PROMOCIJAS DARBS
Zinātniskā doktora grāda
zinātnes doktors (Ph.D.) Lauksaimniecības un
zivsaimniecības zinātnēs, mežzinātnē iegūšanai

AUGSTUMA PIEAUGUMA MAINĪBA PARASTĀS EGLES (*PICEA ABIES* (L.) H. KARST.) TĪRAUDZĒS JUVENILĀ VECUMĀ

Baiba Jansone

VARIATION OF HEIGHT GROWTH OF YOUNG PURE NORWAY SPRUCE (*PICEA ABIES* (L.) H. KARST.) STANDS

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

LATVIJAS VALSTS MEŽZINĀTNES INSTITŪTS "SILAVA"
LATVIAN STATE FOREST RESEARCH INSTITUTE "SILAVA"

LATVIJAS LAUKSAIMNIECĪBAS UNIVERSITĀTE
LATVIA UNIVERSITY OF LIFE SCIENCES AND TECHNOLOGIES

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Promocijas darba zinātniskie vadītāji / *Supervisors*:
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Dr.silv. Āris JANSONS

Promocijas darbs izstrādāts Latvijas Valsts mežzinātnes institūta “Silava” un Latvijas Lauksaimniecības universitātes Memoranda par sadarbību Latvijas meža nozares augstākās izglītības un mežzinātnes attīstībā ietvaros. Doktorantūras studiju laiks Latvijas Lauksaimniecības universitātes Meža fakultātē no 2018. līdz 2020. gadam. Pētījumu, kuru ietvaros ievākts datu materiāls, atbalstītājs ir a/s “Latvijas valsts meži”, un tie realizēti Latvijas Valsts mežzinātnes institūtā “Silava”. Darba izstrāde atbalstīta projekta “LLU akadēmiskā personāla pilnveidošana” (ERAF, Nr. 8.2.2.0/18/A/014) ietvaros. Atsevišķi darbi veikti Meža nozares kompetences centra pētījuma “Metodes un tehnoloģijas meža kapitālvērtības paaugstināšanai” (ERAF, Nr. L-KC-11-0004) un pētījuma “Vitālu egļu audžu izaudzēšanas ekoloģiskie un tehnoloģiskie aspekti” (ESF, Nr. 1DP/1.1.1.2/13/APIA/VIAA/052) ietvaros.

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ANOTĀCIJA

Parastā egle ir ekonomiski nozīmīgākā koku suga Ziemeļeiropā, tādēļ tās ražībai un vitalitātei ir nozīmīga loma reģiona mežsaimniecībā. Koka augstums ir tieši saistīts ar mežaudzes ražību, un to ietekmē gan augšanas apstākļi, gan koku ģenētika. Augstuma pieaugums jaunaudzes vecumā lielā mērā nosaka audzes tālāko attīstību, tādēļ svarīgi vērtēt dažādu faktoru ietekmi uz koku augšanu šajā periodā un iespējas to veicināt ar mežsaimniecības un meža selekcijas paņēmieniem. Promocijas darba mērķis ir raksturot lokālo apstākļu un iedzimtības ietekmi uz juvenila vecuma parastās egles (*Picea abies* (L.) H. Karst.) augstuma pieaugumu stādot atjaunotos hemiboreālajos mežos Latvijā.

Promocijas darbs sastāv no septiņām tematiski vienotām zinātniskajām publikācijām, un to rezultāti liecina par iespējām ievērojami uzlabot egles augšanu jaunaudzes vecumā. Koku augstumu ievērojami un būtiski ietekmē augsnes sagatavošanas veids un augsnes ielabošana ar koksnes pelniem gadu pirms stādījuma ierīkošanas vai papildus barības vielu pievienošana reizē ar stādīšanu, turklāt šo mežsaimniecības darbību ietekme saglabājas vismaz 10 gadus ilgā laika posmā. Labvēlīgu lokālo apstākļu kombinācijas nodrošināšana ievērojami paaugstina egļu ar apikālajiem augusta dzinumiem īpatsvaru jaunaudzēs, kas savukārt palielina kopējo koku augstuma pieaugumu. Starp apikālajiem augusta dzinumiem un koku augstumu pastāv pozitīva atgriezeniskā saite, palielinot koku augstumu jaunaudzes vecumā. Gan augusta dzinumu, gan augstuma pieauguma veidošanās ir ģenētiski determinēta, un egles pluskoku brīvapputes pēcnācēju ģimenēm ar lielāku augstuma pieaugumu augšanas intensitāte kulminē vēlāk, aktīvajā augšanas periodā ir augstāka un saglabājas augsta ilgāk.

ABSTRACT

Norway spruce is economically the most important tree species in Northern Europe; therefore, its productivity and vitality have key role in the forest management of this region. Tree height is directly linked to the productivity of the stand and is affected by growing conditions and tree genetics. Height increment in young stands determines the further development of the stand therefore, it is important to evaluate the effect of various factors on tree height growth during this stage and assess the possibilities to improve it with silvicultural measures and tree breeding. This doctoral thesis aims to assess the effect of microenvironmental conditions and genetics on the height increment of Norway spruce at a juvenile age in planted hemiboreal forests in Latvia. The doctoral thesis summarizes seven thematically linked scientific publications, and their results indicate the possibilities for substantial improvement of the growth of Norway spruce at a juvenile age. Tree height is considerably and significantly affected by the type of soil preparation and soil fertilization with wood ash a year before planting or by applying additional fertilizer during the planting process. Furthermore, the effect of these forest management measures lasts for at least the next 10 years. Providing favorable microenvironmental conditions considerably increases the proportion of spruces with lammas shoots, which in turn, increases the total height increment of these trees. A positive feedback loop exists between the presence of apical lammas shoots and the tree height increment, leading to increased tree height in young stands. The occurrence of lammas shoots and the intra-annual development of the height increment is genetically determined. Growth intensity (mm per day) for progenies from open-pollinated families of plus-trees with larger height increment culminated later in the season, had higher growth intensity at the active growth phase and remained high for a longer period.

SATURS / *CONTENTS*

PUBLIKĀCIJU SARAKSTS / *LIST OF PUBLICATIONS*

Promocijas darba pamatā ir septiņas publikācijas, uz kurām atsauces tekstā veidotas, izmantojot romiešu ciparus:

The doctoral thesis is based on seven publications to which references in the text are indicated with Roman numerals:

I Katrevičs J., Neimane U., **Dzerina**[1] **B.**, Kitenberga M., Jansons J., Jansons Ā. (2018). Environmental factors affecting formation of lammas shoots in young stands of Norway spruce (*Picea abies* Karst.) in Latvia. iForest-Biogeosciences and Forestry, 11(6), 809–815. 10.3832/ifor2539-011

II Neimane U., Zadiņa[2] M., Sisenis L., **Dzerina**[1] **B.**, Pobiaržens A. (2015). Influence of lammas shoots on productivity of Norway spruce in Latvia. Agronomy Research, 13(2), 354–360.

III **Dzerina**[1] **B.**, Girdziušas S., Lazdiņa D., Lazdiņš A., Jansons J., Neimane U., Jansons Ā. (2016). Influence of spot mounding on height growth and tending of Norway spruce: case study in Latvia. Forestry Studies, 65(1), 24–33. 10.1515/fsmu-2016-0009

IV **Jansone B.**, Samariks V., Okmanis M., Kļaviņa D., Lazdiņa D. (2020). Effect of high concentrations of wood ash on soil properties and development of young Norway spruce (*Picea abies* (L.) Karst) and Scots pine (*Pinus sylvestris* L.). Sustainability, 12, 9479. 10.3390/su12229479

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VII **Jansone B.**, Neimane U., Šēnhofa S., Matisons R., Jansons Ā. (2020). Genetically determined differences in annual shoot elongation of young Norway spruce. Forests, 11, 1260. 10.3390/f11121260

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[1] mainīts uzvārds no Džeriņa uz Jansone / *last name changed from Džeriņa to Jansone.*

[2] mainīts uzvārds no Zadiņa uz Kitenberga / *last name changed from Zadiņa to Kitenberga.*

Autoru ieguldījums / *The contribution of the authors*

	I	**II**	**III**	**IV**	**V**	**VI**	**VII**
Ideja / *Original idea*	**BJ**, ĀJ	ĀJ, UN	DL	DL	ĀJ	ĀJ	ĀJ, **BJ**
Pētījuma plāns / *Study design*	**BJ**, UN	UN, **BJ**	**BJ**, DL, AL	DL, **BJ**, MO, DK	**BJ**, ĀJ	**BJ**, ĀJ, RM	**BJ**, UN, ĀJ
Datu ievākšana / *Data collection*	JK, **BJ**, JāJ, UN	UN, **BJ**, AP	**BJ**, UN, ĀJ	MO, DK	OK, MZ, **BJ**	**BJ**, PZ, ID	**BJ**, UN
Datu analīze / *Data analysis*	UN, MK, **BJ**	**BJ**, MZ, LS	**BJ**, JuJ, ĀJ, SG	**BJ**, DL	RM	RM, DD	SŠ, **BJ**
Manuskripta sagatavošana / *Manuscript preparation*	**BJ**, UN	**BJ**, UN	**BJ**, DL	**BJ**, VS,	RM, **BJ**	RM, **BJ**	**BJ**, SŠ, RM
Promocijas darba autora ieguldījums, % / *Contribution of author of the thesis, %*	75	50	70	65	40	40	60

BJ – Baiba Jansone[3], JK – Juris Katrevičs, UN – Una Neimane, MK – Māra Kitenberga[4], JāJ – Jānis Jansons, ĀJ – Āris Jansons, LS – Linards Sisenis, AP – Agris Pobiaržens, SG – Sigitas Girdziušas, DL – Dagnija Lazdiņa, AL – Andis Lazdiņš, JuJ – Jurģis Jansons, VS – Valters Samariks, MO – Modris Okmanis, DK – Dārta Kļaviņa, RM – Roberts Matisons, OK – Oskars Krišāns, MZ – Mārtiņš Zeps, SŠ – Silva Šēnhofa, PZ – Pauls Zeltiņš, DD – Darius Danusevičius, ID – Iveta Desaine.

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[3] mainīts uzvārds no Džeriņa uz Jansone / *last name changed from Džeriņa to Jansone.*

[4] mainīts uzvārds no Zadiņa uz Kitenberga / *last name changed from Zadiņa to Kitenberga.*

PĒTĪJUMA REZULTĀTU PREZENTĒŠANA KONFERENCĒS / *LIST OF CONFERENCES*

Pētījuma rezultāti prezentēti astoņās zinātniskajās konferencēs:
Study results have been presented in seven scientific conferences:

1. **Jansone B.**, Samariks V., Okmanis M., Kļaviņa D., Lazdiņa D. (2020). Effect of wood ash application on soil properties and development of young Norway spruce (*Picea abies* (L.) H. Karst) and Scots pine (*Pinus sylvestris* L.). International Scientific Conference *Forest and forest sector in changing climate*, September 18, 2020. Jelgava, Latvia, referāts */ poster presentation*.
2. **Jansone B.**, Neimane U., Šēnhofa S., Jansons Ā. (2020). Genetically determined differences in annual shoot elongation of Norway spruce. International Scientific Conference *Forest and forest sector in changing climate*, September 18, 2020. Jelgava, Latvia, referāts */ presentation*.
3. **Jansone B.** (2019). Influence of flushing differences on height of Norway spruce at juvenile age. 25th Annual International Scientific Conference *Research for Rural Development 2019*, May 15–17, 2019, Jelgava, Latvia, referāts */ presentation*.
4. **Džeriņa**[5] **B.**, Runģis D. (2018). Influence of seed year on genetic diversity of progenies of Norway spruce seed orchard. 24th Annual International Scientific Conference *Research for Rural Development 2018*, May 16–18, 2018, Jelgava, Latvia, referāts */ presentation*.
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6. Jansons Ā., Neimane U., Rieksts-Riekstiņš J., Puriņa L., **Džeriņa**[5] **B.** (2013). Influence of genetic and climatic factors on formation of lammas growth of Norway spruce and Scots pine. International Scientific Conference *Climate change and tree responses in Central European forests*, September 1–5, 2013, ETH, Zurich, Switzerland, stenda referāts */ poster presentation*.
7. Jansons Ā., Neimane U., Baumanis I., **Džeriņa**[5] **B.** (2011). Factors influencing formation of lammas growth in young Norway spruce (*Picea abies* (L.) Karst.) plantation in Latvia. International Scientific Conference *Climate change:*

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[5] mainīts uzvārds no Džeriņa uz Jansone / *last name changed from Džeriņa to Jansone.*

agro- and forest systems sustainability, Lithuanian research center for agriculture and forestry, Babtai, Lithuania, stenda referāts / *poster presentation*.

8. Jansons Ā., Rieksts-Riekstiņš R., **Džeriņa**[6] **B.**, Baumanis I. (2010). Long term tree breeding trials as tool to monitor tree responses to climate changes. International Scientific Conference *Research, Monitoring and Modeling in the Study of Climate Change and Air Pollution Impacts on Forest Ecosystems*, October 5–7, 2010, COST FP0309, Rome, Italy, referāts / *presentation*.

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[6] mainīts uzvārds no Džeriņa uz Jansone / *last name changed from Džeriņa to Jansone.*

1. DARBA VISPĀRĪGS RAKSTUROJUMS

1.1. Tēmas aktualitāte

Parastā egle (*Picea abies* (L.) H. Karst.) ir ekonomiski nozīmīgākā koku suga Ziemeļeiropā, sastādot aptuveni trešdaļu no reģiona koksnes resursiem – vairāk nekā 18 miljonus hektāru platības, ar koksnes krāju 2700 milj. m^3 (Rytter et al., 2013). Egles koksne galvenokārt izmantota zāģmateriālu ražošanai, un to ražošanas atlikumi arvien vairāk tiek izmantoti bioenerģijas ieguvei (Rytter et al., 2013). Latvijā egles audzes aizņem 19% mežu platības, visbiežāk teritorijas auglīgās minerālaugsnēs ar normālu augsnes mitrumu vērī un damaksnī, un nosusinātās minerālaugsnēs šaurlapju ārenī, attiecīgi veidojot 27%, 22% un 18% no egles mežaudzēm (MSI dati, 2015–2019). Egles vidējais tekošais krājas pieaugums visās mežaudzēs ir 9,7 m^3 ha^{-1}, bet augstākās bonitātes (Ia) audzēs tas sasniedz 14,6 $m^3 ha^{-1}$ (MSI dati, 2015–2019). Augstuma pieaugums jaunaudzes vecumā lielā mērā nosaka audzes tālāko attīstību, tādēļ svarīgi vērtēt dažādu faktoru ietekmi uz koku augšanu šajā periodā un iespējas to veicināt ar mežsaimniecības un meža selekcijas paņēmieniem.

Klimata pārmaiņas var ievērojami ietekmēt mežaudžu augšanu (Kenina et al., 2018). Ziemeļeiropā siltāka klimata apstākļos prognozēta lielāka mežu ražība garāka veģetācijas perioda un lielākas fotosintētiskās efektivitātes dēļ (Menzel & Fabian, 1999; Stöckli & Vidale, 2004; Kolari et al., 2007). Šī gadsimta vidū veģetācijas perioda ilgums, kas šobrīd ir 180–200 dienas, Latvijā var būt par 35–60 dienām garāks, salīdzinot ar tā vidējo garumu periodā no 1961. līdz 1990. gadam (Kļaviņš & Briede, 2011), bet šo apstākļu labvēlīgās ietekmes izmantošanas iespējas var kavēt pieaugoša sausuma un pavasara/rudens salnu ietekme (Gu et al., 2008; Lindner et al., 2010; Zeps et al., 2017).

Uzlaboti augšanas apstākļi veicina augusta dzinumu veidošanos, un tā tiek novērota arvien biežāk (Kvaalen et al., 2010; Søgaard et al., 2011). Augusta dzinumi eglei var būt kā sānzariem (retāk), tā (arī) galotnes dzinumam. Turklāt galotnes dzinumam var būt uzplaukuši viens, daži vai pat visi sānu pumpuri, bet ne centrālais pumpurs (1.1. att.), vai arī centrālais un/vai kādi sānu pumpuri (visbiežāk). Šī darba ietvaros analizēti apikālie augusta dzinumi, kas palielina kopējo kārtējā gada augstuma pieaugumu.

Lai vērtētu apikālā augusta dzinuma nozīmi (vēlama vai nevēlama), nepieciešama informācija par tā veidošanos veicinošiem apstākļiem, kā arī ietekmi uz augšanu un stumbra/koksnes kvalitāti. Apstiprinoties pluskoku ģimeņu atšķirību (iedzimstošai) ietekmei uz apikālā augusta dzinuma attīstību, rastos iespēja zināmā mērā samazināt vai, gluži pretēji, veicināt tā veidošanos.

Zināms, ka piemērota stādmateriāla izmantošana var mazināt klimata (pārmaiņu) ietekmi uz mežsaimniecību (Lindner, 2000; Bolte et al., 2009). Līdz šim selekcija galvenokārt veikta augšanas un stumbra kvalitātes uzlabošanai (Hannerz,

1.1. att. **Augusta dzinumi parastajai eglei**

1993; Kroon et al., 2011), arvien vairāk pievēršoties pazīmēm, kas ietekmē koku adaptāciju klimata pārmaiņām (Ekberg et al., 1985; Namkoong et al., 2012; Zeltiņš et al., 2019; Isabel et al., 2020).

Adaptāciju raksturojošās pazīmes, kā plaukšanas laiks, sausuma izturība, salcietība u.c., ir ģenētiski determinētas (Hannerz, 1998, 1999; Hannerz et al., 1999; Chen et al., 2017; Trujillo-Moya et al., 2018), bet konkrētu populāciju ietvaros šo pazīmju ģenētiskā variācija var būt ierobežota. Straujākai adaptācijai un audžu ražības nodrošināšanai tiek meklēti risinājumi, kombinējot sēklu materiāla pārvietošanu uz klimatiski piemērotākiem reģioniem un selekciju (O'Neill et al., 2014; Klisz et al., 2019; Zeltiņš et al., 2019). Tomēr šo risinājumu efektivitāte ir tieši atkarīga no izpratnes par pieauguma veidošanos ietekmējošajiem faktoriem un to ģenētiski noteikto variāciju, kā arī no stādot atjaunotās platības un tās īpatsvara.

Latvijā aptuveni 90% no egles jaunaudžu platības meža tipos ar auglīgu augsni tiek atjaunota stādot (VMD dati, 2016–2018), un lielākā daļa stādmateriāla (ap 70%) iegūta no sēklu plantāciju sēklām. Stādīšanai ir augstas izmaksas (augsnes sagatavošana, stādi, stādīšana), tomēr, veicot atjaunošanas veidu (pašsēja vai stādīšana) kopējo (salīdzinošo) finansiālo izvērtējumu, vērā jāņem arī jaunaudzes attīstība, iekļaujot agrotehniskās kopšanas nepieciešamību un izmaksas (Uotila et al., 2010). Šādu izvērtējumu apgrūtina gan daudzi iespējamie katras darbības un materiāla varianti, piemēram, dažādi stādmateriāla un augsnes sagatavošanas veidi, atšķirīgas augsnes auglības ietekme uz aizzelšanu, un kombinācijas, gan informācijas trūkums par šo dažādo alternatīvu ietekmi uz koku augšanu.

Koku augšanu iespējams veicināt ar papildus barības vielu pievienošanu. Papildus barošanās elementu ienešana stādīšanas brīdī ir viens no efektīvākajiem augšanas veicināšanas paņēmieniem (Sutton, 1995; Hedwall et al., 2014). Meža augsnes ielabošana ar pelniem palielina augsnes mikroorganismu aktivitāti (Perkiömäki & Fritze, 2005), kā arī stimulē celulozi saturošu organisko savienojumu mineralizāciju (Moilanen et al., 2002; Perkiömäki & Fritze, 2002; Perkiömäki et al., 2004), bet tās ilgtermiņa ietekme uz koku augšanu pētīta reti (Moilanen et al., 2002; Perkiömäki et al., 2004; Saarsalmi et al., 2012). Papildus barošanās elementu ienese var ietekmēt arī koksnes fizikālos rādītājus, tai skaitā spēju nodrošināt barības vielu transportēšanas funkciju pa traheīdām. Egle ir jutīga pret sausumu (Lévesque et al., 2013), turklāt mainīga klimata apstākļos sausuma periodu biežums var pieaugt (Allen et al., 2010; Seidl et al., 2017). Līdz ar to nepieciešams izvērtēt, vai straujāka augšana, kad pieejamas papildus ienestās barības vielas, nerada potenciālu negatīvu ietekmi uz koku vitalitāti.

1.2. Augstuma pieaugums

Augšana augstumā ir svarīga koku izdzīvošanas stratēģija, lai nodrošinātu piekļuvi gaismai un fotosintēzes procesā spētu ražot augšanai nepieciešamās organiskās vielas (Moles et al., 2009; Poorter et al., 2012). Atsevišķi augoši koki pietiekošas gaismas apstākļos veido nemainīgu augstuma un caurmēra attiecību (Mäkelä & Sievänen, 1992), kamēr koki mežā konkurences par gaismu ietekmē relatīvi lielāku resursu daļu izmanto augstuma, nevis caurmēra veidošanai (Mäkelä & Vanninen, 1998; Ilomäki et al., 2003).

Sezonas ietvaros augstuma pieaugumu raksturo sigmoidāla līkne, ar straujāko augšanas intensitāti (mm dienā; *growth intensity*) veģetācijas sezonas vidusdaļā (Chuine et al., 2006; Lanner, 2017). Augšanas uzsākšanu (*onset*) un pārtraukšanu (*cessation*) nosaka gan iekšēji (iedzimtība), gan ārēji (vide) faktori (Hänninen & Kramer, 2007; Salminen & Jalkanen, 2007; Schiestl-Aalto et al., 2013; Gull et al., 2018), un hemiboreālajos un boreālajos mežos šo augšanas posmu norisei atbilstošā laika periodā ir nozīmīga loma sala bojājumu novēršanā (Neimane at al., 2015). Optimālos apstākļos augoši koki spēj nodrošināt efektīvu ūdens transporta funkciju no saknēm uz zaļo vainagu (Sellin, 2001), tādēļ tie var izaugt garāki nekā stresa apstākļos augoši koki. Koka hidrauliskā kapacitāte kontrolē arī kopējo koka augstumu, samazinot augšanu augstumā, kad ūdens vadīšana no saknēm līdz lapotnei kļūst apgrūtināta (Ryan & Yoder, 1997; Ryan et al., 2006).

Augstuma pieaugums var veidoties divos atšķirīgos procesos, no kuriem lielāko daļu koka dzīves laikā aizņem galvenais pieaugums (*predetermined growth*). Galvenais pieaugums veidojas, pagarinoties stumbra posmu aizmetņiem (*stem units*), kas izveidojušies pumpurā iepriekšējā augšanas sezonā (von Wühlisch & Muhs, 1986; Zhang et al., 1992), tādēļ kokiem, kas vecāki par vienu gadu, galveno pieaugumu ietekmē divu sezonu augšanas apstākļi. Stumbra aizmetņu skaitu ietekmē iepriekšējā augšanas sezona, bet katra posma iespējamo garumu ietekmē tekošās sezonas apstākļi un resursu pieejamība (Lanner, 1976; Junttila & Heide, 1981; Junttila, 1986; Mäkinen, 1998; Salminen & Jalkanen, 2005; Lindholm et al., 2009; Schiestl-Aalto et al., 2013; Mäkinen et al., 2018). Arī vecumam ir būtiska ietekme uz koku augšanu (Čermák et al., 2019). Izpētīts, ka viens no galvenajiem meteoroloģiskajiem faktoriem, kas ietekmē egles augšanu reproduktīvajā vecumā, ir iepriekšējās vasaras gaisa temperatūra (Gallego Zamorano et al., 2018), kas saistīta ar resursu novirzīšanu sēklu ražošanai (Miina, 2000; Selås et al., 2002), bet nav noskaidrots, kādi ir galvenie faktori juvenilā vecumā.

Pirmajā dzīves gadā kokiem augstums veidojas atšķirīgā procesā, ko sauc par brīvo augšanu (*free growth*), t.i., stumbra posmu aizmetņi gan veidojas, gan aug (*enlonging*) vienas sezonas ietvaros (Zhang et al., 1992). Tipiski eglei veidojas viens augstuma pieaugums (galvenais pieaugums) vienā augšanas sezonā, bet labvēlīgu apstākļu ietekmē juvenilā vecumā pēc galvenā pieauguma pārtraukšanas novērota brīvā augšana, t.i., pumpura atkārtota plaukšana un augšana pēc iepriekšnoteiktā augstuma pieauguma pārtraukšanas augšanas sezonas beigās (Ehrenberg, 1963; Dormling et al., 1968; Aldén, 1971; Rone, 1985; Cline & Harrington, 2007; Søgaard et al., 2011). Brīvajai augšanai tiek izšķirti divi veidi (von Wühlisch & Muhs, 1986), atkarībā no pumpuru kopas (*bud cluster*) veidošanās. Pēc galvenā pieauguma pārtraukšanas brīvā augšana var sākties no jau izveidotas pumpuru kopas (*sylleptic shoots*, veidojas divi mieturi), vai galvenajam dzinumam turpinot augt bez pumpuru kopas veidošanas (*proleptic shoots*, starp galvenās un brīvās augšanas pieaugumu mieturis neveidojas). Brīvā augšana iespējama ierobežotā laika posmā starp galvenā pieauguma pārtraukšanu un endogēno miera periodu (Lang et al., 1987). Visbiežāk brīvā augšana vērojama augustā, tādēļ izveidotais pieaugums tiek dēvēts par augusta dzinumu (*lammas shoot*, 1.1., 1.2. att.).

Augusta dzinumu veidošanās fizioloģiskie mehānismi (saistība ar ogļhidrātu uzkrāšanas potenciālu, fitohormoniem, fotoperiodu u.tml.) joprojām nav skaidri (Cline & Harrington, 2007), bet novērojumi liecina gan par augšanas un meteoroloģisko apstākļu (Dormling et al., 1968; Aldén, 1971; von Wühlisch & Muhs, 1986; Hallgren & Helms, 1988; Kushida, 2005), gan par ģenētikas (Rone, 1975; Ununger et al., 1988; Danusevičius & Persson, 1998; Danusevičius, 1999; Skrøppa & Steffenrem, 2016) ietekmi. Provenienču pārbaužu stādījumos piecu gadu vecumā Zviedrijas centrālajā daļā egles ar augusta dzinumiem īpatsvars bija no 4% ± 2% proveniencēm ar Zviedrijas ziemeļu izcelsmi līdz 17% ± 3% proveniencēm no Austrijas (Danusevičius & Persson, 1998). Vēl izteiktāks proveniences efekts konstatēts piecu gadu vecumā Norvēģijā, kur egles ar augusta dzinumiem īpatsvars bija 18% Skandināvijas izcelsmes proveniencēm, 28% Latvijas un 54% Slovākijas un Čehijas izcelsmes proveniencēm (Søgaard et al., 2011). Arī deviņām vietējām Norvēģijas populācijām deviņu gadu vecumā bija būtiski atšķirīgs (12% līdz 34%) koku ar augusta dzinumiem īpatsvars (Skrøppa & Steffenrem, 2019). Atšķirības starp ģimenēm bija būtiskas un ievērojamas, trīs proveniencēs ar lielākajām atšķirībām starp ģimenēm koku ar augusta dzinumiem īpatsvars bija 11%–52%, 18%–64% un 0%–39% (Skrøppa & Steffenrem, 2019). Vecākiem kokiem brīvā augšana ir mazāk raksturīga (Ehrenberg, 1963; Rone, 1985; Søgaard et al., 2011), un egles brīvapputes

1.2. att. **Apikālais augusta dzinums parastajai eglei**

pēcnācēju pārbaužu stādījumos kokiem 20 līdz 25 gadu vecumā konstatēta neliela (4% no pazīmes variācijas), bet joprojām būtiska ģimenes ietekme uz augusta dzinumu veidošanos (Steffenrem et al., 2008).

Kopumā labāk augošiem kokiem apikālais augusta dzinums veidojas biežāk, tādējādi vēl vairāk veicinot to augšanu un mežaudzes ražību (Hoffmann, 1965; Rone, 1975; Danusevičius & Persson, 1998). Biežāka augusta dzinumu sastopamība un līdz ar to straujāka koku augšana jaunaudzes vecumā paaugstinātas temperatūras apstākļos ir pierādīta laboratorijas eksperimentos (Johnsen, 1989; Kvaalen & Johnsen, 2008), un arvien biežāka augusta dzinumu sastopamība jaunaudzēs vērtēta kā klimata pārmaiņu sekas (Kvaalen et al., 2010; Søgaard et al., 2011). Augusta dzinumu sastopamība var būt saistīta ar sala bojājumiem to nepietiekamas salcietības dēļ un ar stumbra defektu (dubultās galotnes vai padēlu) veidošanos (Gabrilavičius & Danusevičius, 2003; Pallardy, 2008; Søgaard et al., 2011; Granhus et al., 2019).

1.3. Lokālo apstākļu ietekme

Skujkoku mežaudžu paššējas atjaunošanās auglīgos hemiboreālajos mežos ir apgrūtināta (Holgén & Hånell, 2000). Lai gan sekmīga egles mežaudžu atjaunošanās iespējama gan ar paaugas kokiem pieaugušā mežā (Luguza et al., 2020), gan jaunaudzēs pēc atjaunošanas cirtes veikšanas auglīgajos meža tipos (Luguza et al., 2019), abos gadījumos tā ir laikietilpīga un atkarīga no sēklu pieejamības. Stādītas egles spēj labāk konkurēt ar zemsedzes veģetāciju (Holgén & Hånell, 2000). Turklāt šādas jaunaudzes ir arī ražīgākas nekā dabiski ieaugušās (Gradeckas & Malinauskas, 2005). Tas saistīts gan ar selekcionēta stādmateriāla izmantošanu (Jansons et al., 2015), gan ar augsnes sagatavošanas labvēlīgo ietekmi uz augšanu (Nordborg et al., 2003; Heiskanen et al., 2013).

Augsnes sagatavošanu var veikt, izmantojot dažādas metodes (Mangalis, 2004; Gradeckas & Malinauskas, 2005), no kurām Baltijas valstīs visbiežāk pielietota augsnes sagatavošana vagās ar disku arklu. Augsnes mitrums pēc tās apstrādes ne vienmēr ir piemērots stādu augšanai. Teritorijās ar normālu (noregulētu) mitrumu vagās un pacilās stādītu koku saglabāšanās ir līdzvērtīga, bet paaugstināta mitruma apstākļos saglabāšanās vagās ir ievērojami un būtiski zemāka nekā uz pacilām (Örlander et al., 1990, 1998). Pacilas nodrošina egles augšanai piemērotu augsnes mitrumu, kas ir īpaši svarīgi to izdzīvošanai pirmajos gados pēc stādīšanas (Schlyter et al., 2006).

Līdzīgi kā citas augsnes sagatavošanas metodes, arī pacilas samazina zemsedzes veģetācijas konkurenci, bet šis efekts saglabājas ilgāku laika periodu (Lehtosalo et al., 2010). Piemēram, Somijā ar pacilām gatavotā augsnē agrotehnisko kopšanu bija nepieciešams veikt tikai otrajā līdz ceturtajā gadā pēc stādīšanas relatīvi auglīgā augsnē, un ceturtajā līdz sestajā gadā pēc stādīšanas zemas auglības augsnē (Saksa, 2008; Uotila et al., 2010). Pacilas arī veicina augsnes temperatūras paaugstināšanos vairāk nekā citas augsnes gatavošanas metodes (Örlander et al., 1990; Sutton, 1993), un uzlabo lokālos apstākļus. Koki uz pacilām mazāk cieš no sala (Langvall et al., 2001; Heiskanen et al., 2013) un lielā priežu smecernieka (*Hylobius abietis* (L.)) radītajiem bojājumiem (Örlander et al., 1990; Heiskanen & Viiri, 2005; Saksa, 2008; Heiskanen et al., 2013). Turklāt pacilu virzienā no augšas uz leju veido apgriezta minerālaugsne un humusa slānis, neskarts humusa slānis un minerālaugsne, un izveidotais dubultais augsnes organiskais slānis labvēlīgi ietekmē sākotnējo koku augšanu (Nordborg et al., 2003; Saksa et al., 2005; Hallsby & Örlander, 2013; Heiskanen et al., 2013).

Barības vielu pieejamībai ir būtiska ietekme uz koku augšanu, un augsnes ielabošana ir efektīvākais veids, kā paaugstināt egles mežaudžu ražību (Nohrstedt, 2001; Saarsalmi & Mälkönen, 2001; Sicard et al., 2006). Pelni satur augiem nepieciešamās barības vielas, piemēram, kāliju, kalciju, magniju, fosforu, nātriju (Levula et al., 2000; Demeyer et al., 2001). Augsnes ielabošana ar pelniem samazina augsnes skābumu (pH) un bagātina augsni ar fosforu, kāliju un mikroelementiem (Ingerslev et al., 2014), un platībās, kur slāpeklis nav augšanu limitējošs faktors (īpaši, kūdras augsnēs), tā ievērojami uzlabo koku augšanu (Huotari et al., 2015). Turklāt pelnu izmantošana papildus barošanās elementu ienesei ļauj ilgtspējīgi izmantot koksnes pārstrādes blakusproduktus (barības vielas, kas izvāktas ar koksni, daļēji tiek atgrieztas mežā), kas citādi tiek deponēti kā rūpnieciskie atkritumi poligonos (Knapp & Insam, 2011; Väätäinen et al., 2011; Huotari et al., 2015).

Papildus barošanās elementu ieneses veicinātā straujā augšana skujkokiem var atstāt iespaidu arī uz koksnes uzbūvi (piemēram, šūnu sieniņu biezumu), tādējādi ietekmējot koksnes blīvumu un kvalitāti (Mäkinen et al., 2002; Lundgren, 2004; Cao et al., 2008). Ietekme uz augšanu atkarīga no augsnes ielabošanas līdzekļa izkliedēšanas laika un ķīmiskā sastāva (kontekstā ar augsnes ķīmisko sastāvu) un devas (Ingerslev, 1997; Nohrstedt, 2001). Kopumā papildus barības vielu lokāla pievienošana stādīšanas brīdī veicina stādu augšanu un konkurētspēju ar zemsedzes veģetāciju (Sicard et al., 2006), kam ir nozīmīga loma mežaudzes tālākajā attīstībā (Sutton, 1995; Hytönen & Jylhä, 2008).

1.4. Iedzimtība

Koka augstums ir tieši saistīts ar mežaudzes ražību, un tas tiek lietots kā viens no galvenajiem kritērijiem genotipu atlasei selekcijas procesā (Ekberg et al., 1985; Hannerz, 1993; Danusevičius & Gabrilavičius, 2001; Kroon et al., 2011). Selekcijas efekts konkrētai pazīmei atkarīgs no tās variācijas (iespējas atlasīt vēlamo) un ģenētiski noteiktās daļas šajā variācijā, ko raksturo iedzimstamības koeficients. Kopumā lielāks selekcijas efekts iegūstams, atlasot pazīmes ar augstu iedzimstamības koeficienta vērtību apstākļos (stādījumos), kur konkrētās pazīmes ģenētiski noteiktās atšķirības ir skaidri izteiktas (Kroon et al., 2011). Koka augstums parasti raksturojams ar augstāku iedzimstamības koeficientu nekā caurmērs. Pētījumu apkopojumā Jansson et al. (2013) analizējis egles selekcijas aditīvā ģenētiskā efekta noteiktā iedzimstamības koeficienta h^2 (*narrow sense heritability*) vērtības, kas augstumam ir 0,05–0,36, augstuma pieaugumam 0,04–0,47, caurmēram 0,09–0,27. Atsevišķos gadījumos visa ģenētiskā efekta noteiktais iedzimstamības koeficients H^2 (*broad sense heritability*) sasniedzis 0,54 un augstāku rādītāju (Hannrup et al., 2004; Kowalczyk, 2005). Salīdzinot ar caurmēru, augstumu mazāk ietekmē audzes biezums (konkurences apstākļi) un citi ar mežkopības paņēmieniem maināmi rādītāji. Dažādas pazīmes ir savstarpēji ģenētiski saistītas, un to ģenētiskā korelācija nosaka, kā un cik lielā mērā, atlasot kokus pēc vienas pazīmes, ietekmētas citas pazīmes (Kroon et al., 2011). Augstuma pozitīvā ģenētiskā korelācija ar vairumu stumbra kvalitāti raksturojošo rādītāju (Haapanen, 1997) ļauj to izmantot par nozīmīgāko pazīmi labāko ģimeņu atlasē pēcnācēju pārbaudēs.

Labāko genotipu atlase sniedz ievērojamu mežaudzes krājas un kvalitātes uzlabojumu. Norvēģijā atlasītu egles ģimeņu pēcnācējiem 21 gada vecumā konstatēts par 14% lielāks augstums ($p < 0{,}001$) nekā vietējas izcelsmes provenieņcēm (Skrøppa et al., 2007). Egles selekcija Norvēģijā ļāvusi samazināt aprites ciklu par 5 līdz 10 gadiem un palielinājusi tīro tagadnes vērtību (*net prestent value*) no 30% līdz 400% (Kvaalen (2010) citēts pēc Jansson et al. (2017)), bet Zviedrijā iekšējās atmaksāšanās likme (*internal rate of return*) palielinājusies līdz 5,3%–8,3% (Simonsen et al., 2010).

Fenoloģijai ir nozīmīga loma koku izdzīvošanas un adaptācijas nodrošināšanā. Gan augšanas uzsākšana, gan pārtraukšana ir daļēji ģenētiski determinēta (Hannerz, 1998, 1999), un arī augšanas laiks un ilgums atšķiras starp dažādām provenieņcēm, ģimenēm un kloniem (Skrøppa et al., 1999). Arī meteoroloģiskie faktori ietekmē koku fizioloģisko aktivitāti, piemēram, temperatūra nosaka pumpuru plaukšanas un augstuma pieauguma sākšanas laiku (Hannerz, 1999) un intensitāti (Sarvas, 1973; Danusevičius et al., 1999). Genotipa un vides mijiedarbība nosaka to, ka viena un tā pati pazīme, piemēram, augšanas uzsākšanas laiks konkrētam genotipam dažādos apstākļos var izpausties atšķirīgi (Kroon et al., 2011). Ja šāda mijiedarbība pastāv un ir sasaistāma ar augšanas vai klimatiskajiem apstākļiem vai ģeogrāfisko novietojumu, šo informāciju iespējams izmantot reģionāliem apstākļiem piemērotu populāciju atlasei, tādējādi paaugstinot selekcijas ieguvumu.

Viena no svarīgākajām genotipa un vides mijiedarbībām saistīta ar sala bojājumu risku (Granhus et al., 2009; Søgaard et al., 2009). Boreālajos un arī hemiboreālajos mežos nozīmīga loma koku izdzīvošanā un vitalitātē ir augšanas ritma (*growth rythm*) saskaņotībai ar klimatiskajiem apstākļiem, īpaši agrīnā vecumā. Tas, savukārt, ietekmē koku ātraudzību. Piemēram, genotipi, kas uzrāda labu augšanu vietās ar augstu pavasara salnu risku, var nebūt starp labāk augošajiem kokiem vietās ar zemu salnu risku (Berlin et al., 2014). Klimatam kļūstot siltākam, koki augšanu var uzsākt agrāk (Danusevičius et al., 1999), bet tie tiek pakļauti lielākam sala bojājumu riskam (Polle et al., 1996), jo līdz ar temperatūras paaugstināšanos biežākas un izteiktākas kļūst arī temperatūras novirzes (ekstrēmi) no ilgtermiņa novērojumu vidējās vērtības (Avotniece et al., 2012). Šīs pārmaiņas visizteiktāk skar jaunus, brīvi augošus kokus, īpaši jaunaudzēs pēc atjaunošanas cirtes (Langvall & Löfvenius, 2002). Mazināt genotipa un vides mijiedarbības negatīvo ietekmi var divējādi – gan atlasot katriem konkrētiem vides apstākļiem piemērotus klonus, gan atlasot genotipus, kas uzrāda atbilstošus rezultātus dažādos apstākļos (St Clair & Kleinschmit, 1986). Turklāt eglēm piemīt epiģenētiskā atmiņa (*epigenetic memory*), t.i., pumpuru plaukšanas fenoloģiju, sala noturību (*frost hardiness*) un augšanas uzsākšanas laiku īstermiņā ietekmē rudens temperatūra (Granhus et al., 2009; Søgaard et al., 2008), bet ilgtermiņā – temperatūra embrija veidošanās laikā (Yakovlev et al., 2010; Solvin & Steffenrem, 2019), kas ļauj ātrāk pielāgoties klimata pārmaiņām.

1.5. Promocijas darba mērķis

Promocijas darba mērķis ir raksturot lokālo apstākļu un iedzimtības ietekmi uz juvenila vecuma parastās egles (*Picea abies* (L.) H. Karst.) augstuma pieaugumu stādot atjaunotos hemiboreālajos mežos Latvijā.

1.6. Promocijas darba uzdevumi

Promocijas darbā izvirzīti trīs uzdevumi:

1. raksturot lokālo apstākļu (zemsedzes veģetācijas konkurence un augsnes mitrums) un iedzimtības ietekmi uz egles apikālajiem augusta dzinumiem (**I** un **II**);
2. raksturot barības vielu nodrošinājuma uzlabošanas ietekmi uz egles augstuma pieaugumu (**III**, **IV** un **V**);
3. raksturot egles pluskoku brīvapputes pēcnācēju ģimeņu ikgadējā augstuma pieauguma veidošanās atšķirības (**VI** un **VII**).

1.7. Promocijas darbā izvirzītās tēzes

Promocijas darbā izvirzītas divas tēzes:

1. lokālo apstākļu uzlabošana jaunaudzēs veicina egles apikālo augusta dzinumu veidošanos;
2. iedzimtība ietekmē gan iepriekšnoteiktā augstuma pieauguma veidošanās dinamiku sezonas ietvaros, gan apikālo augusta dzinumu veidošanos.

1.8. Zinātniskā novitāte

Pirmo reizi vērtēta lokālo apstākļu ietekme uz parastās egles apikālo augusta dzinumu veidošanos hemiboreālajos mežos. Tāpat pirmo reizi hemiboreālajos mežos raksturota egles apikālo augusta dzinumu kumulatīvā ietekme uz pirmās vecumklases egles augstumu.

Pirmo reizi Latvijā raksturota stādvietas un augsnes ielabošanas ar koksnes pelniem pirms stādīšanas ietekme uz egles augstumu 10 gadu laika posmā.

2. MATERIĀLI UN METODES

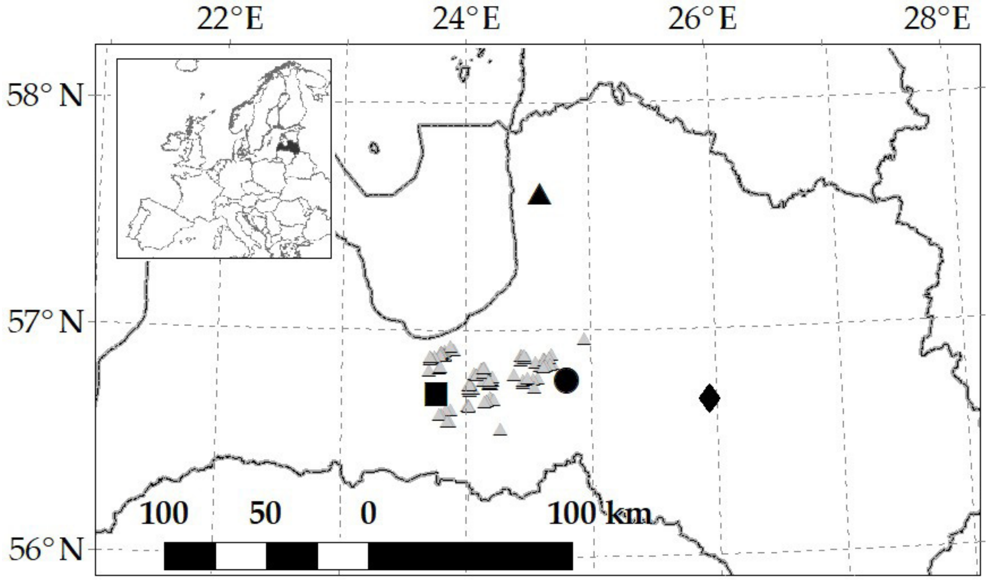
Egles augstuma pieaugums (iepriekšnoteiktais pieaugums un apikālais augusta dzinums) atkarībā no lokālajiem apstākļiem un citiem faktoriem (**I**, **II** un **VII**), stādvietas sagatavošanas veida un papildus barības vielu nodrošinājuma (**III**, **IV** un **V**) un iedzimtības (**VI** un **VII**) vērtēts galvenokārt Latvijas centrālajā daļā (2.1. att.), hemiboreālo mežu zonā (Barbati et al., 2007).

2.1. Augusta dzinumi

2.1.1. Datu ievākšanas metodika

Egles apikālā augusta dzinuma sastopamība, tā veidošanās saikne ar koku augšanas apstākļiem un to izmaiņām, kā arī saistība ar koku augstumu novērtēta stādītās mežaudzēs (**I**) un brīvapputes pēcnācēju pārbaužu stādījumos (**II** un **VII**).

Kopumā nejauši izvēlētas 102 mežaudzes (**I**) trīs līdz septiņu gadu vecumā astoņos meža tipos: damaksnī (Dm, *Hylocomiosa*), vērī (Vr, *Oxalidosa*), slapjajā damaksnī (Dms, *Myrtilloso-sphagnosa*), slapjajā vērī (Vrs, *Myrtilloso-polytrichosa*), šaurlapju ārenī (As, *Myrtillosa mel.*), platlapju ārenī (Ap, *Mercurialiosa mel.*), šaurlapju kūdrenī (Ks, *Myrtillosa turf. mel.*), platlapju kūdrenī (Kp, *Oxalidosa*

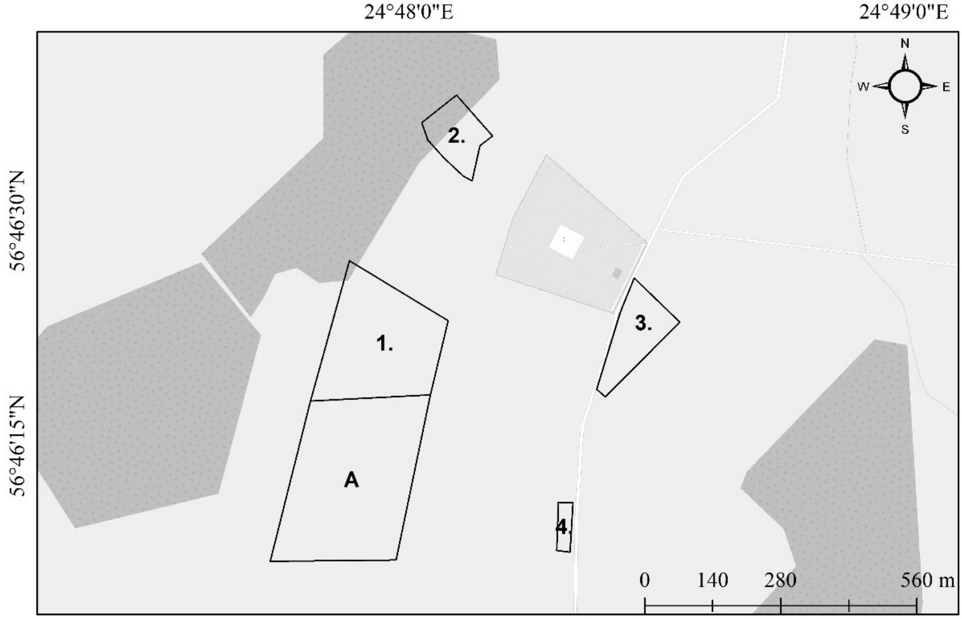


2.1. att. **Pētījuma objektu izvietojums**
Pelēkie trijstūri (▲) – mežaudzes (**I**), melnais aplis (●) – Rembate (**II** un **VII**),
melnais kvadrāts (■) – Jelgava (**VI** un **VII**), melnais trijstūris (▲) – Viļķene (**III**),
melnais rombs (♦) – Kalsnava (**IV** un **V**)

turf. mel.). Dati ievākti 2011. gada nogalē. Atkārtota datu ievākšana veikta daļā šo audžu (21 audzē) 2012. gada nogalē. Visas mežaudzes atjaunotas stādot, mežaudžu platība ≥0,5 ha.

Katrā mežaudzē uz tās garākās diagonāles izveidoti 20 apļveida parauglaukumi (platība 25 m²). Katrā parauglaukumā noteikts egļu skaits ar un bez augusta dzinumiem. Par augusta dzinumu šajā promocijas darbā uzskatīts tikai apikālais augusta dzinums, t.i., galvenā dzinuma galotnes pumpura atkārtota plaukšana un augšana pēc iepriekšnoteiktā augstuma pieauguma pārtraukšanas. Uzskaitīti tikai tie augusta dzinumi, kuru garums sasniedzis vismaz vienu centimetru. Atsevišķi 70 mežaudzēs no iepriekš minētajām (2011. gadā 56 mežaudzēs, 2012. gadā 14 mežaudzēs) vērtēta lokālo apstākļu piemērotība egles augšanai (t.sk., trīs faktori – konkurējošā veģetācija, augsnes mitrums un briežu dzimtas dzīvnieku radīti bojājumi), šos parametrus nosakot katrā parauglaukumā. Katrs faktors vērtēts trīs ballu skalā: a) egles augstuma attiecība pret konkurējošās veģetācijas (t.i., lakstaugi, avenes, krūmi, koki) augstumu 0,5 m rādiusā (1 balle: <0,75; 2 balles: 0,75–1,25; 3 balles: >1,25); b) augsnes mitrums (1 balle: sugai piemērots (atbilstošs) mitruma līmenis; 2 balles: periodiski paaugstināts mitruma līmenis; 3 balles: pastāvīgi paaugstināts mitruma līmenis); c) parauglaukumā bojāto (t.i., bojājumi galvenajam un/vai vairāk nekā 50% sānu dzinumu) koku īpatsvars (1 balle: <1%; 2 balles: 1%–10%; 3 balles >10%). Kopējās lokālo augšanas apstākļu un dzīvnieku radīto bojājumu ietekmes vērtēšanai katram parauglaukumam visu iepriekš minēto faktoru balles summētas, iegūstot no trim (egles augšanai visatbilstošākā) līdz deviņām (visneatbilstošākā) ballēm. Mežaudžu līmenī koku ar augusta dzinumiem īpatsvars aprēķināts kā parauglaukumu vidējā vērtība (± 95% ticamības intervāls); tāpat aprēķināts arī koku ar dzīvnieku radītiem bojājumiem īpatsvars. Meteoroloģiskie dati iegūti no trim tuvākajām meteoroloģiskajām stacijām (Rīgā, Dobelē un Skrīveros).

Egles pluskoku pēcnācēju ģimeņu atšķirības apikālo augusta dzinumu veidošanā, kā arī šo dzinumu attīstības saikne ar koku augstumu, augstuma pieaugumu, pumpuru plaukšanas laiku un sala radītiem bojājumiem vērtēta brīvapputes pēcnācēju pārbaužu stādījumos Ķeguma novada lauku teritorijā, turpmāk tekstā – Rembatē (**II** un **VII**). Rembatē dati ievākti 2 stādījumos: Rembate-A (**II**) un Rembate-B (**II** un **VII**) (2.2. att.). Stādījums Rembate-A ierīkots auglīgā lauksaimniecības zemē (atbilst Vr meža tipam) 2010. gada pavasarī ar trīsgadīgiem kailsakņu stādiem. Pārstāvētas 60 ģimenes 4–8 atkārtojumos, 12 koki parcelē (vienā rindā), stādīšanas attālums 2,5 × 2,5 m. Rembate-B stādījums izvietots četros savstarpēji netālu esošos laukos (turpmāk tekstā "Lauks 1–4") auglīgā lauksaimniecības zemē (atbilst Vr meža tipam) ar nedaudz atšķirīgu augsni un mikroreljefu. Stādījums ierīkots 2005. gada pavasarī ar trīsgadīgiem kailsakņu stādiem, kopumā pārstāvētas 140 ģimenes 3–4 atkārtojumos (attiecīgi pa Laukiem 1–4: 138, 77, 95 un 16 ģimenes) 24 koku parcelēs (četras sešu koku rindas), stādīšanas attālums 2 × 2,5 m. Datu analīzei (**II**) no stādījuma Rembate-B izmantoti mērījumi, kas iegūti Laukos 1, 3, 4 (publikācijā **II** apzīmēti attiecīgi kā 1, 2, 3).



2.2. att. **Rembates brīvapputes pēcnācēju stādījumu izvietojuma shēma: Rembate-A (A), un Rembate-B Lauki (1–4)**

Koku augstums, augstuma pieaugums un augusta dzinumu sastopamība stādījumā Rembate-A vērtēta astotās augšanas sezonas beigās (2014. gada oktobris) 3887 kokiem no 60 ģimenēm, un stādījumā Rembate-B – 10. (2011. gada novembris), 11. (2012. gada oktobris) un 13. (2014. gada novembris) augšanas sezonas beigās, vērtējumam atlasot 3412 kokus no 112 ģimenēm. Pumpuru plaukšana vērtēta stādījumā Rembate-B 11. augšanas sezonas sākumā četru ballu skalā: 1 balle – ļoti vēlu plaukstoši (tekošais pieaugums ≤3 cm); 2 balles – vēlu plaukstoši (3 līdz 6 cm); 3 balles – agri plaukstoši (7 līdz 10 cm); 4 balles – ļoti agri plaukstoši (≥10 cm). Noteikta salnu bojājumu sastopamība.

Ģenētiski determinētās augusta dzinumu veidošanās atšķirības (**VII**) vērtētas stādījumā Rembate-B.

2.1.2. Datu statistiskā apstrāde

Mežaudžu (**I**) koku ar augusta dzimumiem īpatsvara saistība ar audzes biezumu novērtēta ar Spīrmena korelācijas analīzi. Lokālo apstākļu (konkurējošā veģetācija, augsnes mitrums) un dzīvnieku radīto bojājumu ietekme uz koku ar augusta dzinumiem īpatsvaru vērtēta ar bināro loģistisko vispārējo jaukta efekta lineāro modeli (GLMM) programmā R (versija 3.4.3; R Core Team, 2017), izmantojot paketi “lme4” (Bates et al., 2015). Izveidoti trīs modeļi, kuros attiecību starp kokiem ar un kokiem bez augusta dzinumiem parauglaukuma līmenī izmantoja kā atbildes mainīgo. Katrā modelī mežaudzes identifikācijas numurs ņemts vērā kā nejaušais efekts, lai iekļautu iespējamu korelāciju (atkārtoti mērījumi) starp parauglaukumiem no vienas un tās pašas mežaudzes. Pirmajā modelī vērtēta audzes vecuma un meža tipa ietekme, izmantojot datu kopu par 102 mežaudzēm (dati ievākti 2011. gadā). Otrajā modelī vērtēta lokālo apstākļu, dzīvnieku radīto bojājumu un novērojumu veikšanas gada ietekme, izmantojot datu kopu par 70 mežaudzēm (dati ievākti 2011. un 2012. gadā). Balstoties uz šo pašu datu kopu, vērtēta kopējā lokālo apstākļu (atsevišķu faktoru vērtējumu summa) piemērotības ietekme. Vispārināto lineāro hipotēžu tests (pakete “multcomp” (Hothorn et al., 2008)) izmantots gradācijas klašu savstarpējai salīdzināšanai, ja GLMM analīzē faktoru mijiedarbība vai faktors ar vairāk nekā divām gradācijas klasēm uzrādīja būtisku rezultātu.

Parastās egles brīvapputes pēcnācēju koku datu statistiskā apstrāde veikta, izmantojot vienfaktora dispersijas analīzi (**II** un **VII**), Pīrsona korelācijas analīzi (**II** un **VII**) un Hī-kvadrāta (χ^2) *testu* (**II**).

2.2. Stādvietas sagatavošanas veids un barības vielu nodrošinājums

2.2.1. Datu ievākšanas metodika

Izmantotā stādvietas sagatavošanas veida (**III**) un barības vielu nodrošinājuma (**IV** un **V**) ietekme uz augstuma pieaugumu vērtēta vairākos atsevišķos eksperimentos (2.1. att.).

Augsnes sagatavošanas veida ietekme uz koku augšanu (**III**) vērtēta divās platībās (izdalīti četri meža tipi: Dm, Vr, Vrs un Ks), katrā divos atkārtojumos. Pēc atjaunošanas cirtes veikšanas vienā platībā (Dm un Ks) daļa augsnes sagatavota ar rotējošo pacilotāju un daļa sagatavota vagās ar disku arklu, bet otrā platībā (Vr un Vrs) daļa augsnes sagatavota ar rotējošo pacilotāju un daļa atstāta bez augsnes apstrādes. Pēc augsnes sagatavošanas (2008. gada rudenī) stādīti divgadīgi konteinerstādi (augstums no 16 līdz 36 cm (vidēji 23 ± 0,5 cm), sakņu kakla caurmērs no 1,5 līdz 4,5 mm). Turpmākās četras augšanas sezonas abās platībās veikta agrotehniskā kopšana.

Koku kopējais augstums un trīs pēdējo gadu augstuma pieaugumi uzmērīti 2014./2015. gada ziemā, ar precizitāti līdz vienam centimetram. Zarojuma defekti (galotnes bojājumi, padēli) konstatēti nelielam koku īpatsvaram (<2%) bez saistības ar augsnes sagatavošanas veidu vai platību, un šie koki tālākajā datu analīzē nav iekļauti.

Barības vielu nodrošinājuma uzlabošanas ar pelniem ietekme uz parastās egles augšanu (**IV**) vērtēta platībā ar nosusinātu minerālaugsni (As). Stādījumā ietvertas 18 egles parceles ar 15 m buferjoslām starp tām. Pēc nejaušas izvēles katā no tām gadu pirms stādīšanas izkaisīta viena no koksnes pelnu devām: 0 (kontrole), 5 un 10 t ha^{-1}, katra deva lietota sešās parcelēs. Pelnu ķīmiskais saturs (2.1. tabula) bija līdzīgs literatūrā aprakstītajam (Campbell, 1990; Ozolinčius et al., 2011), pH līmenis 12,4. Stādījums ierīkots augsnē ar augstu slāpekļa saturu (Bārdule et al., 2009), tādēļ papildus slāpekļa mēslojums nav pievienots.

2.1. tabula

Eksperimentā izmantoto un literatūrā aprakstīto pelnu ķīmiskais sastāvs

Ķīmiskais elements	Ķīmiskā elementa saturs izmantotajos pelnos, % [1]	Literatūrā aprakstītais ķīmiskā elementa saturs pelnos, % [2,3]
P	0.92	0.30–1.40
K	2.30	1.40–4.20
Ca	22.00	7.40–33.10
Mg	1.50	0.70–2.20
S	0.38	0.40–0.70
Fe	0.39	0.30–2.10
Mn	0.67	0.30–1.30
Zn	0.11	0.0004–0.0820
Cu	0.0054	0.0052–0.0289
Mo	0.0001	-
B	0.0158	0.0022–0.0225
Na	0.09	-

[1] Brūvelis (2005); [2] Campbell (1990); [3] Ozolinčius et al. (2011).

Divgadīgi egles stādi stādīti gadu pēc pelnu izkaisīšanas (2004. gada pavasarī). Divpadsmit mēnešus pēc stādījuma ierīkošanas aptuveni puse stādu izrakti, un tiem noteikta sakņu un stumbra biomasa. Palikušajiem kokiem 10 gadus pēc stādījuma ierīkošanas (2014. gadā pirms veģetācijas sezonas) mērīts augstums un caurmērs krūšaugstumā. Katrā parcelē ievākti augsnes paraugi atkārtotai augiem pieejamo barības vielu satura un augsnes vides reakcijas noteikšanai. Paraugi sagatavoti atbilstoši LVS ISO 11464 (2005) standartam. Noteikts kopējais slāpekļa (N) saturs (LVS ISO 11261 (2002)), augiem pieejamā fosfora (P-PO_4^{3-}) saturs (LVS 398 (2002)) un kālija (K) saturs (ekstrahēts ar amonija acetātu un noteikts ar atomu spektroskopiju).

Augsnes ielabošanas ar komplekso minerālmēslojumu ietekme (**V**) uz egles augstuma pieaugumu vērtēta egles stādījumā damaksnī. Stādījums ierīkots 1982. gadā ar vietējās provenienences četrgadīgiem kailsakņu stādiem, presētas kūdras briketēs "Brika" (Rubtsow, 1979), iepriekš sagatavotā augsnē ar biezumu 4000 koki ha^{-1}, četros 200 koku blokos. Pēc stādīšanas katram kokam visapkārt 10 cm attālumā apbērts minerālmēslojums, nodrošinot devu 14 g N (NH_4NO_3), 6 g P (superfosfāts) un 11 g K (KNO_3) vienam kokam, kas atbilst attiecīgi 56, 24 un 44 kg ha^{-1}. Pirmajā augšanas sezonā divreiz veikta ķīmiskā veģetācijas ierobežošana ap koku, izmantojot simazīnu koncentrācijā 3 kg ha^{-1}.

Koku augstums un caurmērs krūšaugstumā mērīts 2012. gada februārī 586 kokiem, kuriem veikta augsnes ielabošana stādīšanās brīdī, un 592 kontroles kokiem. Augsnes ielabošanas ilgtermiņa ietekmes vērtēšanai 2013. gada oktobrī (mežaudzes vecums 34 gadi) 30 kokiem, ap kuriem tā veikta, un 30 kontroles valdaudzes kokiem bez redzamiem bojājumiem krūšaugstumā veikti 5 mm urbumi ar Preslera pieauguma svārpstu. Izurbtie koksnes paraugi laboratorijā apstrādāti koksnes analīzes sistēmā LignoStation (RinnTECH Inc., Heidelberg, Germany), katram paraugam iegūstot datus par katras gadskārtas kopējo platumu un vēlīnās koksnes platumu (Schinker et al., 2003).

2.2.2. Datu statistiskā apstrāde

Meža tipa un augsnes sagatavošanas veida ietekme uz koku augstumu, kā arī konkurējošās veģetācijas projektīvā seguma un augstuma atšķirības pirms un pēc agrotehniskās kopšanas, un augsnes sagatavošanas veida ietekme uz agrotehniskajai kopšanai nepieciešamo laiku (**III**) vērtēta ar vienfaktora dispersijas analīzi, starpību būtiskuma vērtēšanai izmantots Tukey kritērijs. Augsnes sagatavošanas veida, meža tipa un abu šo faktoru mijiedarbības ietekme vērtēta ar divfaktoru dispersijas analīzi. Augsnes sagatavošanas veida ietekme uz koku augšanu vērtēta arī 100 mežaudzes augstākajiem kokiem ha^{-1} (Donis, 2014). Augsnes sagatavošanas veida ietekme uz koku augstumu vērtēta ar Hī-kvadrāta (χ^2) *testu*, salīdzinot koku sadalījumu augstuma gradācijas klasēs ($h \leq 1{,}5$ m; $1{,}5 < h \leq 2$ m; $2 < h \leq 2{,}5$ m; $h > 2{,}5$ m) katrā meža tipā. Aprēķini veikti programmā SPSS ar 95% ticamības līmeni.

Dažādas minerālmēslojuma devas ietekme (**IV**) uz NPK sastāvu augsnē un uz koku biomasu un dimensijām salīdzināta, izmantojot vispārinātos lineāros modeļus. Devas ietekme vērtēta ar jaukta efekta modeļiem, parceles numuru pieņemot par nejaušu faktoru.

Papildus barības vielas saņēmušo un kontroles koku gadskārtu platumu mērījumu sērijas (**V**) periodam no 1985. gada līdz 2013. gadam šķērsdatētas un to kvalitāte vizuāli un statistiski pārbaudīta programmā COFECHA (Grissino-Mayer, 2001; Speer, 2010). Sērijas, kas uzrādīja nesaderību ar pārējo sēriju kopu, tika noraidītas, atstājot tālākai datu analīzei 24 koku no platības ar ielabotu augsni un 24 kontroles koku paraugus.

2.3. Pluskoku brīvapputes ģimeņu atšķirības

2.3.1. Datu ievākšanas metodika

Ģenētiski determinēto atšķirību (ģimeņu un provenienču līmenī) ietekme uz augstuma pieauguma veidošanos (**VI** un **VII**) vērtēta divos brīvapputes pēcnācēju pārbaužu stādījumos Latvijas centrālajā daļā (2.1. un 2.2. att.).

Stādmateriāla izcelsmes reģiona ietekme uz augstuma pieauguma veidošanos (**VI**) vērtēta stādījumā Ozolnieku novada teritorijā, MPS Jelgavas mežu novadā, turpmāk tekstā – Jelgavā. Jelgavas stādījums ierīkots 2006. gadā meža zemē (As) ar divgadīgiem kailsakņu stādiem, stādīšanas attālums 3 × 2 m. Pārstāvētas divas provenieces no rietumu un četras provenieces no austrumu meža reproduktīvā materiāla ieguves apgabala (Gailis, 1993). Katra provenience pārstāvēta ar 10 pussibu ģimenēm. Katra ģimene pārstāvēta piecos (atsevišķos gadījumos – četros) atkārtojumos, 12 koku parcelēs (trīs četru koku rindas).

Koku pieauguma mērījumi veikti 2010. gadā, septītajā augšanas sezonā. Izvēlēti 1273 koki bez dubultām galotnēm un redzamiem bojājumiem: 843 koki no apvienota centrālā un austrumu un 430 koki no rietumu provenienču reģiona (meža reproduktīvā materiāla ieguves apgabala). Mērījums veikts garākajam dzinumam katru sesto līdz astoto dienu laika posmā no 25. maija līdz 20. jūlijam (deviņas reizes) ar precizitāti līdz 1 mm. Katrā mērījumu atkārtojumā visi koki mērīti vienā un tajā pašā dienā. Koku kopējais augstums pēc pieauguma pārtraukšanas mērīts 10. septembrī.

Ģimenes ietekme uz augstuma pieauguma veidošanos (**VII**) vērtēta egles brīvapputes pēcnācēju pārbaužu stādījumā Rembate-B, Laukā-1 (aprakstu sk. 2.1.1.) un Jelgavā (aprakstu un mērījumu veikšanas metodiku sk. 2.3.1.-VI). Stādījumā Rembate-B mērījumi veikti devītajā augšanas sezonā. Stādījums sākotnēji apsekots katru otro dienu, lai noteiktu pumpuru plaukšanas laiku (*bud burst*), t.i., kad aptuveni pusei no kokiem plauka pumpuri. Augstuma pieauguma mērījumi turpmāk veikti reizi nedēļā kokiem bez redzamiem dzīvnieku, kukaiņu radītiem bojājumiem vai lauztu galotni. Kopumā stādījumā Rembate-B mērījumi veikti 88 ģimenēm, 1766 kokiem (vidēji 20 koki no ģimenes). No Jelgavas stādījumā ievāktajiem datiem ģimenes ietekmes vērtēšanai izmantoti dati par 59 ģimenēm, 1239 kokiem (vidēji 21 koks no ģimenes).

2.3.2. Datu statistiskā apstrāde

Provenienču reģiona ietekme uz augstuma pieauguma sākšanu (binomiāls mainīgais lielums), nedēļas vidējo augšanas intensitāti (mm, dienā), kopējo augstuma pieaugumu un koka augstumu novērojumu perioda sākumā un beigās vērtēta (**VI**), izmantojot lineāros jauktos modeļus (Zuur et al., 2009). Augstuma pieauguma uzsākšanas un pārtraukšanas laika atšķirības vērtētas ar vispārīgajiem modeļiem, ar atlikumu binomiālu sadalījumu un "logit link" funkciju. Provenineces ietekmes uz augšanu vērtēšanai šie modeļi salīdzināti ar dispersijas analīzi.

Augstuma pieauguma līknes raksturošanai un salīdzināšanai (**VII**), katram kokam augstuma mērījumi aproksimēti ar Gompertz vienādojumu (2.1):

$$f(A) = \alpha \exp(-\beta \exp(-kA)) , \qquad (2.1)$$

kur:

α – asimptota (*asymptote parameter*) – maksimālās vērtības koeficients pieauguma izlīdzināšanās laikā jeb stacionārajā fāzē;

β – pārliekuma punkts (*displacement parameter*) – horizontālās nobīdes koeficients, kas raksturo pieauguma tempa izmaiņu uzsākšanas laiku;

k – pieauguma temps – koeficients, kas raksturo attiecību starp maksimālās vērtības koeficientu jeb asimptotu un pārliekuma punktu;

A – novērojuma diena.

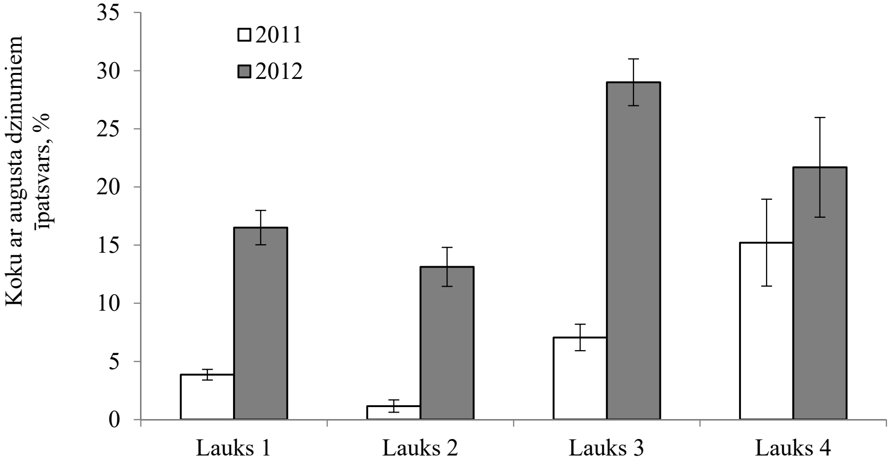
Katra stādījuma ģimenes kārtotas dilstošā secībā pēc to augstuma pieauguma, un pēc ģimenes vidējām vērtībām atlasīti 10% “labāko” un 10% “sliktāko” ģimeņu. Izdalītajām ģimeņu grupām no individuālu koku datiem aprēķināti vidējie pieauguma līkni raksturojošie koeficienti, vidējais augstuma pieaugums, kumulatīvais augstuma pieaugums un kumulatīvais augstuma pieauguma īpatsvars un to 95% ticamības intervāli. Ģimenes ietekme uz šiem rādītājiem noteikta ar vienfaktora dispersijas analīzi, bet saistības starp augšanu raksturojošiem parametriem noteiktas ar Pīrsona korelācijas analīzi.

3. REZULTĀTI UN DISKUSIJA

3.1. Augusta dzinumi

Parastās egles (*Picea abies* (L.) Karst.) jaunaudzes vecumā novērtētajās mežaudzēs un pēcnācēju pārbaužu stādījumos datu ievākšanas periodā (4 gadi) konstatētais koku ar augusta dzinumiem īpatsvars bija robežās no 0% līdz 27%. Brīvapputes pēcnācēju pārbaužu stādījumos konstatētais koku ar augusta dzinumiem īpatsvars bija 6% stādījumā Rembate-A astoņu gadu vecumā un 8,7%, 26,9% un 8,1% stādījumā Rembate-B attiecīgi 10, 11 un 13 gadu vecumā (**II**). Koku īpatsvars ar augusta dzinumiem vismaz vienā no novērojumu gadiem stādījumā Rembate-B bija 32,3% (**II**). Apsekotajās mežaudzēs koku ar augusta dzinumiem īpatsvars vidēji 6,5%, variējot no 0% līdz 25% (**I**). Līdzīgs koku ar augusta dzinumiem īpatsvars (7%) konstatēts Baltijas valstu proveniencēm piecu gadu vecumā stādījumā Zviedrijā (Danusevičius & Persson, 1998), un tādā pašā vecumā Latvijas proveniencēm Norvēģijā (Søgaard et al., 2011), bet atsevišķos gadījumos Norvēģijā mežaudzēs koku ar augusta dzinumiem īpatsvars bijis pat līdz 80% (Kvaalen et al., 2010).

Gan pēcnācēju pārbaužu stādījumos, gan mežaudzēs koku ar augusta dzinumiem īpatsvaram konstatēta nozīmīga starpgadu mainība. Egles mežaudzēs koku ar augusta dzinumiem īpatsvars 2011. gadā bija nedaudz ($p > 0,05$) zemāks nekā 2012. gadā: attiecīgi – 9,1% un 12,9% (**I**). Savukārt pēcnācēju pārbaužu stādījumā Rembate-B (visi lauki kopā) atšķirības starp novērojumu gadiem bija būtiskas ($p < 0,05$) un nozīmīgas: attiecīgi 6,8% un 20,1% (3.1. att.). Augusta

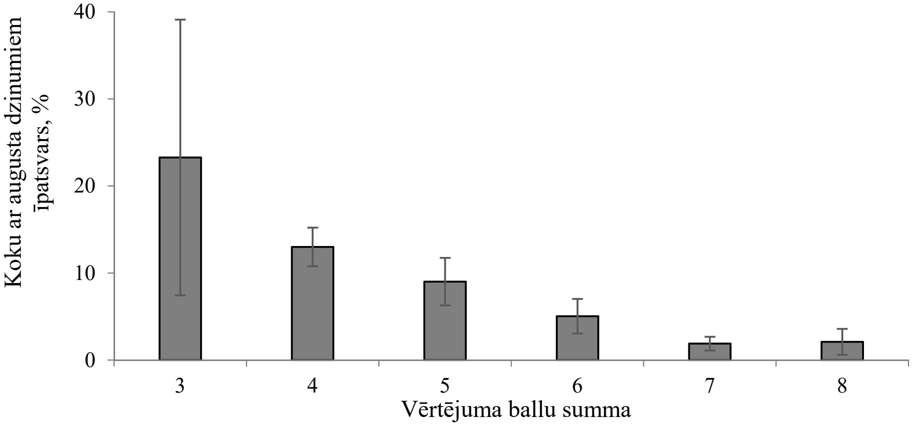


3.1. att. **Vidējais egļu ar augusta dzinumiem īpatsvars (± 95% ticamības intervāls) stādījumā Rembate-B divos uzmērīšanas gados** dzinumu sastopamības mainība tiek saistīta ar meteoroloģisko apstākļu ietekmi, īpaši – gaisa temperatūru to veidošanās laikā (Skrøppa & Steffenrem, 2016). Konstatēts, ka novērojumu veikšanas teritorijā 2011. gadā augusta temperatūra bija nedaudz (vidēji par 3°C) zemāka nekā nākamajā gadā. Analizējot jūlija un augusta temperatūru īsākos laika posmos, 2012. gadā (atšķirībā no 2011. gada) redzams straujš tās pieaugums starp jūlija trešo un ceturto nedēļu (**I**). Iespējams, ka šīs relatīvās meteoroloģisko faktoru izmaiņas atbilstošā augšanas cikla brīdī (ne faktoru vidējās vērtības) ir veicinājušas augusta dzinumu veidošanos. Līdzīgi šāda īstermiņa izmaiņu ietekme palielinātam nokrišņu daudzumam veģetācijas sezonas beigās ir viens no literatūrā biežāk minētajiem augusta dzinumu attīstību stimulējošiem faktoriem (Carvell, 1956; McCabe & Labisky, 1959; Hallgren & Helms, 1988).

Mežaudžu rādītājiem – biezumam, meža tipam un meža tipa-mežaudzes vecuma mijiedarbībai – nebija būtiskas ietekmes uz koku ar augusta dzinumiem īpatsvaru (visos gadījumos $p > 0,05$; **I**), tomēr šāda ietekme iepriekš konstatēta gan vecumam (Ehrenberg, 1963; Aldén, 1971; Rone, 1985; von Wühlisch & Muhs, 1986; Ununger et al., 1988; Søgaard et al., 2011), gan augsnes auglībai (Søgaard et al., 2011). Savukārt stādījumā Rembate-B, kas izvietots savstarpēji netālu esošos laukos auglīgā lauksaimniecības zemē (visi atbilst Vr meža tipam) ar nelielām augsnes un mikroreljefa atšķirībām, koku ar augusta dzinumiem īpatsvars atšķīrās būtiski. Tas bija no 1,2% līdz 15,2% desmit gadu vecumā un no 13,1% līdz 29,0% 11 gadu vecumā, parādot lokālo apstākļu ietekmi uz apikālo augusta dzinumu sastopamību.

Egles mežaudzēs koku ar augusta dzinumiem īpatsvaru ievērojami ietekmējuši gan lokālie apstākļi (zemsedzes veģetācijas konkurence, augsnes mitrums), gan dzīvnieku radīti bojājumi (**I**). Konkurējošās zemsedzes veģetācijas un augsnes mitruma ietekme uz augusta dzinumu veidošanos bija statistiski būtiska ($\chi^2 = 45,0$, $p < 0,001$). Mežaudzēs bez zemsedzes veģetācijas konkurences (vērtējums 1 balle) bija būtiski lielāks koku ar augusta dzinumiem īpatsvars nekā mežaudzēs ar vidēju un lielu konkurenci (2 un 3 balles): attiecīgi – 14,5%, 6,0% un 2,2%. Līdzīgi arī audzēs ar eglei piemērotu augsnes mitrumu koku ar augusta dzinumiem īpatsvars bija lielāks nekā audzēs ar periodiski vai pastāvīgi paaugstinātu augsnes mitrumu: attiecīgi 11,7%, 4,8% un 1,7%. Abos gadījumos statistiski būtiski ($p < 0,05$) no pārējām vērtējuma grupām atšķīrās tikai vislabvēlīgākajos lokālajos apstākļos augošie koki, bet starp pārējām grupām atšķirības nebija būtiskas (**I**). Koku ar augusta dzinumiem īpatsvars bija mazāks dzīvnieku vairāk bojātās audzēs (11,3%, 8,2% un 7,7%, attiecīgi pieaugot vērtējuma ballei), bet atšķirības starp vērtējuma grupām nebija statistiski būtiskas ($p > 0,05$).

Faktoru mijiedarbības analīzes rezultāti liecina, ka katram no šiem faktoriem bija atsevišķa loma augusta dzinumu veidošanās veicināšanā (**I**). Līdz ar to lokālo apstākļu savstarpējai kombinācijai, t.i., zemsedzes veģetācijas konkurences, augsnes mitruma un dzīvnieku radīto bojājumu summāram vērtējumam, bija izteikta būtiska ietekme uz augusta dzinumu veidošanos (3.2. att., **I**). Kokiem, kas auga vislabvēlīgākajos lokālajos apstākļos (vismazākā ballu summa) bija vislielākais



3.2. att. **Vidējais egļu ar augusta dzinumiem īpatsvars (± 95% ticamības intervāls) mežaudzēs atkarībā no lokālo apstākļu (zemsedzes veģetācijas konkurences, augsnes mitruma) un briežu dzimtas dzīvnieku radīto bojājumu vērtējumu summas**

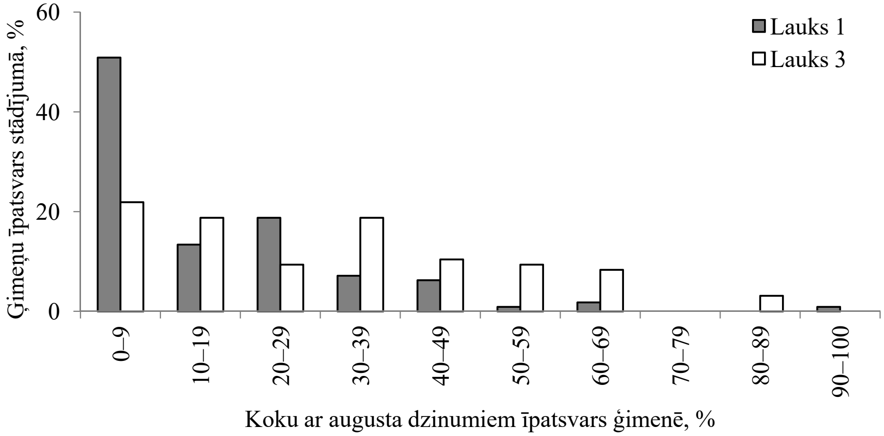
Katrs faktors vērtēts trīs ballu skalā, kur (1) faktora negatīva ietekme uz egles augšanu nav novērota, (2) faktors nedaudz negatīvi ietekmēja egles augšanu un (3) faktors ievērojami negatīvi ietekmēja egles augšanu.

augusta dzinumu īpatsvars. Savukārt, ja vismaz viens no faktoriem kādā audzē novērtēts ar trīs ballēm (ievērojama negatīva ietekme), augusta dzinumu īpatsvars nepārsniedza 10% (**I**). Piemēram, piecus gadus vecā jaunaudzē (Dm) ar izteiktu veģetācijas konkurenci un 22% koku ar redzamiem dzīvnieku radītiem bojājumiem koku ar augusta dzinumiem īpatsvars bija tikai 1,8%, kamēr tāda paša vecuma jaunaudzē tajā pašā meža tipā ar redzamām regulāras zemsedzes veģetācijas ierobežošanas pazīmēm un bez dzīvnieku radītiem bojājumiem koku ar augusta dzinumiem īpatsvars bija 25,5%.

Atkārtoto novērojumu rezultāti liecina, ka augusta dzinumu sastopamības pieaugums varētu būt saistīts ar agrotehnisko kopšanu, kas veikta 2011. gadā (**I**). Piemēram, pēc agrotehniskās kopšanas augšanas sezonas beigās trīs gadus vecā jaunaudzē (Kp) koku ar augusta dzinumiem īpatsvars pieauga no 10% 2011. gadā līdz 26% 2012. gadā, bet piecus gadus vecā jaunaudzē (Dm) – no 18% 2011. gadā līdz 33% 2012. gadā. Līdzīgi, ievērojami lielāka augusta dzinumu sastopamība novērota duglāzijas audzēs pēc konkurējošās veģetācijas ierobežošanas (Roth & Newton, 1996).

Konstatēta būtiska (p < 0,05) ģimenes ietekme uz koku ar augusta dzinumiem īpatsvaru, un šādu koku īpatsvars ģimenēs stādījumā Rembate-B bija no 0% līdz 42%. Labvēlīgos apstākļos, kā tas bija 2012. gadā stādījuma Rembate-B Laukā-3 (auglīgā augsnē, vasarā ar izteiktu gaisa temperatūras paaugstināšanos iepriekšnoteiktā pieauguma veidošanās beigās), apikālo augusta dzinumu veidoja ne tikai lielāks koku īpatsvars ģimenē, bet arī lielāks ģimeņu īpatsvars (3.3. att.).

Pumpuru plaukšanas laiks ir lielā mērā ģenētiski noteikts (Hannerz et al., 1999; Skrøppa & Steffenrem, 2019), un tam konstatēta saikne ar augusta dzinumu

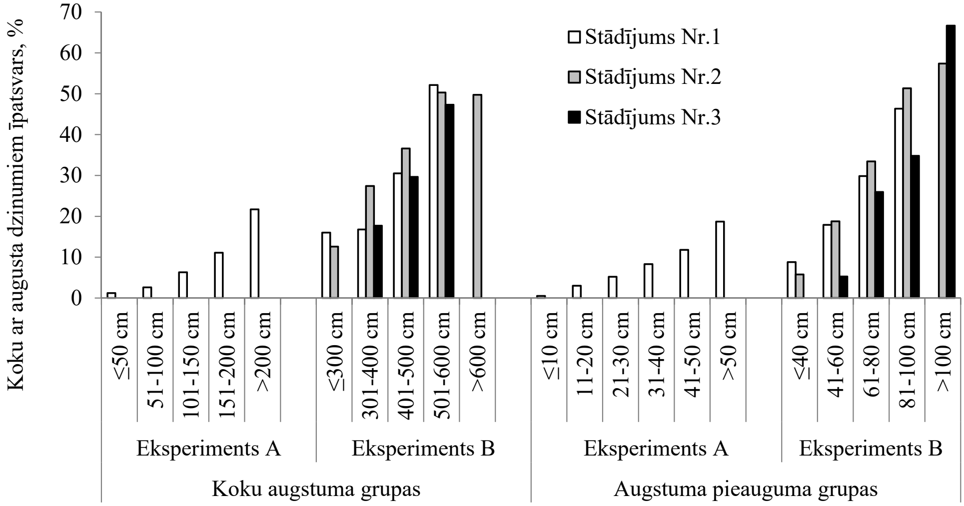


3.3. att. **Ģimeņu īpatsvars ar noteiktu koku ar augusta dzinumiem īpatsvaru stādījumā Rembate-B 11 gadu vecumā**

veidošanos (**II**). Starp agrāk plaukstošajiem kokiem bija proporcionāli vairāk tādu, kas veidoja augusta dzinumus, nekā starp vēlāk plaukstošajiem. Piemēram, otrajā laukā ļoti agri plaukstošo koku grupā (4. plaukšanas balle) 56% veidoja augusta dzinumus, savukārt ļoti vēlu plaukstošo koku grupā (1. plaukšanas balle) – tikai 22%. Katrā no plaukšanas vērtējuma ballēm vidējais augstuma pieaugums bija būtiski ($p < 0,001$) lielāks kokiem ar augusta dzinumiem nekā kokiem bez tiem (**II**). Zviedrijas centrālajā daļā, pretēji šiem rezultātiem, lielāks augusta dzinumu īpatsvars novērots kokiem no vēlu plaukstošām proveniencēm (Danusevičius & Persson, 1998).

Kopumā agrāka plaukšana nodrošināja kokiem priekšrocības, un to augstuma pieaugums bija lielāks nekā vēlāk plaukstošiem kokiem. Tomēr agri plaukstošiem kokiem arī salnu bojājumu risks bija lielāks: bojājumu īpatsvars ļoti agri un agri plaukstošiem kokiem (4. un 3. balle) bija attiecīgi 87% un 2%, kamēr vēlu un ļoti vēlu plaukstošiem kokiem (2. un 1. balle) bojājumi netika konstatēti (**II**). Salnu bojājumiem bija būtiska negatīva ietekme uz augstuma pieaugumu: visagrāk plaukstošo koku (4. balle) augstuma pieaugums kokiem bez salnu bojājumiem bija vislielākais, bet ar sala bojājumiem – vismazākais, atpaliekot pat no visvēlāk plaukstošo koku (1. balle) vidējā pieauguma (**II**). Augusta dzinumu veidošana lielā mērā spēja kompensēt salnu bojājuma negatīvo ietekmi, un kokiem ar augusta dzinumiem salnu radītais augstuma samazinājums bija mazāks nekā kokiem bez augusta dzinumiem (**II**).

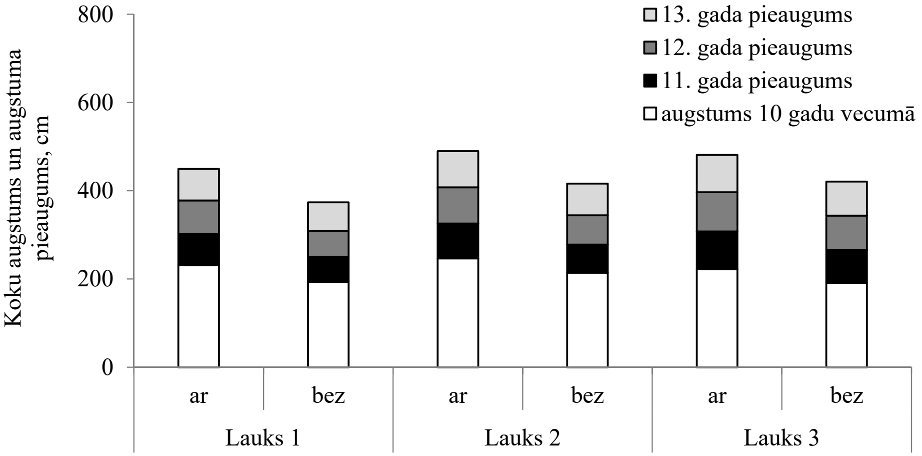
Augusta dzinumu veidošanās saistīta ar koku augstumu. Stādījumā Rembate-A būtiski ($p < 0,001$) lielāks koku ar augusta dzinumiem īpatsvars bija kokiem ar lielāku augstumu, kā arī kokiem ar lielāku pēdējā gada augstuma pieaugumu (3.4. att.), grupās ar augstākām produktivitāti raksturojošo pazīmju vērtībām sasniedzot aptuveni 20%, bet grupās ar zemākajām šo pazīmju vērtībām – tikai aptuveni 1%. Arī stādījuma Rembate-B visos laukos konstatēta līdzīga sakarība – koku grupās ar lielāko augstumu un augstuma pieaugumu augusta dzinumi bija vidēji 47–68% koku, bet lēni augošu koku grupās tie bija tikai 5–18% koku; atšķirības starp grupām bija statistiski būtiskas ($p < 0,001$).



3.4. att. **Koku ar augusta dzinumiem īpatsvars atkarībā no to augstuma un iepriekšējā gada augstuma pieauguma**

Augstuma pieaugums astotajā augšanas sezonā stādījumā Rembate-A bija ievērojami (par 68%) un būtiski ($p < 0,001$) lielāks kokiem ar augusta dzinumiem nekā kokiem bez tiem – attiecīgi 44 ± 2,4 cm un 26 ± 1,7 cm (**II**). Līdzīgi arī stādījumā Rembate-B kokiem ar augusta dzinumiem trīs pēdējo gadu augstuma pieaugums bija statistiski būtiski ($p < 0,001$) lielāks nekā kokiem bez augusta dzinumiem, sasniedzot starpību 10–14 cm. Kumulatīvais efekts šīm augstuma pieauguma atšķirībām bija būtisks ($p < 0,001$): koku augstums 13. augšanas sezonas beigās kokiem ar augusta dzinumiem un kokiem bez tiem stādījumā Rembate-B atsevišķos laukos bija attiecīgi 450 ± 11,8 cm un 374 ± 7,8 cm (Lauks 1), 490 ± 8,1 cm un 416 ± 7,4 cm (Lauks 3, Trial 2), un 481 ± 16,0 cm un 420 ± 12,2 cm (Lauks 4, Trial 3; 3.5. att., **II**). Koki ar augusta dzinumiem tātad bija par 14–20% augstāki nekā koki bez šiem dzinumiem. Arī stādījumā Rembate-A rezultāti bija līdzīgi: astoņu gadu vecumā koku ar augusta dzinumiem vidējais augstums par 29% ($p < 0,001$) pārsniedza koku bez augusta dzinumiem augstumu (attiecīgi 148 ± 5,8 cm un 115 ± 1,4 cm).

Ģimeņu līmenī, stādījumā Rembate-A (**II**) koku īpatsvars ar augusta dzinumiem bija būtiski saistīts ar augstuma pieaugumu ($r = 0,44$; $p < 0,001$), bet ar augstumu korelācija nebija statistiski būtiska ($r = 0,22$; $p = 0,09$). Stādījumā Rembate-B koku īpatsvars ar augusta dzinumiem bija būtiski ($p < 0,01$) saistīts ar augstuma pieaugumu un kopējo augstumu gan stādījumā kopumā (attiecīgi $r = 0,49$ un $r = 0,51$), gan katrā laukā atsevišķi (attiecīgi $r = 0,41...0,71$ un $r = 0,48...0,70$). Sakarība starp koka augstumu un augusta dzinumu veidošanos konstatēta arī iepriekš koku selekcijas stādījumos Latvijā (Rone, 1975) un provenienču pārbaužu stādījumos Zviedrijā (Danusevičius & Persson, 1998).



3.5. att. **Koku augstums desmit gadu vecumā un trīs pēdējo gadu (11.–13. gada) augstuma pieaugums eglēm ar augusta dzinumiem un bez tiem stādījumā Rembate-B**

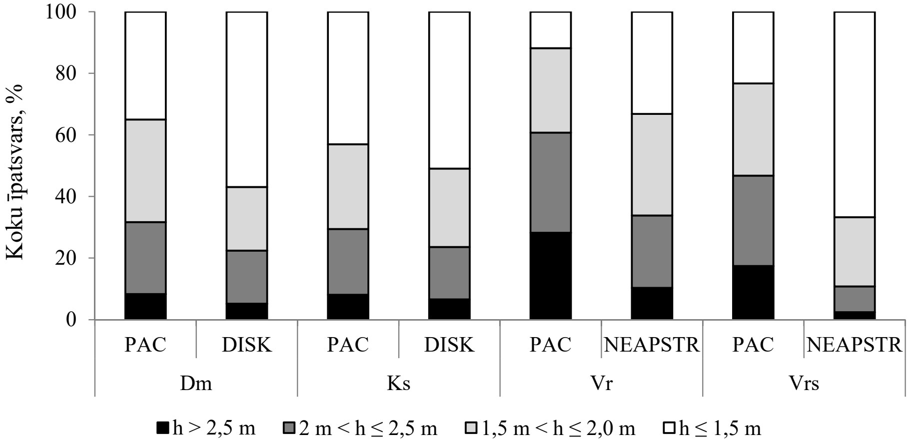
3.2. Stādvietas sagatavošanas veids

3.2.1. Augsnes sagatavošanas ietekme uz augšanu

Koka augstumu astoņu gadu vecumā būtiski ietekmēja meža tips, augsnes sagatavošanas veids un abu šo faktoru mijiedarbība (visi $p < 0,001$, **III**), bet stādījuma atkārtojumam nebija būtiskas ietekmes ($p > 0,05$). Vislielākais koku augstums (neatkarīgi no augsnes sagatavošanas veida) konstatēts kokiem vērī (198 ± 3,8 cm). Līdzīgi arī Lietuvā šāda vecuma koki šajā meža tipā (*Oxalidosa*) sasniedz lielāko augstumu (Gradeckas & Malinauskas, 2005), apliecinot meža tipa piemērotību ražīgu parastās egles mežaudžu veidošanai.

Kokiem, kas stādīti uz pacilām, augstums bija ievērojami un būtiski lielāks nekā kokiem, kas stādīti iepriekš neapstrādātā augsnē (augstuma starpība 27 cm jeb 17,8%) vai vagās (augstuma starpība 55 cm jeb 35,7%). Vērtējot koku īpatsvaru četrās augstuma grupās, visos meža tipos pacilās sagatavotajās platībās konstatēts lielāks augstāko koku īpatsvars salīdzinājumā ar vagās sagatavotajām vai neapstrādātajām platībām (3.6. att.). Koku augstuma atšķirības ar dažādām metodēm gatavotā augsnē bija statistiski būtiskas ($p < 0,05$) vērī un slapjajā vērī, un šāda tendence konstatēta arī damaksnī ($p = 0,05$) un šaurlapju kūdrenī. Līdzīga augsnes sagatavošanas veida ietekme uz egles augstumu konstatēta Somijā (Uotila et al., 2010).

Koku augstuma atšķirības ar pacilotāju gatavotā augsnē, salīdzinot ar citiem augsnes sagatavošanas veidiem, bija būtiskas ($p < 0,05$, **III**) meža tipos minerālaugsnēs ar normālu mitruma režīmu (Dm, Vr), kā arī slapjās minerālaugsnēs (Vrs). Mazāk izteiktas ($p = 0,09$) atšķirības konstatētas šaurlapju kūdrenī. Iespējams, tas saistīts ar sala izcilāšanas (*frost have*) ietekmi, kas Latvijā visbiežāk



3.6. att. **Koku īpatsvara sadalījums augstuma grupās astoņu gadu vecumā ar pacilotāju (PAC) un disku arklu (DISK) sagatavotā augsnē un iepriekš neapstrādātā (NEAPSTR) augsnē damaksnī (Dm), šaurlapju kūdrenī (Ks), vērī (Vr) un slapjajā vērī (Vrs)**

vērojama tieši susinātās kūdras augsnēs (Mangalis, 2004). Somijas centrālajā daļā novērots, ka sala izcilāšana visbiežāk rodas platībās, kur augsne gatavota vagās (Heiskanen et al., 2013). Līdzīgi rezultāti par augstuma pārākumu kokiem, kas stādīti uz pacilām, iegūti vairākos Zviedrijā un Somijā veiktos pētījumos (Saarinen, 2007; Lehtosalo et al., 2010; Uotila et al., 2010; Hallsby & Örlander, 2013). Šajā reģionā konstatētās koku augstuma atšķirības ar dažādām metodēm sagatavotās augsnēs bija mazākas (Örlander et al., 1990, 1998) nekā mūsu pētījumā iegūtajos rezultātos (**III**), kas, iespējams, saistīts ar koku lēnāku augšanu izteiktāka ziemeļu klimata apstākļos.

Pacilu pozitīvā ietekme uz koku augšanu (**III**) saistīta ar paaugstinātu slāpekļa pieejamību (straujāku mineralizāciju) otrajā un trešajā augšanas sezonā (Smolander & Heiskanen, 2007; Nieminen et al., 2012), kas veicina koku virszemes biomasas palielināšanos un sakņu augšanu (Nordborg et al., 2003). Augsnes gatavošana samazina arī lielā priežu smecernieka radītos bojājumus, turklāt šis efekts novērots arī gadījumos, ja stādiem kokaudzētavā veikta apstrāde ar insekticīdu (Heiskanen et al., 2013). Piemēram, pētījumā Somijā pirmajā augšanas sezonā iepriekš neapstrādātā augsnē mizas bojājumi konstatēti 76% egles stādu, savukārt ar pacilām gatavotā augsnē – tikai 1% stādu (Heiskanen & Viiri, 2005). Stādi ar smecernieka radītajiem bojājumiem ir novājināti un veido mazāku augstuma pieaugumu (Heiskanen & Viiri, 2005; Heiskanen et al., 2013). Ņemot vērā, ka pētītās platības (**III**) ierīkotas pēc skujkoku atjaunošanas cirtes veikšanas (t.i., platībās ar vislielāko smecernieka bojājumu risku), augsnes sagatavošana, iespējams, ierobežojusi smecernieka izplatību, tādējādi ietekmējot koku augstuma atšķirības (**III**). Pacilu veidošana labvēlīgi ietekmē arī augsnes temperatūru (Kankaanhuhta et al., 2009; Heiskanen et al., 2016), un kopā ar uzlabotu barības vielu pieejamību un aizsardzību pret smecernieka radītiem bojājumiem veicina stādu labāku ieaugšanu un straujāku sākotnējo augšanu, salīdzinot ar laukumos vai vagās gatavotu augsni.

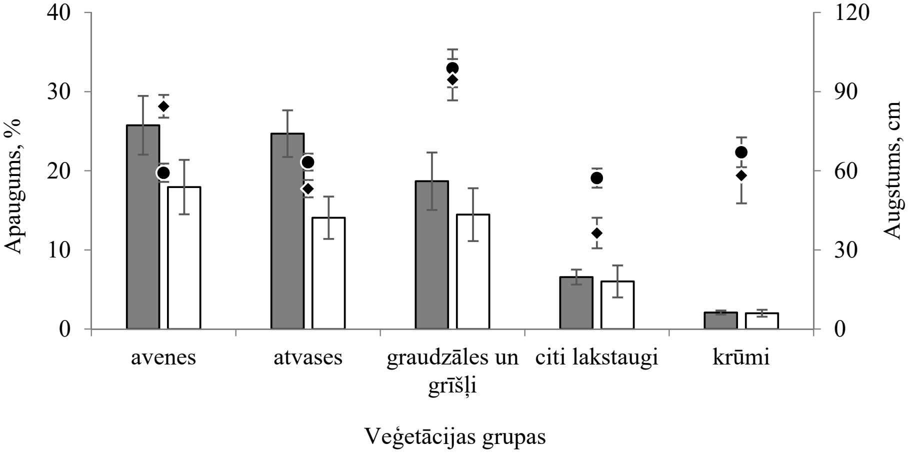
Audzes dominējošo koku pēdējo trīs sezonu augstuma pieaugums ar pacilām sagatavotā augsnē bija lielāks nekā vagās sagatavotā augsnē (**III**). Statistiski būtiskas atšķirības konstatētas damaksnī astotajā augšanas sezonā. Savukārt sestajā augšanas sezonā būtiskas atšķirības nav konstatētas. Astotajā un septītajā sezonā platībās ar pacilās sagatavotu augsni augstuma pieaugums bija lielāks nekā platībās, kur augsnes sagatavošana netika veikta, bet sestajā sezonā būtiskas atšķirības konstatētas tikai slapjajā vērī ($p < 0,05$, **III**). Kopumā iegūtie rezultāti saskan ar konstatēto Somijā: vidējais augstuma pieaugums eglēm, kas stādītas uz pacilām, bija nedaudz lielāks nekā tām, kas stādītas vagās (attiecīgi 23,7 ± 17,4 un 20,6 ± 13,6 cm), un, veidojot kumulatīvu efektu, devītās augšanas sezonas beigās augstuma atšķirības bija būtiskas (Saksa et al., 2005).

3.2.2. Augsnes sagatavošanas ietekme uz konkurējošo veģetāciju

Aizzēlums platības daļā, kur to tieši nav ietekmējis augsnes sagatavošanas agregāts (starp vagām un pacilām), abos augsnes sagatavošanas veidos bija līdzīgs (**III**). Savukārt, vidējais projektīvais veģetācijas segums pirms agrotehniskās kopšanas bija lielāks ar pacilām sagatavotā augsnē, salīdzinot ar vagās sagatavotu augsni: attiecīgi 78% un 54% (**III**). Līdzīgos klimatiskajos apstākļos Lietuvā konstatēts, ka augsnes sagatavošanas veids ietekmē stādu noēnojumu, un līdz ar to arī agrotehniskās kopšanas nepieciešamību. Vismazāk noēnoti ir stādi platās (100 cm) vagās un uz augstām (30 cm) pacilām (Suchockas et al., 2014).

Augsnes sagatavošana palielina konkurējošās veģetācijas sugu daudzveidību (Balandier et al., 2006), bet ne vienmēr augsnes gatavošana izmaina konkurējošās veģetācijas ietekmi uz stādu augšanu. Tās nelabvēlīgā ietekme saistīta tieši ar attālumu līdz stādam, un šo ietekmi var samazināt, palielinot apstrādātās vietas laukumu un apstrādes dziļumu (Suchockas et al., 2014). Platībās, kur augsne sagatavota pacilās un vagās, konkurējošās veģetācijas grupu īpatsvars bija līdzīgs (3.7. att.), un koku/krūmu atvases, avenes (*Rubus ideaeus* L.), graudzāles un grīšļi (*Graminae* un *Cyperaceae* dz.) veidoja lielāko aizzēluma daļu (85% līdz 89%). Arī vidējais svērtais (pēc projektīvā seguma) konkurējošās veģetācijas augstums bija līdzīgs ($p > 0,05$). Pacilās sagatavotā augsnē graudzāļu un grīšļu grupas bija augstākas nekā citas veģetācijas grupas, savukārt, vagās sagatavotā augsnē augstākās veģetācijas grupas bija graudzāles un grīšļi, kā arī avenes (**III**). Graudzāles un grīšļi tiek uzskatīti par nozīmīgāko konkurējošās veģetācijas daļu. Straujās sakņu augšanas dēļ tie intensīvi patērē ūdeni, tādējādi ietekmējot paššējas koku augšanu (Coll et al., 2003). Nepieciešamība ierobežot veģetācijas konkurenci pacilās sagatavotā un vagās sagatavotā augsnē bija līdzīga (**III**).

Veģetācijas projektīvais segums pēc agrotehniskās kopšanas pacilās sagatavotā augsnē bija būtiski zemāks (5%) nekā vagās sagatavotā augsnē (13%), bet tās augstums bija līdzīgs ($p > 0,05$, **III**). Gan pļaušanai nepieciešamais laiks, gan



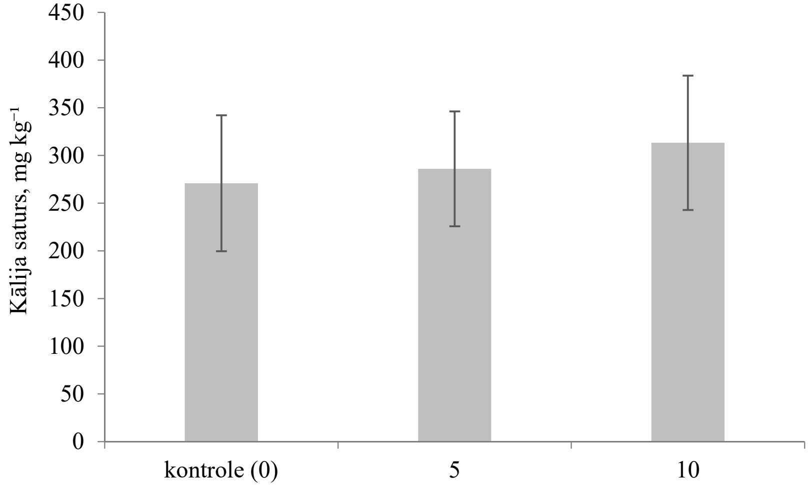
3.7. att. **Konkurējošās veģetācijas projektīvais segums un augstums (abiem ± 95% ticamības intervāls) pirms agrotehniskās kopšanas šaurlapju ārenī pacilās (attiecīgi, pelēkie stabiņi un punkti) un vagās (attiecīgi, baltie stabiņi un rombi) sagatavotā augsnē**

tā īpatsvars no kopējā darbu izpildei nepieciešamā laika bija līdzīgs abiem augsnes sagatavošanas veidiem: 478 min ha^{-1} (67 ± 9,7%) jaunaudzei pacilās sagatavotā augsnē un 462 min ha^{-1} (68 ± 8,3%) jaunaudzei vagās sagatavotā augsnē (**III**).

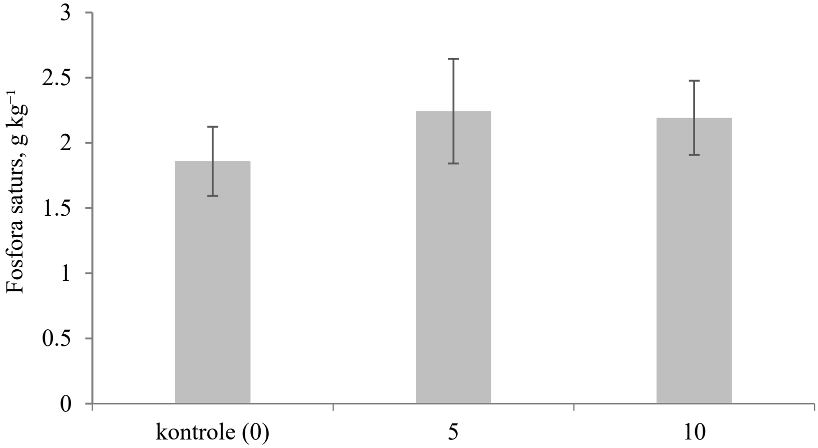
3.2.3. Augsnes ielabošanas ietekme uz koku augstumu

Koksnes sadegšanas procesā vairums augu barošanās elementu saglabājas pelnos, un tie var tikt izmantoti augsnes barības vielu nodrošinājuma uzlabošanai.

Desmit gadus pēc augsnes ielabošanas kālija saturs palielinājās proporcionāli pievienotajai pelnu devai (3.8. att.): kontroles parcelēs kālija saturs bija 270,9 ± 70,3 mg kg^{-1}, bet parcelēs, kas ielabotas ar pelnu devu 5 t ha^{-1} un 10 t ha^{-1}, kālija saturs bija attiecīgi 286,0 ± 60,2 mg kg^{-1} un 313,3 ± 70,5 mg kg^{-1} (**IV**). Līdzīgi ielabošanas ar pelniem pozitīvā ietekme uz kālija deficīta samazināšanu augsnē jau pēc viena gada konstatēta Somijā (Moilanen et al., 2005), turklāt, atkarībā no izmantotās pelnu devas, uzlabotā minerālvielu pieejamība augsnē var saglabāties pat līdz 20–30 gadiem (Moilanen et al., 2002, 2004, 2005). Fosfora satura pieaugums ielabotajās parcelēs bija redzams jau pēc viena gada, tomēr šis ķīmiskais elements šķīst lēni (Nieminen et al., 2005; Callesen et al., 2007), un nepieciešami 3 līdz 4 gadi, lai fosfors augsnē būtu pieejams augiem izmantojamā formā (Moilanen et al., 2002; Nieminen et al., 2005). Desmit gadus pēc augsnes ielabošanas ar 5 t ha^{-1} un 10 t ha^{-1} koksnes pelniem, fosfora saturs augsnē bija attiecīgi 2,24 ± 0,40 un 2,19 ± 0,28 g kg^{-1}, kamēr kontroles parcelēs 1,85 ± 0,27 g kg^{-1} (3.9. att., **IV**). Citos pētījumos konstatēts, ka palielinātā fosfora pieejamība augsnē pēc ielabošanas ar pelniem var saglabāties pat līdz 50 gadiem (Moilanen et al., 2002, 2004, 2005). Slāpekļa vērtības parcelēs ar atšķirīgu pelnu devu bija līdzīgas ($p > 0,05$), no 26,79 ± 3,42 g kg^{-1} kontroles parcelēs līdz 27,42 ± 2,84 g kg^{-1} parcelēs, kuras ielabotas ar 5 t ha^{-1} pelnu devu

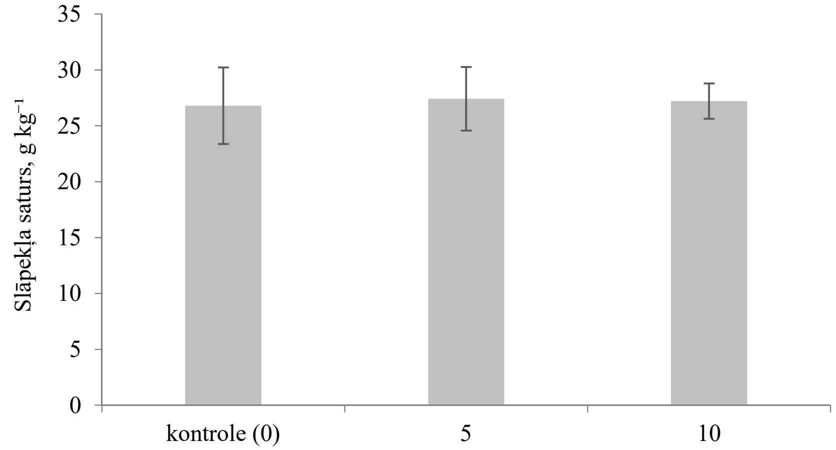


3.8. att. **Kālija saturs augsnē (± 95% ticamības intervāls) parcelēs, kas ielabotas ar atšķirīgu pelnu devu (0 (kontrole), 5 un 10 t ha^{-1}), 10 gadus pēc stādījuma ierīkošanas**



3.9. att. **Fosfora saturs augsnē (± 95% ticamības intervāls) parcelēs, kas ielabotas ar atšķirīgu pelnu devu (0 (kontrole), 5 un 10 t ha^{-1}), 10 gadus pēc stādījuma ierīkošanas**

(3.10. att., **IV**). Koksnes sadegšanas procesā slāpeklis tiek atbrīvots atmosfērā, tādēļ pelnos šis makroelements nav pieejams. Pelnu izmantošanai var būt netieša ietekme uz slāpekļa saturu augsnē – tā veicina paātrinātu organiskās vielas sadalīšanos un organiskā slāpekļa atbrīvošanu augiem pieejamā formā (Moilanen et al., 2002; Genenger et al., 2003; Jäggi et al., 2004). Atsevišķi pētījumi liecina, ka ielabošana ar pelniem var pakāpeniski paaugstināt augsnes organiskā slāņa biezumu (slāpekļa rezervi) palielinātā nobiru apjoma dēļ (Omil et al., 2013), bet desmit gadu periodā pēc augsnes ielabošanas šāds efekts nebija redzams (**IV**). Vienlaikus jāņem vērā,

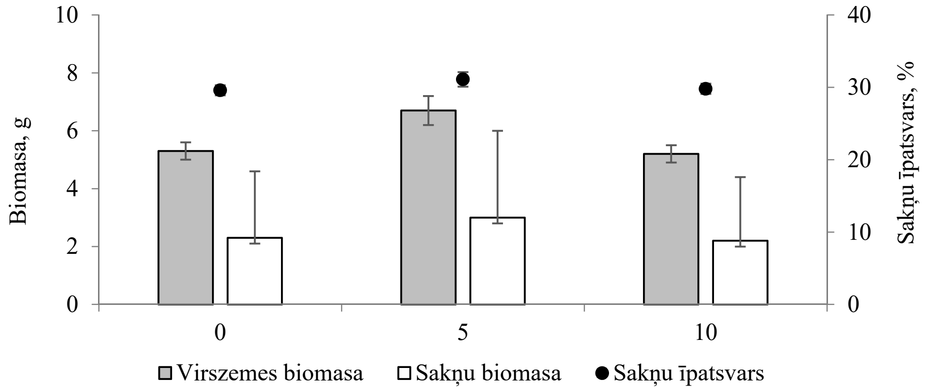


3.10. att. **Slāpekļa saturs augsnē (± 95% ticamības intervāls) parcelēs, kas ielabotas ar atšķirīgu pelnu devu (0 (kontrole), 5 un 10 t ha^{-1}), 10 gadus pēc stādījuma ierīkošanas**

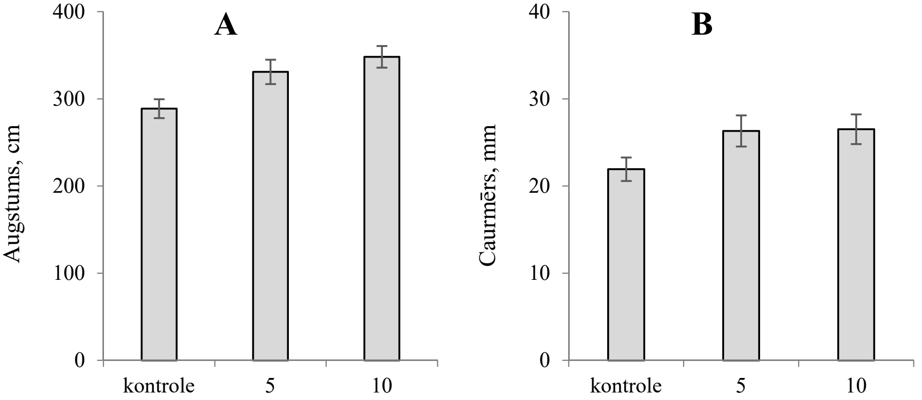
ka papildus atbrīvotais slāpeklis var izskaloties, nonākt atmosfērā slāpekļa oksīdu formā, kā arī to patērē koki un zemsedzes veģetācija. Augsnes ielabošanas mērķis nav slāpekļa satura palielināšana, bet tā pieejamības uzlabošana, un līdz ar to labākas koku augšanas nodrošināšana.

Papildus augu barības vielas veicina stādu sākotnējo augšanu turpmākos pāris gadus, uzlabojot konkurētspēju ar zemsedzes veģetācijas radīto aizzēlumu (Nilsson & Örlander, 1999; Hytönen & Jylhä, 2008). Ielabošana ar pelniem ietekmēja koku biomasas veidošanu jau vienu gadu pēc stādīšanas. Stādu virszemes daļas masas lielākās vērtības konstatētas parcelēs ar pelnu devu 5 t ha^{-1}, salīdzinājumā ar kontroli un 10 t ha^{-1} pelnu devu (3.11. att., **IV**), turklāt atšķirības bija statistiski būtiskas ($p < 0,05$). Novērots, ka arī sakņu masa parcelēs ar 5 t ha^{-1} pelnu devu bija būtiski lielāka ($p < 0,05$) nekā kontroles parcelēs vai parcelēs ar pelnu devu 10 t ha^{-1}. Savukārt sakņu masas īpatsvars parcelēs ar 5 t ha^{-1} bija salīdzinoši lielāks, bet būtiski neatšķīrās no sakņu masas īpatsvara abos pārējos variantos (**IV**).

Desmit gadus pēc stādījuma ierīkošanas pelnu izkliedēšanas ietekme saglabājās, turklāt pieauga līdz ar pelnu devu (3.12. att., **IV**). Caurmērs krūšaugstumā kontroles parcelēs bija 21,9 ± 1,3 mm, bet parcelēs, kas ielabotas ar pelniem 5 t ha^{-1} un 10 t ha^{-1}, caurmērs bija attiecīgi 26,3 ± 1,8 un 26,5 ± 1,7 mm. Augstums kontroles parcelēs bija 289 ± 11 cm, bet parcelēs, kas ielabotas ar pelniem 5 t ha^{-1} un 10 t ha^{-1}, augstums bija attiecīgi 331 ± 14 cm un 348 ± 12 cm. Parcelēs, kur izkliedēti pelni, koku augstums bija par 15% un 21% (attiecīgi, pelnu deva 5 t ha^{-1} un 10 t ha^{-1}) lielāks nekā kontroles parcelēs. Ielabotajās (abas pelnu devas) parcelēs gan augstums, gan caurmērs bija būtiski lielāks (visi $p < 0,05$) nekā kontrolei, bet atšķirības starp parcelēm, kas saņēma pelnu devu 5 un 10 t ha^{-1}, bija nelielas un nebija statistiski būtiskas ($p > 0,05$; **IV**).



3.11. att. **Egles morfoloģiskie parametri (± standartnovirze) parcelēs, kas ielabotas ar atšķirīgu pelnu devu (0 (kontrole), 5 un 10 t ha^{-1}), 12 mēnešus pēc stādījuma ierīkošanas**



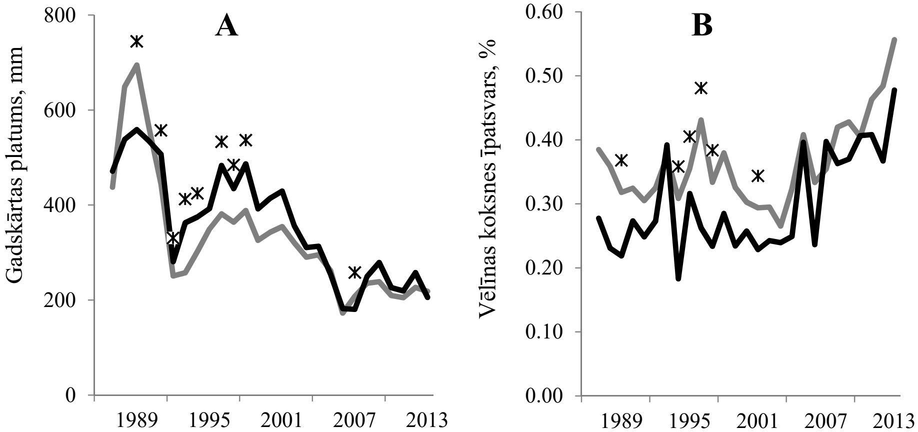
3.12. att. **Koku augstums (A) un caurmērs krūšaugstumā (B) (± 95% ticamības intervāls) parcelēs, kas ielabotas ar atšķirīgu pelnu devu (0 (kontrole), 5 un 10 t ha^{-1}), 10 gadus pēc stādījuma ierīkošanas**

Būtiska ($p < 0,01$) ilgtermiņa augsnes ielabošanas ietekme konstatēta arī kompleksā minerālmēslojuma pievienošanai stādīšanas brīdī (**V**). Papildus barības vielu ienese tikai ap stādu (**V**) radīja līdzīgu efektu, kāds novērots vienlaidus platības ielabošanai (Nohrstedt, 2001; Saarsalmi & Mälkönen, 2001; Cao et al., 2008), bet kopumā bija nepieciešams mazāks minerālmēslojuma daudzums uz platības vienību. Agrīnas augsnes ielabošanas ilgtermiņa efekts uz koku augšanu konstatēts arī Somijas austrumu daļā pirms stādīšanas ielabotajās priežu jaunaudzēs ar minerālaugsni, kur koku augstums 15 gadus pēc augsnes ielabošanas bija par 24% līdz 27% lielāks (pelnu deva attiecīgi 2,5 un 5 t ha^{-1}) nekā kontroles parauglaukumos bez ielabošanas (Saarsalmi & Levula, 2007). Straujāka koku augšana jau vienu gadu pēc ielabošanas ar pelniem (2,5 t ha^{-1}) konstatēta arī vidēja vecuma (pelni ienesti 36 līdz 47 gadu vecumā) egles audzēs (As un Ks meža tipi). Četrus gadus pēc koksnes pelnu izkliedēšanas kumulatīvais papildus krājas pieaugums bija no 8,5 līdz 19,2 m^3 ha^{-1} (Okmanis et al., 2016). Savukārt 64 un 69 gadus vecās priežu audzēs ar minerālaugsni 5 līdz 10 gadus pēc ielabošanas ar pelniem (3 t ha^{-1}) krājas pieaugums bija par 7% līdz 9% lielāks nekā kontroles audzēs, bet šīs atšķirības nebija būtiskas (Saarsalmi et al., 2004).

Salīdzinot konkrētā gadā veidojušās gadskārtas papildus barības vielas saņēmušajiem un kontroles kokiem, vislielākās atšķirības bija redzamas novērojumu perioda pirmajā pusē (3.13. att.).

Pirmos trīs gadus pēc papildus barības vielu ieneses gadskārtas platums bija lielāks kontroles kokiem, savukārt nākošos astoņus gadus gadskārtas platums bija būtiski lielāks papildus barības vielas saņēmušiem kokiem (**V**). Aizkavētā koku reakcija, iespējams, saistīta ar pārāk lielu barības vielu devu vai arī pakāpenisku to pāreju augiem viegli pieejamā formā (Nohrstedt, 2001; Saarsalmi & Mälkönen, 2001), bet tā var būt saistīta arī ar atšķirīgu oglekļa uzkrāšanas stratēģiju kokiem no platības ar ielabotu augsni (Axelsson & Axelsson, 1986).

Kopumā 34 gadu vecumā papildus barības vielas saņēmušiem kokiem šķērslaukums bija par 14% lielāks nekā kontroles kokiem (**V**). Vēlīnās koksnes īpatsvars kontroles kokiem bija lielāks gandrīz visā analizētajā laika posmā, būtiski atšķiroties 1989., 1994. līdz 1997. un 2001. gadā (10 līdz 20 gadu vecumā). Līdzīgi rezultāti par mazāku vēlīnās koksnes īpatsvaru papildus barības vielas saņēmušiem kokiem iegūti arī citos pētījumos (Mäkinen et al., 2002; Zhang, 1995). Kopumā šie rezultāti liecina, ka papildus barības vielu ienese stādīšanas brīdī ietekmēja kokus turpmākos aptuveni 15 gadus (**V**).



3.13. att. **Vidējie gadskārtu platumu mērījumu sērijas parametri kokiem no platības, kur veikta augsnes ielabošana (melnā līkne), un kontroles (pelēkā līkne) kokiem**

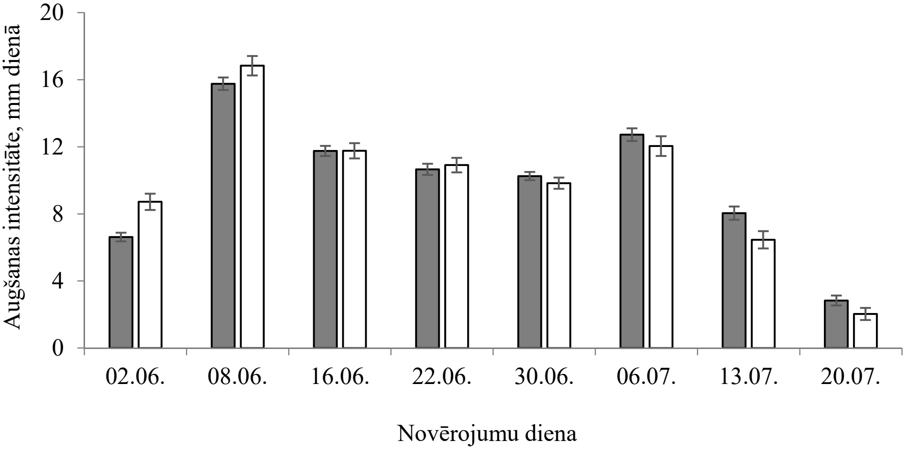
(A) gadskārtas platums, (B) vēlīnās koksnes īpatsvars gadskārtas platumā; būtiskās ($p < 0{,}05$) atšķirības norādītas ar*.

3.3. Pluskoku brīvapputes ģimeņu pieauguma veidošanās dinamika

Augstuma pieauguma veidošanās intensitātes novērtējums ir nozīmīgs, lai prognozētu klimata pārmaiņu ietekmi uz tā summāro garumu un precīzāk atlasītu tādus genotipus, kas šīm pārmaiņām piemērotāki. Sezonas ietvaros augstuma pieaugums nav vienmērīgs, bet tipiski sastāv no trim nosacītiem posmiem: relatīvi lēnākas augšanas uzsākšanas un pārtraukšanas, un intensīvas augšanas starp šiem abiem posmiem (Chuine et al., 2006; Lanner, 2017). Izvērtējot katra posma ietekmi uz kopējo augstuma pieaugumu un ģimeņu augšanas atšķirības šajos posmos, iespējams noteikt to laika posmu sezonas ietvaros, kad vērtējumi jaunos stādījumos var sniegt precīzāku priekšstatu par ģenētiski noteiktajām (ģimeņu) atšķirībām.

Kokiem no atšķirīgiem izcelsmes reģioniem (austrumu un rietumu provenienсes, kopā sešas audzes) augstums un augstuma pieaugums septiņu gadu vecumā bija līdzīgs (atšķirība 1%, p > 0,05), bet sezonas ietvaros konstatēta pieauguma veidošanās intensitātes mainība laikā, ko būtiski ietekmēja ģenētika (provenienсes un ģimenes). Rietumu provenienсes augstuma pieaugumu uzsāka veidot būtiski (p < 0,01) agrāk nekā austrumu provenienсes, un attiecīgi 68,7% un 51,7% koku bija uzsākuši augšanu pirms pirmā mērījuma veikšanas 25. maijā (**VI**).

Augstuma pieauguma veidošanās dinamika abu provenienču reģionu kokiem bija līdzīga. Augšanas intensitāte bija straujāka augšanas sezonas sākumā (3.14. att.), un puse no kopējā pieauguma bija izveidojusies aptuveni 17. jūnijā, t.i., 25 dienas kopš augšanas uzsākšanas. Agrākos pētījumos straujāka augšana konstatēta eglēm no austrumu provenienсēm (Gailis, 1993). Šādu atšķirību starp



3.14. att. **Vidējā augšanas intensitāte (± 95% ticamības intervāls) eglēm no austrumu (pelēkie stabiņi) un rietumu (baltie stabiņi) provenienсēm septītajā augšanas sezonā**
Norādītais datums atbilst aprēķinam izmantotā perioda pēdējai dienai.

proveniencēm trūkumu Jelgavas stādījumā veicināja gan līdzīgs augšanas perioda ilgums un augšanas intensitātes atšķirību izlīdzināšanās sezonas garumā, gan atšķirības pārvietošanas attālumos un stādījuma augšanas (augsnes) apstākļos (**VI**). Rietumu proveniencēm bija būtiski lielāka augšanas intensitāte sezonas sākumā un būtiski zemāka augšanas intensitāte sezonas beigās.

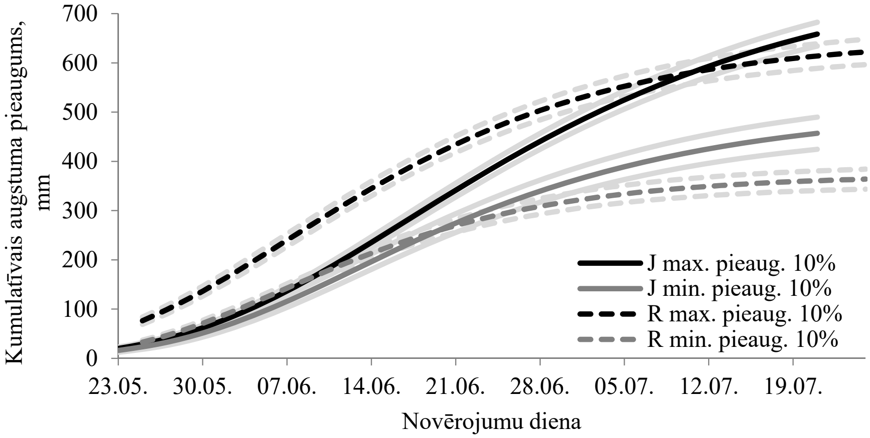
Pēc 8. jūnija augšanas intensitāte samazinājās (3.14. att., **VI**). Tam sekoja krass augšanas intensitātes pieaugums (neatkarīgi no provenieneces) (3.14. att., **VI**), ko visdrīzāk veicinājušas meteoroloģisko apstākļu izmaiņas (Odin, 1972; Cannell & Johnstone, 1978). Augšanas pārtraukšanas laiks proveniencēm būtiski atšķīrās, un pēdējā mērījuma veikšanas dienā (20. jūlijā) izmaiņas augstuma pieaugumā nebija vērojamas 36,6% koku no rietumu proveniencēm un 28,2% koku no austrumu proveniencēm (**VI**).

Kopējais augstuma pieauguma veidošanās periods bija aptuveni 60 dienas ar vidējo augšanas intensitāti 9,2 ± 0,2 mm dienā, un tas notika laika periodā ar dienas garumu vismaz 16,5 stundas (3.14. att., **VI**). Rietumu provenieneces gan uzsāka, gan pārtrauca veidot augstuma pieaugumu aptuveni divas dienas agrāk nekā austrumu provenieneces, norādot uz koku adaptācijas ietekmi uz augstuma veidošanu. Eglēm no izcelsmes vietām ar dažādu ģeogrāfisko garumu augšanas fenoloģiju ietekmē ar gaisa temperatūru saistīti kontroles mehānismi (Heide, 1974; Hannerz, 1998), arī nelielu (mazāku par 300 km) ģeogrāfiskā garuma izmaiņu gadījumā (Danusevičius & Persson, 1998). Egles no austrumu proveniencēm augšanu uzsāka vēlāk, norādot uz piemērošanos izvairīties no pavasara salnām (Dietrichson, 1969; Polle et al., 1996; Langvall & Löfvenius, 2002). Provenieneces reģionam bija lielāka ietekme uz augšanas uzsākšanas laiku (**VI**), pretēji novērotajam Zviedrijas centrālajā daļā, kur proveniencei bija lielāka ietekme uz augšanas pārtraukšanas laiku (Ekberg et al., 1985).

Provenieneces ietekme uz augšanas intensitāti sezonas laikā mainījās (**VI**). Tā bija izteiktāka ($p < 0,05$) pieauguma veidošanas sākumā (pirms 3. jūnija) un beigās (pēc 6. jūlija), bet starp šiem posmiem provenieneces efekts nebija būtisks ($p > 0,21$). Šīs izmaiņas saistītas ar koku piemērošanos iespējamiem sala bojājumiem pavasarī un rudenī (Avotniece et al., 2012). Savukārt laika posmā ar straujāko augšanas intensitāti (no 8. līdz 22. jūnijam) augšanu galvenokārt noteica ārēji faktori (Danusevičius et al., 1999), un atšķirības starp proveniencēm bija nelielas (**VI**).

Augstuma pieauguma veidošanās dinamika sezonas ietvaros (**VII**) sekmīgi aproksimēta ar Gompertz vienādojumu (3.15. att.), iegūstot individuālu koku augšanas līkni raksturojošus koeficientus un to ģimeņu vidējās vērtības. Ģimene būtiski ($p < 0,05$) ietekmēja gan augstuma pieauguma garumu, gan Gompertz vienādojuma koeficientus, kas raksturo augšanas uzsākšanu, pieauguma tempu un augšanas pārtraukšanu. Izņēmums bija ģimenes ietekme uz augšanas uzsākšanu Jelgavas stādījumā ($p > 0,05$), kur koki sāka augt nedaudz vēlāk nekā Rembate-B stādījumā.

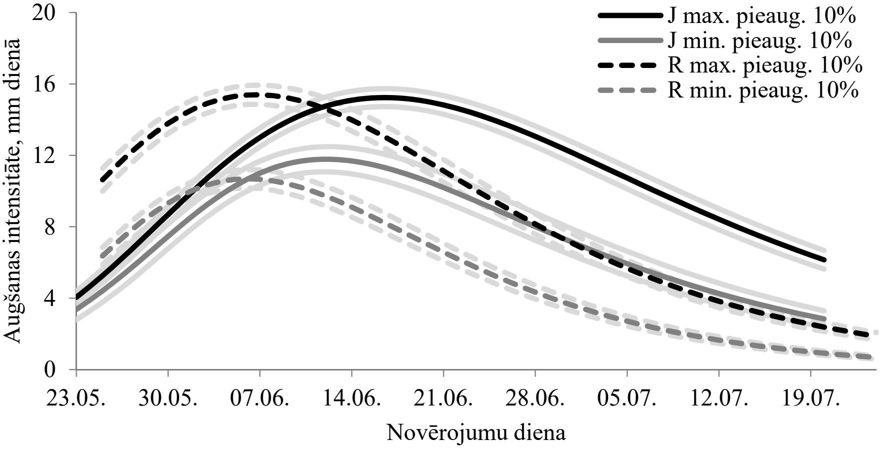
Kopējais augstuma pieaugums labāk augošām ģimenēm bija būtiski un nozīmīgi lielāks nekā sliktāk augošām ģimenēm (**VII**): stādījumā Rembate-B attiecīgi



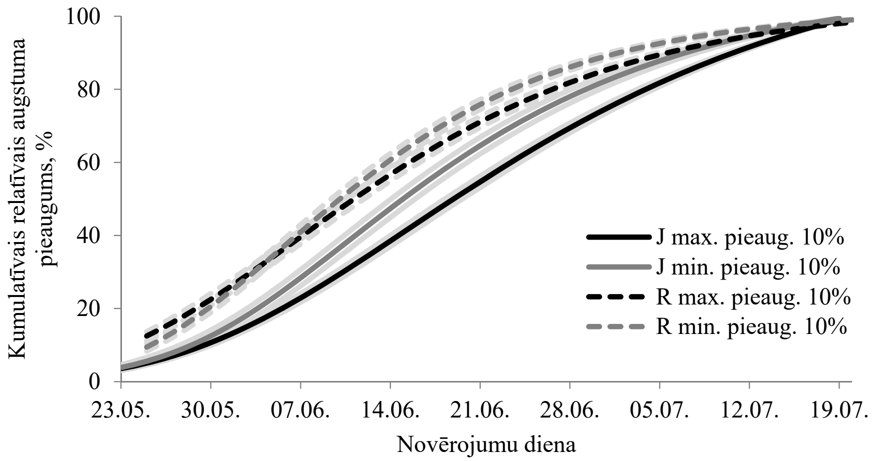
3.15. att. **Aproksimētās Gompertz vienādojuma līknes vidējam augstuma pieaugumam (± 95% ticamības intervāls) Rembates (R) un Jelgavas (J) stādījumā pēc pieauguma labākajām (max. pieaug. 10%) un sliktākajām (min. pieaug. 10%) ģimenēm**

624 ± 26 un 362 ± 20 mm un Jelgavā attiecīgi 664 ± 25 un 462 ± 33 mm. Labāk augošo ģimeņu vidējā augstuma pieauguma pārākums pār sliktāk augošajām ģimenēm saglabājās visu novērojumu periodu.

Labāk augošās ģimenes augstuma pieauguma kulmināciju sasniedza nedaudz vēlāk nekā sliktāk augošās ģimenes (3.16. att.), turklāt pēc tā sasniegšanas labāk augošās ģimenes arī ilgāk saglabāja lielāku pieauguma intensitāti, savukārt sliktāk augošajām ģimenēm pieauguma intensitāte samazinājās straujāk. Kopumā labāk



3.16. att. **Vidējais augstuma pieaugums (± 95% ticamības intervāls) Rembates (R) un Jelgavas (J) stādījumā pēc pieauguma labākajām (max. pieaug. 10%) un sliktākajām (min. pieaug. 10%) ģimenēm**



3.17. att. **Kumulatīvais relatīvais augstuma pieaugums (± 95% ticamības intervāls) Rembates (R) un Jelgavas (J) stādījumā pēc pieauguma labākajām (max. pieaug. 10%) un sliktākajām (min. pieaug. 10%) ģimenēm**

augošās ģimenes raksturoja vienmērīgāka un augstāka augšanas intensitāte un ilgāks pieauguma veidošanās periods (**VII**). Nozīmīgāka ģimenes ietekme uz augšanas intensitāti konstatēta augstuma pieauguma veidošanās otrajā pusē.

Individuālu koku līmenī kopējam augstuma pieaugumam konstatēta cieša, būtiska korelācija ar pieauguma tempu (Gompertz vienādojuma *k* parametrs; attiecīgi Rembatē $r = -0{,}66$, Jelgavā $-0{,}62$, abi $p < 0{,}001$). Šī tendence saglabājās arī ģimeņu līmenī, un ģimenes ar mazāku pieaugumu sasniedza lielāku relatīvo pieauguma intensitāti. Šī sakarība rāda, ka labāk augošām ģimenēm augstuma pieauguma veidošanās ir vienmērīgāk sadalīta kopējā augšanas periodā (3.17. att.), savukārt, sliktāk augošās ģimenes relatīvi lielāku pieauguma īpatsvaru veido intensīvās augšanas posmā (starp uzsākšanas un pārtraukšanas posmiem).

Augstuma pieaugumu ietekmēja arī koku augstums. Augstuma pieaugums cieši korelēja ar koka augstumu sezonas beigās ($p < 0{,}05$), bet korelācija ar augstumu sezonas sākumā bija ievērojami vājāka. Līdzīgi arī pieauguma temps (Gompertz vienādojuma *k* parametrs) pozitīvi korelēja ar koka augstumu sezonas beigās ($r = 0{,}35$), bet korelācijas ar koka augstumu sezonas sākumā lielākoties nebija būtiskas ($r = 0{,}07$, **VII**).

SECINĀJUMI

I Koku ar apikālajiem augusta dzinumiem īpatsvars egles audzēs trīs līdz septiņu gadu vecumā variē no 0% līdz 25%, neatkarīgi no meža tipa (eitrofie un mezotrofie) un audzes vecuma.

II Labvēlīga lokālo apstākļu kombinācija – novērsta zemsedzes veģetācijas konkurence un noregulēts augsnes mitrums – ievērojami un statistiski būtiski ($p < 0{,}001$) palielina egļu ar apikālajiem augusta dzinumiem īpatsvaru jaunaudzēs.

III Iedzimtībai ir nozīmīga ietekme uz apikālo augusta dzinumu sastopamību: koku ar tiem īpatsvars vienā un tajā pašā uzmērīšanas gadā un stādījumā egles pluskoku brīvapputes pēcnācēju ģimenēm bija no 0% līdz 91%, ģimenes ietekme statistiski būtiska ($p < 0{,}05$).

IV Apikālie augusta dzinumi biežāk veidojas ātraudzīgiem un agri plaukstošiem kokiem. Koku ar šiem dzinumiem augstums vidēji par 14–29% lielāks nekā kokiem bez augusta dzinumiem. Nav konstatēta saikne starp apikālajiem augusta dzinumiem un salnu bojājumu varbūtību, turklāt apikālie augusta dzinumi daļēji kompensē pavasara salnu ietekmi uz kopējo pieauguma garumu.

V Mezotrofajos un eitrofajos meža tipos augsnes sagatavošanas veids būtiski ietekmē jaunaudzes koku augstumu. Vidējais koku augstums un augstāko koku īpatsvars ir būtiski ($p < 0{,}05$) lielāks stādījumos, kur augsne sagatavota pacilās, nevis vagās vai negatavotā augsnē. Dominējošo koku augstuma pieauguma atšķirības pacilās un vagās sagatavotā augsnē stādītām eglēm palielinājās no 14% sešu gadu vecumā līdz 20% astoņu gadu vecumā.

VI Divpadsmit mēnešus pirms stādīšanas veiktā augsnes ielabošana ar koksnes pelniem atstāja pozitīvu ietekmi uz augiem pieejamo makroelementu saturu augsnē (kālija un fosfora pievienošana), kā arī veicināja organiskā slāpekļa atbrīvošanos. Uzlabotai makroelementu pieejamībai bija būtiska ietekme uz koku augšanu: desmit gadu vecumā papildus barības vielas saņēmušiem kokiem augstums bija par 15% un 21% (attiecīgi pelnu deva 5 un 10 t ha^{-1}) lielāks nekā kontroles kokiem. NPK minerālmēslojums reizē ar stādīšanu līdzīgi ietekmēja koku pieaugumu līdz 15 gadu vecumam.

VII Egles pluskoku brīvapputes pēcnācēju ģimenēm pieauguma veidošanās dinamika ir ģenētiski noteikta. Ģimenēm ar salīdzinoši lielāku augstuma pieaugumu augšanas intensitāte (mm diennaktī) kulminē vēlāk un saglabājas augsta ilgāk.

PRIEKŠLIKUMI

Darba rezultāti par lokālo apstākļu uzlabošanas ietekmi uz egles apikālajiem augusta dzinumiem un kumulatīvi uz koku augstumu jāietver augšanas gaitas modelēšanas sistēmā, lai precīzāk atspoguļotu mērķtiecīgas šīs koku sugas jaunaudžu apsaimniekošanas sagaidāmo pozitīvo efektu.

Sākotnējā augsnes ielabošanas līdzekļu – minerālmēslojuma un koksnes vai koku mizas pelnu – izmantošana rekomendējama egles audžu pieauguma uzlabošanai, jo to iedarbība saglabājas vismaz 10 gadu ilgā laika periodā.

Rekomendējama genotipu ar apikālajiem augusta dzinumiem atlase selekcijā, jo tā nepalielina salnu vai sala bojājumu risku, bet nodrošina iespējas iegūt lielāku augstuma pieaugumu, mērķtiecīgi veicot ar selekcionētu materiālu atjaunotu jaunaudžu agrotehnisko kopšanu un lokālo apstākļu uzlabošanu. Sagaidāms, ka šo efektu pastiprinās klimata pārmaiņas: biežāki gadi ar augstu gaisa temperatūru iepriekšnoteiktā augstuma pieauguma veidošanās noslēgumā un garāku veģetācijas periodu.

PATEICĪBAS

Autore pateicas Latvijas Valsts mežzinātnes institūta “Silava” Meža selekcijas un adaptācijas radošās grupas kolēģiem, jo īpaši Unai Neimanei un Silvai Šēnhofai, kā arī visiem kopīgi sagatavoto zinātnisko publikāciju autoriem par padomiem, līdzdalību, iedvesmu, pacietību un konstruktīvām diskusijām pētījumu veikšanas laikā, kā arī izteiktajiem komentāriem un iebildumiem, kas palīdzēja nozīmīgi uzlabot sagatavotā darba kvalitāti.

Tāpat autore pateicas LLU Meža fakultātes kolēģiem par piezīmēm, atbalstu un labu vārdu doktorantūras studiju un darba tapšanas ietvaros. Paldies darba vadītājiem un visiem, kas atrada par iespējamu iepazīties ar darba sākotnējām versijām un izteikt savus iebildumus un priekšlikumus uzlabojumiem! Īpašs paldies Kasparam Liepiņam par atvēlēto laiku un kritiku, kas radīja iespēju savlaicīgi novērst daudzas neprecizitātes.

Pētījumu, kuru ietvaros ievākts datu materiāls, finansētājs ir a/s “Latvijas valsts meži”, un tie realizēti Latvijas Valsts mežzinātnes institūtā “Silava”. Autore pateicas par pētījumu iniciēšanu un rezultatīvu sadarbību to realizācijā a/s “Latvijas valsts meži” Izpētes vadītājam Dr.silv. Indulim Brauneram. Darba izstrāde atbalstīta ERAF projekta “LLU akadēmiskā personāla pilnveidošana (Nr. 8.2.2.0/18/A/014)” ietvaros. Atsevišķi darbi veikti Meža nozares kompetences centra pētījuma “Metodes un tehnoloģijas meža kapitālvērtības paaugstināšanai” (ERAF, Nr. L-KC-11-0004) un “Vitālu egļu audžu izaudzēšanas ekoloģiskie un tehnoloģiskie aspekti” (ESF, Nr. 1DP/1.1.1.2/13/APIA/VIAA/052) ietvaros.

1. SCOPE OF THE THESIS

Norway spruce (*Picea abies* (L.) Karst.) is economically the most important tree species in Northern Europe, representing approximately one third of region's wood resources – more than 18 million ha area, with wood volume 2700 million m^3 (Rytter et al., 2013). Spruce wood mainly is used for producing sawn timber, and the residues of production increasingly more are used for bio-energy products (Rytter et al., 2013). In Latvia spruce stands cover 19% of forest area, mostly in territories on fertile mineral soils with normal soil moisture regime (*Oxalidosa* and *Hylocomiosa*) and on drained mineral soils (*Myrtillosa mel.*), representing 27%, 22% and 18%, respectively, from spruce stands (National Forest Inventory (NFI) data, 2015–2019). Mean annual increment of spruce in all forest stands is 9.7 m^3 ha^{-1}, but in the highest site index stands it reaches 14.6 m^3 ha^{-1} (NFI data, 2015–2019). Height increment in young stands to a large extent determines further development of stand, therefore it is important to evaluate the impact of various factors on tree growth during this stage and the possibilities to improve it with forest management measures and forest selection.

Climate change can significantly impact the growth of forest stands (Kenina et al., 2018). In Northern Europe, in conditions of warmer climate, forest productivity is predicted to increase due to longer vegetation period and larger efficiency of photosynthesis (Menzel & Fabian, 1999; Stöckli & Vidale, 2004; Kolari et al., 2007). In the middle of this century the length of vegetation period in Latvia could be two to three weeks longer comparing it with the mean length of vegetation period from 1961 to 1990 (Kļaviņš & Briede, 2011), but the favourable effects of these conditions can be hindered by increasing impact of drought and spring/autumn frosts (Gu et al., 2008; Lindner et al., 2010; Zeps et al., 2017).

Improved growing conditions favours lammas shoots, and it has been observed more often (Kvaalen et al., 2010; Søgaard et al., 2011). Lammas shoots of spruce can be both on lateral branches (rarer) and (also) on top shoot. Furthermore, the top shoot can have one, several or even all lateral buds flushed, but not the central (apical) bud (Fig. 1.1.), or the central and/or some of lateral buds (more often). In this thesis the term 'lammas shoots' is used to describe the second flushing of top (apical) shoot in late summer, which may increase the height increment of current year, unless otherwise specified.

Information about favourable conditions for development of lammas shoots is necessary to evaluate the importance of apical lammas shoot (desirable or undesirable), and also their impact on growth and quality of stem/wood. If the influence of plus-tree family differences (heritable) on the development of lammas shoots would be confirmed, then it would help to reduce or, on the contrary, favour the development of them.

Use of suitable planting material can decrease the impact of climate (change) impact on forestry (Lindner, 2000; Bolte et al., 2009). Up until now selection has

Fig. 1.1. **Lammas shoots of Norway spruce**

mainly been used to improve growth and stem quality (Hannerz, 1993; Kroon et al., 2011), increasingly focusing on traits which influence tree adaptability to climate change (Ekberg et al., 1985; Namkoong et al., 2012; Zeltiņš et al., 2019; Isabel et al., 2020).

Traits that characterise adaptation (such as time of flushing, drought tolerance, frost hardiness, etc.) are genetically determined (Hannerz, 1998, 1999; Hannerz et al., 1999; Chen et al., 2017; Trujillo-Moya et al., 2018), but genetic variation of these traits within specific population can be limited. A search for new solutions to promote a faster adaptation and stand productivity is in process, combining seed material transfer (to climatically more suitable regions) and selection (O'Neill et al., 2014; Klisz et al., 2019; Zeltiņš et al., 2019). However, the effectiveness of these solutions depends directly on the understanding about factors that impact increment development and their genetically determined variation, and also on the area reforested by planting and its proportion.

Approximately 90% young spruce stands of Latvia in forest types on fertile soil have been reforested by planting (State Forest Service data, 2016–2018), and the largest proportion of planting materials (around 70%) come from seeds of seed orchards. Planting is costly (soil preparation, planting material, planting), however, when performing the total (comparable) financial evaluation of reforestation type (self-seeding or planting) the development of young stand has to be taken into account as well by including the need and costs of tending (Uotila et al., 2010). Such evaluation is difficult due to both various possible options and combinations of each measure and material (for example, different types of planting material and soil preparation, differences in the weed competition in different fertility soils), and the lack of information about the impact of these different alternatives on tree growth.

Tree growth can be improved with additional fertilisation. Applying additional fertilisers during the process of planting is one of the most effective measures to improve growth (Sutton, 1995; Hedwall et al., 2014). Soil fertilisation with wood ash increases the activity of soil micro-organisms (Perkiömäki & Fritze, 2005), and also stimulates decomposition of litter and cellulose and decomposition of organic matter – mineralisation (Moilanen et al., 2002; Perkiömäki & Fritze, 2002; Perkiömäki et al., 2004), but its long-term impact on tree growth has been minimally studied (Moilanen et al., 2002; Perkiömäki et al., 2004; Saarsalmi et al., 2012). Supplementation with additional fertilisers can also improve physical indicators of wood, including the ability of nutrients transfer function through tracheas. Spruce is sensitive to drought (Lévesque et al., 2013), furthermore in the conditions of a changing climate the frequency of drought periods can increase (Allen et al., 2010; Seidl et al., 2017). Thereby, it is necessary to evaluate whether a faster growth, when additional fertiliser is applied, does not create a potentially negative effect on tree vitality.

1.1. Height increment

Height growth is an important tree survival strategy to provide access to light and with photosynthesis produce the organic matter needed for growth (Moles et al., 2009; Poorter et al., 2012). Trees growing separately in sufficient light conditions produce a constant height and diameter proportion (Mäkelä & Sievänen, 1992), while trees in forest with the impact of light competition use a relatively larger portion of the resources to increase height rather than diameter (Mäkelä & Vanninen, 1998; Ilomäki et al., 2003).

Within a season the height increment can be described as sigmoid curve with the highest growth intensity (mm per day) in the middle of growing season (Chuine et al., 2006; Lanner, 2017). The onset and cessation of growth are determined both by internal (heritability) and external (environmental) factors (Hänninen & Kramer, 2007; Salminen & Jalkanen, 2007; Schiestl-Aalto et al., 2013; Gull et al., 2018), and in the northern latitude a specific time period of the process in this growth stage has an important role to avert the frost damage (Neimane at al., 2015). Trees in optimal growing conditions can provide effective water transportation function from seeds to foliage (Sellin, 2001), therefore they can grow taller than trees growing in stress conditions. The hydraulic capacity of a tree controls also the total tree height, reducing the height growth when water transportation from roots to foliage becomes difficult (Ryan & Yoder, 1997; Ryan et al., 2006).

Height increment can be formed in two different processes, from which the predetermined growth takes place in the largest part of tree life. Predetermined growth is formed by lengthening of stem units that have been formed in the buds of previous growth season (von Wühlisch & Muhs, 1986; Zhang et al., 1992), therefore for trees older than one year the predetermined growth is influenced by growing conditions of two seasons. The number of stem units in buds is influenced by previous growth season, but the possible length of each unit is influenced by the conditions of current season and the availability of resources (Lanner, 1976; Junttila & Heide, 1981; Junttila, 1986; Mäkinen, 1998; Salminen & Jalkanen, 2005; Lindholm et al., 2009; Schiestl-Aalto et al., 2013; Mäkinen et al., 2018). Age also has a significant impact on tree growth (Čermák et al., 2019). It has been studied that one of the main meteorological factors, which influences the growth of spruce in the reproductive age is air temperature of previous summer (Gallego Zamorano et al., 2018), which is linked to allocating resources to produce seeds (Miina, 2000; Selås et al., 2002), but it has not been clarified which are the main factors during juvenile age.

In the first year of tree life height is formed in a different process, which is called free growth, when both formation and elongation of stem units in buds happen within the same season (Zhang et al., 1992). Typically one height increment (predetermined growth) is formed in one growing season, but in favourable conditions at juvenile age, after the cessation of the predetermined growth, a free growth has been observed, when a repeated bud flush and growth happens at the end of growing season (Ehrenberg, 1963; Dormling et al., 1968; Aldén, 1971; Rone, 1985; Cline & Harrington, 2007; Søgaard et al., 2011). Free growth has two types (von Wühlisch & Muhs, 1986) depending on the development of bud clusters. After cessation of predetermined growth the free growth can begin from sylleptic shoots (two whorls are formed), or predetermined growth continuing to grow without forming proleptic shoots (whorl is not formed in between predetermined growth and free growth). Free growth is possible in a limited time period between the predetermined growth cessation and the endogenous dormant period (Lang et al., 1987). Mostly free growth has been observed in august (*lammas shoot*, Fig. 1.1., 1.2.).

The physiologic mechanisms (relation with accumulation potential of carbohydrates, phytohormones, photoperiods, etc.) of lammas shoots are still not clear (Cline & Harrington, 2007), but observations point to impact of growing and meteorological conditions (Dormling et al., 1968; Aldén, 1971; von Wühlisch & Muhs, 1986; Hallgren & Helms, 1988; Kushida, 2005), and also genetics (Rone, 1975; Ununger et al., 1988; Danusevičius & Persson, 1998; Danusevičius, 1999; Skrøppa & Steffenrem, 2016). In plantations of provenance trails at the age of five years in the central part of Sweden the proportion of spruces with lammas shoots were in 4% ± 2% provenances with northern Sweden origin, 17% ± 3% for provenances from Austria (Danusevičius & Persson, 1998). More pronounced effect of provenance was found for five-year-old spruces in Norway, where the proportion of spruces with lammas shoots was 18% for provenances of Scandinavian origin, but 28% for Latvian and 54% for Slovakian and Czech origin (Søgaard et al., 2011). Also, nine of local Norwegian populations at the age of nine years had significant differences (12% to 34%) in proportion of trees with lammas shoots (Skrøppa & Steffenrem, 2019). Differences between families were significant and substantial, three provenances with the

Fig. 1.2. **Apical lammas shoot of Norway spruce**

largest differences between families with large proportion of trees with lammas shoots were 11%–52%, 18%–64% and 0%–39% (Skrøppa & Steffenrem, 2019). Free growth for older trees is less common (Ehrenberg, 1963; Rone, 1985; Søgaard et al., 2011), and in field trials with open-pollination of progenies of Norway spruce trees at the age 20 to 25 years had little (4% from trait variation), but still significant effect of family on development of lammas shoots (Steffenrem et al., 2008).

In total, better growing trees form lammas shoots more often, therefore advancing their growth and stand productivity even more (Hoffmann, 1965; Rone, 1975; Danusevičius & Persson, 1998). More frequent lammas shoots occurrence, thereby also more rapid tree growth at young stand age, in conditions with increased temperature has been proven in laboratory experiments (Johnsen, 1989; Kvaalen & Johnsen, 2008), and more frequent occurrence of lammas shots in young stands is assessed as a result of climate change (Kvaalen et al., 2010; Søgaard et al., 2011). Occurrence of lammas shoots could be linked to frost damage due to low frost hardiness and with formation of stem defects (double tops or ramicorn branch) (Gabrilavičius & Danusevičius, 2003; Pallardy, 2008; Søgaard et al., 2011; Granhus et al., 2019).

1.2. Impact of micro-environment

Regeneration by self-seeding of coniferous stands in the fertile hemiboreal forests is difficult (Holgén & Hånell, 2000). Even though successful Norway spruce stand regeneration is possible both with undergrowth trees in mature forests (Luguza et al., 2020), and in young stands after clear-cut performed in fertile forest types (Luguza et al., 2019), in both cases it is time-consuming and depends on seed availability. Planted spruces can compete better with ground vegetation (Holgén & Hånell, 2000). Moreover, such young stands are also more productive than naturally regenerated (Gradeckas & Malinauskas, 2005), which is linked to the use of genetically improved planting material (Jansons et al., 2015), and also with the positive effect of soil preparation on growth (Nordborg et al., 2003; Heiskanen et al., 2013).

Soil preparation can be performed using different methods (Mangalis, 2004; Gradeckas & Malinauskas, 2005), one used more often in Baltic States is soil preparation with disc trenching. Soil moisture after soil preparation not always is suitable for seedling growth. Survival of trees planted in territories with normal moisture in trenches and in spot mounds are equal, but in conditions of increased moisture survival in trenches is significantly lower than in mounds (Örlander et al., 1990, 1998). Mounds provide suitable soil moisture for spruce growth, which is essential for their survival in the first years after planting (Schlyter et al., 2006).

Similar to other soil preparation methods, mounds are also decreasing ground vegetation competition, but this effect lasts for a longer period of time (Lehtosalo et al., 2010). For example, in Finland in soils prepared with mounding, cleanings (tendings) was needed only in the second to fourth year after planting in relatively fertile soil, and in the fourth to sixth year after planting in low fertility soil (Saksa, 2008; Uotila et al., 2010). Mounds also helps to increase soil temperature more than in other soil preparation methods (Örlander et al., 1990; Sutton, 1993), and improves micro-environment. Trees on mounds less frequently suffer from frost (Langvall et al., 2001; Heiskanen et al., 2013) and from damages by large pine weevil (*Hylobius abietis* (L.)) (Örlander et al., 1990; Heiskanen & Viiri, 2005; Saksa, 2008; Heiskanen et al., 2013). Furthermore, mounds in direction from top down are made from turned over mineral soil, turned humus layer, untouched humus layer and untouched mineral soil, and the created double organic layer of soil has a positive effect on the initial tree growth (Nordborg et al., 2003; Saksa et al., 2005; Hallsby & Örlander, 2013; Heiskanen et al., 2013).

Availability of nutrients has a considerable impact on tree growth, and initial soil fertilisation is the most effective way to improve the productiveness of Norway spruce stands (Nohrstedt, 2001; Saarsalmi & Mälkönen, 2001; Sicard et al., 2006). Ash contain nutrients needed by plants, for example, potassium, calcium, magnesium, phosphorus, sodium (Levula et al., 2000; Demeyer et al., 2001). Initial soil fertilisation with ash decreases soil acidity (pH) and enriches soil with phosphorus, potassium and micro-elements (Ingerslev et al., 2014), and in territories where nitrogen is not growth limiting factor (especially on peat soils) it is increasing tree growth considerably (Huotari et al., 2015). Furthermore, ash as an initial fertiliser allows sustainable use of wood processing by-products (nutrients that have been removed from forest with wood are partially brought back to forest), which otherwise would be deposited in landfills as industrial waste (Knapp & Insam, 2011; Väätäinen et al., 2011; Huotari et al., 2015).

The rapid growth of conifers favoured by initial fertilisation can also influence the structure of wood (for example, the thickness of cell walls), thus impacting the density and quality of wood (Mäkinen et al., 2002; Lundgren, 2004; Cao et al., 2008). The impact of fertiliser on growth depends on the time of application and chemical composition (in relation to chemical composition of soil) and the doses (Ingerslev, 1997; Nohrstedt, 2001), however, in general a local application of fertiliser during planting favours growth and competitiveness with ground vegetation (Sicard et al., 2006), which has an important role in the further development of forest stand (Sutton, 1995; Hytönen & Jylhä, 2008).

1.3. Heritability

Tree height is closely linked to productivity of forest stand, and it has been used as one of the main parameters in selecting genotypes in selection process (Ekberg et al., 1985; Hannerz, 1993; Danusevičius & Gabrilavičius, 2001; Kroon et al., 2011). Selection effect of a specific parameter depends on its variation (possibility to select the desirable) and the genetically determined part in this variation, which is expressed as heritability coefficient. In general, larger selection effect can be gained by selecting parameters with high heritability coefficient value in conditions (plantations) where genetically determined differences of specific parameters are clearly marked (Kroon et al., 2011). Tree height generally is characterised with higher heritability coefficient than diameter. In the extensive literature review about Norway spruce selection Jansson et al. (2013) has summarised the values of narrow sense heritability (h^2), which for height is 0.05–0.36, for height increment 0.04–0.47, for diameter 0.09–0.27. In some cases the broad sense heritability (H^2) values have even been 0.54 and higher (Hannrup et al., 2004; Kowalczyk, 2005). When compared to diameter, height is less affected by stand density (conditions of competition) and other parameters that can be changed with forest management measures. Different parameters are genetically linked and their genetic correlations determine how and to what extent other parameters are affected by selecting trees by one parameter (Kroon et al., 2011). The positive genetic correlation of height with most of parameters characterising stem quality (Haapanen, 1997) allows to use it as the main parameter to select best families in progeny tests.

Selection of best genotypes provide notable improvement in standing volume and quality of forest stand. Norway spruce progenies of families selected in Norway at the age of 21 years had 14% higher height ($p < 0.001$) than provenances of local origin (Skrøppa et al., 2007). Selection of Norway spruce in Norway has allowed to shorten the rotation period by 5 to 10 years and has increased net present value by more than 30% (Kvaalen (2010) cited by Jansson et al. (2017)), but in Sweden the internal rate of return has increased by 5.3%–8.3% (Simonsen et al., 2010).

Phenology has an important role in providing tree survival and adaptation. Both onset and cessation of growth is partially genetically determined (Hannerz, 1998, 1999; Hannerz et al., 1999), and also time and length of growth differs between different provenances, families and clones (Skrøppa et al., 1999). Also, meteorological factors influence physiological activity of trees, for example, temperature determines the time of bud burst and onset of growth increment (Hannerz, 1999) and intensity (Sarvas, 1973; Danusevičius et al., 1999). The interaction between genotype and environment determines that one single parameter, for example, onset of growth for a specific genotype in different conditions may differ (Kroon et al., 2011). If such interaction exists and can be linked to growing or climatic conditions or geographical location, then this information can be used to select populations suited for aimed conditions, thus increasing the gain from selection.

One of the most important interactions between genotype and environment is linked to the risk of frost damage (Granhus et al., 2009; Søgaard et al., 2009). In northern latitude an important role in tree survival and vitality is the growth rhythm synchronisation with climatic conditions, especial at juvenile stage. That also influences tree productivity. For example, genotypes that show good growth in locations with high risk of spring frosts might not be between best growing trees in locations with low risk of frost (Berlin et al., 2014). With the climate getting warmer, trees can start their growth earlier (Danusevičius et al., 1999), but they are exposed to a larger risk of frost damages (Polle et al., 1996), because with the increase of temperature comes more frequent and distinct temperature deviations (extremes) from the average value of long-term observations (Avotniece et al., 2012). These changes have the largest impact on young, free growing trees, as they are in young stands after clear-cuts (Langvall & Löfvenius, 2002). The negative effect of interaction between genotype and environment can be decreased in two ways – both selecting clones suitable for specific environmental conditions, and selecting genotypes that show acceptable results in such conditions (St Clair & Kleinschmit, 1986). Moreover, Norway spruce has epigenetic memory, when bud burst phenology, frost hardiness and onset of growth in short-term are influenced by autumn temperatures (Granhus et al., 2009; Søgaard et al., 2008), but in long-term – temperatures during the stage of embryo (Yakovlev et al., 2010; Solvin & Steffenrem, 2019), and that allows to adapt to climate change faster.

1.4. Aim of the thesis

The doctoral thesis aims to assess the effect of microenvironmental conditions and genetics on the height increment of Norway spruce at a juvenile age in planted hemiboreal forests in Latvia.

1.5. Thesis objectives

The following three objectives have been set in the thesis:

1. to characterize the effect of the microenvironment (competition of ground vegetation and soil moisture regime) and genetics on lammas shoots of Norway spruce (**I** and **II**);
2. to characterize the effect of an improved nutrient supply on the height growth of Norway spruce (**III**, **IV,** and **V**);

3. to characterize the intra-annual differences in shoot elongation between open-pollinated families of Norway spruce plus-trees (**VI** and **VII**).

1.6. Thesis statements

1. The improvement of microenvironmental conditions in young stands favors the development of lammas shoots.
2. The occurrence of lammas shoots and intra-annual shoot elongation is genetically determined.

1.7. Scientific novelty

For the first time, the effect of microenvironmental conditions on the development of lammas shoots of the Norway spruce is evaluated in hemiboreal forests. In addition, for the first time in these forests, the cumulative effect of lammas shoots on the height of the Norway spruce at a juvenile age is characterized. For the first time in Latvia, the effect of the planting location and soil fertilization with wood ash before planting on the height of the Norway spruce in a 10-year period is characterized.

2. MATERIALS AND METHODS

Height increment of Norway spruce (intra-annual height growth and occurrence of apical lammas shoots) depending on the micro-environmental conditions and other factors (**I**, **II** and **VII**), type of soil preparation and additional nutrients supply (**III**, **IV** and **V**) and genetics (**VI** and **VII**) was assessed mainly in the central part of Latvia (Fig. 2.1.) in hemiboreal forests (Barbati et al., 2007).

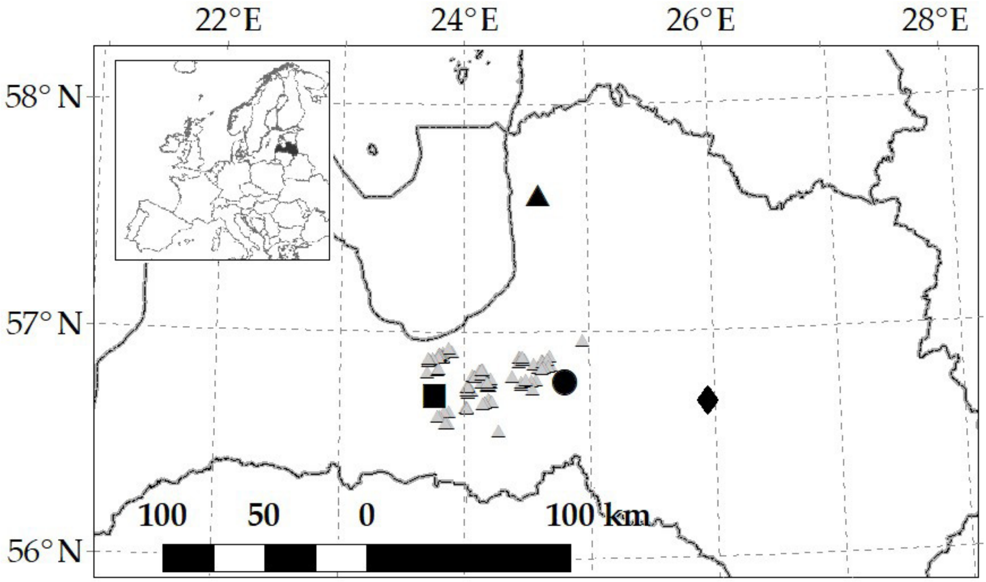


Fig. 2.1. **Location of research sites**
Grey triangles (▲) – forest stands (I), black circle (●) – Rembate (II and VII), black square (■) – Jelgava (II, VI and VII), black triangle (▲) – Viļķene (III), black rhombus (♦) – Kalsnava (IV and V)

2.1. Lammas shoots

2.1.1. Data collection

The presence of apical lammas shoots, the relation of its development with growing conditions and their changes, and also the relation with tree height has been assessed in planted forest stands (**I**) and in experimental plantations of open-pollinated progenies (**II** and **VII**). In this thesis, lammas shoots is used to describe the second flushing of apical (central) bud in late summer after the cessation of intra-annual height growth. Only lammas shoots longer than one centimetre were assessed.

Altogether 102 forest stands (**I**) at the age of three to seven years were randomly selected in eight forest types, where most of Norway spruce stands are: *Hylocomiosa* (Dm), *Oxalidosa* (Vr), *Myrtilloso-sphagnosa* (Dms), *Myrtilloso-polytrichosa* (Vrs), *Myrtillosa mel.* (As), *Mercurialiosa mel.* (Ap), *Myrtillosa turf. mel*. (Ks), *Oxalidosa turf. mel.* (Kp). Data was collected at the end of year 2011. A repeated data collection was performed in some (21) of these stands at the end of year 2012. All forest stands have been reforested with planting, area of stands ≥0.5 ha.

In each stand, on its longest diagonal, 20 circular sample plots (area 25 m²) were placed. In each sample plot the number of spruces with and without lammas shoots were recorded. In 70 from previously mentioned stands, the local suitability for spruce growth was assessed (using three factors – competition by surrounding vegetation, soil moisture regime and browsing damages by ungulates) (in 56 stands in year 2011, in 14 stands in 2012). Each factor had a three-grade scale: a) the ratio between the mean height of spruce and that of the surrounding vegetation within a radius of 0.5 m (Grade 1: <0.75; Grade 2: 0.75–1.25; Grade 3: >1.25); b) soil moisture regime (Grade 1: to sample plots with suitable moisture conditions for spruce; Grade 2: sample plots with periodic excessive moisture; Grade 3: to sample plots with permanent excessive moisture); c) proportion of damaged trees in sample plot (damaged tops and/or more than 50% of lateral shoots) (Grade 1: <1%; Grade 2: 1%–10%; Grade 3: >10%). The total impact of micro-environmental factors and browsing damages was evaluated for each sample plot by calculating the sum of scores (grades) for all three previously mentioned factors, ranging from 3 (best) to 9 (worst). The proportion of trees with lammas shoots at stand level was calculated as the mean value (± 95% confidence interval) of sample plots; the same was done with the proportion of trees with browsing damages. The meteorological data were collected from the three nearest meteorological stations (Riga, Dobele, and Skriveri).

The differences in development of apical lammas shoots of progenies of Norway spruce plus-tree families, and also the relation between lammas shoot development with tree height, height increment, bud burst time and frost damages has been assessed in trials of open-pollinated progenies in Ķegums region, further in text – in Rembate (**II** un **VII**). Data in Rembate were collected in two experimental plantations: Rembate-A (**II**) and Rembate-B (**II** and **VII**) (Fig. 2.2.). Experiment Rembate-A was planted on fertile abandoned agricultural land (corresponding to forest type Vr) in year 2010 using three-year old bare-rooted seedlings. Altogether 60 families in 4-8 replications, 12 trees in block plots, planted with initial spacing spacing 2.5 × 2.5 m were assessed. Experiment Rembate-B was established in four nearby parcels (hereinafter, Field 1–4) on fertile abandoned agricultural land (corresponding to forest type Vr) with slightly different soil and micro-relief conditions. Experiment was established in spring of 2005 using three-year old bare-rooted seedlings, 140 families were represented in 3–4 replications (accordingly, for fields 1–4: 138, 77, 95 and 16 families) 24 trees per block plot (four

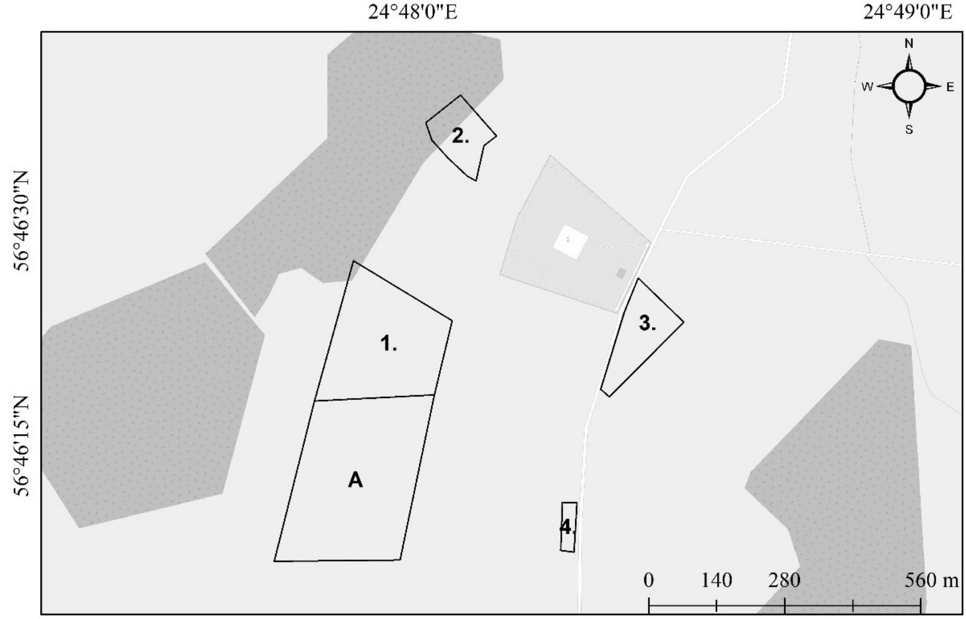


Fig. 2.2. **Location scheme of experiments of open-pollinated progenies: Rembate-A (A), and Rembate-B (Fields 1–4)**

rows of six trees), with spacing 2 × 2.5 m. For data analysis (**II**) from experiment Rembate-B the measurements were made in Fields 1, 3, 4 (in publication **II** used as 1, 2, 3, respectively).

Tree height, height increment and presence of lammas shoots in experiment Rembate-A was assessed at the end of eight growing season (October of 2014) for 3887 trees from 60 families, and in experiment Rembate-B – at the end of 10th (November of 2011), 11th (October of 2012) and 13th (November of 2014) growing seasons, assessing 3412 trees from 112 families. Bud flushing in experiment Rembate-B was assessed at the end of 11th growing season in a four-grade scale: Grade 1 – very late flushing (length of current increment <3 cm); Grade 2 – late flushing (3–6 cm); Grade 3 – early flushing 7–10 cm); Grade 4 – very early flushing (>10 cm). The presence of frost damage was also recorded.

The genetically determined development differences of lammas shoots (**VII**) were assessed in Rembate-B plantation.

2.1.2. Data analysis

The relation between proportions of trees with lammas shoots and stand density (**I**) was assessed with Spearman’s correlation analysis. The impact of micro-environmental factors (competition by surrounding vegetation, soil moisture regime) and browsing damages by ungulates on proportion of trees with lammas shoots was assessed with binary logistic generalised linear mixed-effects model (GLMM) in software R (version 3.4.3.; R Core Team, 2017) using the library ‘lme4’ (Bates et al., 2015). Three models were developed using the relation between trees with and trees without lammas shoots at the sample plot level as a response variable. In each model, the stand ID was set as the random effect to account for possible correlation (repeated measures) among sample plots within the same stand. The first model assessed the impact of stand age and forest type, using the data set of 102 stands (data collected in 2011). The second model assessed the impact of the micro-environmental factors, browsing damages and the impact of year of observation, using data set of 70 stands (data collected in 2011 and 2012). The same data set was used in the third model where the impact of suitability of growing conditions was assessed (calculated as the sum of scores of the three micro-environmental factors). The generalised linear hypothesis tests (in library 'multcomp' of R (Hothorn et al. 2008)) were used as post hoc tests after GLMM analysis, when the interaction of factors or factor showed a significant result by more than two levels.

The statistical data analysis of open-pollinated progenies of Norway spruce trees was carried out using one-factor analysis of variance (**II** and **VII**), Pearson's correlation analysis (**II** and **VII**) and Chi-squared (χ^2) test (**II**).

2.2. Soil preparation type and additional nutrient supply

2.2.1. Data collection

The impact of soil preparation type (**III**) and additional nutrients supply (**IV** and **V**) on height increment has been assessed in several separate experiments (Fig. 2.1.).

The impact of soil preparation type on tree growth (**III**) has been assessed in two locations (representing four forest types: Dm, Vr, Vrs and Ks), each in two replications. After a clear-cut in one of the sites (Dm and Ks) part of land was prepared with spot mounding and the other part with disc trenching, while in other site (Vr and Vrs) part of land was prepared with spot mounding and in part of land no soil preparation was performed. After the soil preparation (in autumn of 2008) two-year old containerized Norway spruce seedlings (height from 16 to 36 cm (average 23 ± 0.5 cm), root collar diameter from 1.5 to 4.5 mm) were planted. Tending (cleaning from competing vegetation) in both locations was performed in the following four growing seasons.

Tree height and annual height increment of the last three years were measured in winter of 2014/2015, with the accuracy of 1 cm. Tree defects (broken tops, ramicorn branches) were recorded in small proportion of trees (<2%) without any relation to soil preparation method or site, thus these trees were excluded from further data analysis.

The effect of additional nutrient supply with wood ash on growth of Norway spruce (**IV**) was assessed in a location on drained mineral soil (As). Plantation contains 18 spruce block plots with 15 m buffer zones between them. Randomly selecting each of them, a year before planting, one of wood ash doses was applied:

0 (control), 5 and 10 t ha^{-1}, each dose was used in six block plots. The chemical composition of ash (Table 2.1.) was similar to the ones mentioned in literature (Campbell, 1990; Ozolinčius et al., 2011), pH level 12.4. Plantation was established on a soil with high nitrogen content (Bārdule et al., 2009), thus no additional nitrogen fertiliser was used.

Table 2.1

Chemical composition of ash used in experiment and published in other literature sources

Chemical element	Level of chemical element in the ash used, % [1]	Level of chemical element in ash of published literature, % [2,3]
P	0.92	0.30–1.40
K	2.30	1.40–4.20
Ca	22.00	7.40–33.10
Mg	1.50	0.70–2.20
S	0.38	0.40–0.70
Fe	0.39	0.30–2.10
Mn	0.67	0.30–1.30
Zn	0.11	0.0004–0.0820
Cu	0.0054	0.0052–0.0289
Mo	0.0001	-
B	0.0158	0.0022–0.0225
Na	0.09	-

[1] Brūvelis (2005), [2] Campbell (1990); [3] Ozolinčius et al. (2011).

Two-year old spruce seedlings were planted year after ash application (spring of 2004). Twelve months after establishing the plantation, approximately half of the seedlings were dug out and their root and stem biomass was evaluated. For the remaining trees ten years after the establishment of plantation (in year 2014, before the beginning of growing season) height and diameter at breast height was measured. Soil samples were collected in each block plot for a repeated evaluation of the composition of nutrients available to plants and the soil reaction. Samples have been prepared according to LVS ISO 11464 Standard (year 2005). The total nitrogen (N) content (LVS ISO 11261 (2002)), the phosphorus available to plants (P-PO_4^{3-}) content (LVS 398 (2002)) and potassium (K) content (extracted with ammonium acetate and determined with atom spectroscopy) was determined.

The effect of initial soil fertilisation (**V**) on spruce height increment was assessed in spruce plantation in *Hylocomiosa* (Dm) forest type. Experimental plantation was established in year 1982 by planting four-year old bare-rooted saplings of local provenance, enclosed in pressed peat capsules “Brika” (Rubtsow, 1979), in a prepared soil with planting density of 4000 trees per ha^{-1}, with 200 trees in four blocks. After planting, each sapling received ring fertilization at 10 cm distance, providing a dose of 14 g N (NH_4NO_3), 6 g P (superphosphate) and 11 g K (KNO_3) for each sapling, which is equal to 56, 24 and 44 kg ha^{-1}, respectively. Twice during the first growing season, chemical weed control, by sprinkling simazine (3 kg ha^{-1}) solution around the saplings, was applied.

In February of 2012, measurement of tree height and diameter at breast height was performed to 586 trees that received initial soil fertilisation and to 592 control trees. To determine the long-term effect of soil fertilisation in October of 2013 (stand age 34) samples were collected from 30 fertilised trees and 30 control dominant trees without visible damages, by using Pressler borer to extract increment cores (5 mm) at breast height. The increment cores were processed in laboratory using the LignoStation wood analysis system (RinnTECH Inc., Heidelberg, Germany), receiving data on total width and latewood width of each tree ring of each sample (Schinker et al., 2003).

2.2.2. Data analysis

Impact of forest type and soil preparation type on tree height, and also the projective covering of surrounding vegetation and height differences before and after tending, and the impact of soil preparation type on the time when tending is needed (**III**) was assessed with ANOVA, Tukey's HSD test was used to assess the differences. The impact of soil preparation type, forest type and the interaction of these factors were assessed with two-factor ANOVA. The impact of soil preparation type on tree growth has also been evaluated for the 100 tallest trees of stand ha^{-1} (Donis, 2014). The impact of soil preparation type on tree growth was assessed with Chi-squared (χ^2) test by comparing the distribution of trees in height classes ($h \leq 1.5$ m; $1.5 < h \leq 2$ m; $2 < h \leq 2.5$ m; $h > 2.5$ m) in each forest type. Calculations were carried out in SPSS programme with 95% confidence interval.

The impact of different fertiliser doses (**IV**) on the content of NPK in soil and on tree biomass and dimensions was compared using general linear models. The impact of dose was assessed with mixed-effects models, taking the number of block plot as the random factor. Time series from 1985 until 2013 of tree rings' widths of trees that received additional nutrients and the control trees (**V**) were crossdated and their quality was verified by a graphical inspection and also statistically evaluated by using the program COFECHA (Grissino-Mayer, 2001; Speer, 2010). The time series, which did not match with the rest of the series were excluded from analysis, leaving samples of 24 trees from fertilised soil and 24 control trees for further data analysis.

2.3. Differences of plus-tree open-pollinated families

2.3.1. Data collection

The impact of genetically determined differences (on the level of families and provenances) on the development of height increment (**VI** and **VII**) has been assessed in two experimental plantations of open-pollinated progenies in the central part of Latvia (Fig. 2.1. and 2.2.).

The impact of planting material's origin on the development of height growth (**VI**) was assessed in a plantation in Jelgava region, in Forest Research Station forests, further in text – Jelgava. The experimental plantation in Jelgava was established in 2006 on forest land (As) with two-year-old bare-rooted seedlings, initial spacing 3 × 2 m. Representing forest reproductive material areas of two provenances from western and four provenances from eastern regions (Gailis, 1993). Each provenance was represented by 10 half-sib families. Each family was represented in five (in some cases – four) replications, in block plots of 12 trees (three rows of four trees).

Measurements of increments were performed in 2010, in the seventh growth season. For measurements 1273 trees without double tops and visible damages were selected: 843 trees from joined central and eastern regions, and 430 trees from western region (provenance regions of forest reproductive material). The length of the main shoots was measured every six to eight days during the period from May 25 to July 20 (nine times) with a precision of 1 mm. The measurements for all trees in each survey were performed at the same day. Tree height after the cessation of height growth was measured on September 10.

The impact of families on development of height increment (**VII**) was assessed in experimental plantations of open-pollinated progenies of Norway spruce in Rembate-B, Field-1 (see description in 2.1.1.) and in Jelgava (description and measurement methods in 2.3.1.-VI). Measurements in plantation Rembate-B were carried out in the ninth growing season. At the beginning plantation was surveyed every second day to determine the time of bud burst (when approximately half of trees were flushing). Following measurements of height increment were carried out once a week for trees without animal, insect damages and broken tops. Altogether, in plantation Rembate-B measurements were carried out for 88 families, 1766 trees (20 trees from family on average). From the data measured in Jelgava, data about 59 families, 1239 trees (21 trees from family on average) were used in the analysis of family effect.

2.3.2. Data analysis

The impact of provenance region on the onset of height increment (binomial variable), the diurnal mean growth intensity (mm per day), total height increment and tree height at the beginning and end of observation period (**VI**) was evaluated using linear mixed-effect models (Zuur et al., 2009). Differences in growth onset and cessation were evaluated with general linear model with binomial distribution of residuals and 'logit' link function. To evaluate the effect of provenance on growth, these models were compared with analysis of variance.

To characterise and compare height increment curves (**VII**), the height measurements of each tree were approximated with Gompertz equation (2.1.):

$$f(A) = \alpha \exp(-\beta \exp(-kA)) \,, \tag{2.1}$$

where:

α – asymptote parameter;

β– displacement parameter;

k – maximum relative intensity;

A – day of measurements.

Families of each plantation were ranked in a decreasing order according to height increment, and 10% of the ‘best’ and 10% of the ‘worst’ families were selected according to the mean values of family effect.

Individual tree measurements were used to calculate mean coefficients of the fitted Gompertz model, mean height increment, mean shoot elongation, cumulative shoot elongation and their 95% confidence level. Relations among shoot elongation parameters was assessed by Pearson correlation. The one-way analysis of variance was used to determine statistically significant differences of shoot elongation parameters among distinguished groups of families. All calculations were done in R (version 3.5.3), at significance level 0.05.

3. RESULTS AND DISCUSSION

3.1. Lammas shoots

The proportion of trees with lammas shoots in the assessed young Norway spruce (*Picea abies* (L.) Karst.) forest stands and experimental plantations of progenies during the data collection period (4 years) ranged from 0% to 27%. The proportions of trees with lammas shoots in experimental plantations of open-pollinated progenies were 6% in the experimental Rembate-A plantation at the age of eight and 8.7%, 26.9%, and 8.1% in the experimental Rembate-B plantation at the ages of 10, 11, and 13, respectively (**II**). The proportion of trees with lammas shoots in at least one of the assessment years at Rembate-B was 32.3% (**II**). In the sampled forest stands, the proportion of trees with lammas shoots on average was 6.5%, ranging from 0% to 25% (**I**). A similar proportion of trees with lammas shoots (7%) was found for provenances from the Baltic States at the age of five years in an experiment in Sweden (Danusevičius & Persson, 1998), and at the same age for provenances from Latvia in an experiment in Norway (Søgaard et al., 2011), but in some cases, in forest stands in Norway, the proportion of trees with lammas shoots reached up to 80% (Kvaalen et al., 2010).

Significant intra-annual variability was found for the proportion of trees with lammas shoots both in experimental plantations of progenies and forest stands. The proportion of trees with lammas shoots in the sampled Norway spruce stands in 2011 was slightly ($p > 0.05$) lower than in 2012, at 9.1% and 12.9%, respectively (**I**). However, in the experimental plantation of progenies Rembate-B (all fields together), the differences between assessment years were significant ($p > 0.05$) and notable: 6.8% and 20.1%, respectively. The presence of variability of lammas shoots is linked to the effect of meteorological conditions, especially the air temperature during development (Skrøppa & Steffenrem, 2016). In the territory of assessment, the air temperature in August of 2011 was slightly (3°C on average) lower than in the next year. Analyzing the temperature in July and August in shorter periods in 2012, in comparison with 2011, a sharp temperature increase was observed between the third and fourth weeks of July (**I**). This relative change in meteorological factors during a specific period of development (not the average values of the factors) may have triggered the development of lammas shoots. A similar effect of short-term changes for increased precipitation at the end of the growing season, which stimulates the development of lammas shoots, is one of the most mentioned factors in the literature (Carvell, 1956; McCabe & Labisky, 1959; Hallgren & Helms, 1988).

Stand parameters, which include density, forest type, and interaction between forest type and stand age, did not have a significant effect on the proportion of trees with lammas shoots (in all cases, $p > 0.05$; **I**); however, such an effect has previously been observed for age (Ehrenberg, 1963; Aldén, 1971; Rone, 1985; von Wühlisch & Muhs, 1986; Ununger et al., 1988; Søgaard et al., 2011) and soil fertility (Søgaard et al., 2011). Nevertheless, in the experiment Rembate-B, which was established on four nearby fertile abandoned agricultural lands (all corresponding to the forest type Vr) with slight differences in soil and micro-relief, the proportion of trees with lammas shoots was significantly different. The proportion was from 1.2% to 15.2% at the age of 10 and from 13.1% to 29.0% at the age of 11, showing the effect of the microenvironment on the presence of apical lammas shoots.

The proportion of trees with lammas shoots in Norway spruce stands has been significantly affected by microenvironmental conditions (competition by surrounding vegetation and the soil moisture regime) and browsing damage (Fig. 3.1, **I**). The effect of competition by the surrounding vegetation and soil moisture regime on the development of lammas shoots was statistically significant ($\chi^2 = 45.0$, $p < 0.001$). Forest stands without competition by the surrounding vegetation (Grade 1) had a significantly higher number of trees with lammas shoots than forest stands with average and high competition (Grades 2 and 3): 14.5%, 6.0%, and 2.2%, respectively. Similarly, in stands where the soil moisture regime was suitable for the Norway spruce, the proportion of trees with lammas shoots was higher than stands with periodic or permanent excessive soil moisture: 11.7%, 4.8%, and 1.7%, respectively. In both cases, only the trees growing in the most suitable microenvironmental conditions had statistically significant ($p < 0.05$) differences from the rest of the evaluation groups, and the differences between the rest of the groups were not significant (**I**). The proportion of trees with lammas shoots was lower in stands with greater browsing damage (11.3% in Grade 1, 8.2%

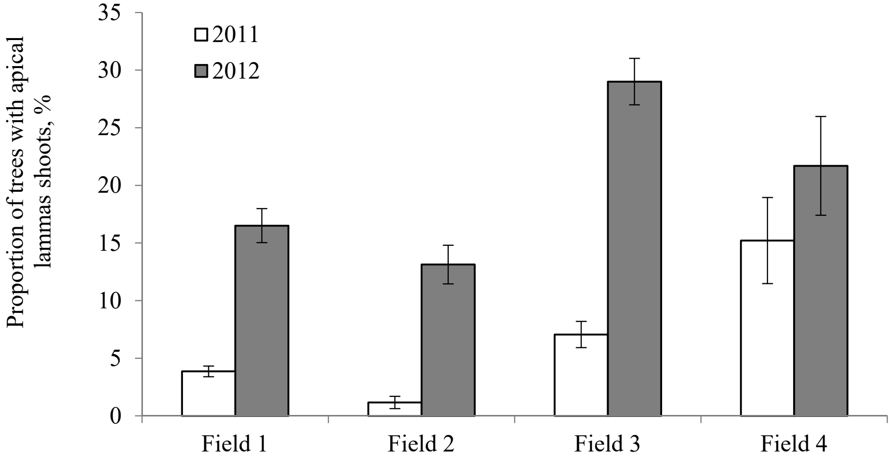


Fig. 3.1. **Proportion of trees with apical lammas shoots (± 95% confidence interval) in Rembate-B for 2011 and 2012**

Each factor was assessed at three grade scales, where (1) the negative effect of the factor on tree growth was not observed, (2) the minimal negative effect of the factor was observed, and (3) the notable negative effect of the factor was observed.

in Grade 2, and 7.7% in Grade 3), but the differences between evaluation groups were not significant ($p < 0.05$).

The results of the interaction analysis revealed that each of these factors had a separate role in favoring the development of lammas shoots (**I**). With that, the combination of all microenvironmental conditions (competition by surrounding vegetation, soil moisture regime, and browsing damage) has a significant effect on the development of lammas shoots (Fig. 3.2, **I**). Trees that grew in the most favorable conditions (the lowest score) had the highest proportion of lammas shoots, whereas, if one of the factors in some stand was evaluated at Grade 3 (a notably negative effect), the proportion of lammas shoots did not exceed 10% (**I**). For example, in a five-year-old stand (Dm) with particularly high competition by surrounding vegetation and with 22% visible browsing damage, the proportion of trees with lammas shoots was only 1.8%, whereas, in a stand of the same age in the same forest type with signs of regular ground vegetation tending and without browsing damage, the proportion of trees with lammas shoots was 25.5%.

The results of repeated assessments demonstrate that the increase in the presence of lammas shoots can be linked to tending (cleaning), which was performed in 2011 (**I**). For example, after tending at the end of the growing season in the three-year-old stand (Kp), the proportion of trees with lammas shoots increased from 10% in 2011 to 26% in 2012, but in a five-year-old stand (Dm), the increase was from 18% in 2011 to 33% in 2012. Similarly, a substantially higher presence of lammas shoots was observed in Douglas fir stands after weed control (Roth & Newton, 1996).

A significant ($p < 0.05$) family effect on the proportion of trees with lammas shoots was determined, and the proportion of such trees in families in the

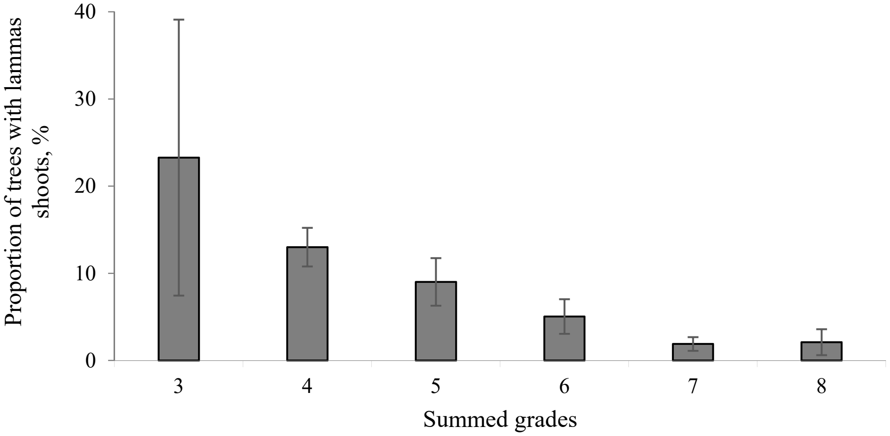


Fig. 3.2. **Proportion of trees with apical lammas shoots (± 95% confidence interval) according to the summed grades of the microenvironment (surrounding vegetation and soil moisture) and browsing damage assessment**

Each factor was assessed at three grade scales, where (1) the negative effect of the factor on tree growth was not observed, (2) the minimal negative effect of the factor was observed, and (3) the notable negative effect of the factor was observed.

experimental plantation Rembate-B was from 0% to 42%. In favorable conditions, which occurred in 2012 at Rembate-B Field 3 (fertile soil during summer with a distinct air temperature increase at the end of the development of the intra-annual height growth), apical lammas shoots formed not only in a larger proportion of trees in the family but also in a larger proportion of families (Fig. 3.3).

The time of bud burst is genetically determined to a large extent (Hannerz et al., 1999; Skrøppa & Steffenrem, 2019), and a link between it and the development of lammas shoots has been observed (**II**). Early-flushing trees had a higher presence of lammas shoots than late-flushing trees. For example, in Field 3, in the group of very early-flushing trees (Grade 4), 56% developed lammas shoots; however, in the group of very late-flushing trees (Grade 1), only 22% developed lammas shoots. In each of the flushing grades, the mean height increment was significantly ($p < 0.001$) higher for trees with lammas shoots than for trees without them (**II**). In the central part of Sweden, in contrast to these results, a higher proportion of lammas shoots was observed for provenances with late-flushing trees (Danusevičius & Persson, 1998).

Altogether, early flushing provided trees with advantages, and their height increment was higher than for later-flushing trees. However, for early-flushing trees, the risk of frost damage was also higher: the proportion of frost damage for very early or early-flushing trees (Grade 4 and 3) was 87% and 2%, respectively, whereas frost damage was not observed for late- or very late-flushing trees (Grade 2 and 1) (**II**). Frost damage had a significant negative effect on height increment: the highest height increment was for very early-flushing trees (Grade 4) without frost damage, but those with frost damage had the lowest increment, even lower than the mean increment of very late flushing trees (Grade 1) (**II**). The development of lammas shoots was able to compensate for the negative effect of frost damage to a large extent, and the decrease in height due to frost damage for trees with lammas shoots was lower than that for trees without lammas shoots (**II**).

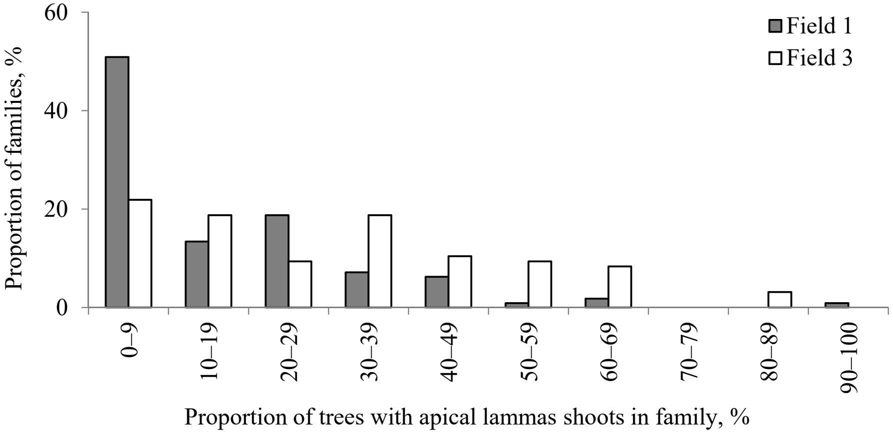


Fig. 3.3. **Proportion of families with a certain proportion of trees with apical lammas shoots within the family at Rembate-B at the age of 11 years**

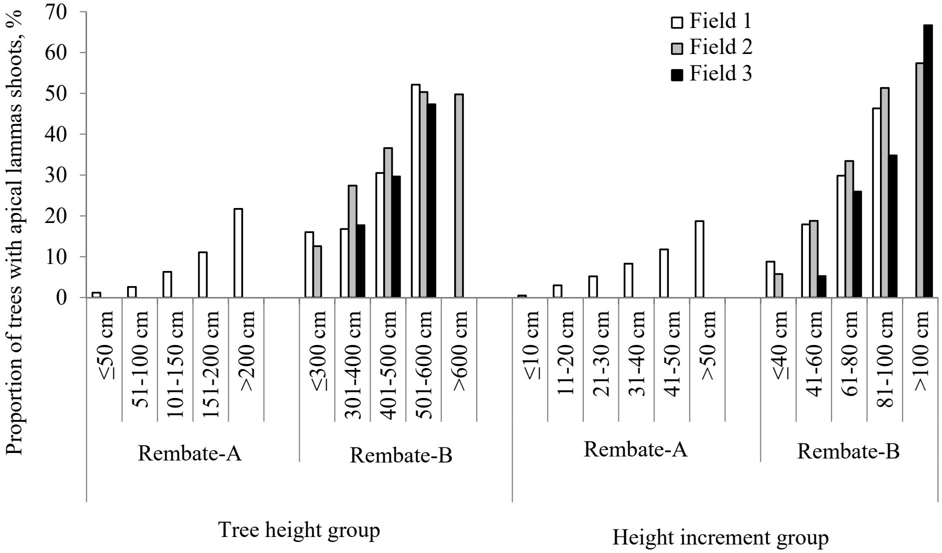


Fig. 3.4. **Proportion of trees with apical lammas shoots according to height and height increment at the previous growing season**

The development of lammas shoots is linked to tree height. In the experimental plantation Rembate-A, a significantly ($p < 0.001$) higher proportion of trees with lammas shoots was found for trees with higher height and higher height increment (Fig. 3.4) and for groups with higher values of productivity parameters reaching approximately 20%. However, in groups of trees with the lowest productivity values, only 1% were found. In addition, in all fields of the plantation Rembate-B, a similar trend was found: trees in groups with the highest height and height increment had, on average, 47% to 68% of trees with lammas shoots, but 5% to 18% were found in groups of slowly growing trees. The differences between the groups were statistically significant ($p < 0.001$).

Height increment in the eighth growing season in the plantation Rembate-A was notably (by 68%) and significantly ($p < 0.001$) higher for trees with lammas shoots than for trees without them at 44 ± 2.4 cm and 26 ± 1.7 cm, respectively (**II**). Similarly, in plantation Rembate-B, the height increment of the last three years for trees with lammas shoots was statistically significantly ($p < 0.001$) higher than for trees without lammas shoots, reaching a difference of 10 to 14 cm. The cumulative effect of such seemingly small quantitative differences on tree height is notable.

The cumulative effect of these height increment differences is significant ($p < 0.001$). The tree height at the end of the thirteenth growing season for trees with and without lammas shoots at the plantation Rembate-B in separate fields were 450 ± 11.8 cm and 374 ± 7.8 cm (Field 1), 490 ± 8.1 cm and 416 ± 7.4 cm (Fields 3 and 2) and 481 ± 16.0 cm and 420 ± 12.2 cm (Fields 4 and 3; Fig. 3.5, **II**), respectively. Trees with lammas shoots were 14% to 20% taller than trees without

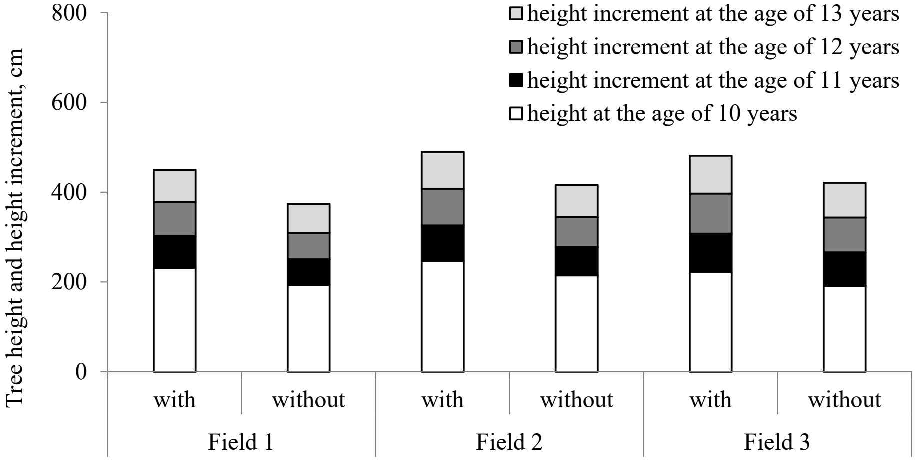


Fig. 3.5. **Tree height at the age of 10 years and height increment of the last three growing seasons (eleventh to thirteenth growing season) for trees with and without apical lammas shoots in Rembate-B**

lammas shoots. In addition, in the plantation Rembate-A, the results were similar. At the age of eight years, the mean height of trees with lammas shoots was 29% ($p < 0.001$) higher than for trees without lammas shoots (148 ± 5.8 cm and 115 ± 1.4 cm, respectively).

On the family level, the proportion of trees with lammas shoots in the plantation Rembate-A (**II**) was significantly related to the height increment ($r = 0.44$; $p < 0.001$), but the correlation with the height was not statistically significant ($r = 0.22$; $p = 0.09$). In the plantation Rembate-B, the proportion of trees with lammas shoots had a significant ($p < 0.001$) correlation with the height increment and with the total height in the plantation in total ($r = 0.49$ and $r = 0.51$, respectively) and each field, separately ($r = 0.41...0.71$ and $r = 0.48...0.70$, respectively). Correlation between the tree height and development of lammas shoots has also been reported in previous tree breeding trials in Latvia (Rone, 1975) and provenance trials in Sweden (Danusevičius & Persson, 1998).

3.2. Soil preparation

3.2.1. Soil preparation effect on height increment

Tree height at the age of eight years was significantly affected (all $p < 0.001$, **III**) by site type, soil preparation type, and interaction between these two factors, but the effect of planting replication was insignificant ($p > 0.05$). Trees on the *Oxalidosa* site type had the largest height (198 ± 3.8 cm), regardless of soil preparation type. Similarly, the largest height was reached for spruce trees growing in the same site type (*Oxalidosa*) at the same age in Lithuania (Gradeckas & Malinauskas, 2005), indicating the suitability of the particular site type for the establishment of productive spruce stands.

Trees that were planted on mounds were notably and significantly higher than trees that were planted on unprepared soil (difference in height of 27 cm or 17.8%) or furrows (difference in height of 55 cm or 35.7%). The assessment of four distinguished groups (by tree height) revealed a larger proportion of the highest trees on mounds at all site types, in comparison to furrows and unprepared soil (Fig. 3.6). Among the studied site preparation methods, differences in height were statistically significant ($p < 0.05$) in *Oxalidosa* and *Myrtilloso-polytrichosa* site types, and the same trend persisted in *Hylocomiosa* ($p = 0.05$) and *Myrtillosa turf. mel.* site types. A similar effect of site preparation type was observed in Finland (Uotila et al., 2010).

Differences in the tree height for spot-mounded sites in comparison to other soil preparation methods were significant ($p < 0.05$, **III**) in site types on dry mineral soils (*Hylocomiosa, Oxalidosa*) and wet mineral soils (*Myrtilloso-polytrichosa*). Such differences were less expressed ($p = 0.09$) on the *Myrtillosa turf. mel.* site type, which was presumably related to the effect of frost heave that mostly occurs on drained peat soil in Latvia (Mangalis, 2004). In the central part of Finland, disk-trenched sites are most susceptible to the occurrence of frost heave (Heiskanen et al., 2013). Superiority in height for trees planted on mounds is also noted in Sweden and Finland (Saarinen, 2007; Lehtosalo et al., 2010; Uotila et al., 2010; Hallsby & Örlander, 2013). The differences in height, however, are smaller (Örlander et al., 1990, 1998) than those found in this study (**III**), which are presumably related to the slower tree growth under a more northern climate.

The positive effect of spot mounding on tree growth (**III**) is associated with

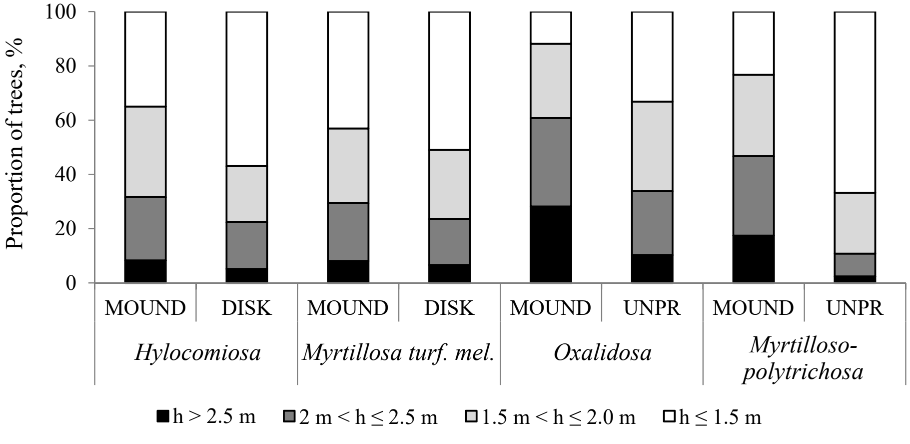


Fig. 3.6. **Proportion of trees according to height groups at the age of eight years on spot-mounded (MOUND), disk-trenched (DISK), and unprepared soil (UNPR) in *Hylocomiosa*, *Myrtillosa turf. mel.*, *Oxalidosa*, and *Myrtilloso-polytrichosa* site types**

the increased availability of nitrogen (increased mineralization) during the second and third growing seasons (Smolander & Heiskanen, 2007; Nieminen et al., 2012) that promotes an increase in aboveground and root biomass (Nordborg et al., 2003). Soil preparation prevents damage by the large pine weevil *Hylobius abietis* (L.). Moreover, such an effect persists even if seedlings in the nursery are treated with insecticide (Heiskanen et al., 2013). For instance, in Finland, during the first growing season, 76% of spruce trees on unprepared soil had damaged bark, whereas damaged bark was found for only 1% of seedlings in spot-mounded sites (Heiskanen & Viiri, 2005). Trees that are damaged by the pine weevil are weakened and have a smaller height increment (Heiskanen & Viiri, 2005; Heiskanen et al., 2013). Considering that the studied stands (**III**) are planted on areas after coniferous clear cutting (i.e., sites with the highest risk of pine weevil damage), soil preparation presumably resulted in a limited occurrence of the pine weevil, thus contributing to the height differences among sites with different soil preparation methods (**III**). Moreover, spot mounding has a positive effect on soil temperature (Kankaanhuhta et al., 2009; Heiskanen et al., 2016). Combined with increased nutrient availability and the limiting effect on the pine weevil, this soil preparation type promotes better seedling establishment and initial growth when compared to disk-trenched and unprepared soil.

For dominant trees, the height increment of the last three growing seasons on spot-mounded sites was higher than that on disk-trenched or unprepared soil (**III**). These differences were statistically significant on the *Hylocomiosa* site type in the eighth growing season, whereas at the sixth growing season significant differences were not found. In the seventh and eighth growing seasons, the height increment on spot-mounded sites was higher than that on the unprepared soil, but in the sixth growing season, significant differences were found only on the *Myrtilloso-polytrichosa* site type ($p < 0.05$, **III**). The obtained results are in agreement with the findings in Finland: the mean height increment for spruce trees planted on mounds is slightly larger than for trees planted in furrows (23.7 ± 17.4 and 20.6 ± 13.6 cm, respectively), and the cumulative effect ensures significant differences at the end of the ninth growing season (Saksa et al., 2005).

3.2.2. Soil preparation effect on competing vegetation

The competing vegetation cover in the area not disturbed by a soil preparation machine (between furrows and mounds) was similar for the spot-mounded and disk-trenched sites (**III**). However, the mean projective cover of competing vegetation before tending was 78% in spot-mounded sites and 54% in disk-trenched sites (**III**). The soil preparation method affects the shading of seedlings and, thus, the necessity for tending. In similar climatic conditions in Lithuania, the least shaded seedlings grow on wide furrows (100 cm) and high mounds (30 cm) (Suchockas et al., 2014).

Soil preparation increases the diversity of competing vegetation species (Balandier et al., 2006) but does not necessarily change the effect of the competing vegetation on the tree height growth. The negative effect of competing vegetation

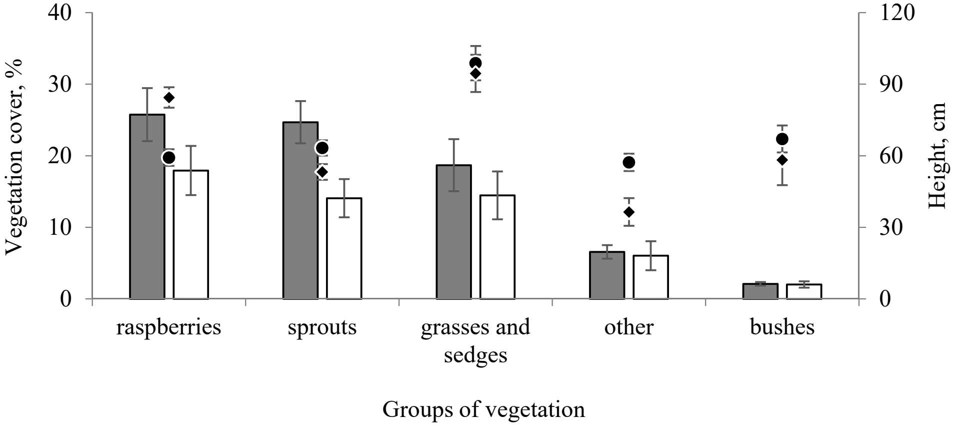


Fig. 3.7. **Projective competing vegetation cover (bars) and height (symbols; all ± 95% confidence interval) before tending in spot-mounded (dark gray bars and points) and disk-trenched (white bars and rhombi) sites on the *Myrtillosa mel.* site type**

is associated with its distance to seedlings and could be reduced by an increased area or depth of the disturbed soil (Suchockas et al., 2014). Spot-mounded and disk-trenched sites had a similar proportion of the competing vegetation groups (Fig. 3.7), and tree/bush sprouts, raspberry (*Rubus ideaeus* L.), grasses, and sedges (families of *Graminae* and *Cyperaceae*) formed the majority of vegetation cover (85% to 89%). In addition, the mean weighted (by projective cover) height of the competing vegetation was similar ($p > 0.05$). In spot-mounded sites, grasses and sedges were higher than the other groups of vegetation, whereas, in disk-trenched sites, the highest vegetation was grasses, sedges, and raspberries (**III**). The grasses and sedges are considered the most important competitors because their rapid root growth requires intensive use of water, thus negatively affecting the growth of seedlings (Coll et al., 2003). In spot-mounded and disk-trenched sites, the necessity for tending was similar (**III**).

After tending, the projective cover of competing vegetation on spot-mounded sites was significantly lower than on disk-trenched sites (5% and 13%, respectively), but its height was similar ($p > 0.05$, **III**). Both the time required for mowing and its proportion of the total time required for tending were similar: 478 min ha^{-1} (67% ± 9.7%) for spot-mounded stands and 462 min ha^{-1} (68% ± 8.3%) for disk-trenched stands (**III**).

3.2.3. Effect of improvement in soil nutrient availability on tree height

After wood combustion, most nutrients are retained in ash and can be used to improve the soil nutrient availability. Ten years after the ash dispersal, the potassium content increased proportionally to the applied dose of ash (Fig. 3.8). In the control parcels, the potassium content was 270.9 ± 70.3 mg kg^{-1}, but in parcels

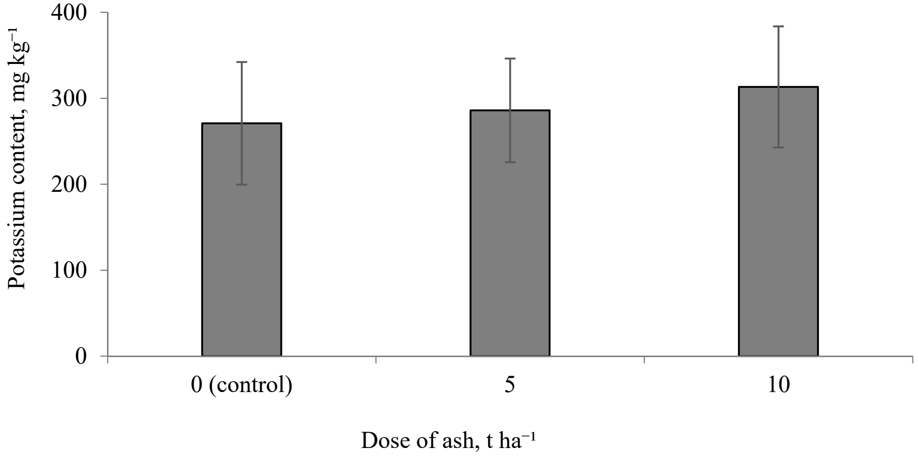


Fig. 3.8. **Potassium content in soil (± 95% confidence interval) 10 years after wood ash dispersal (dose of 0 (control), 5, and 10 t ha^{-1})**

where 5 and 10 t ha^{-1} of ash were applied, the potassium content was 286.0 ± 60.2 and 313.3 ± 70.5 mg kg^{-1} (**IV**). Similar results were observed in Finland, where the potassium deficit in the soil diminished after one year of ash application (Moilanen et al., 2005).

Moreover, depending on the applied dose of ash, the increased nutrient availability in the soil remains for 20 to 30 years (Moilanen et al., 2002, 2004, 2005). An increase in the phosphorus content was notable only one year after application; however, phosphorus dissolves slowly (Nieminen et al., 2005; Callesen et al., 2007); therefore, three to four years are necessary for this nutrient to be present in a plant-available form (Moilanen et al., 2002; Nieminen et al., 2005). Ten years after ash dispersal, the soil phosphorus content in parcels where the applied dose of ash was 5 and 10 t ha^{-1} was 2.24 ± 0.40 and 2.19 ± 0.28 g kg^{-1}, respectively, whereas it was 1.85 ± 0.27 g kg^{-1} in the control parcels (Fig. 3.9, **IV**). Other studies have found that an increased phosphorus amount in the soil after ash application may last for up to 30 to 50 years (Moilanen et al., 2002, 2004, 2005). The soil nitrogen content was similar ($p > 0.05$), regardless of the applied dose of ash, and varied from 26.79 ± 3.42 g kg^{-1} in control parcels to 27.42 ± 2.84 g kg^{-1} in parcels where 5 t ha^{-1} of ash was applied (Fig. 3.10, **IV**).

During wood combustion, nitrogen is released into the atmosphere and, thus, cannot be found in ash. The application of ash, however, has an indirect effect on the soil nitrogen content: increased mineralization of the soil organic matter promotes the release of organic nitrogen into a plant-available form (Moilanen et al., 2002; Genenger et al., 2003; Jäggi et al., 2004). Some studies have indicated that the application of ash might increase the depth of the soil organic layer (nitrogen reserve) due to an increased amount of litter (Omil et al., 2013); however, 10 years after ash application, such an effect was not observed (**IV**). Yet, it should be considered that the released nitrogen might not be found in the soil due to

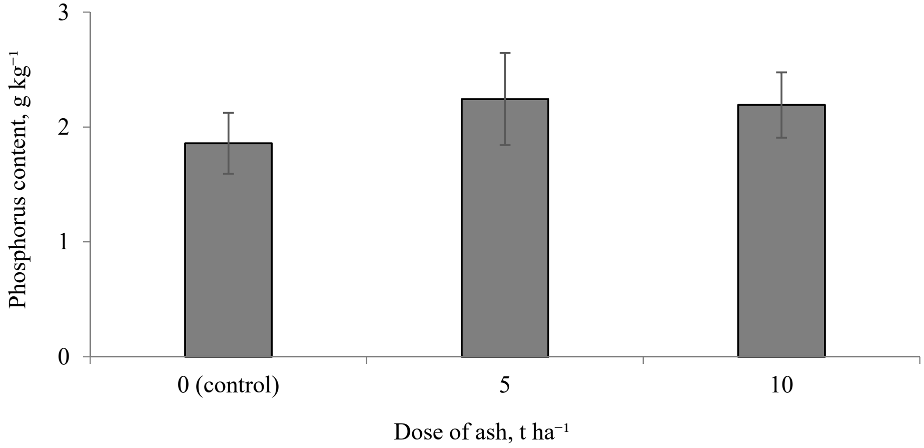


Fig. 3.9. **Phosphorus content in soil (± 95% confidence interval) 10 years after wood ash dispersal (dose of 0 (control), 5, and 10 t ha^{-1})**

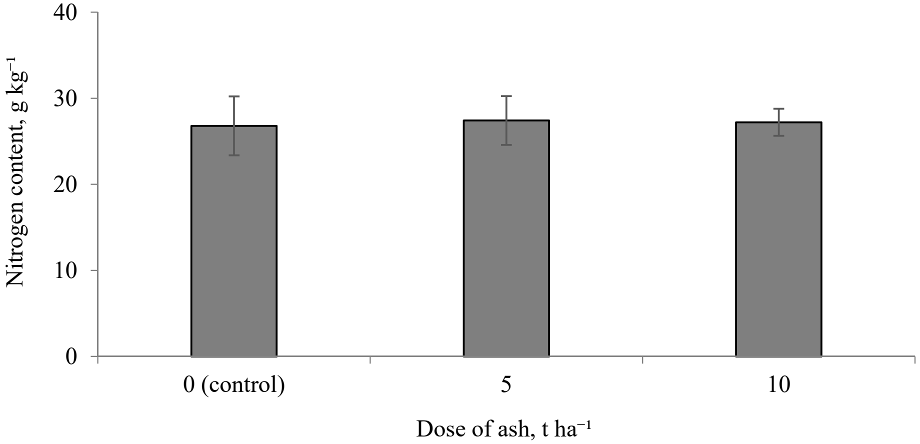


Fig. 3.10. **Nitrogen content in soil (± 95% confidence interval) 10 years after wood ash dispersal (dose of 0 (control), 5, and 10 t ha^{-1})**

leaching and oxidizing into the atmosphere, and it might be used by the trees and competing vegetation. Wood ash application aims to increase its availability for plants to increase their growth, not to increase the nitrogen content in the soil.

The increased availability of nutrients promotes the growth of seedlings, thus increasing their competitiveness with other vegetation for several years (Nilsson & Örlander, 1999; Hytönen & Jylhä, 2008). The positive effect of ash dispersal on tree biomass was found after one year. The highest aboveground biomass was found in the parcels where 5 t ha^{-1} of ash was applied in comparison to parcels where no (control) or 10 t ha^{-1} of ash was applied (Fig. 3.11, **IV**). These differences were statistically significant ($p < 0.05$). Similarly, root biomass was also significantly higher ($p < 0.05$) in parcels where 5 t ha^{-1} of ash was applied in comparison to the

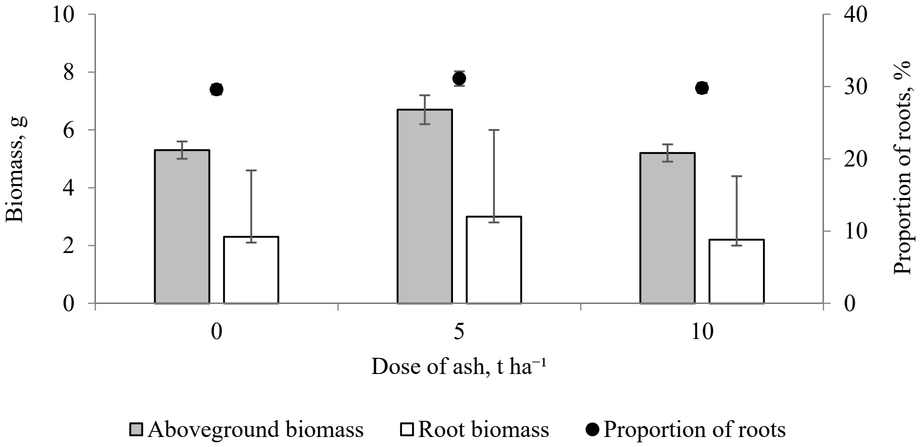


Fig. 3.11. **Morphological parameters (± standard deviation) of trees 12 months after planting in parcels where wood ash was applied (dose of 0 (control), 5, and 10 t ha^{-1})**

parcels where no (control) or 10 t ha^{-1} of ash was applied. The proportion of root mass from total plant biomass in parcels where 5 t ha^{-1} of ash was applied was slightly statistically not significantly higher than in the other parcels (**IV**).

Ten years after planting, a positive effect of ash application on the tree growth remained and was larger for parcels where a higher dose of ash was applied (Fig. 3.12, **IV**). The diameter at breast height was 21.9 ± 1.3 mm in control parcels, and 26.3 ± 1.8 and 26.5 ± 1.7 mm in parcels where 5 and 10 t ha^{-1} of ash was applied, respectively. Similarly, the tree height was 289 ± 11 cm in the control parcels, and 331 ± 14 cm and 348 ± 12 cm in the parcels where 5 and 10 t ha^{-1} of

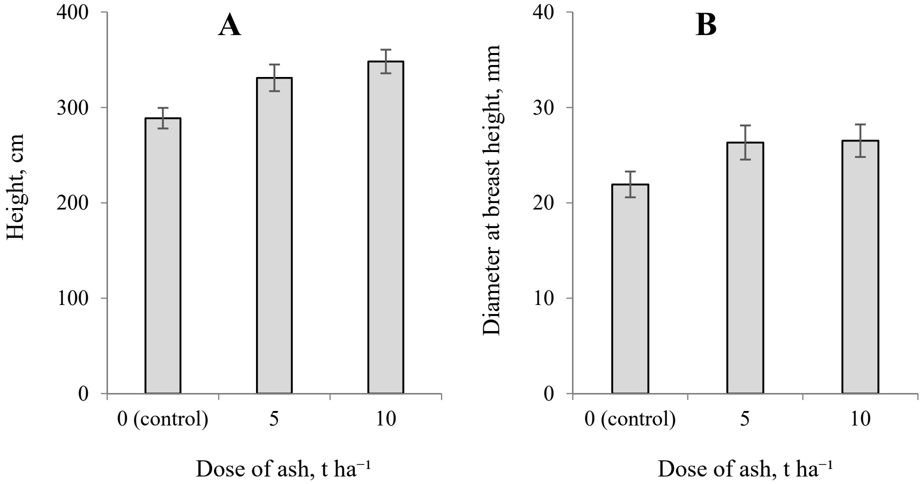


Fig. 3.12. **Tree height (A) and diameter at breast height (B) (± 95% confidence interval) 10 years after wood ash dispersal (dose of 0 (control), 5, and 10 t ha^{-1})**

ash was applied, respectively. In parcels where ash was dispersed, the tree height was 15% and 21% larger (ash doses of 5 and 10 t ha^{-1}) than in control parcels. The tree diameter and height were significantly larger (all $p < 0.05$) in the parcels where ash was dispersed (both ash doses) than in the control parcels. However, the differences between the parcels where 5 and 10 t ha^{-1} of ash was dispersed were small and not significant ($p > 0.05$; **IV**).

A significant ($p < 0.01$) long-term effect of increased soil nutrient availability was found for initial (right after planting) NPK fertilization (**V**). The locally (around the seedling) added nutrients had an effect similar to that of evenly applied fertilizer on the entire stand (Nohrstedt, 2001; Saarsalmi & Mälkönen, 2001; Cao et al., 2008), whereas less fertilizer was needed for the area unit. The long-term effect of the initial fertilization on tree growth was exhibited in pine stands in Finland, where 15 years after wood ash dispersal (2.5 and 5 t ha^{-1}), the tree height was 24% and 27% larger than in the control stands, respectively (Saarsalmi & Levula, 2007). Increased tree growth as soon as one year after ash dispersal (2.5 t ha^{-1}) was found in middle-aged (ash dispersal at the stand age of 36 and 47 years) spruce stands (*Myrtillosa mel.* and *Myrtillosa turf. mel.* site types). Four years after the ash dispersal, the additional volume increment varied from 8.5 to 19.2 m^3 ha^{-1} (Okmanis et al., 2016). In 64- and 69-year-old pine stands on mineral soil, however, the volume increment 5 to 10 years after the ash dispersal (3 t ha^{-1}) was 7% and 9% larger than in the control stands, but these differences were not significant (Saarsalmi et al., 2004).

The comparison of the tree-ring series of fertilized and unfertilized trees demonstrated the largest differences at the beginning of the observed period (Fig. 3.13). For the first three years after fertilization, the tree-ring width was larger for unfertilized trees, whereas, for the following eight years, the tree-ring width was significantly larger for fertilized trees (**V**). The delayed effect, presumably, is associated with the too-high applied dose of nutrients or the gradual release of

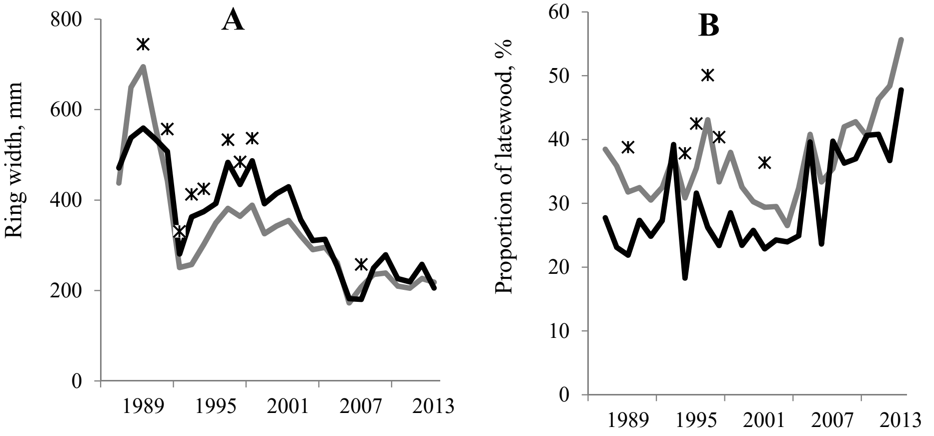


Fig. 3.13. **Mean tree-ring width (A) and proportion of latewood width (B) for time series of fertilized (dark line) and unfertilized (gray line) trees**

Significant ($p < 0.05$) differences are denoted with *.

nutrients in a plant-available form (Nohrstedt, 2001; Saarsalmi & Mälkönen, 2001) but might also be related to a different carbon allocation strategy for fertilized trees (Axelsson & Axelsson, 1986).

At the age of 34 years, fertilized trees had a 14% larger basal area than unfertilized trees (**V**). The proportion of latewood for unfertilized trees was larger for almost all studied periods, with significant differences in 1989, 1994 to 1997, and 2001 (10 to 20 years old). Similar findings of a smaller proportion of latewood for fertilized trees have been reported (Zhang, 1995; Mäkinen et al., 2002). The observed results suggest that the initial (right after planting) fertilization has a long-lasting effect for about 15 years (**V**).

3.3. Differences in shoot elongation dynamics for open-pollinated plus-tree families

The assessment of shoot elongation dynamics is important to forecast the effect of climate changes on the annual height increment and, more precisely, to select genotypes that are suitable for these changes. Within the growing season, shoot elongation is not uniform but typically consists of three distinct phases: a) relatively slow growth onset and b) cessation and c) intense growth between these two phases (Chuine et al., 2006; Lanner, 2017). The analysis of the effect of each distinguished growth phase on the total shoot length and genetic (family) differences for a particular growth phase allows us to determine the time within the growing season when the assessment of young stands could reveal more precise information on genetically determined differences.

Trees with different origins (eastern and western provenances, in total, six stands) had similar heights and height increments (difference 1%, $p > 0.05$) at the age of seven years. However, within the growing season, shoot elongation dynamics between provenances and families varied significantly. Western provenances started shoot elongation significantly earlier ($p < 0.01$) than eastern provenances, and 68.7% and 51.7% of trees, respectively, had started growth before the first measurement on May 25 (**VI**).

Trees from both provenances exhibited similar shoot elongation dynamics. The growth intensity was highest at the beginning of the growing season (Fig. 3.14), and about half of the total shoot length was formed on June 17 (i.e., 25 days after the growth onset). Earlier studies have found more intense growth for eastern provenances (Gailis, 1993), and the lack of such differences in the studied site might be a result of the similar duration of the growing period and the leveling out of the seasonal differences between provenances during the growing period, or it could be related to differences in transfer distance and site (soil) conditions (**VI**). Western provenances had a significantly higher growth intensity at the beginning of the growing season and a significantly lower growth intensity at the end of the growing season.

The growth intensity started to decline after June 8 (Fig. 3.14, **VI**). Regardless of provenance, a sharp increase in growth intensity occurred

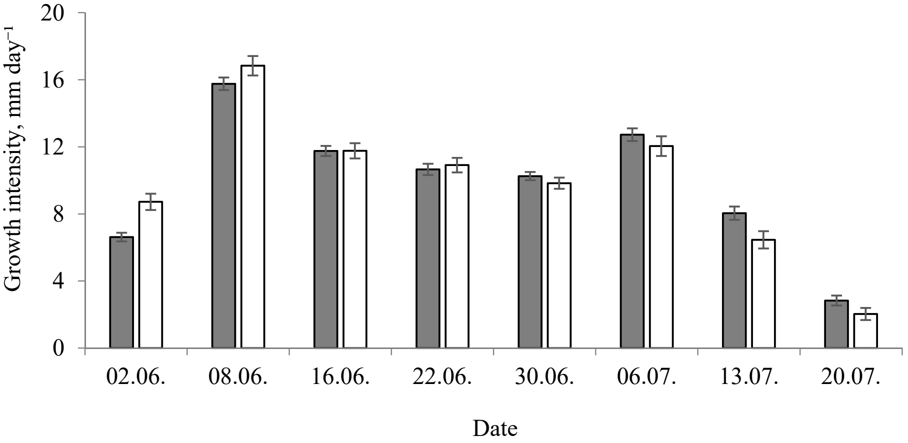


Fig. 3.14. **Mean growth intensity (± 95% confidence interval) for trees from eastern (dark gray bars) and western (clear bars) provenances during the seventh growing season**
The dates correspond to the last day of intervals for which growth rates were calculated.

in the first week of June (Fig. 3.14, **VI**), presumably caused by changes in meteorological conditions (Odin, 1972; Cannell & Johnstone, 1978). The time of growth cessation significantly differed between provenances, and at the last measurement (July 20), no changes in shoot elongation were noted for 36.6% of trees from the western provenances and for 28.8% of trees from the eastern provenances (**VI**).

The growing period was 60 days, with a mean growth intensity of 9.2 ± 0.2 mm day^{-1}, and it occurred during the period with a day length of at least 16.5 hours (Fig. 3.14, **VI**). Western provenances had an earlier growth onset and cessation of about two days compared to the eastern provenances, indicating an adaption of the height formation. The growth phenology for spruce originated from different latitudes is controlled by temperature-related mechanics (Heide, 1974; Hannerz, 1998), even in the case of small (less than 300 km) transfer distances (Danusevičius & Persson, 1998).

Trees from eastern provenances started height growth later than those from western provenances, indicating an adaption to early frost (Dietrichson, 1969; Polle et al., 1996; Langvall & Löfvenius, 2002). The provenance had more effect on the growth onset (**VI**), contrasting findings in central Sweden where provenance has more effect on growth cessation (Ekberg et al., 1985).

The provenance effect on growth intensity varied throughout the growing season (**VI**). The effect was stronger ($p < 0.05$) during the growth onset (before June 3) and during the growth cessation (July 6), but between these growth phases, the provenance effect was not significant ($p > 0.21$). Provenance-determined differences in growth onset and cessation are related to tree adaption to avoid frost damage in spring and autumn (Avotniece et al., 2012), whereas, during the active growth phase (from June 8 to June 22), growth was determined by external factors (Danusevičius et al., 1999), and the differences between provenances were negligible (**VI**).

The dynamics of shoot elongation within the growing season (**VII**) were successfully fitted to the Gompertz model (Fig. 3.15), and the coefficients of the individual tree growth dynamics and family means were obtained. The family was a significant factor ($p < 0.05$) affecting the shoot length and model coefficients that describe the growth onset, intensity, and cessation. The exception was the family effect on the growth onset in Jelgava ($p > 0.05$), where the trees started shoot elongation slightly earlier than in Rembate-B.

Shoot length for the selected top 10% (largest shoots) and bottom 10% (shortest shoots) of families differed notably and significantly (**VII**): 624 ± 26 and 362 ± 20 mm, respectively, in Rembate-B, and 664 ± 25 and 462 ± 33 mm, respectively, in Jelgava. The superiority in shoot length for the top 10% of families in comparison to the bottom 10% of families remained throughout the growing season (Fig. 3.16).

Families with the largest shoots peaked in terms of shoot elongation slightly later than families with the shortest shoots (Fig. 3.16). Additionally, families with the largest shoots maintained a higher growth intensity for a longer period, whereas families with the shortest shoots decreased in growth intensity more rapidly. Overall, families with the largest shoots were characterized by a higher growth intensity that fluctuated less throughout the growing season and by a longer shoot elongation period than families with the smallest shoots (**VII**). The family effect on the growth intensity was stronger during the latter half of the growing season.

At the individual tree level, the shoot length was strongly and significantly related to the growth intensity (Gompertz model coefficient *k*; $r = -0.66$ in

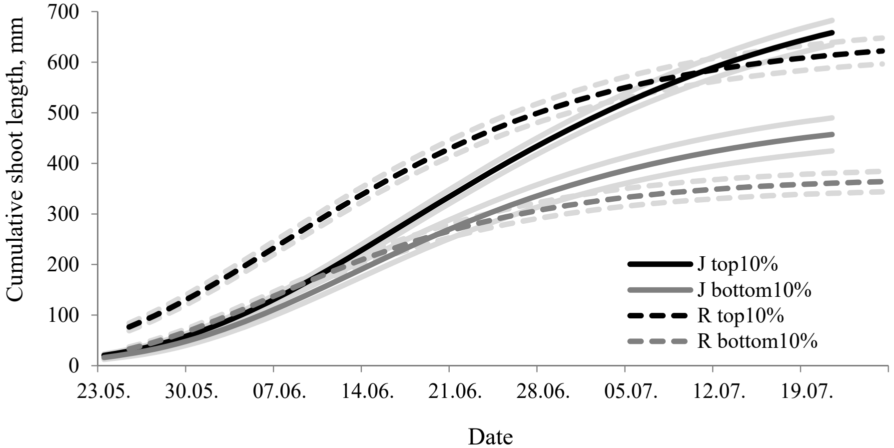


Fig. 3.15. **Approximated Gompertz model of mean shoot length (± 95% confidence interval) in Rembate-B (R) and Jelgava (J) trails for families with the largest (top 10%) and shortest (bottom 10%) shoots**

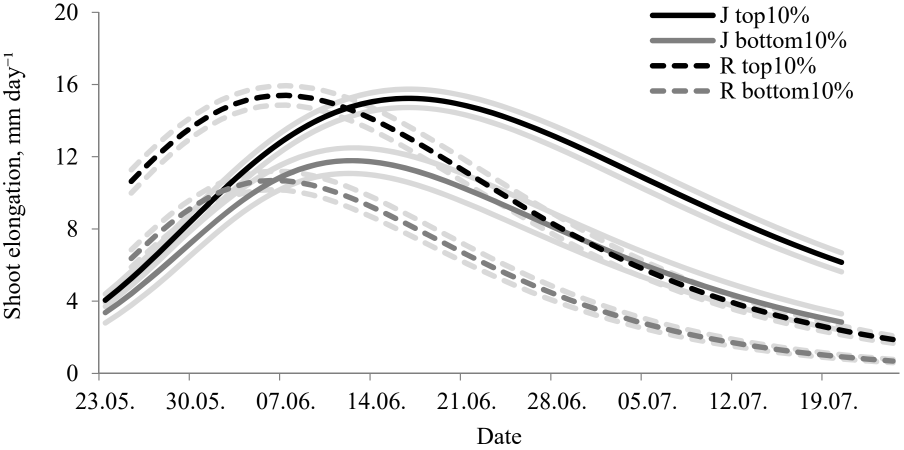


Fig. 3.16. **Mean shoot elongation (± 95% confidence interval) in Rembate-B (R) and Jelgava (J) for families with the largest (top 10%) and shortest (bottom 10%) shoots**

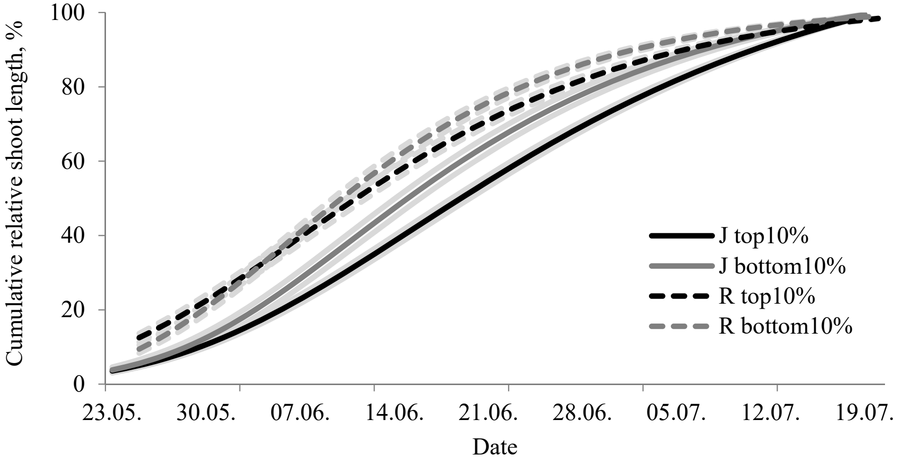


Fig. 3.17. **Cumulative relative shoot length (± 95% confidence interval) in Rembate-B (R) and Jelgava (J) for families with the largest (top 10%) and shortest (bottom 10%) shoots**

Rembate-B, $r = -0.62$ in Jelgava, both $p < 0.001$). This trend remained at the family mean level, and families with shorter shoots had a higher relative growth intensity, indicating that families with larger shoots had a more uniformly distributed shoot elongation within the growing season (Fig. 3.17), whereas families with the shortest shoots formed a larger proportion of shoots during the active growth phase (between the growth onset and cessation phases).

Shoot elongation was also affected by the tree height. The shoot length has a strong relation to the tree height at the end of the growing season ($p < 0.05$) but a substantially weaker relation to the tree height at the beginning of the growing season. Similarly, the growth intensity (Gompertz model coefficient k) is positively correlated to the tree height at the end of the growing season ($r = 0.35$), but the correlation to the tree height at the beginning of the growing season was not significant ($r = 0.07$, **VII**).

CONCLUSIONS

I The occurrence of trees with apical lammas shoots in spruce stands at the age of three to seven years varies from 0% to 25%, regardless of site type (eutrophic to mesotrophic) and stand age.

II A favorable combination of microenvironmental factors, limited competition from surrounding vegetation, and suitable soil moisture, substantially and significantly ($p < 0.001$) increases the occurrence of trees with apical lammas shoots in young stands.

III Genetics (family) has a significant effect ($p < 0.05$) on the occurrence of apical lammas shoots. In the same observation year and trial, the proportion of trees with apical lammas shoots per family ranged from 0% to 91%.

IV Apical lammas shoots are more frequent on fast-growing and early-flushing trees. Trees with apical lammas shoots are, on average, 14% to 29% higher than trees without them. No link was found between the formation of apical lammas shoots and the probability of frost damage. Moreover, apical lammas shoots partly compensate for the negative effect of frost damage on the shoot length.

V In mesotrophic and eutrophic site types, the soil preparation method significantly affects tree height in young stands. The mean tree height and proportion of the highest trees are significantly (both $p < 0.05$) higher in spot-mounded than disk-trenched stands. The difference in the dominant tree height between trees in spot-mounded and disk-trenched sites increased from 14% at the age of six years to 20% at the age of eight years.

VI Ash dispersal 12 months before planting had a positive effect on the plant-available macronutrient content in the soil (adding potassium and phosphorus) and facilitated the release of organic nitrogen. The increased availability of macronutrients significantly affected tree growth. At the age of 10 years, trees that received additional nutrients exceeded the height of the control trees by 15% and 21% (doses of ash at 5 and 10 t ha^{-1}, respectively). Fertilization with NPK right after planting had a similar effect on tree growth for up to 15 years.

VII Shoot elongation dynamics for open-pollinated Norway spruce plus-tree families is genetically determined. Families with longer shoots had a peak in growth intensity (mm per day) later in the growing season, had higher growth intensity at the active growth phase and continued intense growth for a longer period than families with shorter shoots.

RECOMMENDATIONS

The effect of the improvement of the microenvironment on the occurrence of apical lammas shoots and cumulative tree height at a juvenile age should be included in the tree height growth modeling system to reflect the positive effect of targeted management of young spruce stands. The initial (before or right after planting) enrichment of the soil through the application of compound fertilizer or wood ash is recommended to increase the productivity of spruce stands for at least 10 years from the treatment. The selection of genotypes with apical lammas shoots is recommended because it is not related to an increased risk of frost damage, whereas it contributes to a larger height increment, especially when tending occurs and microenvironmental conditions are enhanced in stands planted with improved planting material. This positive effect on growth is expected to be reinforced by climate changes: more frequent years with high temperatures during the cessation of the predetermined height increment and a longer vegetation season.

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Environmental factors affecting formation of lammas shoots in young stands of Norway spruce (*Picea abies* Karst.) in Latvia

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Norway spruce is a relatively fast-growing tree species that is primarily regenerated by planting, which requires significant investments. The formation of lammas shoots (*i.e.*, second flushing in late summer) have been proven to affect the quality and productivity of Norway spruce stands. The aim of our study was to assess the proportion of trees with lammas shoots in young stands of Norway spruce and to investigate the factors affecting their formation. Data have been collected at the end of 2011 in 102 three- to seven-year-old Norway spruce plantations randomly selected across different forest types in the central part of Latvia, and a subset of 21 stands were inventoried again at the end of 2012. In each stand, 20 sample plots were systematically established where trees with and without lammas shoots were counted and micro-environmental factors (moisture, competition, and browsing) were assessed on a three-grade scale. On average, the proportion of trees with lammas shoots was 6.5%. There was no significant effect of the stand age (from 3 to 7 years) on the proportion of trees with lammas shoots nor was there any age-related trend. The effect of forest type on the presence of lammas shoots was not significant. Micro-environmental factors had an important influence on the proportion of trees with lammas shoots. The proportion of lammas shoots in stands with no competition was significantly higher (14.5%) compared to stands with medium and high competition (6.0% and 2.2%, respectively). Similarly, a significantly higher proportion of trees with lammas shoots (11.7%) was observed in sites with normal moisture regime than in sites with slight or notable excess moisture, reaching 4.8% and 1.7%, respectively. Although the influence of browsing damage was not statistically significant, its trend was similar to that observed for competition and moisture regime. Overall, the proportion of trees with lammas shoots was highest in stands showing the most suitable micro-environmental conditions for Norway spruce.

Keywords: Second Flushing, Vegetation Competition, Tending, Moisture Excess, Browsing Damage

Introduction

Norway spruce is the most economically important tree species in the Baltic Sea region, due to its relatively large share in the total forest coverage (Brus et al. 2011), high value of coniferous tree saw logs, and notably shorter rotation period and higher productivity compared to Scots pine (Ekö et al. 2008). In Latvia, Norway spruce is the dominant tree species in 18% of the total forest area (Gadskarta 2016). Most stands (83%) are regenerated by planting, which requires notable investments, starting from tree breeding programs and seed orchard maintenance up to plant production, soil preparation, and the planting itself (Jansons et al. 2015). Norway spruce plantations in Latvia are mainly established in forest types with fertile mineral soils, with normal moisture regime (*Hylocomiosa* and *Oxalidosa*) and drained soil (*Myrtillosa mel.*) accounting for 34%, 39%, and 9%, respectively, of the total annual planted area by this species (Bušs 1976, Gadskarta 2016).

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Changes in climatic conditions might severely affect the survival and development of forest stands (Kenina et al. 2018). Long-term phenological observations across Europe have indicated a trend towards an earlier and longer vegetation period (Stöckli & Vidale 2004), which is predicted to continue in the future. By the middle of this century, the length of the vegetation period in Latvia could increase by two to three weeks in comparison to the mean in 1961-1990 (Klavins & Briede 2012). The response of trees to longer periods of favourable growing conditions might include an increased frequency of formation of lammas shoots (*i.e.*, the second flushing in late summer) after the end of the formation of the predetermined height increment. Formation of lammas shoots has long been studied; however, the underlying physiological mechanisms are not well understood yet (Cline & Harrington 2007). It has been previously reported that the formation of lammas shoots is significantly affected by both meteorological conditions (Dormling et al. 1968, Aldén 1971, Von Wühlisch & Muhs 1986) and genetic factors (Hoffmann 1965, Rone 1975, Ununger et al. 1988, Danusevičius & Persson 1998, Danusevičius 1999, Søgaard et al. 2011).

Genetic determination of lammas shoot formation has been established by analysis of provenance trials. For example, Danusevičius & Persson (1998) reported that the proportion of trees with lammas shoots ranged from 4% ± 2% for provenances from northern Sweden to 17% ± 3% for provenances from Austria at the age of five years in an experiment in Sweden. Significant provenance effects and similar trends (but higher mean values) were reported based on a trial at the same age in Norway. The proportion of trees with lammas shoots was lowest for Scandinavian provenances (18%), followed by Latvian provenances (28%) and Slovak and Czech provenances (54% – Søgaard et al. 2011). Eriksson (2010) reported that, in Austria, the high-altitude provenances do not form lammas shoots, while such shoots are formed by valley-bottom provenances. Provenance and family were significant factors affecting the occurrence of lammas shoots, according to Steffenrem et al. (2008), based on an analysis of open-pollinated progeny trials. However, the family (genetic) contribution to the total variance was relatively low (4%). Lammas growth is often among the traits included in the selection index due to its direct effect on or correlation with the stem and wood quality traits (Jansson et al. 2013). For example, Skrøppa et al. (1999), based on the evaluation of 15 provenances from Finland, Denmark, Germany, and Poland, reported a significant association between the occurrence of lammas shoots at juvenile age and the wood density at the age of 29 years.

Meteorological conditions of the previous year influence the predetermined growth, but conditions of the current year may affect the second flushing (Dormling et al. 1968, Junttila 1986, Von Wühlisch & Muhs 1986). The increased frequency of lammas shoots for Norway spruce due to the rise in temperature has been proven in laboratory conditions (Johnsen 1989, Kvaalen & Johnsen 2008). This increase has been observed in the field in recent years and has been attributed to changes in climatic conditions (Kvaalen et al. 2010, Søgaard et al. 2011).

The second flushing of Norway spruce and other conifer species has been linked to the increased frequency of trees with double leaders and/or spike knots (Gabrilavičius & Danusevičius 2003, Pallardy 2008, Søgaard et al. 2011). In some cases, the occurrence of these stem defects might be caused by several lammas shoots competing for dominance, as well as by insufficient frost hardiness of the apical shoot (and consequently damage) due to lammas growth, at least partly linked to maladaptation of the studied material. Some studies have indicated that most of the spike knots formed in this way disappear in a few years without causing permanent stem damage (Jansons et al. 2016). Formation of lammas shoots is linked to a faster tree growth, thus contributing to increase the productivity of plantations. Indeed, correlations between the mean tree height and the proportion of trees with lammas shoots at five to 13 years of age have been reported in several countries: Germany ($r = 0.93$, $p < 0.01$), Sweden ($r \approx 0.3$, $p < 0.01$), and Latvia (Hoffmann 1965, Rone 1975, Danusevičius & Persson 1998).

A systematic inventory of the frequency of second flushing in Norway spruce has not previously been conducted in Latvia, though lammas shoots are demonstrated to have an increasing frequency and importance in the determination of the productivity and quality of spruce stands. Therefore, the aim of the study is to assess the proportion of trees with lammas growth in young stands of Norway spruce and to identify the environmental factors which affect their formation. The following hypotheses are tested: (i) optimal growing conditions have a positive effect on the formation of lammas shoots in young Norway spruce trees; (ii) tree age has a negative effect on the formation of lammas shoots. This knowledge could be further used in the preparation of recommendations for forest management.

Materials and methods

Data have been collected at the end of 2011 from 102 Norway spruce plantations located in the central part of Latvia (56° 37′-56° 57′ N, 23° 37′-24° 49′ E – Fig. 1). Three- to 7-year-old stands (in 2011) were randomly selected across different forest types (Tab. 1). A subset of 21 stands was further surveyed at the end of 2012. All the selected stands have been established using reproductive material from local seed orchards. The area of each stand was at least 0.5 ha and their elevation ranged from 10 to 40 m a.s.l.

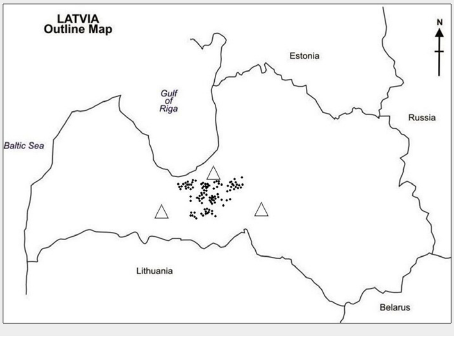


Fig. 1 - Location of sampled Norway spruce stands (dots) and meteorological stations (triangles) in Latvia.

The climate in the study area is predominantly characterised by western winds bringing warm and moist air masses from the Baltic Sea and the Atlantic. According to the Latvian Environment, Geology, and Meteorology Centre (LEGMC 2012), the mean annual temperature in the region is +5.9°C. The average temperature of the warmest month (July) is +17.0°C (mean maximum temperature +21.5°C), and the annual precipitation is 667 mm. Data from the three nearest meteorological stations (Riga, Dobele, and Skriveri) were used to analyse the possible influence of meteorological conditions on lamma shoot formation (Fig. 1).

In each stand, 20 sample plots (radius 2.82 m, area 25 m^2) were placed at regular distance along its longest diagonal. The number of trees with and without current season lammas shoots was recorded in each sample plot. A lammas shoot was defined as the second flushing of the apical or lateral buds of the top shoot, reaching at least 1 cm in length.

The growing conditions of trees in the plots were quite different and not always favourable, due to recent changes in habitat characteristics (*e.g.*, the presence of a beaver dam across the melioration ditch) and browsing pressure (according to the State Forest Service, the density of roe deer, *Capreolus capreolus* L., was 30-40 inds. per 1,000 ha on average). Thus, for each plot the suitability of micro-environmental factors was assessed in a subset of 70 stands (56 in 2011, 14 in 2012) using a three-grade scale which considered the following factors:

- competition by the surrounding vegetation (within a radius of 0.5 m from the spruce tree), including herbaceous plants, shrubs, and sprouts of other tree species; a score (grade) was assigned to each plot based on the ratio between the mean height of trees and that of the surrounding vegetation (Grade 1: < 0.75; Grade 2: 0.75-1.25; Grade 3: > 1.25);
- moisture regime: Grade 1 was assigned to plots showing normal conditions, Grade 2 to plots with periodic excessive moisture, and Grade 3 to those showing permanent excessive moisture (*e.g.*, due to clogging of a drainage system);
- browsing damage was recorded for trees with damaged tops and/or more than 50% of lateral shoots; a score was assigned to each plot based on the proportion of trees affected by browsing (Grade 1: < 1%; Grade 2: 1%-10%; Grade 3: > 10%).

The proportion of trees with lammas shoots (*i.e.*, the number of trees with lammas shoots out of the total number of trees) at the stand level was calculated as the mean value (± 95% confidence interval) of sample plot proportions. The proportion

Tab. 1 - Number of plots sampled in the Norway spruce stands considered in this study, according to stand age and forest type.

Forest type	Year of observation	No. stands	Age (years)						Total
			3	4	5	6	7	8	
Hylocomiosa	2011	26	118	153	208	18	-	-	497
	2012	5	-	20	20	59	-	-	99
Oxalidosa	2011	9	-	20	74	54	17	-	165
	2012	4	-	-	20	38	19	-	77
Myrtilloso-sphagnosa	2011	13	83	76	43	-	16	-	218
Myrtilloso-polytrichosa	2011	5	-	56	39	-	-	-	95
	2012	1	-	-	19	-	-	-	19
Myrtillosa mel.	2011	24	69	39	19	191	116	-	434
	2012	4	-	18	-	-	37	20	75
Mercurialiosa mel.	2011	6	-	-	57	55	-	-	112
	2012	1	-	-	-	-	20	-	20
Myrtillosa turf. mel.	2011	15	39	72	106	10	37	-	264
	2012	5	-	20	20	57	-	-	97
Oxalidosa turf. mel.	2011	4	37	-	-	-	39	-	76
	2012	1	-	20	-	-	-	-	20
Stands of all types	2011	102	346	416	546	328	225	-	1861
	2012	21	-	78	79	154	76	20	407

of trees with browsing damage was calculated in the same way. Spearman's correlation analysis was used to assess the relation between the proportion of trees with lammas shoots and stand density. To assess the effect of the above factors on the proportion of trees with lammas shoots, a binary logistic generalised linear mixed-effects model (GLMM) was implemented in software R ver. 3.4.3 (R Core Team 2017) using the library "lme4" (Bates et al. 2015). Three models were developed using the relation between trees with and without lammas shoots at the plot level as the response variable. In all models, the stand ID was set as random effect to account for possible correlation (repeated measures) among sample plots within the same stand. The first model included stand age and forest type as predictors using the whole set of 102 stands inspected in 2011. The second model included the three micro-environmental factors (competition, moisture and browsing damage) and the year of observation as predictors, which were tested on the subset of 70 stands described above. Using the same data subset, a third model was developed which included the suitability of growing conditions as predictor, which was calculated as the sum of scores (grades) for all three micro-environmental factors, ranging from 3 (best) to 9 (worst). Generalised linear hypothesis tests, as implemented in the R library "multcomp" (Hothorn et al. 2008), were used as *post-hoc* tests after GLMM when the interaction of the factor or factors with more than two levels were significant compared to the mean proportions between levels.

Results

The proportion of trees with lammas shoots across the sampled stands ranged from 0% to 25% and was 6.5% on average. It was slightly higher in 2012 than in 2011 (in stands sampled in both years, the proportion was 12.9% and 9.1%, respectively), but differences between years were not statistically significant ($\chi^2 = 0.5696$, $p = 0.450$). Initial spacing in all stands was similar, but due to the differences in survival, the density at the age of assessment ranged from 800 to 3600 trees ha^{-1}. The differences in stand density had no statistically significant relation to the proportion of trees with lammas shoots.

There were no notable differences in air temperature in the period of formation of lammas shoots (end of July to the beginning of August) between 2011 and 2012. The mean diurnal temperature in the last week of July and the first week of August at the Riga meteorological station was 20.4 and 20.7 °C, respectively. In Dobele, it was 18.6 and 19.3 °C, respectively, and in Skriveri it was 19.4 and 19.4 °C, respectively. However, a sharp temperature increase by the end of July 2012 in comparison to the slight decrease in the same period of 2011 was observed (Fig. 2). Temperature differences between the third and fourth weeks of July were 5 to 5.8 °C in 2012, but only 0.3 to 0.5 °C in 2011.

Minor changes in precipitation in the first week of August were observed in 2012 as compared to the last week of July (a slight increase in Dobele and decreases in Skriveri and Riga). In contrast, in 2011 (with a lower frequency of trees with lammas shoots), a sharp decrease in the amount of precipita-

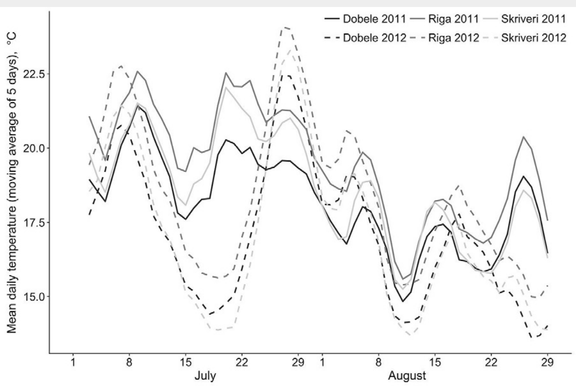


Fig. 2 - Mean daily temperature (moving average of five days) at three meteorological stations (Riga, Dobele, and Skriveri) in July-August 2011 and 2012 (data: LEGMC 2012).

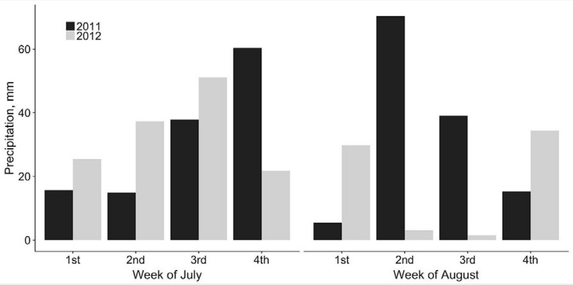


Fig. 3 - Weekly amount of precipitation in July-August 2011 and 2012 (average of three meteorological stations – Riga, Dobele, and Skriveri; data: LEGMC 2012).

tion in the first week of August in comparison to the last week of July was observed (from 29 mm to 0 mm in Skriveri, from 46 mm to 3 mm in Riga, and from 106 mm to 14 mm in Dobele). In the second and third weeks of August, there was a lower amount of precipitation in 2012 than in 2011: 0.3-5 mm and 31-80 mm per week, respectively (Fig. 3).

There was no significant effect of stand age on the proportion of lammas shoots (χ^2 = 0.2175, *p* = 0.641) nor was there an age-related trend. The highest mean proportion of trees with lammas shoots was reached in 7-year-old stands, while the lowest value was observed in 6-year-old stands (Fig. 4). Notable variation in the proportion of trees with lammas shoots was detected for stands at different ages within a particular forest type; for example, in *Myrtillosa mel.* the proportions were 12.7%, 4.0%, and 10.8% at the ages of 4, 6, and 7 years, respectively. The effect of the forest type on the presence of lammas shoots was not significant (χ^2 = 3.6892, *p* = 0.815). The highest and lowest proportion of trees with lammas shoots was detected in *Mercurialiosa mel.* and *Oxalidosa turf.mel.*, respectively (Fig. 5). Also, the nteraction between forest type and stand age did not significantly affect the frequency of lammas shoots (χ^2 = 5.0154, *p* = 0.6581).

Fig. 4 - Mean proportion of trees with lammas shoots (± 95% CI) in spruce stands of different ages.

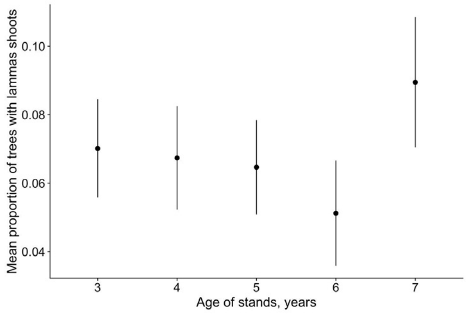
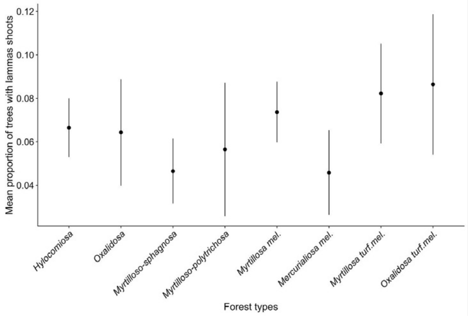


Fig. 5 - Mean proportion of trees with lammas shoots (± 95% CI) in spruce stands of different forest types.



Micro-environmental factors had an important influence on the proportion of trees with lammas shoots (Fig. 6). The effect of competition from the surrounding vegetation and moisture regime was statistically significant (χ^2 = 45.0218, *p* < 0.001). The proportion of trees showing lammas shoots in stands with no competition (Grade 1) was significantly higher (14.5%) in comparison to stands with medium (Grade 2) and high (Grade 3) competition (6.0% and 2.2%, respectively), being the difference between the two latter grades not significant (*p* = 0.066). Similarly, there was a significantly higher proportion of trees with lammas shoots (11.7%) in sites with a normal moisture regime (Grade 1) than in sites with periodic (Grade 2: 4.8%) or permanent (Grade 3: 1.7%) excessive moisture. Similar to that observed for competition, the difference between Grade 2 and Grade 3 of moisture was not significant (*p* = 0.184). Although the influence of the browsing damage was not statistically significant (*p* = 0.094), the observed trend was similar to that detected for competition and moisture regime. The proportion of trees with lammas shoots was 11.3%, 8.2%, and 7.7% in Grade 1, Grade 2, and Grade 3, respectively. The effect of the interactions (of the second or third level) was not significant, suggesting that each factor had independent influence on the formation of lammas shoots.

Finally, the combination of the scores for all micro-environmental factors (moisture, competition, and browsing pressure) revealed a clear significant trend (Fig. 7). The highest proportion of trees with lammas shoots occurred in the most favourable conditions (lower score). If at least one of the factors scored 3 in any stand (a notable negative influence), the proportion of trees with lammas shoots in that stand did not exceed 10%.

Discussion

The average proportion of trees with lammas shoots in our study (7% ± 1%) was similar to that found for Norway spruce provenances from Baltic States at the age of five years in an experiment in Sweden (Danusevičius & Persson 1998). An even higher proportion of trees with lammas shoots was found in Norway, based on the analysis of the national forest inventory sample plots (located at an elevation up to 200 m a.s.l.). Moreover, Kvaalen et al. (2010) reported that as many as 80% of trees had lammas shoots in two of the 58 sample plots analyzed.

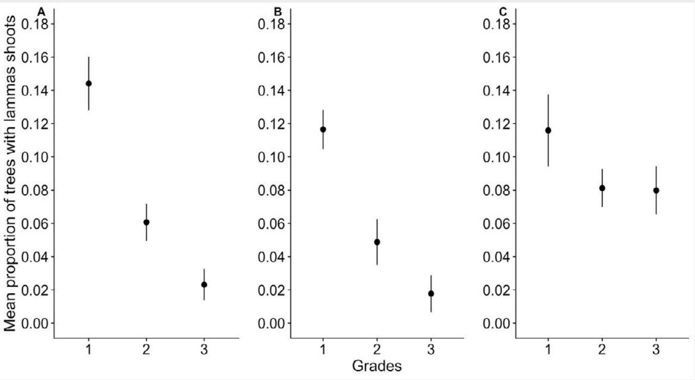


Fig. 6 - Mean proportion of trees with lammas shoots (± 95% CI) in spruce stands with different micro-environmental factors characterised by (A) competition of surrounding vegetation, (B) excessive moisture, and (C) browsing damage. Each factor was assessed in a three-grade scale, where (1) the negative effect of the factor on growth of the spruce was not observed, (2) the minimal negative effect of the factor was observed, and (3) the notable negative effect of the factor was observed.

The formation of predetermined and additional height increment is defined by meteorological conditions, such as temperature and precipitation, in combination with the photoperiod (Dormling et al. 1968, Aldén 1971, Von Wühlisch & Muhs 1986, Gabrilavičius & Danusevičius 2003). Skrøppa & Steffenrem (2016) described the negative relationship between the presence of lammas shoots and the timing of shoot growth for full-sib families in a provenance trial of Norway spruce in the fifth growing season, pointing out that the occurrence of lammas shoots is generally positively associated with a favourable climate and soil fertility. Analysis of different coniferous tree species, such as red pine (*Pinus resinosa* Ait.), white pine (*Pinus strobus* L.), California red fir (*Abies magnifica* A. Mur.), and white fir (*Abies concolor* (Gord. and Glend.) Lindl.), suggests that abundant precipitation at the end of the vegetation period can stimulate the formation of lammas shoots (Büsgen 1929, Carvell 1956, McCabe & Labisky 1959, Hallgren & Helms 1988). This is in contrast to our results, where a lower proportion of trees with lammas shoots was observed in 2011 – a year with higher amounts of precipitation in the middle part of August in comparison to 2012, but only slightly higher than the long-term average and with an increase of precipitation only two weeks after the end of the predetermined height growth. After the completion of the predetermined height growth (second part of July), a sharp temperature increase was observed in the year 2012, along with the highest proportion of trees with lammas shoots. The results suggest that a relative change (not necessarily the mean values of any of the meteorological parameters temperature and precipitation) at the right period of the annual cycle of tree growth could trigger the formation of lammas shoots. In addition, there might be some indirect influence of spring temperatures since previous studies have suggested that earlier flushing trees are more likely to form lammas shoots (Neimane et al. 2015, Skrøppa & Steffenrem 2016), presumably due to the longer period between the end of the predetermined growth and the drop in temperature in autumn. However, the observations in the current study were conducted in autumn, and the spring phenology data were not available.

A decrease in the frequency of formation of lammas shoots with tree age was observed in a number of studies (Büsgen 1929, Ehrenberg 1963, Aldén 1971, Rone 1985, Von Wühlisch & Muhs 1986, Ununger et al. 1988, Søgaard et al. 2011). For example, in a Norway spruce trial in Norway, 38% of 5-year-old trees had lammas shoots, in contrast to 22% at 6 years and 17% at 7 years. This trend was similar in almost all represented provenances (Søgaard et al. 2011). In contrast, no age-related trend was observed in our study. Prolonging or expanding the study (adding one more inventory or older stands) could further improve our understanding of this phenomenon. After analysing the genetic and environmental variation of internodal and whorl branch formation (including whorls formed by lammas growth) for open-pollinated families of Norway spruce at the age of 27 years, Steffenrem et al. (2008) pointed out that, the effects at the juvenile stage might be confounded with the year (meteorological) effect. Retrospective study has also demonstrated higher frequency of the occurrence of extra whorls formed by lammas growth in sites with higher soil fertility

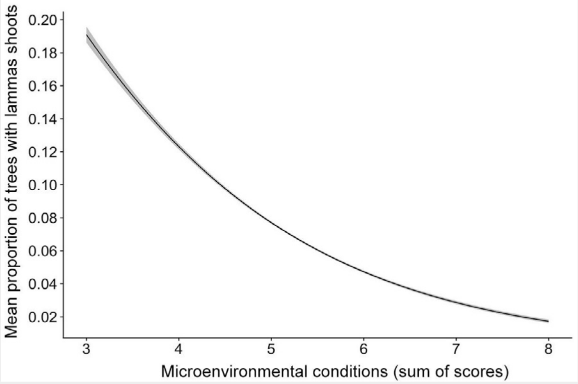


Fig. 7 - Mean proportion of trees with lammas shoots (shown by the black line) with the 95% CI (grey band on both sides of the line) in the Norway spruce stands analyzed in relation to the suitability of the growing conditions (*x*-axis), expressed as the sum of grades (scores) for three micro-environmental factors (competition, moisture, and browsing). For each factor, its negative effect on Norway spruce growth was quantified as: (1) not observed or negligible; (2) minimal; (3) notable.

(assessed in terms of site indices). In other studies carried out on Norway spruce in south-eastern Norway, the forest type (*i.e.*, availability of nutrients) was one of the major factors determining the proportion of trees with lammas shoots: by height index H_{40} = 11 and H_{40} = 23, the proportion of trees with lammas shoots was 5%-25% and 30%-90%, respectively (Søgaard et al. 2011). We did not find significant differences in the proportion of trees with lammas shoots between forest types representing growing conditions for more than 90% of the spruce-dominated stands in Latvia (data: NFI 2010). However, the range of site indexes included in our study (roughly corresponding to H_{40} = 8-22) was smaller than that of the aforementioned study (H_{40} = 8-26 – Søgaard et al. 2011).

Our results showed that differences in the proportion of trees with lammas shoots (even within forest types or stand ages) were strongly linked to micro-environmental factors like moisture, competition, and browsing pressure. For example, in a 5-year-old stand belonging to the *Hylocomiosa* forest type with little evidence of tending and therefore a high competition of herbaceous plants and shrubs, as well as visible browsing damage on 22% of trees, only 1.8% of the individuals had lammas shoots, while the proportion was 25.5% in another 5-year-old stand of the same forest type with visible signs of regular tending and no browsing damage. Similar to our results, Roth & Newton (1996) found a notable increase in the occurrence of lammas shoots for the Douglas fir after weed control.

Sporadic observations gathered during our study (conducted in 2011 and 2012) also suggest that an increase in frequency of lammas shoots might be linked not only to differences in weather conditions between the years but also to the effect of tending conducted in 2011. For example, in a 3-year-old *Oxalidosa turf. mel.* forest type stand, where vegetation control was done in the second part of the vegetation period of 2011, the proportion of trees with lammas shoots increased from 10% in 2011 to 26% in 2012. Similarly, in a 5-year-old *Hylocomiosa* stand, it increased from 18% in 2011 to 33% in 2012.

Browsing damage could notably reduce carbon accumulation capacity and growth of Norway spruce trees. However, it did not show as much pronounced effect on the formation of lammas shoots as the other two micro-environmental factors assessed in this study. Low average browsing pressure (average share of damaged trees 10.7%) and the intensity of damage – a notable effect on height increment was only observed in a few cases – could be the possible reasons for the limited influence of this factor.

For the preparation of recommendations for forest regeneration and tree breeding, further studies should address the issue of actual risks (mainly the formation of long-lasting stem defects) and the long-term positive relationship to growth which could be associated with the formation of lammas shoots.

Conclusions

The proportion of trees with lammas shoots in juvenile (from 3 to 7 years) Norway spruce stands ranged from 0% to 25% and was 6.5% on average. Improvement of micro-environmental conditions (intensive forest management) increased the proportion of trees with lammas shoots in juvenile Norway spruce stands, but there was no clear link between the occurrence of lammas shoots and the age of stands or the forest type.

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Influence of lammas shoots on productivity of Norway spruce in Latvia

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Abstract. The Norway spruce is widely spread in Eastern Europe and it is managed mainly for the production of sawlogs, though its logging residues are now increasingly used for the production of wood chips for bioenergy. The growth of the Norway spruce is and will be affected by climatic changes; one of the possible effects might be an increase in the frequency of trees with lammas shoots. Therefore, the aim of this study was to assess the influence of lammas shoots on the length of height increment of young Norway spruce in Latvia. Tree height and height increment was repeatedly measured and the presence of lammas shoots, bud flushing grades and frost injuries were assessed in two young (8–13 years) open-pollinated progeny tests in the central part of Latvia (56°46´N, 24°48´E). The mean portion of trees with lammas shoots in one experiment was 6% at the end of 8th growing season. In another experiment, it was 8.7%, 26.9% and 8.1% at the end of 10th, 11th and 13th growing seasons, respectively; 32.3% of trees had lammas shoots at least in one of three seasons. Faster growing and earlier flushing trees had a significantly higher frequency of lammas shoots. Lammas shoots increased the length of annual height increment by 10 to 14 cm, resulting in a 14–20% taller tree height at the age of 13 years. The reduction of height increment as a result of frost damages for very early flushing trees was less pronounced for trees with lammas shoots than without them.

Key words: height increment, tree height, open-pollinated family.

INTRODUCTION

The Norway spruce is the most important commercial tree species in Northern European countries. It occupies 18 million ha of forest land, with a total growing stock of 2,700 million m^3 – which is a third of the wood resources in the region (Rytter et al., 2013). The Norway spruce is grown mainly for sawlog production; however, its sawdust and logging residues are increasingly used for bioenergy production. For example, the amount of wood chips produced from logging residues in Latvia's state forests has increased from 3 thousand m^3 in 2006 to 380 thousand m^3 in 2013 (Latvijas valsts meži, 2012). Harvest residues from the Norway spruce, consisting of branches and tops, are an important source of biomass energy in Finland and Sweden (Rytter et al., 2013). In Latvia, it was found that the biomass of dead and living branches forms 6.4% and 17.4% of the total above-ground biomass in 40-year old Norway spruce stand, respectively (Lībiete-Zālīte & Jansons, 2011).

Due to the economic importance of coniferous trees, a substantial amount of studies have been carried out to understand the possible effects of climatic changes on their vitality and growth (Gabrilavičius & Danusevičius, 2003; Bergh et al., 2005; Jansons et al., 2013a; Jansons et al., 2013b). Long term phenological observations in Latvia and other European countries have indicated a trend towards an earlier start of the spring (–0.54 days year^{-1}) and a longer (0.96 days year^{-1}) vegetation period (Stöckli & Vidale, 2004). This trend is predicted to continue in the future and, in combination with increasing temperatures, will lead to more frequent formation of lammas growth – additional height increment in the second half of the vegetation period. Formation of lammas shoots can lead to increased frequency of frost damages (Gabrilavičius & Danusevičius, 2003; Søgaard et al., 2011) and up to a 40% higher frequency of double leaders (Søgaard et al., 2011). In contrast, a significant correlation between the proportion of trees with lammas shoots and stem quality at provenance mean level was not found for young Norway spruce in Sweden (Danusevičius & Persson, 1998). It is suggested that the formation of lammas shoots could increase height increment of the trees (Rone, 1975), however, this effect has rarely been quantified. Therefore, the aim of our study was to assess the influence of lammas shoots on height increment of young Norway spruce in Latvia.

MATERIALS AND METHODS

The study was carried out in two Norway spruce experiments, planted on fertile abandoned agricultural land (corresponding to the *Oxalidosa* forest type), hereafter referred to in this text as ‘A’ and ‘B’, at ages of 8 and 13 years, respectively. Both experiments were located in the central part of Latvia (56°46´N, 24°48´E). According to the data from the nearest meteorological station (Skriveri) of the Latvian Environment, Geology and Meteorology Centre, long-term average annual temperature was +6.1 °C, and the sum of precipitation was on average 717 mm per year. Experiment B was located in three fields of close proximity, with slightly different soil and micro-relief conditions, hereafter referred to in this text as ‘trials.’ Tree height, length of the last season height increment and presence of lammas shoots were assessed at the end of the 8th growing season for 3,887 trees from 60 open-pollinated families in experiment A (October 2014), and at the end of the 10th (November 2011), 11th (October 2012), and 13th (November 2014), growing seasons for 3,412 trees from 112 open-pollinated families in experiment B. Bud flushing grade was assessed in experiment B trial 2 (1930 trees) at the beginning of 11th growing season (June 2012) using a four grade scale: grade 1 = very late flushing (length of current increment < 3 cm), grade 2 = late flushing (3–6 cm), grade 3 = early flushing (7–10 cm), grade 4 = very early flushing (> 10 cm). Also the presence (or absence) of spring frost damage on shoots was noted.

Data analysis was carried out using ANOVA, correlation and χ^2 test and the mean values ± confidence intervals were calculated.

RESULTS AND DISCUSSION

Mean height at the age of 8 years in experiment A was 117 ± 1.4 cm and height increment was 27 ± 0.6 cm. During the 8th growing season, lammas shoots formed for 6% of trees. Tree height at the age of 13 years in the each of the three trials of experiment

B was 394 ± 6.8 cm, 442 ± 5.8 cm, 439 ± 10.2 cm, and the mean height increment in the last 3 years in each of the trials was 64 ± 1.1 cm, 72 ± 0.9 cm, 80 ± 1.7 cm, respectively. Differences in height increment between the trials were statistically significant ($P < 0.001$); therefore, a separate analysis of lammas shoots (characterized as the presence of them in at least one of the three years of assessment) was carried out for each of them. The proportion of trees with lammas shoots in a particular year at the end of 10th, 11th and 13th growing seasons in experiment B was 8.7%, 26.9% and 8.1%, respectively, and lammas shoots in at least one of the assessment years were found for 32.3% of trees.

The proportion of the Norway spruce trees with lammas shoots in this study was in a range of previously reported results from other countries. For example, in Sweden, in trials at the age of 5 years, 7% of spruces from Baltic State provenances had lammas shoots (Danusevičius & Persson, 1998); in Norway, in trials at the same age, 28% of spruces from Latvian provenances had lammas shoots (Søgaard et al., 2011).

In experiment A, the proportion of trees with lammas shoots was highest (reaching 20%) in classes of trees with the largest height and height increment, but was lowest (approximately 1%) in the classes of trees with slowest growth (Fig. 1); differences between the classes were statistically significant ($P < 0.001$).

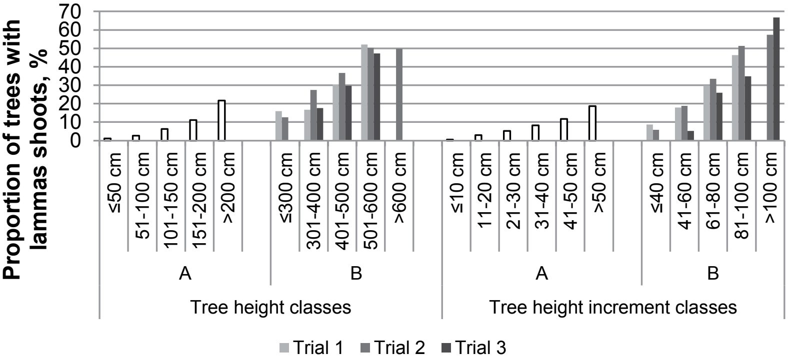

Figure 1. Proportion of trees with lammas shoots in experiment A (at the end of the 8th growing season) and B (at the end of at least one of the three assessment seasons) in different tree height and height increment classes.
In trial 1 (experiment B) trees of height increment 81–100 cm were clustered together with trees of height increment > 80 cm, and trees of height 501–600 cm were clustered together with trees of height > 500 cm.
In trial 3 (experiment B) trees of height increment 41–60 cm were clustered together with trees of height increment ≤ 60 cm, and trees of height 301–400 cm were clustered together with trees of height ≤ 400 cm.

Analyses of each of the trials in experiment B revealed a similar trend – faster growth was associated with higher frequency of lammas shoots: on average, 47–68% of the trees in the class with the largest height and mean height increment had lammas shoots, but lammas shoots were present in only 5–18% of the class with the smallest (the slowest growing) trees. The difference in the proportion of trees with lammas shoots between the classes was statistically significant ($P < 0.001$).

A significant association between tree height and frequency of presence of lammas shoots was also previously reported in Latvia in an analysis of more than 100 stands (Neimane et al., 2015, submitted) and tree breeding trials (Rone, 1975), as well as from analysis of provenance trials in other countries (Hoffmann, 1965). Significant positive correlation ($r \approx 0.3$; $P < 0.01$) was found at provenance mean level between tree height and proportion of trees with lammas shoots in analyses of a trial including 107 Swedish and 16 Eastern European spruce provenances at the age of 5 and 9 years (Danusevičius & Persson, 1998). In experiment A of this study, the proportion of trees with lammas shoots at family mean level had significant positive correlation with height increment ($r = 0.44$; $P < 0.001$) and weaker, non-significant correlation with tree height ($r = 0.22$; $P = 0.09$). Similarly, in experiment B, the proportion of trees with lammas shoots at family mean level had statistically significant ($P < 0.01$) correlation with tree height (when all trials were analysed together ($r = 0.49$) and separately ($r = 0.41...0.71$)) and height increment ($r = 0.51$ and $r = 0.48...0.70$, respectively).

In experiment A, the height increment of the 8th growing season for trees with lammas shoots (44 ± 2.4 cm) was notably (by 68%) and significantly ($P < 0.001$) larger than for trees without them (26 ± 1.7 cm) (Fig. 2). Similarly, in experiment B, spruces with lammas shoots had significantly ($P < 0.001$) larger mean height increment of the last three years than spruces without them: mean differences in these particular trials were from 10 to 14 cm.

Figure 2. Height increment of trees with and without lammas shoots (height increment of the 8th growing season in experiment A; mean height increment of the last 3 years in experiment B).

The cumulative influence of these seemingly small differences was notable (and significant – $P < 0.001$): at the end of the 13th growing season, the height of trees with lammas shoots was on average 450 ± 11.8 cm, while those without lammas shoots averaged at 374 ± 7.8 cm in trial 1; in trial 2 – 490 ± 8.1 cm and 416 ± 7.4 cm, respectively; in trial 3 – 481 ± 16.0 cm and 420 ± 12.2 cm, respectively (Fig. 3). Thus, trees with lammas shoots were 14–20% taller than trees without them. Also, in experiment A, trees with lammas shoots were 29% taller than trees without them (148 ± 5.8 cm vs. 115 ± 1.4 cm, $P < 0.001$).

The additional height increment due to lammas shoots might be dependent on the absolute length of the height increment. To evaluate whether this was the case, in each trial, trees with lammas shoots and trees without them were sorted according to height increments in descending order, and four groups (equal number of trees in each group) were formed. For example, in trial 2, the number of trees with lammas shoots in each group was 688/4 = 172, but without them was 1242/4 = 310. Height increment in each of the four groups was significantly ($P < 0.001$) higher for trees with lammas shoots than for trees without them in each of the trials.

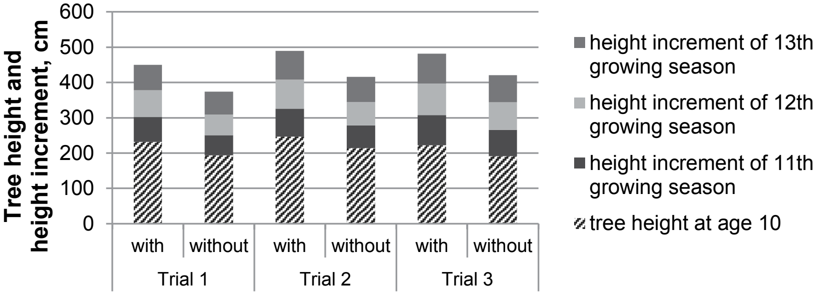

Figure 3. Height and height increment of trees with and without lammas shoots in trials 1–3 of experiment B ('with' – trees with lammas shoots; 'without' – trees without lammas shoots).

The frequency of lammas shoots was linked not only to tree height increment, but also to their bud flushing phenology: earlier flushing trees had a higher frequency of lammas shoots. For example, in trial 2, for trees with flushing grade 4 (very early), 56% of trees had lammas shoots, but in grade 1 (very late), only 22%. Within every flushing grade, the mean height increment was significantly ($P < 0.001$) higher for spruces with lammas shoots than without them (Fig. 4).

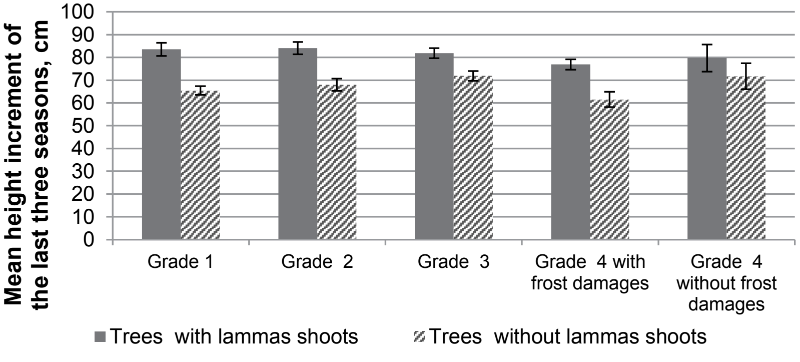

Figure 4. Height increment of the last three seasons for trees with and without lammas shoots in different bud flushing grades in trial 2 of experiment B.

This contrasts the observations by Danusevičius & Persson (1998), who found a higher proportion of trees with lammas shoots for provenances with later flushing. Frost damages were not observed for very late and late flushing trees (grades 1 and 2), but were observed for 2% of early flushing and 87% of very early flushing trees (grades 3 and 4). The reduction of height increment as a result of frost damages for very early flushing trees was less pronounced for trees with lammas shoots than for those without them (Fig. 4).

CONCLUSIONS

Results indicate that lammas shoots are linked to an increase in height increment and can reduce the impact of frost damages on the length of height increment. Increased frequency of the formation of lammas shoots due to climatic changes would raise the height increment of the Norway spruce.

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Influence of spot mounding on height growth and tending of Norway spruce: case study in Latvia

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Abstract. Norway spruce is commonly regenerated by planting and disc trenching is by far the most widely used soil preparation method in Latvia; however, in specific site conditions other methods might be beneficial. Therefore aim of our study was to assess influence of spot mounding on early growth and tending of Norway spruce in hemiboreal forests. Spot mounding was compared with disc trenching or no soil preparation in central part of Latvia (57° N 24° E) in five different forest types, where two-year-old containerized Norway spruce seedlings were planted. Influence of soil preparation method on tending was assessed in the same region in two different sites in a single forest type on drained fertile mineral soil. Spot mounding had positive effect on the height increment of the dominant trees at the 6th to 8th growing season. Mean height of Norway spruce at the end of 8th growing season on mounds significantly exceeded that on unprepared soil: 179 ± 6.5 and 152 ± 6.2 cm, respectively. Similarly mean height on mounds was significantly larger than on furrows: 209 ± 3.9 and 154 ± 4.0 cm, respectively. Projective vegetation cover before the tending was significantly higher in spot-mounded, but after – in disc trenched sites. Networking time for brash-saw operators in spot-mounded (478 min/ha^{-1}) and disc trenched (462 min/ha^{-1}) sites was similar ($p > 0.05$). Overall, spot mounding ensured more suitable microenvironment resulting in higher productivity of planted trees and had no negative effect on quality or efficiency of tending, therefore its wider use is recommended.

Key words: soil preparation method, height increment, weed control, *Picea abies*.

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Introduction

Norway spruce (*Picea abies* (L.) Karst.) occupies significant forest areas and is one of the most cultivated tree species in Baltic Sea region countries. For example, in Latvia, based on data from National Forest Inventory, its stands cover 17% from the total forest area and, according to data of State Forest Service, in 2015 altogether 6531 ha was regenerated with this tree species. Natural regeneration of coniferous trees in hemiboreal forests on fertile soils after the clear-cut is very unlikely and/or time consuming. It has been demonstrated already in middle of previous century, when large-scale inventory found, that more than 70% of the clear-cuts in coniferous forests in such site conditions naturally regenerate with broadleaved trees (Sarma, 1959). Also studies indicate that planted spruce stands have considerably higher productivity than naturally regenerated ones (Gradeckas & Malinauskas, 2005). It is achieved partly

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due to realization of tree breeding results (Jansons *et al.*, 2015) and partly due to positive influence of soil preparation (Nordborg *et al.*, 2003; Heiskanen *et al.*, 2013).

Various soil preparation methods, like ploughing, disc trenching, soil inversion, mounding (Mangalis, 2004; Gradeckas & Malinauskas, 2005) can be applied; however in Baltic States by far most commonly used is disc trenching. Conditions created by disc trenching or ploughing are not always optimal for the seedlings. For example, Örlander *et al.* (1990, 1998) have found that survival of trees planted on furrows is similar to that of trees planted on mounds in sites with normal moisture regime, but notably and significantly lower in wet sites. Also other studies have concluded that mounds creates favourable moisture regime that is essential for early survival of Norway spruce (Schlyter *et al.*, 2006). Planting on mounds improves not only the survival, but also initial growth of the trees (Nordborg *et al.*, 2003; Hallsby & Örlander, 2013; Heiskanen *et al.*, 2013). Young trees on mounds are less likely to be affected by frosts (Langvall *et al.*, 2001; Heiskanen *et al.*, 2013) and better protected from pine weevils (Örlander *et al.*, 1990; Heiskanen & Viiri, 2005; Saksa, 2008; Heiskanen *et al.*, 2013) that tend to avoid rather large open soil area around the seedling (Wallertz, 2009). Furthermore, mound excluded competition from surrounding vegetation for a longer period of time than furrows (Lehtosalo *et al.*, 2010). For example, in Finland it was found, that in sites where spot mounding was applied, tending was needed only in 2nd–4th year after planting in relative fertile soil, and in 4th–6th year in poor soil (Saksa, 2008; Uotila *et al.*, 2010). Therefore, some authors (Uotila *et al.*, 2010) suggest that financial assessment of forest regeneration shall include not only planting (and survival of planted trees), but also tending: its frequency (number of occasion), quality and time spent (costs). Time spent for soil preparation (and thus also the costs and potential for their reduction) had been analysed in numerous studies (Rantala *et al.*, 2010; Liepiņš *et al.*, 2011). However, there is still very limited information on time spent for tending in the context of soil preparation method in Baltic States.

Most of above mentioned studies had been carried out in boreal forest with different climatic conditions and soil fertility (important both for tree as well as ground vegetation growth) than in hemiboreal forests. Therefore, the aim of our study was to estimate influence of spot mounding on early growth and tending of Norway spruce in hemiboreal forests.

We hypothesised that spot mounding has significant positive influence on tree height increment in comparison to disc trenching or no soil preparation. Larger tree height consequently would ensure faster tending in sites prepared by spot mounding (though trees are not planted in rows) than in sites prepared by disc trenching.

Material and Methods

Evaluation of influence of spot mounding on growth of Norway spruce was based on trials from central part of Latvia (57°36′ N 24°36′ E), located in middle of hemiboreal forest zone (Barbati *et al.*, 2007). Data on tree height were collected in Norway spruce stands established in two clear-cut areas (sites), two replications per site. In autumn of 2008 in one of the sites spot mounding and disc trenching was applied, while in other site spot mounding and no soil preparation was done. In study sites in total 5 different forest types (classified according to Bušs, 1976): *Myrtillosa, Hylocomiosa, Oxalidosa* (mineral soil, normal moisture regime, arranged according to increasing soil fertility), *Myrtillosa turf. mel.* (peat soil, drained, fertile), *Myrtilloso-polytrichosa* (mineral soil, wet, fertile), were represented.

Planting was carried out immediately after soil preparation (in autumn) using two year old containerized Norway spruce seedlings with similar size in each of the sites and treatments: height ranged from 16 to 36 cm (average 23 ± 0.5 cm), root collar diameter: from 1.5 to 4.5 mm. Planting material in both sites was from the same provenance region (category: selected), grown in the same nursery. After planting in both sites regular treatment according Latvian forestry practice was applied, i.e. clearing from competing vegetation during first 4 growing seasons.

In winter of 2014/2015 height of all Norway spruce trees as well as last three years annual height increment was measured with the accuracy of 1 cm. Also defects (broken tops, spike knots) were evaluated and recorded, however frequency of trees with them was low (< 2%) and no specific tendencies in relation to soil preparation method or site were detected. As this study focuses on the height of vital trees, data of damaged trees were excluded from further analysis.

Tending time and quality was evaluated in *Myrtillosa mel.* forest type (mineral soil, drained, fertile), since it is characterized by fast growth and high density of competing ground vegetation, representing the most challenging conditions for this work. Also for this part of the study two clear-cut areas (sites) were used. In each of the sites spot mounding and disc trenching (two replications per site) was applied before the planting. Similar containerized seedlings than in the first part of the study were planted and, at the time of tending (end of first vegetation season after planting), had reached mean height of 28 ± 0.7 cm.

In each parcel (defined by replication and site) four blocks of 0.25 or 0.5 ha (depending on size of the parcel) were systematically placed. On the longest diagonal of the blocks 10 circular plots (r = 2.82 m, area 25 m^2) were systematically (even distances between the centres) marked out. In each of these plots assessment of ground vegetation (projective area) was carried out before and after the tending based on ICP Forest method (ICP Forest, 2011), distinguishing five groups of plants (shrubs, sprouts, half-shrubs, grasses, other ground vegetation). Also area of bare soil in each plot, created in process of soil preparation, was measured. Inventory was carried out by a single person to ensure comparability of the estimates. Mean height of each vegetation group was measured in each plot (accuracy 0.1 m). Tending was carried out by 5 brush saw operators (the same persons working in areas where spot mounding and disc trenching was used) in the end of August. Networking time (period when the brush-saw was operated) as well as total working time of the operators in each of the blocks was recorded (accuracy 0.1 min).

Data analysis was carried out in SPSS applying ANOVA and χ^2 test. To characterise the variance, 95% confidence interval was used. One-way analysis of variance and Tukey's HSD test was used to assess the differences of tree height (and height increments) between particular forest types and soil preparation methods. To evaluate the impact of soil preparation method, forest type, and interaction of both factors, two-way analysis of variance was used. Impact of the soil preparation method on height growth of trees was also characterised using dominant trees: highest, corresponding to density 100 trees ha^{-1} (Donis, 2014).

The relation between tree height and soil preparation method was also evaluated comparing distribution of trees in different height classes (h > 2.5 m; 2 < h ≤ 2.5 m; 1.5 < h ≤ 2 m; h ≤ 1.5 m), in each of forest type separately; χ^2 test was use to assess the differences of distribution. The differences of projective cover and height of competing vegetation before and after tending, as well as the differences of the networking time (and its proportion from total working time) for sites with different soil preparation were assessed by one-way analysis of variance and Tukey's HSD test.

Results and Discussion

Growth of Norway spruce in relation to soil preparation method

The forest type ($p < 0.001$), soil preparation method ($p < 0.001$) as well as interaction of both factors ($p < 0.001$) had significant effect on the height of trees at age of 8 years; however statistically significant influence of replication was not detected ($p > 0.05$).

Regardless of soil preparation method, the highest (198 ± 3.8 cm) mean tree height was found on *Oxalidosa* forest type. Similarly, largest mean height of Norway spruce seedlings at the same age had been found in *Oxalidosa* forest type also in Lithuania (Gradeckas & Malinauskas, 2005), conforming the suitability of this forest type for establishment of productive spruce stands.

Mean tree height on mounds notably and significantly exceeded that on unprepared soil (height difference 27 cm, corresponding to 17.8%) or furrows (55 cm, 35.7%). Similar results were obtained also in analysis of the distribution of trees in different height classes: the proportion of highest trees was significantly higher in spot-mounded sites (Figure 1).

Consequently, mean height of dominant trees in spot-mounded sites exceeded that on disc-trenched ones significantly ($p < 0.05$) in all forest types (Figure 2).

Detailed analysis demonstrated that differences in tree height distribution between soil preparation methods were significant in *Myrtillosa*, *Oxalidosa* and *Myrtilloso-polytrichosa* forest types. Similar trend was noted in *Hylocomiosa* and in *Myrtillosa turf. mel.* forest types, however, these differences were non-significant ($p = 0.05$ and $p = 0.53$, respectively). Differences were more pronounced, when trees growing on mounds were compared with those growing in unprepared soil: in these circumstances one

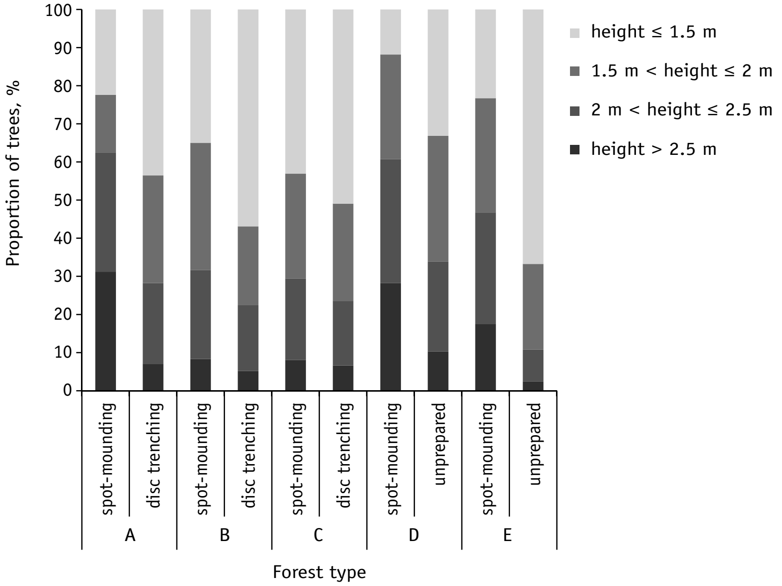

Figure 1. Distribution of trees in height groups at the age of 8 years in different forest types: *Myrtillosa* (A), *Hylocomiosa* (B), *Myrtillosa turf. mel.* (C), *Oxalidosa* (D), *Myrtilloso-polytrichosa* (E).

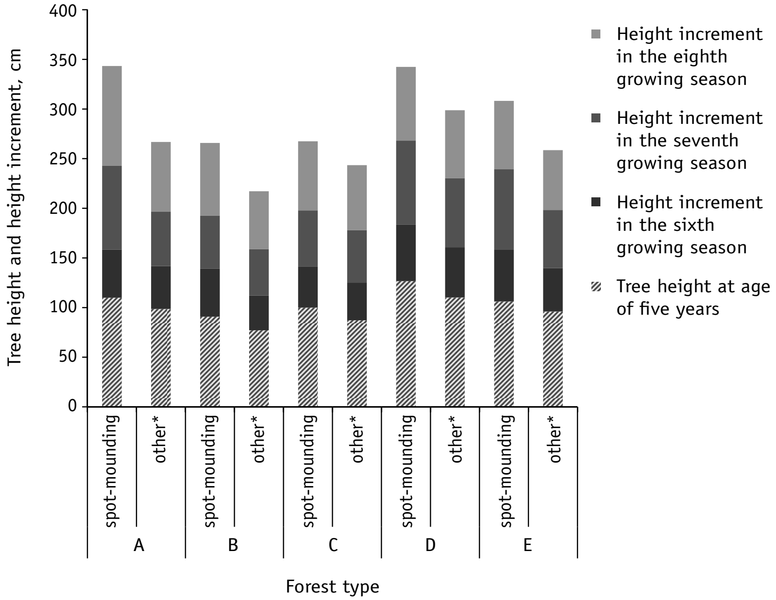

Figure 2. The total height and the height increment during last 3 growing seasons of the one hundred highest trees per ha^{-1} at the age of 8 years.
* other: disc trenching in *Myrtillosa* (A), *Hylocomiosa* (B), *Myrtillosa turf. mel.* (C), unprepared soil in *Oxalidosa* (D), *Myrtilloso-polytrichosa* (E).

third of trees in *Oxalidosa* forest type and as much as two thirds in *Myrtilloso-polytrichosa* forest type were lower than 1.5 m. Similar influence of soil preparation method on tree height distribution in young Norway spruce stand was found also in Finland (Uotila *et al.*, 2010).

Differences in mean height of the trees (Figure 3) were significant ($p < 0.05$) in most of the forest types – on mineral soil with normal moisture regime (*Myrtillosa, Hylocomiosa, Oxalidosa*) and on wet mineral soil (*Myrtilloso-polytrichosa*). Less pronounced ($p = 0.09$) differences were found on drained peat soil (*Myrtillosa turf. mel.*), presumably due to impact of frost heave. Frost heave primarily affects areas on drained peat soils in Latvia (Mangalis, 2004). Study in central Finland found that it has been present mainly on areas with ditch mounded and inverted soil (Heiskanen *et al.*, 2013).

Similar to our results, superior height growth of trees planted on mounds had been found also in numerous studies in Sweden and Finland (Saarinen, 2007; Lehtosalo *et al.*, 2010; Uotila *et al.*, 2010; Hallsby & Örlander, 2013). Even so the reported (Örlander *et al.*, 1990, 1998) differences in tree height between the soil preparation methods were smaller than those found in our study, presumably due to slower growth in more northern climatic conditions. Positive effect of spot-mounding might be a results of improved availability of nitrogen (faster mineralization) at the second and third growing season (Smolander & Heiskanen, 2007; Nieminen *et al.*, 2012) thus increasing the biomass and root growth of seedlings (Nordborg *et al.*, 2003). In this respect both soil treatments with humus removal as well as planting in un-prepared soil yielded the worst results (Nordborg *et al.*, 2003). These

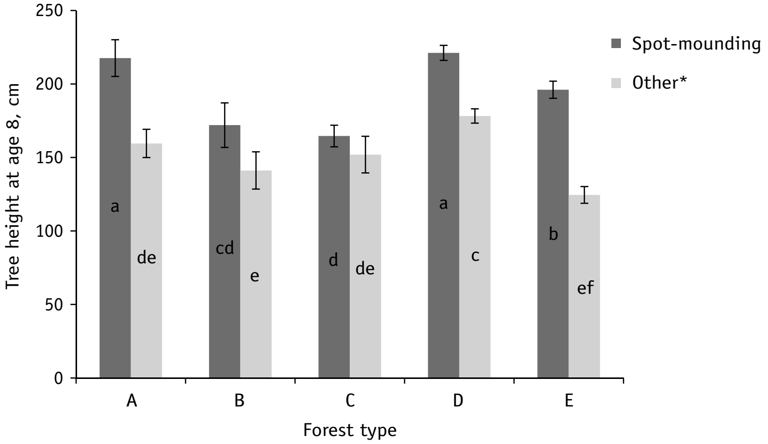

Figure 3. Tree height (± confidence interval) in relation to soil preparation and forest type at the age of 8 years.
* other: disc trenching in *Myrtillosa* (A), *Hylocomiosa* (B), *Myrtillosa turf. mel.* (C), unprepared soil in *Oxalidosa* (D), *Myrtilloso-polytrichosa* (E). Arithmetic means denoted by the same letter show non-significant differences ($p > 0.05$).

findings are in line with our results where largest height differences were found between spruces growing on mounds and on unprepared soil (Figure 3). Lack of soil scarification leads to much more frequent pine weevil damages even if the plants are treated by insecticide in the nursery (Heiskanen *et al*., 2013). For example, study in Finland had found 76% of Norway spruce seedlings gnawed in unscarified spots during first growing season in field in contrast to only 1% gnawed on mounded spots (Heiskanen & Viiri, 2005). Seedlings damaged by pine weevil were less vigour and had smaller height increment (Heiskanen & Viiri, 2005; Heiskanen *et al*., 2013). Since our trials were established in fresh coniferous clearcuts, usually most affected by pine weevil, reduction of impact of this insect might be an important factor causing the observed differences in tree height distribution (Figure 1).

Mounding had produced better establishment and initial growth of Norway spruce plantations than patching or disc trenching due to combination of reduced seedling damage, improved thermal conditions and improved availability of nutrients (Kankaanhuhta *et al*., 2009; Heiskanen *et al*., 2016). Improved vigour in first years may have led to larger height increment of trees later on, as demonstrated by our results (Figure 2). Height increment of dominating trees of the last three growing seasons was larger in spot-mounded sites in comparison to disc-trenched ones. It showed significant differences in *Myrtillosa* and *Hylocomiosa* forest types during the eighth growing season, and in *Myrtillosa* type during the seventh growing season; however no significant differences were found during the sixth growing season. Height increment of the eighth and seventh year in areas with spot-mounding was higher also than in areas without soil preparation, but in the sixth growing season significant differences were found only in *Myrtilloso-polytrichosa* forest type ($p < 0.05$). Inter-annual differences in the results might be caused by variation of meteorological conditions affecting height

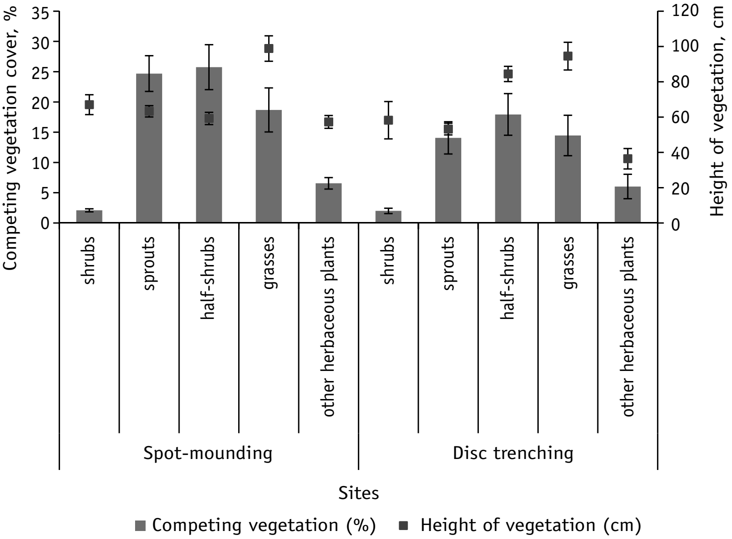

Figure 4. The projective cover (± confidence interval) and height of competing vegetation (± confidence interval) before tending in *Myrtillosa turf. mel.* forest type.

increment. Overall our results are in line with findings in Finland, demonstrating that mean height increment of spruces planted on mounds was slightly higher than for those planted in furrows (23.7 ± 17.4 and 20.6 ± 13.6 cm, respectively) leading to significant differences in height of trees at the end of 9th growing season (Saksa *et al.*, 2005).

Tending in relation to soil preparation method

Our results showed no differences in the abundance of ground vegetation on sites with spot mounding and disc trenching, if adjusted for the area of un-prepared soil. However, the actual mean projective cover of ground vegetation before the tending was significantly higher in spot-mounded sites in comparison to disc-trenched sites: 78 and 54%, respectively.

Earlier studies in similar climatic conditions had found, that soil preparation method determines the shading of seedlings and thus the need for tending; the least shaded were seedlings planted on wide (100 cm) furrows and 30 cm high mounds (Suchockas *et al.*, 2014). So both of the soil preparation methods analysed in our study can yield similar results in relation to vegetation competition. Soil preparation increases the ground vegetation species richness (Balandier *et al.*, 2006), but not necessarily its impact to seedlings. Impact of ground vegetation is related to its vicinity to the seedling and delayed by soil preparation depth and width (Suchockas *et al.*, 2014).

The sprouts, half-shrubs and grasses were the most abundant (85–89%) type of competing vegetation in both spot-mounded and disc-trenched sites. The proportion of these vegetation groups was similar within sites with different soil preparation methods (Figure 4).

The mean weighted (the projective cover used as weights) height of vegetation was similar ($p > 0.05$) for sites with both types

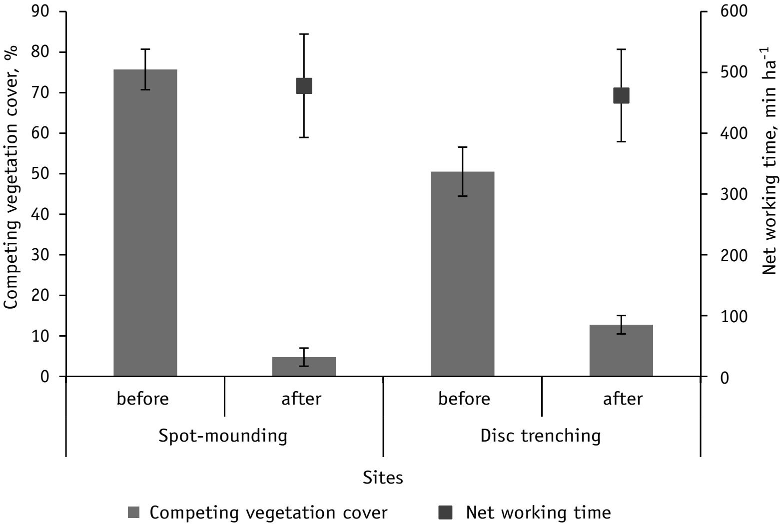

Figure 5. The competing vegetation cover (± confidence interval) before and after tending, and net working time (± confidence interval) in spot-mounded and disc-trenched sites.

of soil preparation. The height of grasses significantly exceeded that of other vegetation groups in spot-mounded sites. In disc-trenched sites, grasses and half-shrubs (mostly raspberries) were significantly higher than other vegetation groups. Similarly, grasses were the dominant ground vegetation type in second and third year after the clearcut in forest types on fertile soil also in Lithuania. Height of weeds were similar on ploughed berms and mounds (Suchockas *et al.*, 2014). Grasses had been noted as most significant competitors, capable to reduce height-growth of seedlings, primarily due to fast root growth and consequently intensive water uptake by graminoids (Coll *et al.*, 2003). In order to reduce this impact, need for tending was similar in both disc-trenched and spot-mounded sites.

The projective covers of vegetation after tending was significantly lower in spot-mounded (5%) in comparison to disc-trenched (13%) sites (Figure 5) and the mean height of it did not differ significantly ($p > 0.05$). Statistically significant impact of replication on vegetation cover was not detected.

The networking time, as well as its proportion from total working time was similar ($p > 0.05$) for sites with different soil preparation: 478 min/ha^{-1} (67 ± 9.7%) and 462 min/ha^{-1} (68 ± 8.3%) in spot-mounded and disc-trenched sites, respectively.

Conclusions

Soil preparation method had significant effect on height of Norway spruce trees at the age of 8 years: planting on mounds resulted both in higher mean height as well as larger proportion of highest trees in comparison to planting on furrows or in unprepared soil. The difference between height increment of dominant (the highest 100 trees ha^{-1}) trees in spot-mounded and disc-trenched sites increased gradually along with the age of the trees: from the average of 7 cm (14%) during the sixth growing season to 17 cm (20%) during the eighth growing season. Tending in site prepared by spot mounding was as effective as in site prepared by disc trenching, reducing the vegetation cover to a negligible 5 and 13%, respectively. Also the speed of the operation was unaffected by soil preparation method.

Overall the results suggest a great potential of spot mounding to improve the early growth of planted Norway spruce stands.

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MDPI

Article

Effect of High Concentrations of Wood Ash on Soil Properties and Development of Young Norway Spruce (*Picea abies* (L.) Karst) and Scots Pine (*Pinus sylvestris* L.)

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Abstract: Wood ash recycling can be a reasonable method for energy producers to decrease waste problems. Using wood ash as a fertilizer or liming material could improve soil macro and micronutrient content in peat soils. Therefore, the effect of wood ash on Norway spruce (*Picea abies* (L.) Karst) and Scots pine (*Pinus sylvestris* L.) juvenile growth and nutrient content in the soil after spreading wood ash in medium to high doses before and after planting seedlings was investigated in peat forests in the Eastern part of Latvia. The aim of the study was to evaluate the effect of high doses of wood ash on soil properties and the growth of planted Norway spruce and Scots pine seedlings up to 10 years after experiment establishment. Wood ash was applied a year before planting seedlings in doses of 5 and 10 t ha^{-1} and right after planting in concentrations of 5, 10, 15, and 20 t ha^{-1}. Changes in macronutrient content (i.e., phosphorus [P], and potassium [K]) and tree height and diameter at breast height were measured at one and 10 years after establishing the experiment. Fertilization one year prior to planting the seedlings exhibited a positive response on tree height and diameter growth compared to fertilization after the seedlings were planted. Soil samples from fertilized plots one year after establishment contained more P and K in the soil than the control plots. Wood ash application of the highest doses did not reach the overdose limit, as the tree growth (height and diameter at breast height) results of fertilized plots were similar to those of the control fields; therefore, no significant negative effect on tree growth was discovered.

Keywords: fertilization; forest regeneration; liming; seedling growth; wood ash

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1. Introduction

Wood ash application intensifies the increase of available nutrients in forest soils and improves forest production, however the effects of wood ash on tree growth differ between peat and mineral soils [1–5]. Wood ash fertilization has a long-lasting pH neutralizing effect on the soil organic layer and wood ash application counteracts soil acidity after forest harvesting of whole tree biomass (including logging residues and, in some cases, even roots) for energy production [4–6]. Therefore, wood ash could be used as an alternative mineral fertilizer and liming material because it primarily consists of metal oxides, hydroxides, carbonates, salts, and soil minerals [6,7]. Recycling ash may contribute to sustainable forest management, and it can be an environmentally acceptable solution to the waste problems of energy producers [8]. In Latvia, wood chip ash is deposited on waste disposal sites; thus, only a minor portion is used for fertilization and liming in farms. However, according to the State Plant Protection Service registry data, interest in wood ash as a fertilizer has grown in the last few years, and currently, 24 companies have registered wood ash as a liming material.

Studies on the effect of wood ash application and soil chemistry of forest ecosystems have been carried out in Fennoscandia [8,9], and several small-scale experimental trials of wood ash usage for forest soil fertilization and liming were established in Latvia [10–13]. These studies have found that the utilization of ash by moving it back to forest mineral elements after the burning of organic matter for energy production could be defined as the "recycling of nutrients", "fertilizing", and "liming". These methods are effective for stabilizing soil pH, enriching the soil with phosphorus (P), potassium (K), and micronutrient elements (zinc, boron, copper, etc.), especially in peat soils (due to the fact that wood ash does not contain nitrogen, however peat soils are nitrogen rich in comparison to mineral soils where nitrogen is the growth limiting element), and decreasing the need to deposit wood ash in waste disposal sites or landfills [14–24].

In general, no short-term growth effect of wood ash application has been found on mineral soils; however, recycling wood ash and using it as a fertilizer with other macronutrients or fertilizers may affect stand growth in different ways over a longer period [5]. On nitrogen (N) rich organic soils, a substantial growth increase is usually seen [25,26]. However, wood ash application can deplete organic carbon (C) in locations with N-rich soil [27]; therefore, experiments and investigations are needed to determine the potential and ecological consequences of wood ash recycling. The application of wood ash leads to changes in mycorrhizal fungi communities, increased species richness, and higher Shannon diversity index in fertilized plots compared to control plots [28].

The share of wood as a renewable fuel for energy and the increase in pellet production are factors that re-actualize investigations about the effect of wood ash as a source of nutrient elements for forest trees in the long term, therefore such investigations were done on experimental fields established several years ago. If forests within the Nordic and Baltic regions functioned as a "deposit" for the wood ash coming from the total harvest of wood for energy within the region, then the forests would receive an average of 0.2 to 0.5 t ha^{-1} of dry wood ash within one rotation period [8]. Recommended wood ash doses in the rotation period are 1–2 t ha^{-1} and 0.7–1.5 t ha^{-1} for Norway spruce (*Picea abies* (L.) Karst) and Scots pine (*Pinus sylvestris* L.), respectively [29]. In the trial, high doses of wood ash are used to determine both positive and negative effects on plant development at an early stage and to assess the effects on the nutrient elements in the soil. Therefore, the aim of this study is to characterize the influence of high doses of wood ash on soil properties and the growth of Norway spruce and Scots pine seedlings up to 10 years after planting.

2. Materials and Methods

2.1. Study Site

The research site is located in the Kalsnava district in the central part of Eastern Latvia (56°42′ N. latitude, 25°50′ E. longitude), approximately 150 km from the Baltic Sea. The research area is located on the border between continental and marine climate conditions. The average air temperature is +5 °C to +6 °C (January −5 °C to 6 °C, July +16 °C to +18 °C). The average precipitation in previous years before planting was 797 mm [10]. The experiment was established on restoration site on homogenous drained fertile (grass) peat soil in the forest type *Myrtillosa mel.* [30]. Experimental plots were divided into 4 random blocks and total study site area was 0.2 ha, thus a single experimental plot size on average was 2.7 m^2. The study site design is presented in Klavina et al. [31]. Soil was prepared manually in each plot, the understory plants were removed, and the top soil layer was overturned.

The study site consists of 46 experimental plots (with 50 cm buffer zones between the plots) established with two tree species: Norway spruce and Scots pine. Altogether 18 spruce plots and 28 pine sample plots were established with two years old spruce containerized seedlings and one year old pine containerized seedlings obtained from JSC "Latvia's State Forests" tree nursery. The seedlings met basic operational standards in terms of seedling morphological parameters. In each experimental plot, approximately 70 containerized seedlings were planted in rows with 0.5 × 0.5 m spacing (Figure 1). The experimental plots of the Norway spruce consisted of randomly assigned plots with six replications for control and twelve replications with fertilization. Wood ash in doses of 0 (control group) and 5 and 10 t ha^{-1} (medium dose before) was applied in May 2003—one year before the spruce stand establishment. For Scots pine, the experimental plots consisted of randomly assigned plots with 6 to 8 replications for each type, where wood ash was applied a year prior to planting (in May 2003) in doses of 0 (control group) and 5 and 10 t ha^{-1} (medium dose before). In May 2004, in each plot seedlings were planted and the wood ash with doses of 0 (control group), 5 and 10 t ha^{-1} (medium dose after), or 15 and 20 t ha^{-1} (high dose after) was applied afterwards. Wood ash was applied manually on all the study plots (same method prior and after planting) with a surface spread approach.

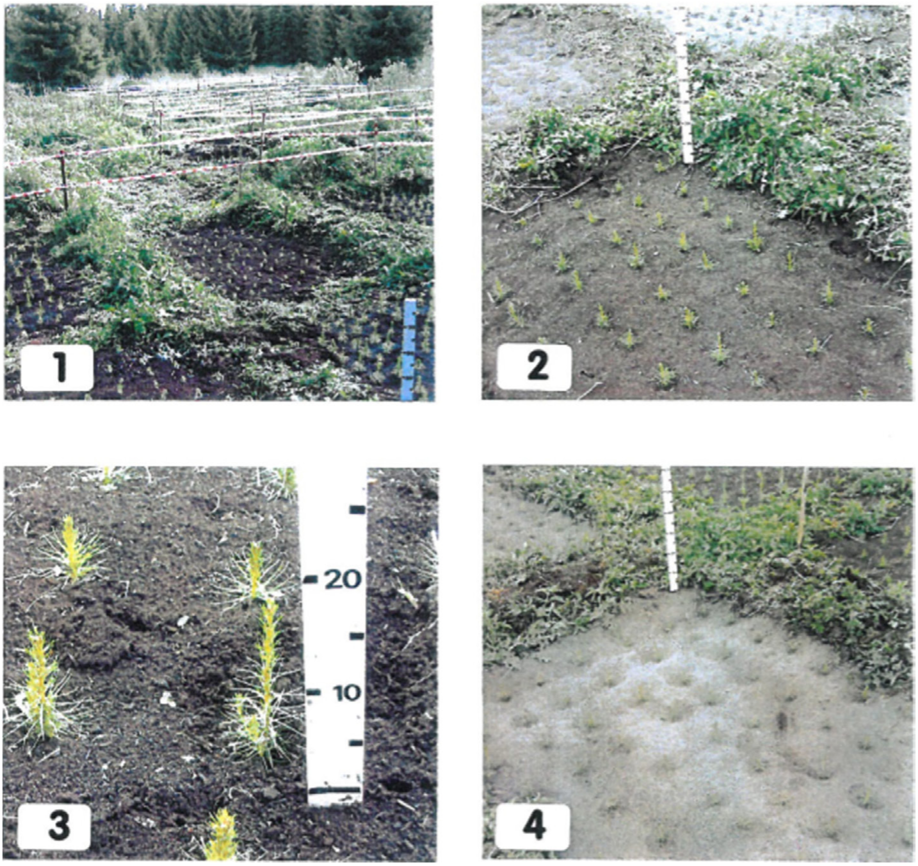

Figure 1. Experimental plots of wood ash fertilization (1 = experimental plots in the year 2004, 2; 3 = plots fertilized one year before planting seedlings, 4 = experimental plot fertilized right after planting seedlings) [10].

The medium dose (5 to 10 t/ha^{-1}) of wood ash was calculated and assumed to last for a 5-year period, with the high dose (15 to 20 t ha^{-1}) of wood ash calculated to last for a 10-year period. The ash used for the experiment was alkaline (pH = 12.44); its nutrient content was average compared to that found by other scientists (Table 2). The experiment soil analysis established that the trial was conducted on an N-rich site; therefore, no additional N fertilizer was added.

One year after the experiment establishment, approximately half of the seedlings were removed from the sample plots for the investigation of root and stem biomass. Moreover, 10 years after the establishment of the experiment, the tree height and diameter at breast height (DBH) of the surviving and standing dead trees were measured. Originally, standing dead trees were measured to assess information of tree dimensions (H and DBH) at which self-thinning due to species competition occurred and at what wood ash doses. A sampling of the soil for nutrient analysis was conducted in each plot. Soil samples were taken from every experimental plot at four depths (0–10 cm, 10–20 cm, 20–40 cm, 40–80 cm).

Soil samples were prepared for analyses according to the LVS ISO 11,464 (2005) standard, and the parameters evaluated in the soil samples were the total N content using the modified Kjeldahl method according to LVS ISO 11,261 (2002). The available phosphorus ($P\text{-}PO_4^{-3}$) content was determined according to LVS 398 (2002), and the exchangeable K was extracted with ammonium acetate and determined using flame atomic emission spectroscopy.

2.2. Data Analysis

The generalized linear model was used to determine the significance of differences among the plots with various wood ash treatments. Mixed effect models were used for analysis where the plot ID was taken as a random factor, and the year of fertilization and dose combination were used as influencing factors.

3. Results

3.1. Fertilization Effect on Soil Chemical Composition one Year Afterwards

Wood ash is a source of K, and after fertilization, additional amounts of macronutrient elements are available for tree development. The K content in the soil of the pine sample plots one year after the application of wood ash increased two to six times in comparison to the control plots, depending on wood ash concentration (Figure 2). The content of K in the control plots was an average of 6.1 ± 2.0 mg kg^{-1}, but after treatment with wood ash, the K content in the soil increased two to six times in the first year (differences are statistically significant). In the sample plots where wood ash was applied in medium doses (5 to 10 t ha^{-1}) before planting the seedlings, the K content was 11.9 ± 2.1 mg kg^{-1}. However, treatment with medium doses (5 to 10 t ha^{-1}) right after planting resulted in K increases of up to four times (25.5 ± 9.5 mg kg^{-1}), but high doses (15 to 20 t ha^{-1}) of wood ash resulted in a K content of 37.8 ± 9.8 mg/kg, which increased up to six times in comparison to the control field. In the spruce sample plots, the K amount in the control field was 6.0 ± 1.7 mg kg^{-1}. In plots where wood ash was applied before planting, K increased to 7.9 ± 2.0 mg kg^{-1}; however, no significant differences were observed.

Phosphorus (P) is one of the problematic or even lacking macronutrient elements in acid peat soils. The content of P in the soil after the application of wood ash was higher in comparison to the pine control plots. The average amount of P in the control plots was 0.22 ± 0.06 g kg^{-1}, but after a year of the ash treatment, the P content in the soil increased by approximately two to three times in all sample plots (Figure 3). The lowest amount of P (0.43 ± 0.26 g kg^{-1}) between plots (excluding the control) occurred with the medium dose (5 to 10 t ha^{-1}) of ash applied a year before planting. The application of medium doses of ash after planting resulted in a significant increase in P content to 0.53 ± 0.17 g kg^{-1}, but treatment with high doses (15 to 20 t ha^{-1}) of ash exhibited the highest content of P in the soil at 0.57 ± 0.14 g kg^{-1}. In spruce sample plots, the P content in the soil increased in fertilized plots in comparison to the control plots. The lowest P amount in the soil was observed in the control plots (0.31 ± 0.05 g kg^{-1}); however, in the fertilized plots, the P content increased to 0.53 ± 0.18 g kg^{-1}. The differences were noticeable but not statistically significant ($p > 0.05$) between the control and fertilized spruce plots.

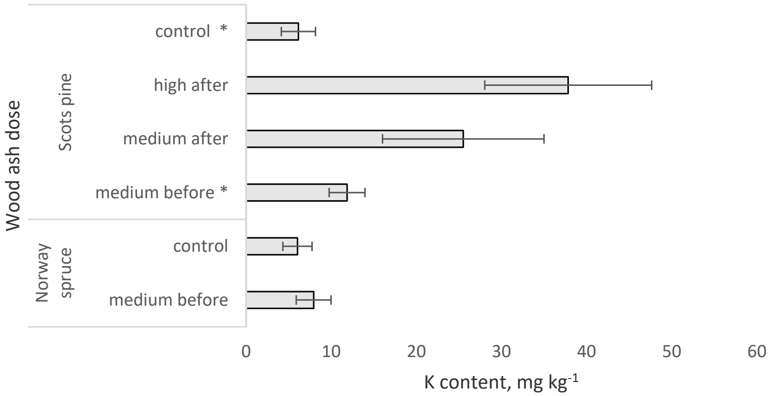

Figure 2. Content of potassium (K) in the soil a year after planting the seedlings fertilized using different wood ash doses (5 to 10 t ha^{-1} = medium dose before planting seedlings, 5 to 10 t ha^{-1} = medium dose after planting seedlings, 15 to 20 t ha^{-1} = high dose after planting seedlings, and control = untreated plots, 0 t ha^{-1}; SP: Scots pine, NS: Norway spruce; the confidence interval is represented by vertical error bars, * indicates significant differences between treatments).

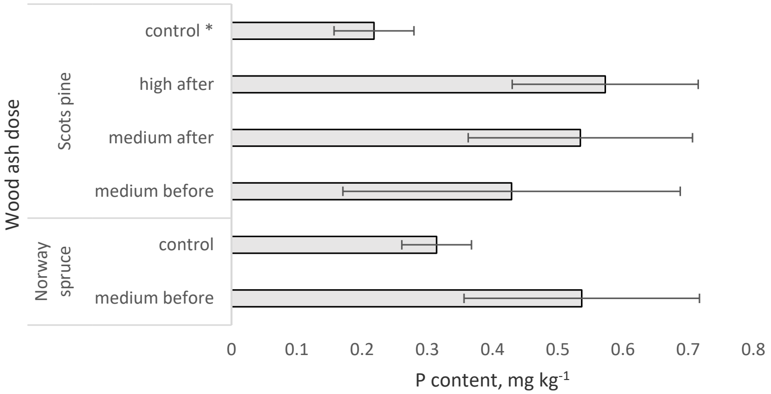

Figure 3. Content of phosphorus (P) in the soil a year after planting seedlings fertilized using different wood ash doses (5 to 10 t ha^{-1} = medium dose before planting seedlings, 5 to 10 t ha^{-1} = medium dose after planting seedlings, 15 to 20 t ha^{-1} = high dose after planting seedlings, and control = untreated, 0 t ha^{-1} plots; SP: Scots pine, NS: Norway spruce; the confidence interval is represented by vertical error bars, * indicates significant differences between treatments).

After wood combustion, most nutrients (except N) are retained in the ash, and the ash can be used for soil amendment, altering the soil properties. The ammonium (NH_4) content in the soil of pine plots varies from 9.3 ± 1.4 g kg^{-1} (high dose after planting) to 12.3 ± 3.0 g kg^{-1} (medium dose prior to planting); however, the changes are not significant after wood ash application with any dose; thus, the highest nitrogen content after one year was observed in plots where ash was applied a year before planting the pine seedlings (Figure 4). Similar tendencies were observed in spruce plots, where the highest N content was observed in sample plots where wood ash was applied (10.8 ± 0.9 g kg^{-1}), and the lowest amount was in control plots (9.6 ± 2.1 g kg^{-1}). However, no significant differences were observed.

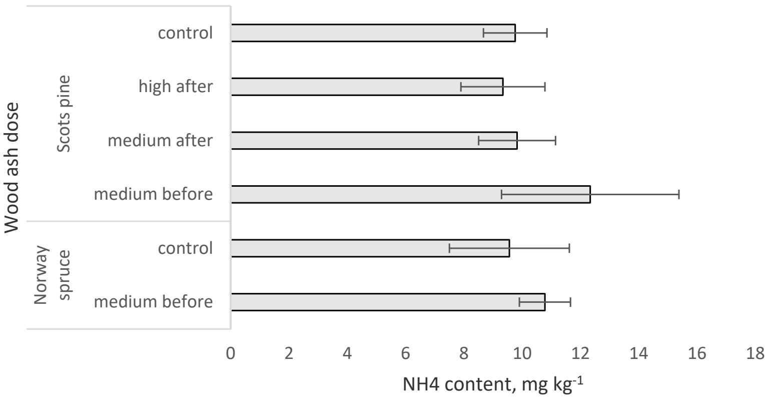

Figure 4. Content of NH_4 in the soil a year after planting seedlings fertilized using different wood ash doses (5 to 10 t ha^{-1} = medium dose before planting seedlings, 5 to 10 t ha^{-1} = medium dose after planting seedlings, 15 to 20 t ha^{-1} = high dose after planting seedlings, and control = untreated plots, 0 t ha^{-1}; SP: Scots pine, NS: Norway spruce; the confidence interval is represented by vertical error bars).

3.2. Ten Years after Fertilization

After 10 years, no significant difference ($p > 0.05$) was observed between sample plots; however, in a 10-year period, the P content available for plants in soil in pine control fields was 1.8 ± 0.31 g kg^{-1} (Figure 5). In pine dominated plots where wood ash was applied a year before planting, the content also reached 1.8 ± 0.37 g/kg. The application of a medium dose of ash after planting resulted in a P content increase to 1.6 ± 0.24 g kg^{-1}, but treatment with high doses (15 to 20 t ha^{-1}) increased the P content in the soil to 1.7 ± 0.27 g kg^{-1}. In spruce plots, the P content in control plots was 1.86 ± 0.27 g kg^{-1}, while in fertilized plots the P content reached 2.2 ± 0.34 g kg^{-1}.

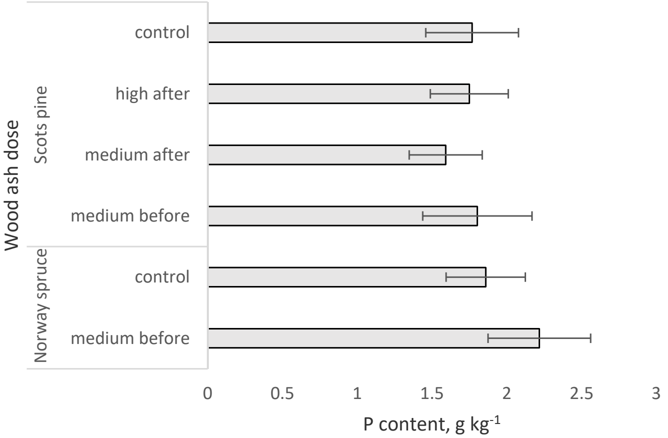

Figure 5. Content of phosphorus (P) in the soil 10 years after planting seedlings fertilized using different wood ash doses (5 to 10 t ha^{-1} = medium dose before planting seedlings, 5 to 10 t ha^{-1} = medium dose after planting seedlings, 15 to 20 t ha^{-1} = high dose after planting seedlings, and control = untreated plots, 0 t ha^{-1}; SP: Scots pine, NS: Norway spruce; the confidence interval is represented by vertical error bars).

Ten years after the application of wood ash, differences in K content between treated and untreated plots are not as marked because the control plots have the highest K content (372.5 ± 102.1 mg kg^{-1}) in comparison to other pine-dominated plots (Figure 6). However, in spruce plots, the situation is inverted because the K content in control plots had a value of 270.9 ± 71.3 mg kg^{-1}, but in fertilized plots, the K content was 299.6 ± 65.3 mg kg^{-1}. In addition, the N content in the soil 10 years after wood ash application did not differ statistically significantly between tree species or wood ash doses. The N content in the soil varied from 25.4 ± 1.8 g kg^{-1} (medium dose before planting) to 27.6 ± 2.0 g kg^{-1} (control group) in pine-dominated plots and from 26.8 ± 3.4 g kg^{-1} (control) to 27.3 ± 2.2 g kg^{-1} (fertilized) in spruce sample plots.

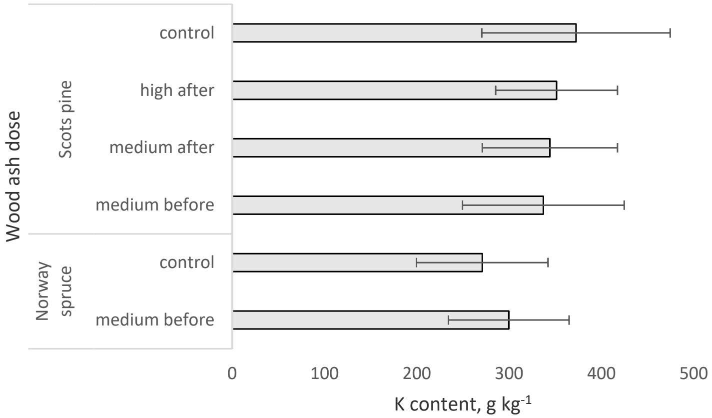

Figure 6. Content of potassium (K) in the soil 10 years after planting seedlings fertilized using different wood ash doses (5 to 10 t ha^{-1} = medium dose before planting seedlings, 5 to 10 t ha^{-1} = medium dose after planting seedlings, 15 to 20 t ha^{-1} = high doses after planting seedlings, and control = untreated plots, 0 t ha^{-1}; SP: Scots pine, NS: Norway spruce; the confidence interval is represented by vertical error bars).

3.3. *Growth of Fertilized Trees*

Fertilization effects on pine seedling morphological parameters differed between applied wood ash doses and the control plot (Table 1). After one year, the plots where wood ash was applied a year before planting had higher values than the control plot in all analyzed parameters (seedling height, aboveground biomass, root mass, and root mass and plant mass proportions). The Scots pine height in the control plots was 15.2 ± 0.3 cm. In plots where fertilization was carried out in medium doses before planting, the tree height was 15.8 ± 0.4 cm. Overall, applying fertilizers in medium doses prior to planting pine seedlings has a positive effect on tree biomass growth.

Further, the analysis was applied to pine dominated plots where fertilization was done right after planting seedlings. No significant differences ($p > 0.05$) were observed for sample plots with medium to high doses after planting compared to control fields after one year of establishment (Table 1). Applying medium doses of wood ash after planting had lower results than in control fields where the tree height was 15.2 ± 0.3 cm, but in plots with medium and high doses, the height was 14.9 ± 0.3 cm. A similar trend was observed for aboveground biomass where the control plots had higher values than the medium to high dose sample plots.

Fertilization effects on spruce growth and biomass one year after establishing the experiment between control and sample plots were analyzed where the wood ash application was carried out a year before planting. The control plot had lower values in all analyzed parameters (aboveground biomass, root mass, and root mass/plant mass proportion), and the fertilization effects on root biomass and root and plant mass proportion differed significantly between experimental plots, thus wood ash application improved seedling morphological development (Table 1).

Table 1. Pine and spruce seedling morphological parameters (mean value ± standard deviation) one year after applying wood ash in various doses (5 to 10 t ha^{-1} = medium before, 5 to 10 t ha^{-1} = medium after, 15 to 20 t ha^{-1} = high after, and 0 t ha^{-1} = control) [10].

Variant	Tree Species	Seedling Height, cm	Aboveground Biomass, g	Root Mass, g	Root Mass % From Plant Mass
Control	Scots pine	15.2 ± 0.3	3.11 ± 0.13	1.19 ± 0.05	27.7 ± 0.6
Medium before	Scots pine	15.8 ± 0.4 *	3.71 ± 0.17 *	1.43 ± 0.08 *	28.0 ± 0.8
Medium after	Scots pine	14.9 ± 0.3	2.90 ± 0.11	1.26 ± 0.06	30.2 ± 0.7
High after	Scots pine	14.9 ± 0.3	2.83 ± 0.12	1.16 ± 0.06	29.7 ± 0.7
Medium before	Norway spruce	-	0.60 ± 0.04 *	0.26 ± 0.02 *	30.5 ± 0.9 *
Control	Norway spruce	-	0.53 ± 0.03	0.23 ± 0.02	29.6 ± 0.7

* indicates statistically significant differences ($p < 0.05$) between treatments [10].

Pine growth was not significantly affected by the amount of wood ash application after the stand establishment (planting); however, some tendencies were observed after a 10-year period (Figure 7). The application of ash one year prior to the planting had a positive effect on the height growth of pines (increasing from 3.8 ± 0.4 m in the control plots to 4.4 ± 0.6 m in the fertilized plots with a medium dose before planting), and the effect was not dependent on the dose of wood ash. The lowest height of trees (3.3 ± 0.4 m) was monitored in plots where high doses of wood ash were applied after planting.

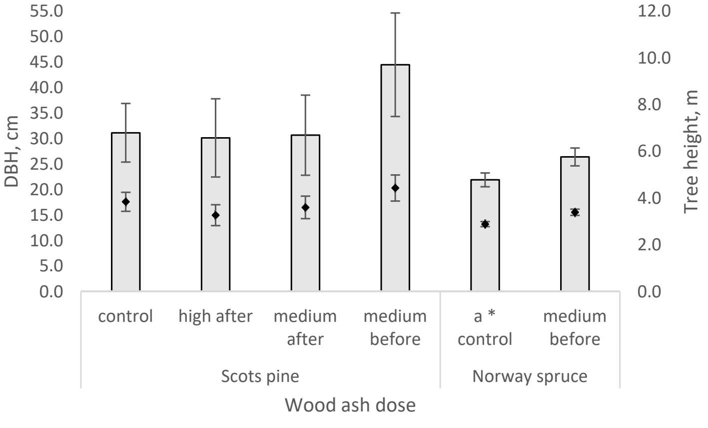

Figure 7. Mean diameter at breast height (DBH) and height of trees planted on sample plots using different wood ash fertilization doses (5 to 10 t ha^{-1} = medium dose before planting seedlings, 5 to 10 t ha^{-1} = medium dose after planting seedlings, 15 to 20 t ha^{-1} = high dose after planting seedlings, and control = untreated plots, 0 t ha^{-1}; SP: Scots pine, NS: Norway spruce) 10 years after establishment (gray bars indicate DBH, black dot denotes tree height, and the confidence interval is represented by vertical error bars, * indicates significant differences of DBH between treatments, a—indicates significant height differences between treatments).

No significant DBH differences were observed for pine plots where the application of ash was done a year after, however the application of ash one year before planting had noticeable positive effect on pine radial growth (Figure 7). The tree DBH for control fields was 31.2 ± 5.8 mm, but for plots fertilized prior to planting, the DBH was 44.5 ± 10.2 mm. Other fertilized plots exhibited rather similar results, yet lower values than those of the control fields. Overall, applying wood ash one year before planting seedlings demonstrates a noticeably higher but non-significant difference in tree height and DBH in comparison to any other sample field.

Wood ash application has significantly positive ($p < 0.05$) effects on the spruce height and diameter growth after 10 years for wood ash application in comparison to the control treatment (Figure 7). The DBH for the control plot after 10 years was 21.9 ± 1.4 mm, whereas in the fertilized sample plots, the DBH increased to 26.4 0 ± 1.8 mm. In addition, the height increment also differed significantly between sample plots. The tree height in the control plot was 2.9 ± 0.11 m, but in the fertilized plots, the height reached 3.4 ± 0.13 m.

3.4. Dead Standing Tree Parameters

Scots pine height of alive trees in sample plots ranged from 1.45 to 5.08 m, 1.3 to 6.03 m, 1.2 to 6.65 m and 1.59 to 5.41 m in control plots, plots fertilized prior planting, plots fertilized after planting with medium doses and plots fertilized with high doses, respectively. In spruce sample plots, the tree height of alive trees ranged from 1.25 to 4.43 m and 0.64 to 5.03 m in control and fertilized plots, respectively.

After 10 years, the average height of dead standing trees in spruce sample plots was 1.75 ± 0.31 m and 1.63 ± 0.1 m in control and fertilized plots, respectively. In pine dominated plots, the average height of dead standing trees was 1.46 ± 0.05 m, 1.74 ± 0.39 m in control and plots fertilized prior to planting, respectively. In pine sample plots where wood ash was applied after planting the seedlings in medium and high doses, the average tree height was 2.13 ± 0.31 m and 2.52 ± 0.57 m, respectively.

4. Discussion

Wood ash chemical content used in our experiment was average compared to chemical content used in other fertilization studies (Table 2). Soil chemical content of different wood ash application doses is summarized in Supplementary Material (Table S1).

Table 2. Chemical content of wood ash used for the experiment, %.

Elements	Wood Ash Chemical Content, % [10]	Range of Wood Ash Chemical Content in Other Studies, % [32,33]
Phosphorus (P)	0.92	0.3–1.4
Potassium (K)	2.30	1.4–4.2
Calcium (Ca)	22.0	7.4–33.1
Magnesium (Mg)	1.50	0.7–2.2
Silicon (S)	0.38	0.4–0.7
Iron (Fe)	0.39	0.3–2.1
Manganese (Mn)	0.67	0.3–1.3
Zinc (Zn)	0.11	0.0004–0.0820
Copper (Cu)	0.0054	0.0052–0.0289
Molybdenum (Mo)	0.000125	
Boron (B)	0.0158	0.0022–0.0225
Sodium (Na)	0.093	

Some of the most prominent effects of wood ash application are the decreased soil acidity, and increased mineralization rate of forest soil [8]. Some of the elements in wood ash are quickly leached into the soil, for example, content of K can be found in the soil at deeper levels shortly after the application of ash [9]. In our study, the content of K between the control and experimental plots differed substantially, as the wood ash treatment increased the soil K content up to six times in plots with high doses (Figure 2). Similar results have been reported in Finland, where wood ash fertilization already had a positive effect on potassium deficit decrease in soil one year after ash application [19]. However, the lowest K content in the soil was found for plots (excluding control plots) where the wood ash was applied a year before planting, which demonstrates the quick K infiltration process. Such an increase in K content in the soil testifies to the lack of availability of this element for trees, as presumably, K can be a limiting factor for growth in the sample fields. No significant differences were observed for spruce-dominated sample plots. After 10 years, the differences were not as pronounced, as the K content in the soil was similar in all the study plots (Figure 6).

On drained peatlands the availability of P and K limits tree growth; therefore, a significant increase in needle mass and content of both macronutrients in the soil can be observed in the wood ash fertilized stands after a long period [19]. In this experiment, after one year, the content of P increased significantly in pine-dominated plots where ash was used after planting seedlings. More wood ash resulted in a higher content (Figure 3); such results have also been reported by I. Stupak [8]. Even with an ash application with high doses, no significant differences were observed after the 10-year period (Figure 5). For spruce-dominated plots, the P content in the fertilized plots increased noticeably in comparison to the control plots, and the differences can be observed even after 10 years; however, the differences were not statistically significant.

Fertilization experiments in Nordic countries performed in Scots pine stands showed that N was the only element that demonstrated a significant effect on tree growth [34]. However, the soil in the study site was N rich; therefore, additional macronutrients for growth were not added, except the wood ash which is rich in P, K, and other micronutrient elements (Table 1). The N content in the soil at one and 10 years after the wood ash application did not statistically significantly differ between tree species or wood ash doses (Figure 4). Trees use N in their growth processes; therefore, the N content decreases after planting seedlings, but the application of wood ash initiates the decomposition of organic soil [15,18,35]. A higher content of N in the soil after fertilization with wood ash was observed, and plants use it for their metabolic processes. The obtained tree biomass could be a result of the decomposition of organic soil; however, after 10 years, these processes slow down.

Tree height and DBH 10 years after wood ash fertilization did not exhibit big differences for plots where fertilization was applied after planting the seedlings. However, in plots where fertilization was done before planting, the tree height and DBH were larger compared to the control fields (Figure 7). Height and DBH in the fertilized spruce sample plots were significantly higher than in the control fields. Applying fertilizers before planting lets the macronutrients leach into the soil, which made it easier for spruce seedlings to absorb these elements efficiently right after planting. Our findings are in accordance with previous studies, where the initial fertilization effect can significantly increase tree dimensions up to 15 years after fertilizer application [36].

High doses of wood ash fertilizer did not result in an increase in tree height or DBH for Scots pine. The study results showed rather similar average height values compared to the control plots. The height of the trees was the lowest in plots where the most wood ash was used and was the highest in fields where fertilization was done before planting the seedlings (Figure 7). Similar results have been reported in previous studies where high doses (up to 20 t ha^{-1}) of wood ash were not found to be toxic or cause significantly lower growth parameters for trees [37,38]. Therefore, a limiting factor for growth might be other nutrients that are not applied with the wood ash. Most often in studies, the addition of N is recorded as the only treatment, which can provide a significant tree biomass increase on mineral soils [6]. Furthermore, studies from Estonia, where young Scots pines growing on mineral soils were examined, showed no significant differences in the height and radial growth of trees on plots treated with 2.5 to 5 t ha^{-1} of wood ash [39], but an increase occurred after the application of 3 t ha^{-1} with 150 kg ha^{-1} of N [22]. Therefore, the role of N in the soil is an important factor. However, as mentioned, in the current study, the N content in the soil was sufficient, and no significant differences between sample plots were observed (Figure 4).

From the economic point of view, the transportation and mechanized spreading of wood ash are expensive processes. The initial fertilization is a technically simpler method than the application of fertilizer after planting and later before thinning the trees. Therefore, applying wood ash fertilizer in higher intensity prior planting could be practiced in forest management. The application of high doses of wood ash, despite their high expenses, did not improve pine growth more than in other fertilized plots. Wood ash application in different doses prior planting had a positive influence on spruce growth parameters. Soil properties increased in all plots where ash was used; thus, on peatlands, fertilization can increase P and K content even in high doses. Therefore, it is economically acceptable to use lower doses of ash but apply them before planting seedlings because spruce sample plots exhibit better results than control plots. In contrast, the application of wood ash did not cause increased decaying or mortality. The mortality could be explained with species competition, as the average height of dead standing tree was low (close to minimal tree height in the sample plot). Therefore, the analyzed wood ash does not have a significant negative influence on tree growth even with high doses.

5. Conclusions

Wood ash is a long-term fertilizer and liming material with a significant effect on P and K content in the soil of pine-dominated plots in the first year after application of wood ash. The effect of fertilization is still present in the soil even 10 years after planting the seedlings. Using fertilizers in medium doses (5 to 10 t ha^{-1}) a year prior to planting increases tree biomass in the short term and significantly increases the tree height and DBH in the long term in spruce stands compared to the control plots. In plots where the same amount of wood ash (5 to 10 t ha^{-1}) was applied after seedlings were planted, the results of the tree height and DBH are similar or lower compared to the control plots. High doses of wood ash have growth parameters that are similar to the control plots, but despite the higher content of soil macronutrient elements, high doses of wood ash do not seem to reach the overdose limit. Therefore, an economically acceptable and sustainable management option for wood ash application would be to apply medium doses of wood ash a year prior to planting rather than using high doses.

Supplementary Materials: Supplementary materials are available online at http://www.mdpi.com/2071-1050/12/22/9479/s1.

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V

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Effect of initial fertilization on 34-year increment and wood properties of Norway spruce in Latvia

Jansons Ā., Matisons R., Krišāns O., Džeriņa B., Zeps M. (2016). Effect of initial fertilization on 34-year increment and wood properties of Norway spruce in Latvia. Silva Fennica vol. 50 no. 1 article id 1346. 8 p.

Highlights

- The initial fertilization increased the productivity of *Picea abies* increasing stem volume by 17% at the age of 34 years.
- The tree-ring width was affected for up to15 years.
- The fertilization did not affect mean tree-ring density, although the latewood density was increased.

Abstract

Initial fertilisation, when the fertilizer is supplied during the plantation, is applied to improve the competitive ability of the seedlings and hence to increase their growth and productivity; however, fertilization could also alter wood properties and timber quality. In this study, the dimensions and tree-ring parameters – width, proportion of latewood, maximum and mean density, mean earlywood and latewood density – of initially fertilized (by 14, 6 and 11 g of N, P and K per seedling, respectively) Norway spruce (*Picea abies* Karst.) growing in an experimental plantation in Kalsnava, Latvia (temperate climate region) were assessed. The fertilization significantly increased the dimensions of trees in long-term (ca. 17% increase of stemwood volume). The analysis of tree-ring width suggested that the duration of the effect was ca. 15 years. The maximum and latewood density were higher for the fertilized trees only in a few years. The mean and earlywood density of tree-rings were mainly similar for both treatments. Altogether, considering the one-time application of a limited amount of fertilizer, such treatment had notable and lasting effect on Norway spruce.

Keywords tree-rings; wood density; proportion of latewood; high-frequency densitometry; legacy effect; *Picea abies*
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1 Introduction

Fertilization is one of the most effective means of increasing the productivity of stands, especially for the nutrient-demanding species (Nohrstedt 2001; Saarsalmi and Mälkönen 2001; Sicard et al. 2006). However, fertilization also alters wood properties such as cell wall thickness, affecting wood density and hence the quality of timber (Mäkinen et al. 2002; Lundgren 2004; Cao et al. 2008). The gain from the fertilization might depend on the timing and manner of its application, as the positive effect might be diminished by e.g. competition (Nohrstedt 2001) or leakage (Ingerslev 1997). Still, the positive effect of fertilization of young Norway spruce (*Picea abies* Karst.) has been shown to persist up to eight years (Tamm 1965). The initial fertilization, when a limited amount of fertilizer is applied locally, before or during the plantation, has been used to boost the early growth of seedlings/saplings of spruce and hence to improve their competitive ability (Sicard et al. 2006), which strongly affects further development of a stand (Sutton 1995; Hytönen and Jylhä 2008). However, a rather small effect of such management on the increment has been reported (Sutton 1995). The effect of the initial fertilization on tree-ring properties and hence the physical strength and/or conductive properties of wood has been studied poorly. The aim of this study was to evaluate the effect of the initial fertilization on growth and tree-ring properties of Norway spruce in Latvia. We hypothesised that fertilization had a lasting effect on tree-ring properties.

2 Materials and methods

The study was carried out in the eastern part of Latvia (56°42′N, 25°57′E). The topography of the site was flat with elevation ca. 110 m a.s.l.; soil was loamy. Climate is mild, the mean annual temperature is ca. +6 °C; the monthly mean temperature ranges from –6.4 to +17.1 °C in January and July, respectively. The growing season extends for ca. 180 days. The annual sum of precipitation is ca.700 mm; approximately half of it falls during the June–September period.

The experimental plantation of Norway spruce was established in 1982 in *Hylocomiosa* forest type (Bušs 1976), planting 4-year-old bare-rooted saplings from a local provenance, enclosed in pressed peat capsules “Brika” (Rubtsow 1979), in prepared soil with the density of 4000 trees per ha, in four blocks by 200 trees within each. Directly after the planting, each sapling received ring fertilization at 10 cm distance, 14, 6 and 11 g of N (NH_4NO_3), P (superphosphate) and K (KNO_3) per sapling (equalling 56, 24 and 44 kg ha^{-1}), respectively. The treatment was applied for the entire blocks. Chemical weed control, by sprinkling simazine (3 kg ha^{-1}) solution around the saplings, was applied twice during the first year.

In October 2013, a 5-mm increment core at the breast height was collected from 30 fertilized and 30 control undamaged dominant trees. In the laboratory, the increment cores were processed using the LignoStation wood analysis system (RinnTECH Inc., Heidelberg, Germany). A high-resolution (50 microns) wood density profile was acquired for each core using high-frequency probe (Schinker et al. 2003). For each tree-ring, 1) width, 2) latewood width, 3) mean density, density of 4) earlywood and 5) latewood and 6) maximum density was measured. The part of the tree-ring with density > 50% of the maximum density was considered as latewood. Additionally, data on height and diameter at 1.3 m height of 586 fertilized and 592 control trees were obtained from the inventory conducted in February 2012.

Considering that the outermost tree-ring(s) were sometimes lost during the sampling, the measured time series were crossdated and their quality was verified by a graphical inspection and statistically using the program COFECHA (Grissino-Mayer 2001), based on the tree-ring width. The time series, which had inconsistent dating, i.e. a match with the rest of the series both with and without a certain lag, were not used to avoid errors (Supplementary file 1, available at http://dx.doi.org/10.14214/sf.1346). The time series of the measured tree-ring parameters of 24 fertilized and 24 control trees were crossdated consistently and passed the quality check. The comparison of tree-ring parameters of the analysed and the rejected trees is shown in Supplementary file 2. The proportion of latewood width (latewood width/tree-ring width) was calculated to describe the composition of tree-rings. The similarity of mean time series of the fertilized and control trees was described by Pearson correlation and Gleichläufigkeit (GLK) coefficients (Speer 2010). The tree-ring parameters for each year, mean time series of parameters and dimensions between the fertilized and control trees were compared by a t-test.

3 Results

The initial fertilization resulted in significantly (p-value < 0.01) higher dimensions (by ca. 3% and 7% and 17% for height, diameter and volume of stem, respectively) of spruce at the age of 34 years (Fig. 1). Statistics of the crossdated time series of the tree-ring parameters are shown in Table 1. The fertilization affected wood properties of Norway spruce as shown by the significant differences in mean values of some tree-ring parameters between the fertilized and control trees. The maximum and latewood density was significantly higher and the mean proportion of latewood was significantly lower for the fertilized trees (Table 1). The annual variation amongst the tree-ring parameters differed notably, but it was similar for the fertilized and control trees, and the mean

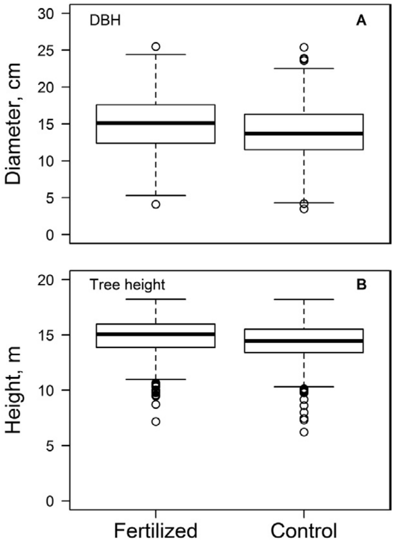

Fig. 1. Height (A) and diameter at breast height (DBH) (B) of fertilized and control Norway spruce in winter of 2012 at the age of 34 years. Line shows median, box represents 1st and 3rd quartile, whiskers mark range (not exceeding 150% of interquartile distance) and circles denote outliers of the datasets.

Table 1. Statistics of tree-ring parameters (minimum (MIN), maximum (MAX) and mean (MEAN) values and their standard deviation (SD) and coefficient of variation (VAR)) of crossdated datasets and p-values of differences (DIFF) in mean values of mean time series of tree-ring parameters of fertilized and control Norway spruce in Kalsnava, Latvia.

	MIN	MAX	MEAN	SD	VAR	DIFF
Maximum density, kg m^{-3}						
Fertilized	258	1087	832	128	0.15	< 0.01
Control	376	1061	811	116	0.14	
Mean density, kg m^{-3}						
Fertilized	170	713	489	82	0.17	0.69
Control	144	760	495	86	0.17	
Mean earlywood density, kg m^{-3}						
Fertilized	84	638	400	86	0.22	0.42
Control	39	649	399	96	0.24	
Mean latewood density, kg m^{-3}						
Fertilized	229	931	692	113	0.16	< 0.01
Control	276	881	672	108	0.16	
Tree-ring width, mm						
Fertilized	0.59	9.20	3.54	1.65	0.47	0.65
Control	0.37	9.85	3.37	1.54	0.46	
Proportion of latewood						
Fertilized	0.06	0.88	0.32	0.15	0.49	< 0.01
Control	0.05	0.94	0.37	0.16	0.45	

time series calculated for them were rather synchronous (GLK > 0.55) (Table 2). The strength of the correlation between mean time series differed for the parameters (Table 2), it was weaker for the maximum and latewood density (0.40 and 0.53, respectively), suggesting that fertilisation has affected their patterns of annual variation.

When the tree-ring parameters of fertilized and control trees were compared on the annual bases, most of the significant differences occurred in the first part of the analysed period (Fig. 2). In the beginning of the analysed period, tree-ring width was higher for the control trees for three years, but then it became significantly higher for the fertilized trees for the next eight consecutive years (up to 1998). Thus fertilization resulted in an additional 0.003 m^2 of basal area (ca. 14%) per tree at the age of 34 years. In contrast, the proportion of latewood was higher for the control trees during most of the analysed period, but the differences were significant only in 1989, 1994–1997 and in 2001 (age 10–20 years). Maximum and latewood density was higher for fertilized trees during the first 12 years of the analysed period (until 1998), but the differences were significant only in a few years (1989, 1991 and 1994 or 1995). Such differences suggested that the effect of

Table 2. Pearson correlation (r) and Gleichläufigkeit (GLK) coefficients calculated between mean time series of crossdated datasets of tree-ring parameter of fertilized and control Norway spruce in Kalsnava, Latvia for 1987–2013.

	r	GLK
Maximum density	0.40	0.77
Mean density	0.70	0.81
Earlywood density	0.66	0.69
Latewood density	0.53	0.55
Tree-ring width	0.88	0.81
Proportion of latewood	0.80	0.58

the initial fertilization lasted for ca. 15 years. Mean tree-ring density was similar for the fertilized and control trees during most of the analysed period; however, this parameter was significantly higher for the control trees in 2004 and 2006. Earlywood density was the only tree parameter, which showed no significant differences between the treatments (Fig. 2 E).

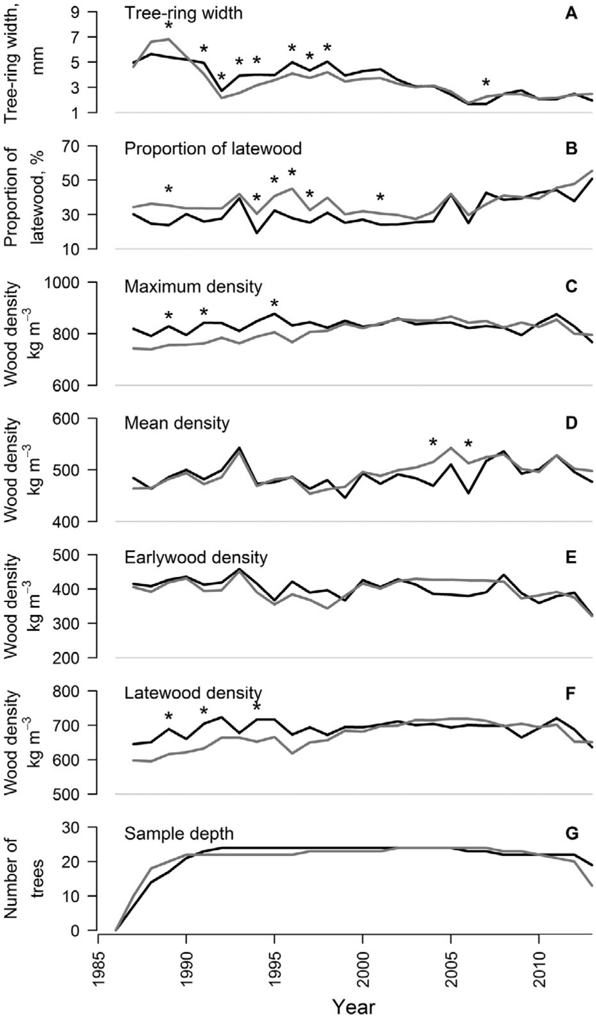

Fig. 2. Mean measurement (tree-ring width (A); proportion of latewood in tree-ring (B); maximum (C) and mean (D) wood density of tree-ring; earlywood (E) and latewood (F) density) time series and sample depth (G) of fertilized (black line) and control (grey line) Norway spruce. Asterisks indicate significance (p-value < 0.05) of differences between fertilized and control trees.

4 Discussion

The local application of initial NPK fertilization on saplings increased the dimensions of Norway spruce at the age of 34 years (Fig. 1), suggesting lasting effect of such treatment as previously observed in Central Europe (Sicard et al. 2006). The duration of the effect was evidenced by the significant differences in tree-ring width, proportion of latewood and maximum density for up to 15 years (Fig. 2 A, B). Generally, the fertilisation efficiently boosted early growth of the saplings, likely relieving them from the competition during the next years (Nilsson and Örlander 1999; Hytönen and Jylhä 2008). The reaction of Norway spruce to local fertilization (Fig. 1) was similar to that when the entire area of stand has been evenly fertilized (Nohrstedt 2001; Saarsalmi and Mälkönen 2001; Cao et al. 2008), although less nutrients were added per ha. Still, an inverse reaction to fertilization of radial increment was observed in the very beginning of the analysed period (Fig. 2 A). This might be explained by a slight over dosage of fertilizer, burdening early growth (Nohrstedt 2001; Saarsalmi and Mälkönen 2001), which, apparently, decreased after ca. 8 years, releasing the increment. Alternatively, this might be related to the differences in patterns of carbon allocation in the fertilized saplings (Alexsson and Alexsson 1986).

The differences in other tree-ring parameters during the first half of the analysed period were more consistent (Fig. 2). The fertilization decreased the proportion of latewood (Fig. 2 B) as previously observed by Mäkinen et al. (2002), likely decreasing the hardiness of heartwood (Zhang 1995). The fertilization also increased the maximum and latewood density (Fig. 2 C, F) that might be related to the differences in carbon allocation (Alexsson and Alexsson 1986). Nevertheless, this did not alter the mean tree-ring density (Fig. 2 D) as the contribution of the increased latewood density was likely countervailed by the higher proportion of the low-density earlywood. The earlywood is formed by thin-wall conducting cells; thus, its density was altered negligibly. The mean density of the fertilized trees was significantly lower compared to the control in 2004 and 2006 (Fig. 2 D) that might be related to higher environmental sensitivity of the faster growing trees (Martin-Benito et al. 2008).

5 Conclusions

The locally applied initial NPK fertilization increased the dimensions of Norway spruce at the age of 34 years and affected wood properties. The duration of the effect was ca. 15 years, likely due to the advances provided by higher rates of early growth. Nevertheless, the effect of fertilization was dual. Although fertilization improved the yields, it also increased the proportion of the softer earlywood. Hence, fertilisation did not affect mean tree-ring density; however, formation of a wider earlywood and denser latewood increased heterogeneity of wood.

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Total of 19 references.

Supplementary files

Available at http://dx.doi.org/10.14214/sf.1346

1: Details of the series checking (1_Series_checking.pdf).
2: The main statistics of the entire and crossdated datasets (2_Basic_statistics.pdf).

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Genetic control of intra-annual height growth in 6-year-old Norway spruce progenies in Latvia

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Coupling growth with periods of favourable weather conditions minimizes risks of frost damage and maximizes annual height increment. The phenology of the formation of height increment is therefore a trait related to the adaptability of trees to annual weather fluctuations. Strong genetic control of the timing of the onset and cessation of shoot elongation has been reported for Norway spruce, but little is known about its fluctuations that occur during the growth period. The strength of the genetic control of the height growth rate was assessed for young (6 years old) Norway spruce progenies originating from six open-pollinated stands from two local provenance regions. In 2010, the length of the growing period for the studied trees was ca. 60 days. Trees from the more continental provenance region, which had later onset and cessation of height growth (by ca. 2.5 days), exhibited slightly lower increments (by ca. 1%). Accordingly, the provenance region had a significant effect on height growth at the beginning and end of the growing period. Nevertheless, considerable genetic control of the growth rate was found throughout the entire growing period (particularly at the beginning and cessation, $h_a^2 \geq 0.20$), except for a week-long interval around mid-summer ($h_a^2 = 0.07$). Similarly, the coefficient of additive genetic variation suggested that breeding could be applied for the improvement of height growth intensity throughout the season. The phenotypic correlations between weekly growth rates and tree height (before growth) were mostly non-significant, suggesting varying mechanisms of control, hence possibility for simultaneous improvement of the traits by breeding.

Keywords: Height Growth Rate, Growing Period, Heritability, *Picea Abies*, Local Populations

Introduction

The effect of climatic changes on forests varies regionally and locally (Wilmking et al. 2004, Lindner et al. 2010), raising challenges for management systems worldwide (Millar et al. 2007). In Northern Europe, warming is expected to enhance forest productivity *via* an extension of vegetation period and intensification of photosynthesis (Menzel & Fabian 1999, Kolari et al. 2007), yet the increasing effects of water deficit and late/early frosts might notably counteract such improvements (Gu et al. 2008, Lindner et al. 2010, Zeps et al. 2017). To mitigate the negative effects of a changing climate, an application of the improved forest regeneration material has been advised (Lindner 2000, Bolte et al. 2009), emphasizing the importance of tree breeding for future forestry (Namkoong et al. 2012). Currently, tree breeders have focused mainly on traits related to growth capacity and stem quality (Ekberg et al. 1985, Hannerz 1993, Kroon et al. 2011), yet the traits related to adaptability appear particularly topical under shifting conditions (Hannerz 1998, Namkoong et al. 2012). Ekberg et al. (1985) showed that traits important for adaptation have higher within-population variability than growth capacity does; nevertheless, to include such traits in selection programmes, detailed information about their genetic control is necessary.

Tree height is among the main traits related to the growth capacity and productivity of stands; hence, it has been used for the selection of best genotypes (Ekberg et al. 1985, Hannerz 1993, Danusevičius & Gabrilavičius 2001, Kroon et al. 2011). The height increment of Norway spruce (*Picea abies* Karst.) is determined by the number of growth initials formed in the preceding year and their elongation (Cannell & Johnstone 1978). In addition, "free", *i.e.*, undetermined lammas growth (Cannell & Johnstone 1978, Hannerz et al. 1999), which increases the productivity of stands (Neimane et al. 2015), can occur. The height growth of Norway spruce is seasonal, and most of the annual increment is formed rapidly during the first part of summer (Owens & Molder 1984, Chmura 2006), although additional growth can occur afterwards, if conditions are favourable (Neimane et al. 2015).

The susceptibility of newly formed tissues (shoots) to environmental risks varies throughout the season, thus the coupling of periods of cell division and tissue maturation with favourable conditions is crucial for growth (Dietrichson 1969, Langvall & Löfvenius 2002, Muffler et al. 2016). Accordingly, timing and intensity of growth, which vary geographically, seasonally, and

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depending on genetic and environmental factors (Slaney et al. 2007), can be considered as adaptive traits related to height growth and productivity (Hannerz et al. 1999). Such adaptive traits have been shown to have an even greater effect on the productivity of Norway spruce over a longer term than the traits related to growth capacity (Hannerz et al. 1999, Danusevičius & Gabrilavičius 2001, Chmura 2006). In addition, traits related to the timing of growth are age-independent, hence are crucial for long-term predictions of tree responses (Hannerz et al. 1999).

The physiological activity and growth of Norway spruce are controlled primarily by photoperiod (Aronsson 1975, Partanen et al. 1998), while temperature causes certain shifts in the date of budburst and thus the initiation of the height increment (Hannerz 1999) and intensity of shoot elongation (Sarvas 1973, Danusevičius et al. 1999). In a warming climate, which also implies increasing variability in terms of weather extremes in springs (Avotniece et al. 2012), height growth can start earlier (Danusevičius et al. 1999), exposing newly formed shoots to damage from late frosts (Polle et al. 1996), particularly in the case of unsheltered trees, *e.g.*, after clear cuts (Langvall & Löfvenius 2002). The termination of height growth coincides with the initiation of cold hardening in response to the decreasing photoperiod (Dormling 1973, 1993, Beck et al. 2004). Accordingly, Danusevičius & Gabrilavičius (2001) and Kohmann & Johnsen (2007) showed that Norway spruce populations/clones with later onset and cessation of growth suffered considerably less frost damage, were more productive, and had better stem form. Such differences have been related to the requirements in terms of heat and day-length for the initiation and cessation of growth, which vary among provenances (Sarvas 1973, Danusevičius & Gabrilavičius 2001). Considering the importance of phenology for the survival and adaptation of species, strong genetic control (heritability) has been estimated for the timing of budburst and growth cessation (Hannerz 1998, 1999, Hannerz et al. 1999), implying photoperiodic and thermal regulation. Nevertheless, the annual height increment is a result of continuous elongation and maturation processes; hence, detailed information about the genetic control of intra-annual shoot elongation can be helpful for a deeper assessment of the susceptibility of growth to environmental conditions (Skrøppa 1982). Ekberg et al. (1985) reported a slight increase in the genetic variance component of the height increment with the advance of the growing period for Norway spruce in populations in Sweden. Still, insufficient information is available on the genetic control of height growth during various stages of shoot elongation for other populations (Kroon et al. 2011).

The aim of this study was to assess the intra-annual height growth pattern and the strength of genetic control (heritability) of the height growth rate (GR) of Norway spruce individuals originating from the western and eastern provenance regions of Latvia. We hypothesized that genetic control fluctuated during the height growth period, being the highest at the initiation and cessation of growth. We also hypothesized that intra-annual GRs were not correlated with tree height, but rather controlled independently.

Material and methods

Field trial and measurements

A field trial of progenies of Norway spruce plus-trees from six open-pollinated stands (Fig. 1) representing two local provenance regions (western and eastern – Gailis 1993) from the western part of the species range was studied. The naturally regenerated seedlots (stands where seeds were collected) were growing in lowland conditions (50-150 m above sea level) on dry, mesotrophic mineral (silty or sandy) soils. The studied trial was established in 2006; two-year-old, bare-rooted seedlings were planted in forest land in dry, mesotrophic mineral soil (*Hylocomiosa* stand type). Ten open-pollinated half-sib families per seedlot (20 and 40 families representing the western and eastern provenance regions, respectively – Fig. 1) were tested. Each family was represented by five (for a few families, four) randomized replications of plots containing 4 × 3 trees (3190 trees planted in total; 48-60 trees per family). The spacing of trees was 3 × 2 m.

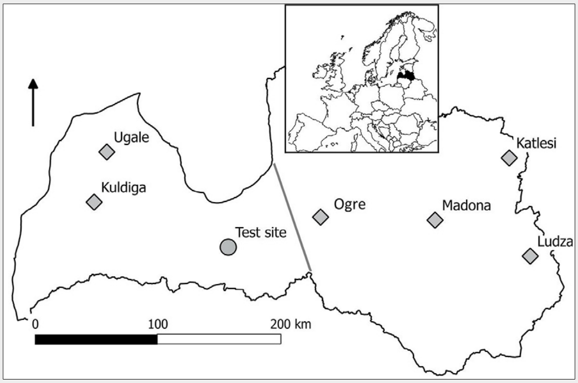

Fig. 1 - The provenances of the tested Norway spruce (squares) and location of the trial (circle). Grey line demarcate two provenance regions of Norway spruce in Latvia.

The climate in the central part of Latvia is moist continental (Lindner et al. 2010). During 2005-2015, the mean (± standard deviation) annual temperature was 7.8 ± 0.6 °C; the mean monthly temperature ranged from -3.5 ± 3.3 to 18.9 ± 1.6 °C in January and July, respectively (Harris et al. 2014). The vegetation period, when mean diurnal temperatures exceeded 5 °C, extended from mid-April to mid-October. The mean annual precipitation was 656 ± 91 mm, yet the highest monthly precipitation occurred during the summers (June-September period, ca. 75 ± 30 mm per month). The climate in the central part of Latvia is warmer (annual temperature was ca. 1.5 °C higher, and the vegetation period is longer by ca. 10 days) and drier (annual precipitation was ca. 150 mm lower) than both the western and eastern parts of the country (Harris et al. 2014). In 2010, the daily minimum temperature was constantly above 0 °C from May through September, although the beginning of May was warmer than the long-term mean for that period (Fig. 2a). The highest amount of precipitation occurred in July and August. The precipitation-free periods were up to a week long. During the growing period of 2010 (May 15-Jul 31), the mean diurnal temperature and precipitation were 17.3 ± 4.8 °C and 265 mm, respectively, which were similar to the long-term means. During the July-September period in 2009, when the primordia of the studied increment were formed, the diurnal temperature ranged 14.0-29.7 °C, with the mean value of 16.2 ± 2.6 °C; the mean 10-day precipitation sum was 17.5 ± 15.4 mm.

Within the trial, 1273 trees (430 and 843 trees representing the western and eastern provenance regions, respectively) were selected for measurements. Forked and/or damaged trees were excluded. In 2010, at the age of six years, the lengths of the main shoots of the selected trees were measured every 6-8 days during the period from May 25 to July 20 (nine surveys) with a precision of 1 mm. The measurements for all trees were done during the same day to reduce errors associated with growth. In addition, tree height after the cessation of

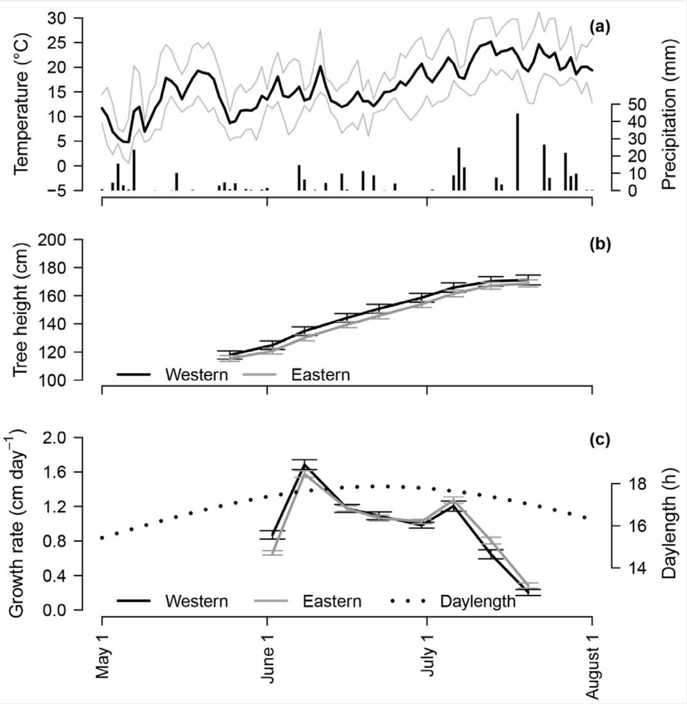

Fig. 2 - Mean (black bold line), minimum and maximum (fine grey lines) daily temperature and precipitation (bars) at the trial site (a), mean height (b), and height growth rate of studied Norway spruce originating from the western and eastern regions of Latvia, and daylength (c) during the seventh growing period in 2010. In (b) and (c), whiskers indicate 95% confidence intervals. In (c), the dates correspond to the last day of intervals, for which growth rates were calculated.

height growth (September 10) was measured.

Data analysis

For each tree, weekly GRs (mm day^{-1}) were calculated. The effect of provenance region on the timing of growth initiation (as a binomial variable), weekly GRs, total height increment, and tree height at the beginning and end of the observation period was assessed using linear mixed models (Zuur et al. 2009) of the following form (eqn. 1):

$$Y_{ijk}=\mu+P_i+(F_{j(i)})+(R_k)+Z_{ijk1}+E_{ijk} \qquad (1)$$

where Y_{ijk} was the response variable; μ was the overall mean; P_i was the fixed effect of provenance region *i*; ($F_{j(i)}$) was the random effect of family *j*, nested within provenance region *i*; (R_k) was the random effect of replication *k*; Z_{ijk1} was the value of the response parameter in the preceding period (numeric covariate, where applicable); and E_{ijk} was the residual error term. The differences in growth onset and cessation were assessed with a generalized model using a binomial distribution of the residuals and a "logit" link function. The analysis of variance of the models was used to determine the strength of the effect of provenance throughout the growing period.

For the assessment of the strength of the genetic control of intra-annual growth patterns (genetic parameters), which is based on the family and family × environment variance components, the models were transformed to (eqn. 2):

$$Y_{ijkl}=\mu+P_i+R_k+(F_j)+(F_{j(i)}\cdot R_k)+Z_{ijk1}+E_{ijkl} \qquad (2)$$

where P_i was the fixed effect of provenance region *i*; R_k was the fixed effect of replication *k*; (F_j) was the random effect of family *j*; ($F_{j(i)} \cdot R_k$) was the random effect of the family × replication interaction; Z_{ijk1} was the value of the response parameter from the preceding period (numeric covariate, where applicable); and E_{ijk} was the residual error term.

The narrow sense (additive) individual-tree heritability coefficient (h_a^2) for weekly GR, shoot length, and tree height was calculated based on family variance according to Falconer & Mackay (1996 – eqn. 3)

$$h_a^2=\frac{4\cdot\hat{\sigma}_f^2}{\hat{\sigma}_f^2+\hat{\sigma}_{fb}^2+\hat{\sigma}_e^2} \qquad (3)$$

where $\hat{\sigma}_f^2$, $\hat{\sigma}_{fb}^2$ and $\hat{\sigma}_e^2$ were the estimated variance components of family, family × replication interaction, and residual, respectively. The mean heritability at the family level (h_f^2), which describes the representability of heritability of traits by the experimental design, was calculated as (eqn. 4):

$$h_a^2=\frac{4\cdot\hat{\sigma}_f^2}{\hat{\sigma}_f^2+(\hat{\sigma}_{fb}^2/r)+(\hat{\sigma}_e^2/rn)} \qquad (4)$$

where *r* was the number of replications, and *n* was the harmonic mean of the number of observations per plot. The standard errors for h_a^2 and h_f^2 were estimated using approximation by Dickerson (1969). The coefficient of additive genetic variation (CV_a), which indicates the amount of variance in a trait that could be altered by breeding (Falconer & Mackay 1996), was calculated as follows (eqn. 5):

$$CV_a=\frac{\sqrt{\hat{\sigma}_f^2}}{\mu} \qquad (5)$$

Phenotypic Pearson's correlation analysis based on individual observations as well as on family means was used to quantify the linkage among the studied traits. Trees were used as observations, and replication was considered to be the statistical unit. The analyses were conducted in SAS using

Tab. 1 - The effect of provenance region on height growth rate during the growing period, tree height prior and after the height measurements in 2010, and genetic parameters: additive heritability coefficient (h_a^2), family mean heritability coefficient (h_f^2), and coefficient of additive genetic variation (CV_a) for these traits. (SE): standard error.

Param	Period	Effect of provenance region		Genetic parameters		
		F-value	*p*-value	h_a^2 ± SE	h_f^2	CV_a
Height growth rate	May 25-June 2	8.11	<0.01	0.73 ± 0.16	0.81	0.31
	June 2-June 8	2.66	0.11	0.48 ± 0.12	0.66	0.11
	June 8-June 16	0.01	0.93	0.07 ± 0.04	0.21	0.06
	June 16-June 22	0.22	0.66	0.24 ± 0.08	0.61	0.15
	June 22-June 30	1.35	0.26	0.28 ± 0.09	0.63	0.14
	June 30-July 6	1.55	0.21	0.31 ± 0.04	0.58	0.13
	July 6-July 13	4.42	0.03	0.61 ± 0.18	0.77	0.26
	July 13-July 20	3.97	0.04	0.20 ± 0.07	0.50	0.48
Tree height	In 2009 (before observation)	0.35	0.56	0.31 ± 0.11	0.65	0.11
	In 2010 (after observation)	0.46	0.50	0.39 ± 0.12	0.71	0.08
	Increment (shoot length)	0.27	0.65	0.30 ± 0.10	0.60	0.08

PROC MIXED, PROC LIMMIX, and PROC CORR (SAS Institute Inc. 2004).

Results

During the seventh growing period, the mean tree height increased from 114.5 ± 1.7 to 169.6 ± 2.0 cm (Fig. 2b). Trees from the western provenance region were slightly taller (ca. 1%) compared with trees from the eastern region; yet, considering the experimental design (random effects, among which family and block had the highest variance), these differences were not significant (p-value > 0.50). The same was observed for total shoot length at the end of the seventh growing period.

The onset of height growth was significantly (p-value < 0.01) earlier for trees from the western provenance as compared to the eastern provenance region, because 68.7 and 51.7% of trees had initiated shoot elongation prior to the first measurement on May 25, respectively. A significant difference (p-value < 0.05) was also observed for growth cessation, because 36.6% and 28.2% of trees from the western and eastern provenance regions had completed height increment (showed zero GR) prior to the final measurement on July 20, respectively. Accordingly, the height growth period was estimated to be ca. 60 days long (mean GR = 0.92 ± 0.02 cm day^{-1}), and it occurred when the day-length was ≥ 16.5 h (Fig. 2c).

In 2010, shoot growth was faster during the first part of the season (Fig. 2c), and 50% of the height increment were completed around the 17th of June (ca. 25 days since growth onset). Initiation and cessation of the height growth of trees from the western provenance region appeared ca. 2 days earlier. Accordingly, they showed significantly higher GR at the beginning and significantly lower GR at the cessation of the growing period. Although GR showed a decreasing tendency after June 8, a sudden improvement in growth, irrespective of provenance region, was observed during the first week of July, which coincided with a warmer and dryer period (Fig. 2a).

The effect of provenance region on GR varied during the season (Tab. 1). The strongest provenance effect was observed at the beginning and at the cessation of the growing period (before June 3 and after July 6; p-values < 0.05), while it was weak around mid-summer (p-value > 0.21). A similar seasonal pattern was observed for the additive heritability, as the highest h_a^2 coefficients (>0.30) were observed at the beginning and end of the season. Nevertheless, during the mid-part of the growing period, h_a^2 remained mostly intermediate (Falconer & Mackay 1996). The h_f^2 was generally higher (mean h_f^2 = 0.60) and less variable throughout the season. The pattern of CV_a was similar to the effect of provenance region, ranging from 0.06 to 0.48 in the middle and at the end of the growing period, respectively. The heritability for tree height and shoot length was high ($h_a^2 \geq 0.31$ and $h_f^2 \geq 0.65$), yet the genetic variation in these traits was low ($CV_a \leq 0.11$).

Significant phenotypic correlations were observed among the studied traits. The height increment of 2010 was strongly correlated with the terminal tree height (*r* = 0.56, p-value < 0.001), yet the correlation with the initial height of trees was considerably weaker, although significant (*r* = 0.10, p-value < 0.01). Similarly, the GRs throughout the season were positively correlated with the terminal tree height (mean *r* = 0.35), yet the correlations with the tree height prior to the growing period were mostly non-significant (mean *r* = 0.07 – Tab. 2). The correlations among the weekly GRs ranged from -0.14 to 0.67 and had an explicit tendency to decrease with an increasing interval between the measurements due to the autocorrelation of growth. Nevertheless, the similarity of GRs in consecutive periods was higher during

Tab. 2 - Phenotypic Pearson's correlation coefficients (the upper diagonal part) and their p-values (the lower diagonal part) among the height growth rate (GR) and tree height before and after growing period of 2010.

Parameter, Period	GR, May 25-June 2	GR, June 2-June 8	GR, June 8-June 16	GR, June 16-June 22	GR, June22-June 30	GR, June 30-July 6	GR, July6-July 13	GR, July13-July 20	Height, before	Height, after
GR, May 25-June 2	-	0.47	0.18	0.21	0.07	0.02	-0.12	-0.14	0.02	0.22
GR, June 2-June 8	<0.001	-	0.19	0.47	0.39	0.35	0.25	0.04	0.07	0.38
GR, June 8-June 16	<0.001	<0.001	-	0.21	0.54	0.47	0.39	0.15	0.03	0.31
GR, June 16-June 22	<0.001	<0.001	<0.001	-	0.51	0.48	0.41	0.16	0.04	0.34
GR, June 22-June 30	0.01	<0.001	<0.001	<0.001	-	0.67	0.63	0.29	0.04	0.41
GR, June 30-July 6	0.43	<0.001	<0.001	<0.001	<0.001	-	0.62	0.29	0.16	0.48
GR, July 6-July 13	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	-	0.42	0.16	0.45
GR, July 13-July 20	<0.001	0.14	<0.001	<0.001	<0.001	<0.001	<0.001	-	0.06	0.24
Height, before	0.58	0.01	0.34	0.17	0.13	<0.001	<0.001	0.05	-	0.88
Height, after	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	-

the second part of the growing period from June 22 to July 13. The family mean correlations (not shown) showed a highly similar pattern, although family mean GRs in the May 5-June 2 period and those later periods were negatively correlated.

Discussion

The height increment of Norway spruce (Fig. 2) was similar to that in other stands within the region (Rone 1984, Neimane et al. 2015). Although Gailis (1993) observed a faster height growth for Norway spruce from eastern Latvia, the lack of such a difference in the studied trial might be related to similar transfer distances (Fig. 1) or to the effects of a drier climate at the trial site. In addition, Norway spruce from both provenance regions had growing periods of similar length (ca. 60 days), explaining the comparable height increments.

The height growth patterns of Norway spruce from both provenance regions were similar. The highest GR was observed at the beginning of the growing period, followed by a gradual decrease (Fig. 2c) that can be related to the concentration of growth hormones after the onset of growth (Pallardy 2008). The additional lammas growth, which occurred during the June 30-July 6 period, irrespectively of provenance region, was likely triggered by the increased temperature and solar radiation following the period of cooler and more humid weather (low precipitation – Odin 1972, Cannell & Johnstone 1978, Neimane et al. 2015).

Although the pattern of height growth of the studied Norway spruce was similar (Fig. 2), the phenology differed by provenance region (Tab. 1), indicating possible local adaptations to climate, as the photoperiod was the same. The specifics of the temperature-related control mechanisms have been identified as the main cause of longitudinal differences in growth phenology of Norway spruce (Heide 1974, Hannerz 1998), even on a small geographic scale (< 300 km – Danusevičius & Persson 1998). The Norway spruce from the eastern part of Latvia, where the climate was harsher, had significantly later onset and cessation of height growth (Tab. 1), indicating better adaptation to the late frosts (Dietrichson 1969, Polle et al. 1996, Langvall & Löfvenius 2002). Accordingly, the provenance region had a stronger effect on the timing of growth onset than cessation, in contrast to the findings of Ekberg et al. (1985) in central Sweden. Apparently, in the milder climate of the Baltic States (compared with central Sweden), where summers are warmer, the late frosts mainly have had an effect on Norway spruce growth (particularly in the eastern part of Latvia – Rone 1984), thus determining a stronger genetic control of growth onset (Tab. 1). The increasing effect of late frosts on plant growth has been attributed to the warming of climate (Gu et al. 2008). Nevertheless, the genetic control of GR, as illustrated by the differences between the provenance regions (Tab. 1), was significant only during rather short periods after the onset and before the cessation of growth, likely following the probability of frosts (Avotniece et al. 2012). During the period of fastest height growth in June 8-22, GR was controlled mainly by external factors, as noted previously by Danusevičius et al. (1999), while the differences between the provenance regions were negligible (Tab. 1).

The studied traits showed high heritability, as the h_a^2 mostly exceeded 0.20 (Tab. 1), implying that they might be improved by breeding (Falconer & Mackay 1996). The reliability of the genetic parameters calculated based on the studied trait was good, as the h_f^2 (Tab. 1) prevailingly exceeded 0.50 (Falconer & Mackay 1996). Considering the additive genetic variation of the studied traits (CV_a – Tab. 1), the highest effect of breeding might be expected for the GR at the beginning and cessation of growth, as also shown by the differences among the provenance regions. Nevertheless, the heritability of GR during the middle of summer did not reach minimum values (except for the GR in the period June 8-16), suggesting that these traits might be influenced by selection at the family level. Tree height showed high h_a^2 values, yet the CV_a was low, as observed in similar studies, indicating strong genetic control but limited variability (Hannerz et al. 1999). The GR throughout the season was independent of tree height (Tab. 2), allowing for selection for productivity and adaptability. The increment of trees is autoregressive (Cook 1985), and such a pattern was observed for the intra-annual GR (Tab. 2). Nevertheless, stronger correlations between consecutive GRs during the middle compared with the cessation of the growing period might be explained by the utilization of current assimilates for growth (Axelsson & Axelsson 1986).

Conclusions

The studied provenances of Norway spruce showed similar height increments, intra-annual height growth patterns, and length of growing period, yet they differed by growth phenology, indicating adaptation to slightly different climates. Considering that phenology is a trait that is highly important for adaptation, the intensity of growth (GR) throughout the season showed strong genetic control, particularly at the beginning and cessation of the growing period, when the probability of frost was the highest. The control mechanisms of growth phenology (and intensity of height growth during the season) and growth capacity (total annual height increment) appeared to be independent, suggesting that both traits might be simultaneously improved by tree breeding to increase the productivity and sustainability of Norway spruce under a changing climate.

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Genetically Determined Differences in Annual Shoot Elongation of Young Norway Spruce

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Abstract: The annual shoot elongation could be described by a non-linear growth model to characterize differences in its dynamics among spruce genotypes, the effect of each shoot elongation phase on the total shoot length, and the genetic differences for a particular growth phase. The terminal shoot length was measured in two open-pollinated progeny trials of Norway spruce on average once per week during the ninth growing season. For the analysis, 10% of families with the longest annual increment (shoot) and 10% with the shortest were selected for each trial. The Gompertz model was fitted to individual tree data, and the mean values of its coefficients for each group of families were obtained. Family significantly ($p < 0.001$) affected total shoot length and all growth rhythm parameters, with similar trends reported in both studied sites. Heritability of Gompertz model coefficients in most cases exceeded that of the tree height. The superior10% of families started shoot elongation slightly but non-significantly earlier (all $p > 0.05$) than the other groups of families and had more intense shoot elongation (mm per day) during the entire growing season. A strong negative relation was found between the slope coefficient of the cumulative shoot elongation lines and the total height increment. The group of families with the longest increment had flatter relative shoot elongation lines, indicating relatively more evenly distributed growth within the growing season. In contrast, families with the shortest increment tended to accumulate a higher proportion of height increment during the active growth phase and reduced relative growth intensity more rapidly. The 10% of families with the largest annual increment showed superior characteristics in all shoot elongation phases, resulting in 30–40% longer shoots compared to the 10% of families with the smallest annual increment. The significant differences in Gompertz model coefficients indicate that genotypes with favorable growth patterns might be selected.

Keywords: *Picea abies*; height growth intensity; increment development; intra-annual growth dynamics; Gompertz model

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1. Introduction

Norway spruce (*Picea abies* (L.) Karst.) is the most economically important tree species in Northern Europe, constituting about one-third of the wood resources in the region [1]. The genetic improvement of spruce began in the late 1940s [2]. Since then, the selection of superior genotypes has notably improved yield and stem quality. The reported gain for best-performing families is 21–25% for height [3] and 10–25% for stem volume [2] compared to unimproved trees. Hence, breeding has led to a reduced rotation length by 5–10 years and an increased net present value by 30–400% in Norway [2] and has increased the internal rate of return by 5.2–8.3% in Sweden [4].

In Northern Europe, climate change is associated with an extended vegetation period [5] that could enhance forest productivity but is counteracted by limitations due to early/late frosts [6,7]. Therefore, tree survival and vitality, especially at a young age, largely depend on the synchronicity between the growth rhythm and climate. The growth onset and cessation are partly genetically determined [8–10], and growth timing and duration differ among provenances, families, and clones [11,12]. An application of the improved (suitable) forest regeneration material could mitigate the adverse effects of the changing climate on forestry [13,14]. Hence, traits related to adaptability have gained increased importance in tree breeding [15,16].

Superior height growth is the main trait used for genotype selection for various reasons. An early height growth provides information on the growth potential of the tested material [17–19], has reasonably high heritability [20–23], and is the earliest well-expressed trait [17]. Tree height is less affected by the environment and competition than other easily measurable characteristics, such as stem diameter [24], and is used to express site productivity through site index [25,26]. Total tree height is compounded by yearly height increments. Annual height growth variation has not been extensively studied, presumably due to the technical limitations in measurements, with some insights into inter-annual variation related to meteorological conditions (e.g., [27–29]) and seasonal dynamics of height growth (e.g., [30–32]).

The intra-annual height growth rhythm follows a sigmoid pattern that could be described using non-linear growth models, such as Gompertz's model [33]. This model's coefficients describe three growth phases (growth onset, active growth, and growth cessation), providing data to assess the growth dynamics between families of a particular species, the effect of each divided phase on the total shoot length, and the genetic (family) differences for a particular growth phase. Based on this knowledge, genotypes with desired traits (e.g., larger height increment) could be selected more precisely.

In this study, we aimed to characterize the genetically determined differences of annual shoot elongation dynamics for superior and inferior families. We hypothesized that a higher shoot length is formed for trees with an earlier growth onset and more intense elongation at the beginning of the growth period.

2. Materials and Methods

The elongation of the terminal shoot was studied in two open-pollinated progeny trials of Norway spruce (*Picea abies* (L.) Karst.) in the central region of Latvia, in Ķegums (56°46′ N, 24°48′ E) and Ozolnieki (56°43′ N, 23°46′ E) municipalities (throughout the paper "Rembate" and "Jelgava," respectively).

The Rembate trial was located on abandoned agricultural land, corresponding to the *Oxalidosa* forest type (local classification by Bušs [34]). The trial was established in 2005, planting three-year-old bare-rooted seedlings, representing a total of 104 families in three or four replications of 24 tree plots (four rows of six trees) with a spacing of 2 × 2.5 m. In total, 9485 trees were planted in the trial, with an average of 91 progenies per family.

The Jelgava trial was established in forest land on drained peat soil, corresponding to the *Myrtillosa mel*. forest type [34]. The trial was established in 2006, planting two-year-old bare-rooted seedlings, representing a total of 60 families in three or four replications of 12 tree plots (three rows of four trees) with a spacing of 3 × 2 m. In total, 2736 trees were planted in the trial, with an average of 46 progenies per family. Each trial consisted of a different set of open-pollinated families of plus-trees selected across Latvia.

In both trials, measurements of the current year terminal shoot length were done during the ninth growing season (age from seed). In May, trials were monitored every second day to determine the time of budburst, that is, when about half of the trial trees had started bud flush. The shoot length was measured by a single person once per week for randomly selected trees, omitting trees with damages (browsed, pest infected, or lost top shoot). Measurements were stopped when about half of the trial trees had a weekly increment less than 3 mm. The monitored period was 61 days in Rembate and 59 days in Jelgava. In total, 1766 trees from 88 families in Rembate (on average, 20 trees per family) and 1239 trees from 59 families in Jelgava (on average, 21 trees per family) were measured.

In each trial, families were ranked according to their mean shoot length. We selected 10% of the superior and 10% of inferior families, considering the number of families per trial and the commonly used selection intensity in tree breeding practices in Latvia. The divided groups of families are referred to as "superior10%", "inferior10%", and "rest" throughout the paper. The coefficients of the Gompertz model (1) were calculated for each tree. The Gompertz model fits the sigmoidal curve of the annual shoot elongation and is commonly used in biological studies [33]. The model divides the growth curve into three phases: lag, exponential, and stationary growth. The model coefficient α represents the maximal value at the stationary phase (upper asymptote), coefficient β describes the length of the lag phase, and coefficient k is the growth rate (affects the slope) at the exponential growth phase [33]. Trees that had outlier values of Gompertz model coefficients were omitted from further analysis (seven trees in Rembate and 17 trees in Jelgava). For each group of families, the arithmetic mean coefficients of the model, mean height increment, mean shoot elongation, and cumulative shoot elongation were calculated:

$$f(SL) = \propto \exp(-\beta \exp(-\mathrm{k}A)) \tag{1}$$

where SL is the shoot length, α is the asymptote parameter, β is the displacement parameter, k is the maximum relative intensity, and A the day of measurements.

The estimates of narrow-sense individual-tree heritability (h^2) for the Gompertz model coefficients (α, β, and k) and tree variables (tree height and total shoot length) were calculated as:

$$h^2 = \frac{4 \times \hat{\sigma}_f^2}{\hat{\sigma}_f^2 + \hat{\sigma}_{bf}^2 + \hat{\sigma}_e^2} \tag{2}$$

where $\hat{\sigma}_f^2$, $\hat{\sigma}_{bf}^2$, and $\hat{\sigma}_e^2$ are the estimated variance components of the family, family × replication interaction, and the residual, respectively.

The coefficients of additive genetic variation (CV_a) for the Gompertz model coefficients (α, β, and k) and tree variables (tree height and total shoot length) were estimated as:

$$CV_a = \sqrt{4\hat{\sigma}_f^2} \times \frac{100}{\overline{x}} \tag{3}$$

where $\hat{\sigma}_f^2$ is the estimated variance components of the family and $\overline{x}$ is the phenotypic mean.

Linear mixed-effects models (LME) as implemented in R 4.0.3 [35] packages lme4 [36] and lmerTest [37] were used to test the influence of the group of families (superior10%, inferior10%, and rest) on the Gompertz model coefficients (α, β, and k) and tree variables (tree height and total shoot length). As there were multiple trees per plot and multiple plots per family, family and plot identification numbers (ID) were used as nested random factors in the models:

$$y_{ijk} = \mu + P_i + \left(p_{jk}\right) + \varepsilon_{ijk} \tag{4}$$

where y_{ijk} is the tree level response variable of the kth tree from the ith group of families in the kth plot, nested within the jth replication, P_i is the fixed effect of the ith site, p_{jk} is the random effect (intercept) of the kth plot within the family, and ε_{ijk} is the experimental error.

Residuals plots were used to assess heteroscedasticity. Problems with heteroscedasticity were found for models of coefficients β and k, so those variables were log-transformed. A comparison among the estimated marginal means as implemented in R package emmeans [38] was used to compare levels of factor group of families (superior10%, inferior10%, and rest) if the LME showed a significant effect. In the lmerTest models where the influences of family on coefficients and tree variables were tested, only the sample plot ID was used as a random factor.

The Spearman correlation coefficients between Gompertz model coefficients (α, β, and k) and total shoot length were calculated. A correlation analysis was conducted using two data levels: (1) all data for the Rembate and Jelgava trials separately, and (2) the mean family values for the Rembate and Jelgava trials separately.

3. Results

The measurements of the terminal shoot length were successfully fitted to the Gompertz model, obtaining coefficients describing shoot elongation (Figure 1A). In both trials, the family had a significant effect (all $p < 0.001$) on total shoot length and on the coefficients of growth onset, cessation, and maximal relative growth intensity.

Shoot elongation patterns showed differences among the divided groups of families (Table 1), and the trend was consistent in both studied sites. The maximum value of the shoot length (described by model coefficient α) differed significantly ($p < 0.001$) between the groups of families in both trials. The difference in total shoot length between the superior10% (largest annual increment) and inferior10% (lowest annual increment) families was 42% (624 ± 26 vs. 362 ± 21 mm) in Rembate and 29% (662 ± 26 vs. 468 ± 33 mm) in Jelgava.

Table 1. Gompertz model coefficients, total shoot length (±95% confidence level), and growth intensity of families in Rembate and Jelgava. The groups of 10% of the superior, 10% of the inferior, and the rest families were divided according to their mean shoot length. α—asymptote parameter; β—displacement parameter; k—maximum relative intensity; SL—shoot length; GI–growth intensity; R—Rembate; J—Jelgava. Different letters within the same column and trial indicate significant ($p < 0.05$) difference between the groups.

Trial	Group of Families	Gompertz Model Coefficients			SL, mm	GI, mm day^{-1}
		α	β	k		
R	superior10%	652 ± 29 a	2.54 ± 0.12 a	0.071 ± 0.002 a	624 ± 26 a	10.2 ± 0.4 a
	rest	518 ± 10 b	2.83 ± 0.05 a	0.079 ± 0.001 b	499 ± 9 b	8.1 ± 0.1 b
	inferior10%	373 ± 21 c	2.93 ± 0.14 a	0.087 ± 0.002 c	362 ± 21 c	5.9 ± 0.3 c
J	superior10%	754 ± 36 a	4.15 ± 0.14 a	0.057 ± 0.002 a	662 ± 26 a	11.3 ± 0.4 a
	rest	636 ± 13 b	4.21 ± 0.08 a	0.065 ± 0.001 b	558 ± 10 b	9.4 ± 0.2 b
	inferior10%	520 ± 41 b	4.59 ± 0.31 a	0.073 ± 0.004 c	468 ± 33 c	7.8 ± 0.6 c

In both trials, the model coefficient β (describing the lag of the growth onset) was slightly but non-significantly lower (all $p > 0.05$) for the superior10% families, indicating a similar timing of the start of the height increment as those of other groups of families (Table 1).

Corresponding to differences in total height increment, groups of superior10% families had higher (all $p < 0.001$) mean growth intensity than groups of rest and inferior10% of families. Shoot elongation (mm per day) of the superior10% families was consistently higher in comparison to the inferior10% families during the entire growing season (Figure 1C). Moreover, shoot elongation of the superior10% families peaked slightly later. For inferior10% families, the peak of elongation was delayed one day in Rembate and four days in Jelgava (Figure 1C).

At the peak of the maximal shoot growth (7th of June in Rembate and 16th of June in Jelgava), the superior10% families had formed 39% and 40% of the total shoot length, respectively. For the inferior10% families, 36% of the total shoot length in Rembate and 38% in Jelgava were formed at the peak of the maximal shoot growth.

The slope of cumulative shoot elongation lines (described by the model coefficient k), however, had an opposite trend to growth intensity (Table 1), with a strong negative relation between the slope coefficient and the total height increment at the individual tree level ($r = -0.71$ in Rembate and $r = -0.66$ in Jelgava, both $p < 0.001$). This relation remained at the family mean level ($r = -0.75$ in Rembate and $r = -0.61$ in Jelgava, both $p < 0.001$), and the slope of the cumulative shoot elongation lines was flatter for groups with a larger annual increment (Figure 1B).

The heritability coefficient (h^2) for tree height was 0.24 ± 0.10 (± standard error) in Rembate and 0.31 ± 0.09 (± standard error) in Jelgava (Table 2). The heritability coefficients of the distinct growth phases (described by Gompertz model coefficients) were higher in the Rembate trial than in the Jelgava trial. They were higher for relative growth intensity during the active growth phase (coefficient k) and lag of the growth onset (coefficient β) than for the maximal value of shoot length. The coefficient of additive genetic variance (CV_a) was the highest for β, reaching 17% in both trials. All other analyzed growth parameters (coefficients of Gompertz model, tree height, and total shoot length) had an additive genetic variance of 4–8% (Table 2).

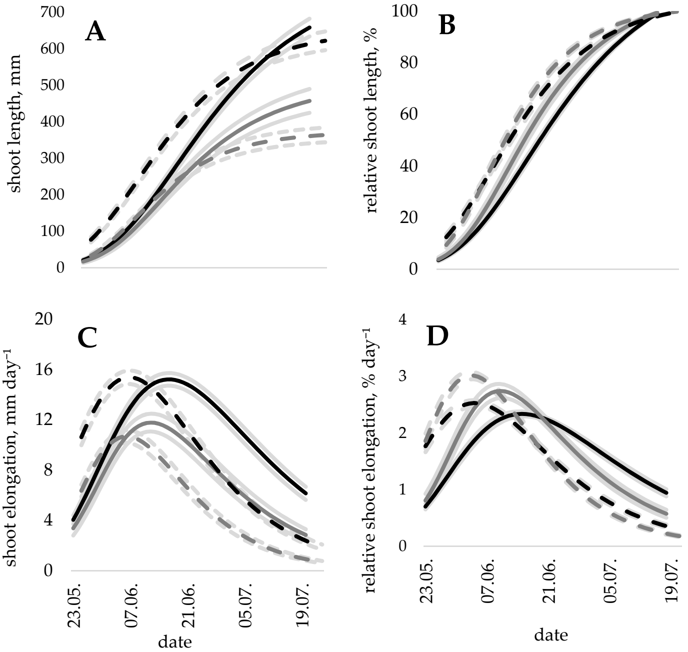

Figure 1. (**A**) the total shoot length and (**B**) relative shoot length, (**C**) shoot elongation and (**D**) relative shoot elongation (±95% confidence level indicated by shadow along the curves) for 10% of fastest-growing (black lines) and 10% of slowest-growing (grey lines) families in Rembate (dashed lines) and Jelgava (solid lines) trials.

Table 2. Heritability coefficient (h^2) and coefficient of additive genetic variance (CV_a) for Gompertz model coefficients (α, β, and k) and tree variables (tree height and total shoot length) in the Rembate and Jelgava trials. SE—standard error; α–asymptote parameter; β—displacement parameter; k—maximum relative intensity.

Trial	Parameters	h^2 ± SE	CV_a, %
Rembate	α	0.21 ± 0.011	8
	β	0.97 ± 0.08	17
	k	0.30 ± 0.10	5
	Tree height	0.24 ± 0.10	7
	Shoot length	0.23 ± 0.11	8
Jelgava	α	0.03 ± 0.05	6
	β	0.16 ± 0.06	17
	k	0.19 ± 0.08	7
	Tree height	0.31 ± 0.09	7
	Shoot length	0.08 ± 0.10	4

4. Discussion

In this study, individual tree data on current year shoot elongation were fitted to the Gompertz model, and the mean parameters of 10% of families with the largest annual increment, 10% of families with the shortest annual increment, and the rest of families were assessed. During the growing season, height growth is not constant, and the obtained results reveal genetic differences (among families) for the biological shoot elongation trend with slow growth during the elongation onset and cessation and high growth intensity in the middle of the growth period [28,39].

Trees in the studied trials started growth at a distinct time, and trees in the Rembate trial had earlier growth onset than trees in Jelgava. The growth rhythm parameters are controlled by environmental factors [40–43]. However, considering the small distance between the sites (about 70 km), the lag in growth onset could be related to differences in microclimatic conditions [44] or the represented set of families rather than by meteorological conditions.

Within each trial, groups of families followed similar shoot elongation patterns, and significant differences in growth rhythm were found between groups of families. The time lag of the growth onset was non-significantly different between groups of families, indicating no effect of the earlier start of shoot elongation on total shoot length. Similarly, a weak relation or no relation between growth onset and annual shoot length was found in earlier findings on Norway spruce [31,45]. The estimated Gompertz parameter on growth onset characterizes the time lag between the start of the shoot elongation to the curve inflection point for active growth. Earlier bud flush is typically related to frost damages [46]. However, trees with earlier shoot elongation are not necessarily exposed to frost damage, since the pattern of height growth intensity after the budburst varies between the families. The small difference in the time lag of growth onset between families could also be related to the origin of the parent material. All tested material was from the open-pollinated families of locally selected plus-trees, which usually adapt well to climate due to their earlier start of growth and avoidance of frost damage [47].

As expected, superior10% families showed faster shoot elongation during the beginning of the growing season, probably associated with a high proportion of the remobilized stored nutrients during the bud break [48,49]. However, superior families also had relatively more evenly distributed growth within the growing season in comparison to families with a lower annual increment that tended to accumulate a higher proportion of height increment during the active growth phase. Accordingly, superior families maintained higher relative growth intensity during the second half of the growing season, while inferior10% families reduced their relative growth intensity more rapidly.

We found no differences in the shoot elongation period, although it has been found to be moderately related to annual shoot length [45] and the primary factor explaining 80% of shoot length variation among provenances in Norway spruce provenance trials [30]. In accordance with our obtained results, the growth rate was found to determine shoot length for Latvian provenances planted in provenance trials in Norway [30]. Similarly, the growth rate in the middle of the active elongation period is shown to be strongly related to the annual shoot length [45]. However, the active growth period's slope coefficient was negatively linked with shoot length (Figure 1B), indicating the greater importance of the active growth period for families with shorter annual increments. Similar results are observed among spruce provenances, and those with shorter annual increment had higher (above mean) rates of elongation [30]. During the active shoot elongation phase, growth is determined more by the environment than by genetics [32]; therefore, slow-growing families are more prone to influences from yearly meteorological conditions.

Observations at the individual tree level have also shown differences in growth rhythm related to tree status within stand [28]. Within the same stand, dominant spruce trees have a more even elongation rate during the growing season, while suppressed trees have delayed growth initiation and a high elongation rate [28]. Our results revealed a similar pattern, as tree height could be used as an indicator for tree status within a trial and is directly affected by shoot length. However, while a correlation between tree height and total shoot length was strong in Rembate, in Jelgava this link was rather weak, indicating the effect of other factors (e.g., initial stage of a competition) on tree growth. Spruce at a young age might form proleptic shoots, and the relation between tree height and annual shoot length might be diminished, as this additional shoot increment adds to the total tree height. The studied trials are established on forest types likely to promote the occurrence of proleptic shoots [50]. However, we did observe a sudden increase in shoot elongation during the observed period.

Most of the Gompertz model coefficients had reasonably high h^2, although differences in the coefficient values between groups of families were relatively small. The estimated heritability of Gompertz model coefficients in most cases exceeded that of tree height. Our obtained heritability for tree height was similar between the trials and is within a range of those calculated for a height of *Pinus pinaster* at the age of 10 years [51] and for *Pinus sylvestris* at the age of 11 to 20 years [52]. A considerably higher heritability of the upper asymptotic height and maximum growth rate was found in a study of *Picea glauca* during the first growing season [17], but it represents free growth as opposed to the predetermined growth analyzed in the current study. The estimated heritability coefficients of growth rhythm parameters had rather different levels between the trials. A large variation in narrow-sense heritability and genetic coefficient of variation for growth parameters between trials was also found in other studies [8,53], indicating the effect of trial conditions and the included set of families on parameters describing the genetic determination of the particular traits.

Overall, the more vigorous families started to grow earlier, grew faster and at a more stable rate, and ceased growth later. The parameters of the growth curves presented in this study are based on the growth curve fitted for one season and thus require some caution. First, the cumulative shoot elongation's seasonal dynamic varies by year [28], as the annual shoot elongation is susceptible to short-term environmental variation [54]. Second, genetic correlations among height growth traits are not stable and change with tree development, at least at a young age [31,55]. Therefore, the obtained relationships among growth parameters should be verified over a longer time span and, preferably, a larger set of genotypes. The obtained results, however, offer valuable insights into genetic differences in growth dynamics that could be applicable to the selection of genotypes with superior height growth.

5. Conclusions

The juvenile shoot elongation patterns for Norway spruce families are genetically determined, and families with larger shoot lengths have higher growth intensity at the active growth phase that remains higher later in the growing season than that of families with shorter annual increments. The significant differences in Gompertz model coefficients indicate that genotypes with favorable growth patterns might be selected to improve the volume production and adaption to climate change.

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