010 and represented by:

1) costs of tree breeding activities, obtained from practical experience in the Latvian State Forest Research Institute 'Silava' according to activities needed to carry out each of the alternatives (FEN, VEG, GEN);
2) costs of seed orchard establishment and maintenance, obtained from the JSC 'Latvia's State Forests', that owns the productive birch seed orchards in Latvia;
3) costs of regeneration: plants, soil preparation, planting, and two extra cleanings, information from the results of the tenders of the JSC 'Latvia's State Forests'.

The differential benefit is represented by additional yield and shorter rotation time (cutting by target diameter, if possible) of the stands regenerated by the selected reproductive material. Values of genetic gain for each of alternatives, scale and timing of tree breeding works were partly assessed using the 'Breeding Cycle Analyser' (Danusevicius and Lindgren, 2002a, b) with genetic gain per unit of time as the target to be maximized (Table 1).

Genetic gain of an improved stand expressed relative to diameter and height growth of an unimproved stand was calculated based on constant proportional advantage approach (Ahtikoski, 2000).

Growth models for traditional (high initial density, delayed, low intensity thinnings) and targeted (aimed to maximize the mean diameter and total volume of trees at the final felling age, and characterized by low initial stand density) silvicultural systems and thinning regimes, the same for naturally regenerated and planted (improved) stand were chosen, based on recommendation of P. Zālītis and J. Jansons (2009). The assortment structure in thinning and final felling was calculated according to the algorithm developed by R. Ozolins (Ozoliņš, 2002). The assortment prices for the years 2006 - 2010 were obtained from Central Statistical Bureau and JSC 'Latvia's State Forest'. Assortments were set as follows: first grade logs (top diameter exceeds 25.9 cm, length 4.9 m), second grade (18 - 25.9 cm, 4.9 m), third grade (14 - 17.9 cm, 4.9 m), pulpwood (6 - 13.9 cm, 3 m), firewood (3.0 - 5.9 cm, 2 m).

Area of seed orchard was based on minimal number of clones to ensure genetic diversity as well as predicted seed needs, assuming that all birch stands on fertile soils would be clear-felled and replanted with improved material. Selected set of clones is set to be used for 24 years, since none of the alternatives could switch to new set of clones of higher genetic quality faster than that.

Table 1

Scale and timing of tree breeding works based on different alternatives used in analysis

Size of breeding material and duration of different phases		Tree breeding alternative		
		FEN	VEG	GEN
Duration of activity, years	Recombination	6	6	6
	Time before	2	4	2
	Testing of progenies	25	12	14
	Time after	-	-	5
	Time before	-	-	2
	Testing of candidates	-	-	12
	Total time	33	22	41
Size of breeding material	Number of families	150	150	150
	Number of trees per family	300	100	120
	Number of candidates	-	40	25
	Number of progenies/ramets per candidate	-	40	35

To ensure unbiased comparison between regeneration methods and breeding alternatives, net present value (NPV) was calculated with the interest rate 3%.

Results and Discussion

Results reveal that NPV of tree breeding costs are highest in VEG alternative, followed by GEN (60% of VEG costs) and FEN (40%). Genetic gain of FEN alternative is approximately 79% of the other alternatives that is according to theory (Falconer and Mackay, 2004) and reflects increased precision of selection, based on progeny testing. In the current situation (prices and costs of the year 2010, on average a bit below 500 ha y^{-1} birch planting used, predictions of genetic gain for height and diameter 14% for FEN and 18% for VEG and GEN, targeted and traditional silviculture applied in equal proportions of area) highest differential benefit is achieved with VEG alternative (88 LVL ha^{-1}), followed by GEN (51 LVL ha^{-1}) and FEN (34 LVL ha^{-1}). Influence of amplitude of different genetic gains is presented in Figure 1.

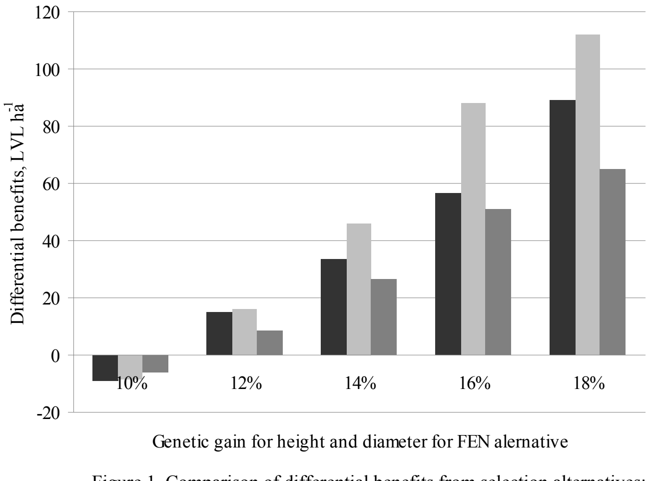

Figure 1. Comparison of differential benefits from selection alternatives:
FEN VEG GEN

Genetic gain for other alternatives calculated proportionally to that of FEN selection alternative
Assumed, that birch planting will be carried out 500 ha y^{-1} and targeted and traditional silviculture applied in equal proportions of area.

Results reveal that superiority of selection based on clonal testing (VEG) remains across the range of genetic gain levels, that exceed 10%, and is increasing in absolute value, as higher the genetic gain is. It is in line with conclusions of L.-G. Stener and G. Jansson (2005) that also noted superiority of vegetative (clonal) testing.

Figures of genetic gain used in this study are in line with other published estimates: at the age of 10 years, 10% gain in height and 18% in diameter has been found for silver birch (Stener and Jansson, 2005). Other studies report no notable difference in genetic gain at the age of 10 and 20 - 36 years, the absolute value being 29% for yield (Hagqvist and Hahl, 1998) that would roughly correspond with 14% increase in height and diameter. Genetic gain 10% - 25% at age 21 - 32 years are estimated (for height) and 20% predicted for yield at mature age for Scots pine (Jansson, 2007; Andersson et al., 2006; Ståhl and Jansson, 2002) for the first breeding cycle. Considerable decrease in genetic variation have been found between wild population and selected plus trees, but the next steps of selection, based on progeny testing corresponds to only marginal changes in genetic variation (Bouffier et al., 2008). Therefore, it can be assumed that the possibility of further improvement in next breeding cycle remains the same as in the first one.

Value of differential benefits is influenced not only by genetic gain, but also by annual planting area and fluctuation in assortment prices (Table 2).

Table 2

Differential benefits from selection alternatives, LVL ha^{-1}

Assortment prices as in year	Annual planting area and selection alternative								
	500 ha y^{-1}			5000 ha y^{-1}			7500 ha y^{-1}		
	FEN	VEG	GEN	FEN	VEG	GEN	FEN	VEG	GEN
2010	34	88	51	71	162	95	72	165	97
2009	24	73	42	62	147	86	63	150	88
2008	143	280	164	181	354	208	182	357	210
2007	169	327	191	206	401	235	208	404	237
2006	85	181	105	122	255	150	124	258	151

Genetic gain for height and diameter 14% for FEN and 18% for VEG and GEN alternatives
Assumed that and targeted and traditional silviculture applied in equal proportions of area

Annual planting area has a profound effect on value of differential benefits: as it increases from 500 ha year^{-1}, planted during the last decade on average, up to 5000 ha year^{-1} the differential benefits increases by 60% on average, ranging from 25% to more than doubling. It is related to constant costs involved in equation – the more the area increases, the lower are the costs of seed orchard establishment and maintenance per one hectare planted with material grown from selected seeds. Tight link between economic value of tree breeding process and the size of the area, where selected forest reproductive material is utilized, is also noted by other authors (Ledig and Porterfield, 1982).

Fluctuation of wood prices has remarkable influence on the value of differential benefits: difference between the lowest and highest estimate for the same alternative and annual area of planting varies 2.4 – 5.0 times. That indicates the importance of selection of proper final harvest time, based on market conditions in order to reap highest benefits from the use of selected material in forest regeneration. Results also demonstrate that rather conservative genetic gain estimate ensures positive differential benefits from tree breeding and use of selected material, even with the least beneficial alternative and in years with the lowest wood prices.

Silvicultural system has a notable influence on stand parameters. Results demonstrate that stands with 'targeted' management regime, involving only one commercial thinning ensures notably higher differential benefits than stands with 'traditional' one regardless of selection alternative or wood price conditions (Figure 2). Main cause of it is faster diameter increment in 'targeted' management, providing opportunity to shorten rotation period as well as to obtain higher proportion of most valuable assortments. In the study we were not able to address aspects of genotype-silvicultural system (like initial spacing, intensity of pre-commercial thinning etc.). Only few studies of this aspect have been carried out in the region based on very limited Scots pine material. They indicate that genotype – initial spacing interaction might have a practical importance (Roth et al., 2007; Persson, 1994). Selection of assortments in our study is based only on dimensions, and quality is not considered. However, studies demonstrate that up to 90% of proportion of veneer logs from tree is determined by branch quality (Hagqvist, 2001). Genetics is even more important than the silviculture in determining quality traits of birch, like natural pruning (Zālītis and Zālītis, 2002), branch diameter and angle (Hagqvist and Hahl, 1998), wood quality (Koski and Rousi, 2005). Genetics has significant effect even on slenderness of trees (Kroon et al., 2008). Therefore, increased quality and proportion of the most valuable assortments could be an important part of differential benefit from use of selected material and shall be addressed in further studies, as soon as there is sufficient data from National forest inventory and older birch trials. Average proportion of elite-grade logs could be determined also by equations, developed by P. Zalitis and colleagues (Zālītis et al., 2002), but it does not allow to consider the additional gain from quality improvement. Constant proportional advantage, adding the genetic gain to parameters of unimproved stand at any age, is used in our study. However, genetic gain could be different at different age, and thinning regime could be optimized to reap highest benefits from the use of selected material.

Considering the above mentioned – thinning regime not optimized, quality traits not estimated and elite veneer assortment not assessed – as well as probability, that no extra cleanings might be needed for planted stand in comparison to naturally regenerated. It can be stated that the results of our study are close to the lowest limit of estimates of differential benefits from the use of selected material.

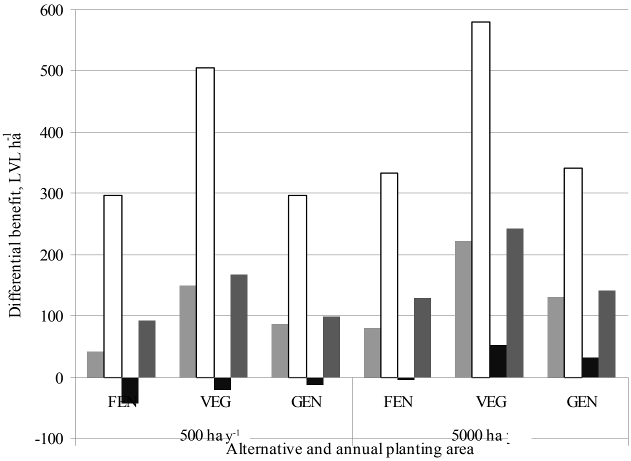

Figure 2. Influence of silvicultural system applied on the differential benefits from forestry in the year of high (2007) and low (2009) wood prices:
2007 traditional 2007 targeted 2009 traditional 2009 targeted
Genetic gain for height and diameter 14% for FEN and 18% for VEG and GEN alternatives.

Interest rate used in the study – 3% – might seem rather low, but it is in line with values usually used in economic analysis in forestry (Pentinten, 1999; Pesonen and Hirvelä, 1992).

Conclusions

1. Differential benefits from forest regeneration with selected birch material in comparison to natural regeneration, in areas with the highest site indexes (Ia-II) with 3% interest rate and at least part of the stands managed in order to maximize radial increment, is positive
2. Selection of best individuals based on clonal testing is the most expensive, least time consuming alternative that ensures highest differential benefits across the range of genetic gain levels, that exceed 10%, and is increasing in absolute value, as higher the genetic gain becomes
3. Factors like annual planting area, silvicultural system used for management of planted stand, and fluctuation of wood prices have a profound effect on value of differential benefits, therefore need to be considered in order to maximize it.

Acknowledgements

Development of calculation model has been carried out in research project, funded by JSC 'Latvia's State Forests', further analysis and preparation of manuscript: by ESF project "Importance of Genetic Factors in Formation of Forest Stands with High Adaptability and Qualitative Wood Properties" (Contract No 2009/0200/1DP/1.1.1.2.0/09/APIA/VIAA/146).

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Effect of Breeding on Income at First Commercial Thinning in Silver Birch Plantations

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Received: 17 February 2020; Accepted: 13 March 2020; Published: 15 March 2020

Abstract: The economic importance of fast-growing tree species like silver birch (*Betula pendula* Roth.) is increasing due to growing demand for timber. Tree breeding provides the opportunity to increase the timber supply and thus ensure the most efficient use of forest land. Application of the results of a breeding program—the planting of young stands—is costly, and information on (potential) early income for the landowner from this investment is scarce. Therefore, the aim of this study was to characterize the gain from the use of improved silver birch material at the first commercial thinning. Material was collected from an open-pollinated progeny trial of 524 silver birch plus-trees at the age of 14 years in the central part of Latvia. Incomes from the first thinning were calculated at low and high timber prices. Heritability of growth traits (assessed as diameter at breast height) and timber value at first thinning were similar. Both timber market fluctuations and genetics had a notable impact on economic outcome: the internal rate of return for the selected best-performing families was 9.4% and 8.3% in the case of high and low timber prices, respectively; on average, for all families in the trial the figures were 8.1% and 6.7%, respectively. Results indicate profitability for investments in planting of improved regeneration material, even at a young age, in hemiboreal forests.

Keywords: *Betula pendula*; genetic gain; revenue; forest regeneration

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1. Introduction

The economic importance of fast-growing pioneer tree species is increasing due to the growing demand for timber both for solid wood products and chemical processing [1,2]. Silver birch (*Betula pendula* Roth), with its high productivity on agricultural land, is suitable for such purposes and less affected by biotic factors (browsing, insect and fungus damages) than conifers [3]. Therefore, it has been included in tree breeding programs to select the most productive genotypes [4]. However, tree-breeding programs are costly; therefore, the assessment of practical economic gain is essential [5]. Moreover, silver birch usually has abundant natural regeneration and most clear-cuts of the species are regenerated this way, rather than by replanting [6]. Solid information on the economic gains realized from the rather high establishment costs of planting is needed to encourage this practice (and the use of germplasm from tree breeding). In northern Europe, the internal rate of return for improved Norway spruce was 5.3%, but for Scots pine from a third round of seed orchards was 7% [7,8]. Such rates were notably higher than in stands regenerated from unimproved material [9]. It demonstrates the economic gains possible for forest owners and the potential to reduce the rotation period, thus ensuring higher wood supply for processing [10,11]. However, the values were estimated (calculated) based on the genetic gain, not actual harvests, and did not include information on silver birch.

Improved birch ensures the opportunity to achieve tree dimensions suitable for sawlogs and plywood in a reduced period of time [3,12]. For example, use of improved Scots pine resulted in a 20-year shorter rotation cycle and a substantial financial benefit: an increase of net present value (at a 2% interest rate) by up to 32%–60% [13]. However, profitability from the use of improved material depends not only on the predicted income but also a reduction of expenses such as establishment and management costs, e.g., less tending necessary [8]. Furthermore, improved material might be more resistant to several environmental factors, which reduces risks [14]. The gain from improved material can be achieved even at a young age [2], but economic evaluations of effect on income from early thinning are still quite rare [14]. The aim of the study is to characterize the gain from improved silver birch material from the first commercial thinning at the age of 14 years.

2. Materials and Methods

2.1. Trial and Measurements

The studied trial of silver birch was located in the central part of Latvia (56°44′ N, 24°49″ E). The elevation was ca. 220 and 75 m a.s.l., and the topography was flat. The mean annual temperature was 6.4 °C; the mean monthly temperature ranged from −4.4 °C in February to +17.4 °C in July. The mean annual precipitation was ca. 630 mm.

The trial was established in 1999 on former agricultural land, corresponding to the *Oxalidosa* forest type with mesotrophic, dry, silty soil. It consisted of open-pollinated (half-sib) families of plus-trees of silver birch, selected across the whole territory of Latvia (55°40′–58°05′ N, 20°58′–28°14′ E). One-year-old containerized seedlings with an initial density of 2500 trees ha^{-1} (2 × 2 m) were planted. No management except weed control during the first year was done prior to thinning. The experimental design was complete randomized blocks. Each family was represented in one to five replications (32-tree blocks); only families represented in at least 3 replications (524 in total) were assessed. In 2014, at the age of 14 years, stem diameter at breast height (DBH) and tree height were measured for each living tree before the harvest and removed trees noted after the harvest. In total, 84% of the initially planted trees had survived until harvesting; each replication (block-plot) contained from 24 to 32 trees. The harvesting was performed by chain saws (motor-manual) to reduce damage to the remaining trees; timber was transported by a forwarder. Thinning from below was performed; basal area was reduced from 14.62 to 7.52 m^2 ha^{-1}.

2.2. Data Analysis

For each tree, stemwood volume was calculated according to the local model [15] as:

$$V = 0.909 \cdot 10^{-4} H^{0.717} DBH^{0.167 \lg(H) + 1.757} \quad (1)$$

where, H is height of the tree (in m) and DBH is stem diameter at breast height (in cm).

The assortment outcome from each harvested tree was calculated using the model developed by Ozoliņš [16] and modified by J. Donis (unpublished). The parameters used in the calculation for each assortment are shown in Table 1. To demonstrate the influence of market fluctuations on the income, low (in 2014) and high (2018) timber prices were used (Table 1).

Table 1. Assortment classes by diameter at the top end and monetary value with low and high timber prices.

Assortment	Length, m	Diameter at the Top End, cm	Price, EUR m^{-3}		Proportion of the Harvested Volume, %
			Low (in 2014)	High (in 2018)	
Sawlogs	3.0	12.0	47	56	1.3
Firewood	3.0	10.0	37	50	14.3
Pulpwood	3.0	6.0	35	54	59.3
Energy-wood	3.0	3.0	22.5	30	25.1

Genetic parameters were calculated using three largest (by DBH) trees per family and replication. To assess the heritability of the traits (DBH, stemwood value, and proportion of industrial timber), variance and covariance components (σ) were estimated using the mixed model analysis with the restricted maximum likelihood approach in SAS (Version 9, SAS Institute, Cary, NC, USA) [17] as follows:

$$y_{jkl} = \mu + B_j + F_k + BF_{jk} + \varepsilon_{jkl} \tag{2}$$

where y_{jkl} is the observation of the lth tree from the kth family in the jth replication; μ is the overall mean; B_j is the fixed effects of the jth replication; F_k is the random effect of the kth family, and BF_{jk} is a random interaction effect of the jth replication and the kth family, respectively; ε_{jkl} is the residual error.

Considering the randomized block design of the trial, heritability (h^2) was estimated as:

$$h^2 = \frac{4 \times \sigma^2{}_f}{\sigma^2{}_f + \sigma^2{}_{bf} + \sigma^2{}_e} \tag{3}$$

where $\sigma^2{}_f$, $\sigma^2{}_{bf}$, and $\sigma^2{}_e$ are the estimated variance components of the family, family × replication interaction, and the residual, respectively. Standard errors of h^2 were calculated using Dickerson's approximation [18].

The coefficient of additive genetic variation (CVa) describing the extent of genetic variability for the quantitative traits [19], was calculated as:

$$\mathrm{CV_a} = \sqrt{4}\hat{\sigma}_f^2 \times \frac{100}{\bar{x}} \tag{4}$$

where $\bar{x}$ is the phenotypic mean and $\hat{\sigma}_f^2$ is the additive genetic variance.

Genetic gain (GG) was calculated using a 10% selection intensity (i) [19]. The net wood value (NWV), net present value (NPV) and internal rate of return (IRR) were calculated as the economic indicators for the harvested timber. To assess the economic effect of breeding, the indicators were calculated for the trial mean, as well as for the top and bottom 10% of the families, ranked by the GG of DBH.

For each tree, sawlog income was calculated as:

$$I = \frac{\left(1.013 \times 0.958 + (-0.112) \times DBH^{0.203}\right)}{(0.958 + DBH^{0.203})} \tag{5}$$

where DBH is the stem diameter at the breast height (cm).

To calculate NWV, the following equation was used:

$$NWV = \mathrm{I}_{income} - \mathrm{H}_{costs} \tag{6}$$

where $\mathrm{I_{income}}$ is income from harvesting and $\mathrm{H_{costs}}$ is the harvesting costs (Central Statistical Bureau of Latvia).

Income and costs were included in the analysis by calculating NPV, which was calculated as the discounted value of the future expected net cash flow.

$$NPV = \frac{(NWV - E_{costs})}{(1 + r)^n} \tag{7}$$

where $\mathrm{E_{costs}}$ is the establishment costs (low and high prices), r is the discount rate (3% and 5%), and n is the number of years (14). The establishment costs were acquired from the Central Statistical Bureau of Latvia.

To estimate the profitability of the potential investment, the IRR was calculated using the following equation:

$$IRR = r_a + \frac{NPV_a}{NPV_a - NPV_b}(r_b - r_a) \quad (8)$$

where r_a is the lower discount rate (3%); r_b is the higher discount rate (5%); NPV_a is NPV at r_a; and NPV_b is NPV at r_b discount rate.

3. Results

3.1. Heritability of Traits

The mean DBH and tree height (± confidence interval) in the silver birch trial at the age of 14 years was 9.1 ± 0.2 cm and 13.4 ± 0.2 m, respectively; standing volume (yield) was 91 ± 1.9 m^3 ha^{-1}. Heritability for timber value and for the usual trait of selection (DBH) was very similar. However, the proportion of industrial timber (sawlogs and pulpwood) was less heritable. The coefficients of additive genetic variation (CV_a) ranged from 3.7% to 22.7% for the proportion of industrial timber and timber value, respectively (Table 2). Genetic gain values had a similar trend as the CVa. There were negligible differences in genetic gain from direct selection or selection by DBH.

Table 2. Coefficients of heritability (h^2), genetic variation (CV_a) and genetic gain (GG) of progenies of plus-trees of silver birch plantation at the age of 14 years.

Trait	Heritability Coefficients h^2± Standard Errors	Coefficients of Additive Genetic Variation CV_a, %	Genetic Gain GG_10% direct	Genetic Gain GG_10% DBH
DBH	0.49 ± 0.08	8.4	8.9	8.9
Proportion of industrial timber (sawlogs and pulpwood)	0.18 ± 0.07	3.7	1.7	1.6
Timber value (low prices)	0.49 ± 0.08	22.7	26.9	26.3
Timber value (high prices)	0.50 ± 0.075	20.0	22.9	22.5

3.2. Monetary Value of the Selected Trees

For the trees subjected to thinning, the DBH and height were 8.0±0.3 cm and 13.0 ± 0.4 m, respectively. The remaining trees had a mean DBH of 10.0 ± 0.3 cm and height of 10.0 ± 0.4 m (Figure 1). The volume of harvested industrial timber on average was 28.0 ± 0.8 m^3 ha^{-1}.

Income from the thinning differed greatly with fluctuations of timber market: with low timber prices, it was 1275 ± 29 EUR ha^{-1} on average; with high, 1863±33 EUR ha^{-1} (Table 3). Similar differences were observed with NWV (Figure 1): the top-performing families reached 1424 ± 86 EUR ha^{-1} with high timber prices, and 616 ± 39 EUR ha^{-1} with low prices; corresponding mean figures in an open-pollinated plus-tree progeny trial were statistically significantly lower: 1030 ± 25 EUR ha^{-1} and 426±11 EUR ha^{-1}, respectively. Selected (best performing) families had NPVs (with a 3% discount rate) from 370 to 741 EUR ha^{-1}. Moreover, for the best-performing families, NPVs at a high timber price and low discount rate were 50% higher compared with the trial mean; at a low timber price, the improvements were 35%. IRR for the worst-performing families reached 2.9% in an unfavorable timber market, and 4.5% in a favorable one. These figures were very different for best-performing families: 8.3% and 9.4%, respectively (Table 3).

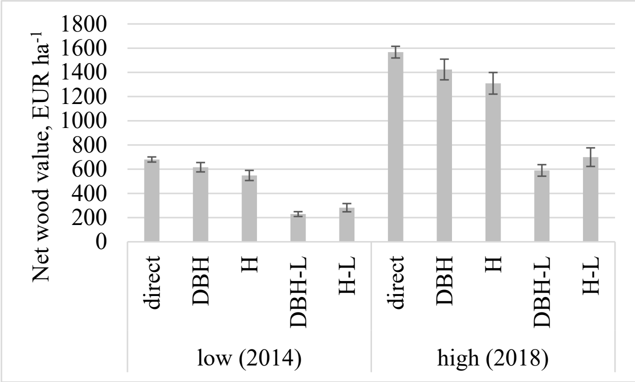

Figure 1. Net wood value of the thinning at the age of 14 years, based on low or high timber prices and selection of 10% best or worst (-L) families either directly (by value) or indirectly (by DBH or by height at the age of 10 years).

Table 3. The economic indicators of the selected trees of the silver birch trial at the first thinning at the age of 14 years.

Timber Price	**Trial Mean**				**Top 10% Families**			**Bottom 10% Families**		
	WV, EUR ha^{-1}	**NPV**		**IRR, %**	**NPV**		**IRR, %**	**NPV**		**IRR, %**
		3%	**5%**		**3%**	**5%**		**3%**	**5%**	
High (2018)	1863 ± 33	741	451	8.1	1484	1018	9.4	106	−33	4.5
Low (2014)	1275 ± 29	370	171	6.7	780	484	8.3	−7	−117	2.9

WV—total value of the harvested timber.

4. Discussion

The estimated heritability (Table 2) implies a high potential for improvement of DBH and timber value [20] by breeding. The estimated heritability was higher than observed for birch in Norway (0.23; [21]) and in Sweden (0.32; [2]). The increased values of higher genetic gain might be related to diverse population structures of birch in Latvia [22], which is a result of the post-glacial recolonization of vegetation in northern Europe. Accordingly, a higher genetic diversity allowed obtaining a broader spectrum of phenotypes, hence the intensive selection of the material was efficient [23]. The CV_a for DBH was relatively low, which might be explained by the effect of stand competition [2,3,24], but the higher coefficients for the timber value might be explained by the cumulative effect of DBH and tree height. Nevertheless, the estimated genetic gain from the 10% top-performing families was similar to other studies. For instance, Stener and Jansson [2] and Hagqvist and Hahl [25] found 18% and 11% gains for DBH when first-generation seeds were compared with ordinary seed material at the age of 7 to 12 years. Such genetic gains from improved material supports the reliability of genotypic selection and the effect of breeding [3].

The calculated sales value of the timber from the trial roughly corresponded to the actual value (obtained from the forest owner, pers. com.). NPV was positive for the mean and the top-performing families at the age of 14 years. This could, at least in part, be attributed to low establishment costs: good quality planting material ensured a need for only one tending. Compared to conventional stands of Scots pine in Sweden [12], the estimated NPV of the top-performing families of silver birch at the age of 14 was high: 2305 and 1488 EUR ha^{-1}, with high and low timber prices, respectively. It indicates high potential for the application of improved reproductive material of birch in commercial forestry with the possibility of early return on investments. Simonsen et al. [26] and Jansson et al. [7] indicates that genetically improved material significantly increases tree growth with lower investment costs. However, Jansson et al. [7] indicated that, with 5.3% IRR, the income is still low due to increasing establishment and harvesting costs, which might not be met by the improved growth rates.

In Latvia, the establishment and management costs would not increase as fast as in Sweden, due to the parity of the costs. Estimated IRR for the mean and top-performing families resulted in good profitability even when timber price is low; the values ranged from 6.7% to 8.3%, thus exceeding those of naturally regenerating stands [7]. These values might be lower if lower planting density is used, due to smaller harvested volume. Similarly, the value would be reduced with an even earlier thinning, aiming to improve the growth of the remaining birch. Thus, additional calculations using growth models would be useful to optimize the planting density. The main value of this study is to demonstrate the practical gain obtained from an actual, large (23.1 ha) thinning area at an early age, and the actual value added by the tree breeding.

5. Conclusions

Breeding ensures substantial income for the landowner at the age of first commercial thinning. Net wood value (timber value minus harvesting costs) of the top-performing families was significantly higher than the mean in the trial in any of the assessed timber market condition. Investment in regeneration with improved planting stock can ensure a positive net present value (at a 3% interest rate) already at the age of 14 years in hemiboreal conditions.

Author Contributions: Ā.J. and A.G. conceived the original research idea and methodology. A.P. was responsible for data collection. A.G. and A.K. wrote the original draft, R.M., P.Z., Ā.J. reviewed and edited the draft. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by ERDF grant number 1.2.1.1/18/A/004

Acknowledgments: The study was carried out as a part of Forest Competence Centre (ERDF) project "Technologies for efficient transfer of genetic gain in plant production and forestry" (1.2.1.1/18/A/004), and part of the material was collected in Latvian state forests (LVM) project "Tree breeding for selection of superior forest reproductive material".

Conflicts of Interest: The authors declare no conflict of interest.

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2026