EIROPAS DIŽSKĀBARŽA (*FAGUS SYLVATICA* L.) KOKAUDŽU ATJAUNOŠANĀS UN AUGŠANA LATVIJĀ

Līga Jansone

REGENERATION AND GROWTH OF EUROPEAN BEECH (*FAGUS SYLVATICA* L.) STANDS IN LATVIA

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

LATVIJAS LAUKSAIMNIECĪBAS UNIVERSITĀTE
LATVIA UNIVERSITY OF LIFE SCIENCES AND TECHNOLOGIES

Mg.silv. **LĪGA JANSONE**

EIROPAS DIŽSKĀBARŽA (*FAGUS SYLVATICA* L.) KOKAUDŽU ATJAUNOŠANĀS UN AUGŠANA LATVIJĀ

REGENERATION AND GROWTH OF EUROPEAN BEECH (FAGUS SYLVATICA L.) STANDS IN LATVIA

PROMOCIJAS DARBS
mežzinātņu doktora zinātniskā grāda iegūšanai

DOCTORAL THESIS
for acquiring the Doctor's degree of Forest sciences

Salaspils 2019

ANOTĀCIJA

Eiropas dižskābardis ir pret vētru ietekmi noturīga, ēncietīga, pārnadžu maz bojāta un daudzviet arī komerciāli nozīmīga koku suga. Latvija atrodas ārpus šīs koku sugas dabiskās izplatības areāla, taču klimata pārmaiņu prognozes liecina, ka jau šī gadsimta laikā visa mūsu valsts teritorija būs tā augšanai piemērota. Faktisko dižskābarža izplatību Latvijā noteiks galvenokārt mežsaimnieciski lēmumi. To pieņemšanai nepieciešama pamatojoša informācija, tādēļ promocijas darba mērķis ir novērtēt Eiropas dižskābarža audzēšanas potenciālu Latvijā klimata pārmaiņu kontekstā. Promocijas darba ietvaros vērtētas lielākā daļa mūsu valsts teritorijā esošo šīs koku sugas mežaudžu.

Konstatēts, ka notikusi sekmīga dižskābarža adaptācija Latvijā: mūsu valsts rietumu daļā dižskābarža dabiskā atjaunošanās ir sekmīga gan pēc vienlaidus atjaunošanas cirtes, līdz 50 m no meža malas, gan zem audzes vainagu klāja arī tādos gaismas apstākļos, kas nav piemēroti citām koku sugām. Dižskābarža gadskārtu platumu ietekmē galvenokārt ar mitruma deficītu saistīti klimatiskie rādītāji (temperatūra, nokrišņi) vasarā un rudens sākumā. Ņemot vērā klimata izmaiņu prognozes, šīs koku sugas audžu ierīkošanai būtiski izvēlēties teritorijas ar stabilu un pietiekamu augsnes mitruma nodrošinājumu. Izveidotie dižskābarža augšanas gaitas vienādojumi un dati no parauglaukumiem mežaudzēs liecina, ka šīs koku sugas otrās paaudzes koku ātraudzība Latvijā ir lielāka nekā pirmajai paaudzei; tā ir arī lielāka nekā Zviedrijas dienvidu daļā un salīdzināma ar citām saimnieciski nozīmīgām koku sugām Latvijā.

Latvijas rietumu daļā iespējams izveidot ražīgas dižskābarža audzes, izmantojot jau esošajās šīs koku sugas audzēs Latvijā ievāktu sēklu materiālu. Piemērotākais sēklu avots ir šī promocijas darba izstrādes ietvaros atlasītie pluskoki. Nepieciešams izveidot sēklu plantācijas stabilas sēklu bāzes nodrošināšanai nākotnē. Rekomendējama plašāku provenienču izmēģinājumu ierīkošana, ietverot tajos materiālu arī no areāla daļām, kur raksturīgs augsts mitruma deficīts vasaras periodā, kā arī plašākas eksperimentālās pārbaudes, vērtējot šīs koku sugas provenienču un atsevišķu genotipu piemērotību Latvijas austrumu daļas klimatiskajiem apstākļiem.

ABSTRACT

European beech is resistant to wind damages, shade-tolerant, in many countries commercially significant and it rarely affected by cervids. Currently Latvia is outside of its natural distribution areal. However, according to the prognosis of climate change, already in this century all territory of our country will be suitable for beech. Its actual spread in Latvia will primarily be determined by forest management decisions. Such decisions require scientific information, therefore aim of the thesis work is assess the growth potential of European beech in Latvia in context of climate change. Thesis are based on data from majority of known beech-dominated forest stands in Latvia.

Adaptation of European beech in Latvia has been successful: regeneration of it is successful in western part of our country both in open area (clearcut) up to 50 m from edge of mature stand and under canopy, even in light conditions that are not suitable for regeneration of other tree species. Width of annual rings for European beech is mainly affected by climatic factors related to water deficit (temperature, precipitation) during summer and beginning of autumn. It causes reduction or even briefly stops radial increment until the complete replenishment of stem water storage. Considering predicted climate change it is important to plant European beech only in areas with sufficient soil moisture availability. Growth models of European beech, developed as part of this thesis work, and data from sample plots in forest stands, indicate that increment of second generation of this tree species in Latvia is higher than that of first generation; it is also higher than in southern part of Sweden and comparable to that of other commercially important tree species in Latvia.

Productive European beech stands can be established in western part of Latvia, using seed material from local seed sources, specifically – from plus-trees selected as part of research for this thesis. Simultaneously establishment of seed orchards to ensure secure seed supply is necessary. Continuous experimental work, establishing comprehensive provenance trials, including reproductive material also from the parts of European beech natural distribution range with high water deficit during summer and testing suitability of provenances and specific genotypes for eastern Latvia, is sensible.

SATURS / *CONTENTS*

PUBLIKĀCIJU SARAKSTS / *LIST OF PUBLICATIONS*

Promocijas darba galvenie rezultāti apkopoti 8 publikācijās:
The main results of thesis are compiled in 8 publications:

I.   **Puriņa, L.**, Neimane, U., Džeriņa, B., & Jansons, Ā. (2013) Eiropas dižskābarža (*Fagus sylvatica* L.) atjaunošanos ietekmējošie faktori. Mežzinātne, 27(60), 67–76.

II.   **Jansone, L.**, Matisons, R., & Adamovičs, A. (2019) Light requirements of regeneration of European beech at its northeasternmost stand in Europe – a case study in Latvia. Iesniegts Forestry Studies.

III.   **Puriņa, L.**, Matisons, R., Jansons, Ā., & Šēnhofa, S. (2016) Survival of European beech in the central part of Latvia 33 years since the plantation. Silva Fennica, 50(4), article id 1656, doi: 10.14214/sf.1656.

IV.   **Purina, L.**, Adamovics, A., Katrevics, J., Katrevica, Z., & Dzerina, B. (2016) Growth of *Fagus sylvatica* in young mixed stand: case study in central Latvia. Research for Rural Development, 2, 21–26.

V.   Matisons, R., Šņepsts, G., **Puriņa, L.**, Donis, J., & Jansons, Ā. (2018) Dominant height growth of European beech at the northeasternmost stands in Europe. Silva Fennica, 52(1), article id 7818, doi: 10.14214/sf.7818.

VI.   Krišāns, O., **Puriņa, L.**, Mesters, D., Kāpostiņš, R., Rieksts-Riekstiņš, J., & Jansons, Ā. (2016) Intra-annual radial growth of European beech – a case study in north easternmost stand in Europe. Forestry Studies | Metsanduslikud Uurimused, 65, 34–42. ISSN 14069954.

VII.   Matisons, R., **Puriņa, L.**, Adamovičs, A., Robalte, L., & Jansons, Ā. (2017) European beech in its northeasternmost stands in Europe: Varying climate-growth relationships among generations and diameter classes. Dendrohronologia. 45, 123–131, doi: 10.1016/j.dendro.2017.08.004.

VIII.   Jansons, Ā., Matisons, R., **Puriņa, L.**, Neimane, U., & Jansons, J. (2015) Relationships between climatic variables and tree-ring width of European beech and European larch growing outside of their natural distribution area. Silva Fennica, 49(1), article id 1255, doi: 10.14214/sf.1255.

Autoru ieguldījums / *The contribution of the authors*

	I	II	III	IV	V	VI	VII	VIII
Ideja / *Original idea*	**LJ***, AJ	AJ	AJ	AJ, **LJ***	AJ	AJ, OK	AJ, RM	AJ, RM
Pētījuma plāns / *Study design*	AJ, **LJ***	AJ, RM	AJ	AJ, **LJ***	AJ, RM	AJ, OK	AJ, **LJ***, RM	AJ, **LJ***, RM
Datu ievākšana / *Data collection*	BJ**, **LJ***	AA, **LJ***	**LJ***, SS	AA, BJ**, JK, **LJ***, ZK	GS, **LJ***	DM, JR, **LJ***, OK, RK	AA, **LJ***, LR	JJ, **LJ***, UN
Datu analīze / *Data analysis*	**LJ***, UN	**LJ***, RM	**LJ***, RM	**LJ***	GS, JD, RM	**LJ***, OK	**LJ***, RM	**LJ***, RM
Manuskripta sagatavošana / *Manuscript preparation*	**LJ***	**LJ***, RM	**LJ***, RM	**LJ***	**LJ***, RM	**LJ***, OK	**LJ***, RM	**LJ***, RM

AA – Andis Adamovics, AJ – Aris Jansons, BJ – Baiba Jansone, DM – Davis Mesters, GS – Guntars Snepsts, JD – Janis Donis, JJ – Janis Jansons, JK – Juris Katrevics, JR – Juris Rieksts-Riekstins, **LJ – Līga Jansone**, LR – Linda Robalte, OK – Oskars Krisans, RK – Rolands Kapostins, RM – Roberts Matisons, SS – Silva Senhofa, UN – Una Neimane, ZK – Zaiga Katrevica.

* mainīts uzvārds no Puriņa uz Jansone / *changed the last name from Purina to Jansone*;
** mainīts uzvārds no Džeriņa uz Jansone / *changed the last name from Dzerina to Jansone*.

1. DARBA VISPĀRĪGS RAKSTUROJUMS

1.1. Tēmas aktualitāte

Eiropas dižskābardis (*Fagus sylvatica* L.) ir izplatītākā koku suga lapu koku mežos Centrāleiropā. Šobrīd tā areāls ziemeļos plešas līdz Vācijas ziemeļdaļai, Dānijai, Zviedrijas dienviddaļai, Polijai. Austrumu robeža sasniedz Ukrainu, Moldāviju, Bulgāriju. Areāla dienvidu daļa ietver Balkānu pussalu, Apenīnu kalnus, Sicīliju, Spāniju (Leugnerová, 2007). Latvija atrodas ārpus dižskābarža dabiskās izplatības areāla, un mūsu valstī šī koku suga sastopama izolētās platībās. Tomēr tiek prognozēts, ka jau līdz 21. gadsimta beigām dažādu sugu izplatības areāli var būtiski mainīties klimata pārmaiņu dēļ (Hickler *et al.*, 2012). Eiropas teritorijā sagaidāma galvenokārt sugu pārvietošanās ziemeļu virzienā (Walther *et al.*, 2002; Kullman, 2008). Prognozes liecina, ka Eiropas dižskābarža augšanai piemērotais areāls līdz gadsimta vidum ietvers arī visu Latvijas un Igaunijas teritoriju (Kramer *et al.*, 2010). Tomēr šīs koku sugas faktisko izplatību noteiks saimnieciskā darbība. Dabiski dižskābardis izplatās lēni, jo tā sēklas ir salīdzinoši smagas. Sēklas izplata putni un peļveidīgie grauzēji; pētījumi liecina, ka vidējais sēklu izplatīšanās attālums ir aptuveni 30 m no sēklu koka, tālākā distancē izplatās nenozīmīga daļa no visām sēklām (Dobrovolný, & Tesař, 2010). Latvijas rietumu daļā veikts pētījums liecina, ka dižskābarža dabiskās izplatīšanās ātrums varētu būt 3.4 m gadā (Sabule L., 2009). Sēklu ražas gadi dižskābardim ir reti un neregulāri, literatūras avotos norādīti dažādi intervāli. Izteikti bagātīga raža sagaidāma apmēram ik pēc četriem līdz sešiem gadiem (Peňa *et al.*, 2010), pēc citu autoru datiem – ik pēc sešiem līdz deviņiem gadiem (Giesecke *et al.*, 2007; Vanders, 1960a). Dižskābardis labi apputeksnējas tikai svešapputes ceļā, tā putekšņi ir salīdzinoši smagi un lido nelielu attālumu, tāpēc gados ar mazāk bagātīgu ziedēšanu svešapputе ir apgrūtināta, kā rezultātā šādos gados lielākā daļa sēklu ir tukšas (Vanders, 1960a). Pēc bagātīga sēklu ražas gada paaugā sastopami pat 350 000 un vairāk dižskābaržu sējeņi uz hektāra, no kuriem pēc gada ir izdzīvojusi aptuveni puse (Vanders, 1957). Dižskābarža izplatīšanos ap sēklu avotiem ietekmē arī intensīva jaunaudžu kopšana – ja nogabalā kā mērķa suga nav noteikts dižskābardis, tad, veicot jaunaudzes kopšanu, tiks atstāti tikai atsevišķi eksemplāri, nevis saglabāti visi dzīvotspējīgie dižskābarži.

Pētījumi Eiropā liecina, ka dižskābardis ir pret vētru ietekmi noturīga, ēncietīga, pārnadžu maz bojāta un daudzviet arī komerciāli nozīmīga koku suga. Ņemot vērā šīs īpašības, kā arī sagaidāmo klimata izmaiņu pozitīvo ietekmi uz dižskābardi vairākumā Baltijas jūras reģiona (Hanewinkel *et al.*, 2013), jau šobrīd atsevišķās valstīs tiek veicināta tā plašāka izmantošana. Ir būtiski detalizēti raksturot dižskābarža atjaunošanos un augšanu ietekmējošos faktorus Latvijā, radot pamatu šīs koku sugas plašākai pielietošanai mežsaimniecībā. Dižskābarža koksne tiek uzskatīta par vērtīgu, tā ir dekoratīva, un tiek izmantota iekštelpu

apdarē, durvīm, mēbelēm, parketam, kā arī finiera un papīra ražošanā (von Wühlisch, 2008; Born, 2011). Koksnes kvalitāte ir atkarīga no stumbra īpašībām, audzes kopējās kvalitātes, augsnes īpašībām un atbilstošas audzes apsaimniekošanas (Poljanec, & Kadunc, 2013).

Pēc literatūras datiem var secināt, ka dižskābarža stādījumi Latvijas teritorijā ierīkoti jau ap 18. gadsimta vidu, izmantojot tos muižu un pilsētu parkos un apstādījumos (Freibe, 1805). Pirmās zināmās mežaudzes ierīkotas 18. gadsimta beigās (Vanders, 1960b). Lai gan dižskābardis Latvijā ir introducēta suga, tomēr jau 20. gadsimta vidū K. Vanders uzskatījis, ka dižskābardis ir pilnīgi naturalizējies Kurzemē (Vanders, 1957). Par to liecina dižskābarža sastopamība pat trīs stāvos un dažādos vecumos stādītajās mežaudzēs, kā arī parkos. Dižskābardis Latvijā atjaunojas dabiski gan zem koku vainagu klāja, gan apkārtējās teritorijās (Bolte *et al.*, 2007; Laiviņš, 2010). Par veiksmīgu sugas adaptēšanos liecina arī tas, ka šīs sugas audzēs koksnes krāja neatpaliek no vietējām koku sugām (Dreimanis, 2006). Pagaidām Latvijas centrālā un austrumu daļa tiek uzskatītas par nepiemērotām dižskābarža audzēšanai, jo šajās teritorijās raksturīga izteikti zema temperatūra ziemā, kas var būt limitējošais faktors dižskābardim (Bolte *et al.*, 2007). Tomēr, ņemot vērā jau līdz šim novēroto un arī prognozēto vidējās temperatūras pieaugumu, ko daļēji izraisa temperatūras palielināšanās ziemas periodā (Lizuma *et al.*, 2007), augšanas apstākļi šajā teritorijā kļūst piemērotāki dižskābardim, un ir lietderīgi ierīkot eksperimentālos stādījumus un atlasīt šiem apstākļiem piemērotākās ģimenes.

Līdzšinējos pētījumos Dr.habil. Māris Laiviņš veicis dižskābaržu kartēšanu Latvijas teritorijā, aprakstījis augu sabiedrības dižskābarža audzēs un ierīkojis divus pastāvīgos parauglaukumus otrās paaudzes audzēs (sākotnēji no Vācijas ievesto pirmās paaudzes koku pēcnācēji). Tajos noteikti taksācijas rādītāji, atmirušās koksnes apjoms, vainagu veselības stāvoklis un projekcija (Laiviņš, 2010). Plašāku taksācijas rādītāju raksturošanu, atkārtoti pārmērot pastāvīgos parauglaukumus, nodrošinājis prof. A. Dreimanis (Dreimanis, 2005, 2006). Tomēr nav pietiekamas informācijas par augstuma pieauguma dinamiku. Ir analizēta gadskārtu platumu korelācija ar meteoroloģiskajiem apstākļiem ilgtermiņā samērā nelielai paraugkopai, konstatējot vasaras sausuma negatīvo ietekmi uz radiālo pieaugumu (Sabule I., 2009), bet nav analizētas paaudžu atšķirības reakcijā uz meteoroloģiskajiem apstākļiem, kā arī meteoroloģisko apstākļu ietekme uz radiālo pieaugumu sezonas ietvaros.

1.2. Promocijas darba mērķis

Novērtēt Eiropas dižskābarža audzēšanas potenciālu Latvijā klimata pārmaiņu kontekstā.

1.3. Promocijas darba pētnieciskie uzdevumi

1. Raksturot dižskābarža dabisko atjaunošanos ietekmējošos faktorus izcirtumā un zem audzes vainagu klāja, un otrās paaudzes koku ģenētisko daudzveidību.
2. Raksturot dižskābarža otrās paaudzes stādījumu saglabāšanos un augšanu relatīvi skarbos apstākļos Latvijas centrālajā daļā.
3. Novērtēt dižskābarža augšanas gaitu.
4. Raksturot meteoroloģisko faktoru ietekmi uz dažādu dimensiju dižskābaržu caurmēra pieaugumu.

1.4. Promocijas darba tēzes

1. Dižskābarža dabiskā atjaunošanās Latvijā ir sekmīga gan zem vecās audzes vainagu klāja, gan izcirtumos.
2. Otrās dižskābarža paaudzes augšanas gaita un jutība pret klimatiskajiem faktoriem ir atšķirīgas salīdzinājumā ar pirmo paaudzi.

1.5. Zinātniskā novitāte

Pirmo reizi salīdzināta dažādu paaudžu dižskābaržu reakcija uz klimatiskajiem faktoriem audzēs, kas atrodas uz ziemeļaustrumiem no šīs koku sugas izplatības areāla robežas. Pirmo reizi Baltijā novērtēta dižskābarža saglabāšanās zem audzes vainagu klāja vairākas desmitgades pēc stādīšanas, ģenētiskā daudzveidība divām šīs koku sugas paaudzēm, kā arī raksturots augstuma pieaugums.

1.6. Zinātniskā darba aprobācija

Pētījuma rezultāti prezentēti 7 konferencēs:

1. Oskars Krisans, Roberts Matisons, **Liga Purina**, Endijs Baders, Aris Jansons (2017) Climatic signals in tree-rings: native vs. introduced tree species case study in Latvia. International meeting "Non-native tree species for European forests – experiences, risks and opportunities", February 6–8, 2017, Prague, Czech Republic.
2. **Liga Purina**, Andis Adamovics, Juris Katrevics, Zaiga Katrevica, Baiba Dzerina (2016) Growth of *Fagus sylvatica* in young mixed stand: case study in central Latvia. Annual 22nd International Scientific Conference "Research for Rural Development 2016", May 18–20, 2016, Jelgava.

3. Roberts Matisons, **Līga Puriņa**, Linda Robalte, Āris Jansons (2016) Climatic factors affecting radial growth of *Fagus sylvatica* in Latvia. 4th International Conference of Dendrochronologists and Dendroecologists from the Baltic Sea Region "BaltDendro 2016", August 22–25, 2016, Annas Tree School, Latvia.

4. Oskars Krišāns, **Līga Puriņa**, Dāvis Mesters, Rolands Kāpostiņš, Āris Jansons, Juris Rieksts-Riekstiņš (2016) Intra annual changes of intensity of radial growth of European beech (*Fagus sylvatica* L.) in western Latvia. 4th International Conference of Dendrochronologists and Dendroecologists from the Baltic Sea Region "BaltDendro 2016", August 22–25, 2016, Annas Tree School, Latvia.

5. **Līga Puriņa**, Ilze Pušpure, Baiba Džeriņa, Āris Jansons (2016) Regeneration of Fagus sylvatica at the edge of its northern distribution limits. 4th International Conference of Dendrochronologists and Dendroecologists from the Baltic Sea Region "BaltDendro 2016", August 22–25, 2016, Annas Tree School, Latvia.

6. **Liga Purina**, Roberts Matisons, Aris Jansons (2015) Regeneration and climate-growth sensitivity of European beech in Latvia. International scientific conference "Knowledge Based Forest Sector", November 4–6, 2015, Riga, Latvia. Poster presentation.

7. Āris Jansons, Roberts Matisons, Jānis Jansons, **Līga Puriņa**, Endijs Baders (2015) High-frequency variation of tree-ring width of several tree species in Latvia. International scientific conference on dendrochronology "Climate and human history in the Mediterranean basin", October 18–23, 2015, Antalya, Turkey.

2. MATERIĀLS UN METODES

Pētījumam dati ievākti dižskābarža lielākajās audzēs Latvijā: Talsu, Madonas, Tērvetes, Aizputes un Priekules novadā (2.1. att.).

- ● - atjaunošanos ietekmējošie faktori / *factors affecting regeneration*
- ▲ - otrās paaudzes ģenētiskā daudzveidība / *genetic diversity of second generation*
- ★ - otrās paaudzes saglabāšanās un augšana / *survival and growth of second generation*
- ✚ - augstuma pieauguma veidošanās / *formation of cumulative primary growth*
- ✕ - caurmēra pieaugumu ietekmējošie meteoroloģiskie faktori / *meteorologic factors affecting secondary growth*

2.1. att. Dižskābarža izplatība Latvijā (pelēkie punkti, dati: Latvijas dendrofloras atlants) un dažādiem pētījuma uzdevumiem izvēlēto objektu izvietojums

Pētījumā analizēti vairāku paaudžu koki. Ar pirmo paaudzi saprot audzes, kuras stādītas, izmantojot Vācijas ziemeļu daļā ievāktas sēklas, audžu vecums aptuveni 100–140 gadi. Otro paaudzi veido pirmās paaudzes pēcnācēji, izauguši no vietējā sēklu materiāla.

2.1. Gaismas apstākļu ietekme uz dižskābarža dabisko atjaunošanos

Lai izzinātu gaismas apstākļu ietekmi uz dižskābarža dabisko atjaunošanos zem vainagu klāja, Talsu novadā ierīkoti 11 transekti dižskābarža tīraudzē, Eiropas baltegļu audzē ar bērzu, ozolu, egļu un dižskābaržu piemistrojumu, kā arī lapu koku mistraudzē. Meža tips – vēris, audžu vecums aptuveni 120 gadi. Transekti ierīkoti cauri dižskābarža paaugas grupām, tie sadalīti 2 × 2 m kvadrātos bez atstarpēm starp tiem. Katrā posmā atsevišķi uzskaitīta dižskābarža un citu koku sugu paauga, uzmērīts tās augstums. Katra kvadrāta centrā veikta vainagu

klāja fotografēšana, lai varētu aprēķināt gaismas rādītājus. Fotogrāfijas uzņemtas ar Nikon Coolpix E8400 kameru, aprīkotu ar platleņķa (*fish-eye*) objektīvu (DSLR 4.9 mm-203) (Regent Instruments Inc., Quebec, Canada), kamera novietota 1.4 m augstumā virs zemes. Eiropas baltegles audzē ierīkotajos transektos papildus ievākti šādi dati: katrā transekta 4 m posmā noteikts tālākā pie paaugas grupas piederošā dižskābarža attālums no transekta abās tā pusēs (lai iegūtu priekšstatu par paaugas grupas aizņemto platību un formu), katrā 4 m posmā abās transekta pusēs uzskaitīts tuvākais pirmā stāva koks, kas ietekmē paaugas grupas gaismas apstākļus, noteikta arī tā suga un caurmērs. Visos virzienos 30 m attālumā no transekta uzskaitīti visi pirmā un otrā stāva dižskābarži, uzmērīts to augstums, caurmērs un attālums no transekta, kā arī noteikta piederība tuvākajam parauglaukuma 4 m posmam.

Gaismas apstākļi transekta posmos aprēķināti, izmantojot WinScanopy 2006a programmu (Regent Instruments Inc., Quebec, Canada). Dižskābarža tīraudzē un lapu koku mistraudzē aprēķināta tiešā, izkliedētā un kopējā gaisma (mol m^{-2} diena^{-1}), Eiropas baltegļu audzē noteikti šādi parametri: vainagu klāja izrobojums, vainagu klāja atvērums, tiešās gaismas īpatsvars un kopējās gaismas īpatsvars, kas ir relatīvas vērtības un tiek izteiktas procentos.

Dižskābarža dabiskās atjaunošanās novērtēšanai izcirtumos ierīkoti parauglaukumi Aizputes novadā, netālu no Kazdangas. Izvēlētas 3 jaunaudzes pēc vienlaidus atjaunošanas cirtes, kurām blakus atrodas audzes ar vairākiem pieaugušiem dižskābaržiem, kas kalpo kā sēklu avots dabiskai atjaunošanai. Tajās ierīkoti kopā 79 parauglaukumi, katrs 25 m^2 platībā. Parauglaukumiem noteikts attālums līdz tuvākajai audzei, kurā atrodami pieauguši dižskābarži, tajos uzmērīti visi dižskābarži un citu sugu koki, nosakot katram caurmēru un augstumu, kā arī noteiktas lakstaugu sugas un to individuālais un kopējais projektīvais segums, kā arī Ellenberga vērtības lakstaugu sugām.

2.2. Otrās paaudzes ģenētiskā daudzveidība

Priekules un Talsu novadā analizēta pirmās un otrās paaudzes dižskābaržu ģenētiskā daudzveidība. Šim nolūkam divās audzēs vēra meža tipā ievākti koksnes paraugi no pirmās paaudzes kokiem (vecums 112–118 gadi) un audžu centrā 20 × 20 metru platībā ievākti lapu paraugi no visiem otrās paaudzes dižskābaržiem. Kopumā analīzē iekļauti 45 pirmās paaudzes un 106 otrās paaudzes koki no audzes Priekules novadā un attiecīgi 63 un 101 koks no audzes Talsu novadā. Paraugu ģenētiskā analīze veikta LVMI Silava Molekulārās ģenētikas laboratorijā.

2.3. Dižskābarža otrās paaudzes stādījumu saglabāšanās un augšana Latvijas centrālajā daļā

Relatīvi skarbos apstākļos Latvijas centrālajā daļā Madonas novadā novērtēta otrās paaudzes dižskābarža stādījuma saglabāšanās zem vainagu klāja. Stādījums ierīkots 1983. gadā 90 gadus vecā priežu audzē ar bērza un egles piemistrojumu. Augsne normāla mitruma, auglīga, mālaina, ar skābu reakciju. Meža tips damaksnis. Audzes platība 3.5 ha. Sēklu materiāls ņemts no dižskābarža audzēm Talsu novada Šķēdē, stādi izaudzēti Meža pētīšanas stacijas kokaudzētavā Madonas novadā. Stādīšana veikta rindās, ar vidējo attālumu starp stādiem 0.83 m, attālums starp rindām variē no 3.5 m līdz 8.5 m. Iestādīti aptuveni 5000 stādi. Līdz 33 gadu vecumam saglabājušies 3975 dižskābarži. Katram no tiem noteikta telpiskā atrašanās vieta (koordinātu tīklā), uzmērīts caurmērs, augstums un maksimālais vainaga rādiuss, kas noteikts pēc garākā zara.

Otrās paaudzes stādījumu saglabāšanās novērtēta arī Tērvetes novadā, 12 gadus pēc dižskābaržu – egļu mistraudzes ierīkošanas izcirtumā. Stādījums izvietots līdzenā, auglīgā, mālainā normāla mitruma minerālaugsnē, meža tips vēris. Stādīts rindu mistrojumā. Izmantoti 2-gadīgi egles stādi no kokaudzētavas un dižskābarža mežeņi no pauagas Talsu novada Šķēdē. Pirms stādīšanas sagatavota augsne. Attālums starp stādiem 2.5 m, attālums starp rindām variē no 2 līdz 3 m. Audzē uzmērītas visas egles un dižskābarži, nosakot tiem augstumu un caurmēru. Dižskābaržiem noteikts arī lielākais vainaga rādiuss, eglēm uzmērīts pēdējo 3 gadu augstuma pieaugums. Abu sugu kokiem veikti urbumi ar Preslera pieauguma svārpstu pēc iespējas tuvāk sakņu kaklam. Iegūtie koksnes paraugi izžāvēti līdz gaissausam stāvoklim, laboratorijā noslīpēti, manuāli uzmērīts gadskārtu platums, lietojot LINTAB 5 (RinnTECH) mērījumu sistēmu ar precizitāti 0.01 mm.

2.4. Augšanas gaita

Talsu novadā 10 dižskābarža audzēs nozāģēti divi valdaudzes koki katrā audzē, lai ievāktu datus par augstuma pieauguma veidošanos. Visas audzes atradās 5 km rādiusā, līdzīgos apstākļos, auglīgā, normāla mitruma minerālaugsnē. Audžu vecums aptuveni no 70 līdz 140 gadiem. Paraugkoki izvēlēti no valdaudzes, veselīgi, ar vienu stumbru, bez būtiskiem redzamiem bojājumiem, pēc iespējas izvairoties no konkurences efekta (Brunner, Nigh, 2000). No stumbra izzāģēti paraugi 0.2 m un 1.3 m augstumā, un tālāk ik pēc 2 metriem. Paraugi tika žāvēti, slīpēti, un gadskārtas saskaitītas ar mikroskopa palīdzību. Katrā augstumā tika noteikts koka vecums.

2.5. Meteoroloģisko faktoru ietekme uz dažādu dimensiju dižskābaržu caurmēra pieaugumu

Meteoroloģisko faktoru ietekme uz dažādu dimensiju dižskābaržu caurmēra pieaugumu pētīta Talsu novadā. Divi atšķirīgu paaudžu koki aprīkoti ar dendrometriem caurmēra pieauguma veidošanās dinamikas novērtēšanai sezonas ietvaros. Koki izvēlēti dižskābaržu – priežu mistraudzē, mālainā normāla mitruma minerālaugsnē, meža tips damaksnis. Abi koki atradās 8 m attālumā viens no otra. Pirmās paaudzes kokam augstums 34 m, krūšaugstuma caurmērs 55 cm, vecums 127 gadi. Otrās paaudzes kokam augstums 12.6 m, krūšaugstuma caurmērs 16 cm, vecums 43 gadi. Stumbra caurmēra izmaiņu monitorēšana veikta krūšaugstumā, fiksēta ik pēc 10 minūtēm ar dendrometru DRL26C (EMS Brno, Czech Republic). Informācija par meteoroloģiskajiem datiem audzē iegūti no blakus novietotās mobilās meteostacijas (Vantage Pro2, Davis Instruments, USA). Augsnes ūdens potenciāls mērīts ar tensiometriem (T8, UMS GmbH, Germany).

Lai novērtētu gadskārtu platumu ietekmējošos faktorus ilgākā laika posmā, pētījums veikts trijās dižskābarža audzēs Talsu novadā, izvēloties 45 dažādu Krafta klašu kokus katrā audzē, un vienā audzē Priekules novadā (9 koki). Visas audzes atrodas salīdzinoši līdzenā reljefā, normāla mitruma auglīgā, mālainā minerālaugsnē. Dižskābaržos ar Preslera pieauguma svārpstu veikti katrā divi urbumi krūšaugstumā no pretējām pusēm. Gadskārtu platums mērīts manuāli, izmantojot Lintab 5 sistēmu (Rinntech, Heidelberg, Germany) ar precizitāti 0.01 mm. Nomērīto gadskārtu sēriju kvalitāti (datējumus) pārbaudīja, veicot vizuālu un statistisku šķērsdatēšanu ar COFECHA programmu (Grissino-Mayer, 2001), t. i., pārbaudīja sēriju mainības savstarpējo saskaņību.

3. REZULTĀTI UN DISKUSIJA

3.1. Dižskābarža dabisko atjaunošanos ietekmējošie faktori izcirtumā un zem audzes vainagu klāja, un otrās paaudzes ģenētiskā daudzveidība

Vainagu klājs aiztur lielāko daļu saules gaismas, un pamežu un paaugu sasniedz mazāk nekā 20% no kopējās gaismas (3.1. att.). Dižskābarža paaugas koku augstums vidēji cieši korelē ar gaismas apstākļiem zem vainagu klāja.
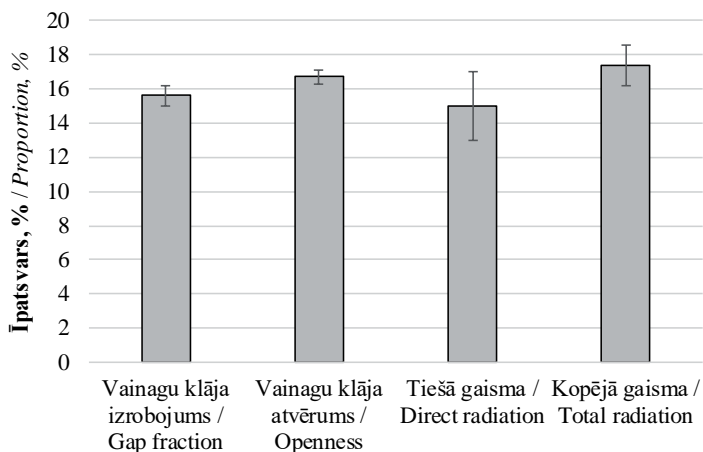
3.1. att. Gaismas apstākļus raksturojošo parametru vidējās vērtības (± 95% ticamības intervāls)

Abās dižskābarža tīraudzēs visi aprēķinātie gaismas parametri bija savstarpēji būtiski saistīti, un tiem bija līdzīga izkliede (variācijas koeficients ~40%). Izkliedētā un kopējā gaisma bija galvenie limitējošie faktori lielākajai daļai paaugas sugu (izņemot egli). Viszemākais izkliedētās gaismas slieksnis, kā arī kopējās gaismas vērtība novērota dižskābardim un osim (attiecīgi 0.37 un 0.66 mol m^{-2} dienā) (3.1. tab.). No konstatētajām paaugas un pameža sugām visaugstākais izkliedētās gaismas slieksnis bija balteglei un pīlādzim (attiecīgi 0.75 un 1.05 mol m^{-2} dienā). Parauglaukumos zem pieaugušās audzes uzskaitītās dižskābarža paaugas koku skaits variēja no 2500 līdz 13 000 uz hektāra, kas pārsniedz Latvijas normatīvajos aktos norādīto minimāli nepieciešamo koku skaitu jaunaudzē (1500 uz ha).

3.1. tabula

Aprēķinātās un uzmērītās gaismas parametru vērtības

Koku suga	Gaisma (mol m^{-2} dienā)			
	Aprēķinātā		Faktiskā (uzmērītā)	
	Izkliedētā	Kopējā	Izkliedētā	Kopējā
Dižskābardis	0.37 (2.48%)	0.19 (0.42%)	0.28 (1.9%)	0.66 (1.45%)
Egle	-	-	0.68 (4.61%)	1.45 (3.19%)
Baltegle	0.79 (5.32%)	2.42 (5.31%)	0.70 (4.74%)	1.89 (4.15%)

Izcirtumos ierīkotajos paraglaukumos konstatēto augu sugu Ellenberga vērtības neatšķīrās būtiski atkarībā no attāluma līdz meža sienai. Var uzskatīt, ka visā izcirtumā augšanas apstākļi bija samērā vienmērīgi, un dižskābarža atjaunošanos ietekmēja citi faktori. Sakarība starp dižskābaržu skaitu un augstumu netika konstatēta (p = 0.92). Analizējot citu vērtēto pazīmju (novērojumu vieta, paraglaukumu attālums līdz meža sienai, citu kokaugu skaits un to augstums, augu sugu skaits, lakstaugu un sūnu projektīvais segums) iespējamo saikni ar dižskābaržu skaitu un augstumu, konstatēts, ka dažādās novērojumu vietās būtiski neatšķīrās dižskābaržu skaits (p = 0.30), turpretī to augstuma atšķirības bija būtiskas (p < 0.001).

Vidējais dižskābaržu jaunaudzes biezums bija 2520 ±720 koki ha^{-1} (robežās no 400 līdz 11 200). Pīrsona korelācijas analīzē konstatēts, ka dižskābaržu biezumam pastāv būtiska (p < 0.05) negatīva korelācija ar citu kokaugu skaitu (r = -0.32), ar sūnu projektīvo segumu (r = -0.31) un ar paraglaukumu attālumu līdz meža sienai (r = -0.38) (3.2. att.).
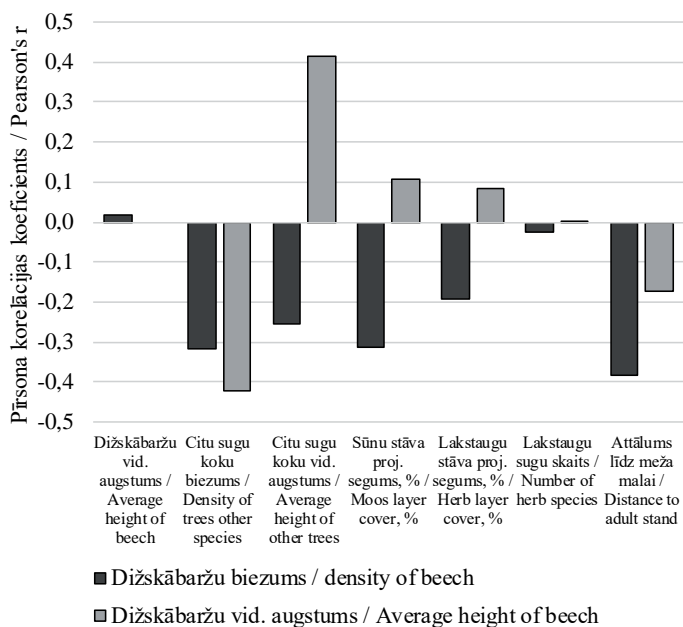
3.2. att. **Dižskābarža biezumu un augstumu ietekmējošie faktori**

Veicot daudzfaktoru lineārās regresijas analīzi (vispirms visām pazīmēm, un tad atkārtojot pēc nebūtisko pazīmju – vieta, sugu skaits, sūnu segums, lakstaugu segums – pakāpeniskas izslēgšanas), konstatēts, ka dižskābaržu skaitu būtiski (p < 0.05) ietekmēja citu kokaugu skaits un to augstums, kā arī attālums līdz meža malai; modelim R^2 = 0.34.

Vidējais dižskābaržu augstums bija 201 ±25.8 cm. Pīrsona korelācijas analīzē konstatēts, ka dižskābaržu augstumam pastāv būtiska ($p < 0.01$) negatīva korelācija ar citu kokaugu skaitu ($r = -0.42$) un būtiska pozitīva – ar citu kokaugu augstumu ($r = 0.57$). Veicot daudzfaktoru lineārās regresijas analīzi, konstatēts, ka būtiska ietekme ir tikai vietai (pārējām analizētajām pazīmēm $p > 0.23$). Tālākā analīze veikta katrai novērojumu vietai atsevišķi un konstatēts, ka tikai vienā no objektiem daudzfaktoru lineārās regresijas modelis ir būtisks. Atkārtojot analīzi šim objektam (vietai) pēc pakāpeniskas nebūtisko pazīmju izslēgšanas, konstatēts, ka modelim $R^2 = 0.57$, un dižskābaržu augstumu būtiski ($p < 0.05$) ietekmēja citu sugu koku klātbūtne (biezums) un to augstums.

Dižskābardis sekmīgi atjaunojas (vismaz 1500 koki uz ha) izcirtumos pēc vienlaidus atjaunošanas cirtes, ja pietiekami netālu (līdz 50 m) atrodas sēklu avots.

Veicot ģenētiskās analīzes, Talsu novada dižskābaržu audzes parauglaukumā 53% no analizētajiem otrās paaudzes kokiem tika identificēts vismaz viens no vecāku kokiem, bet Priekules novada audzē – 42%. Visbiežāk vecāku kokiem tika konstatēts pa vienam pēcnācējam – Talsu novadā 8 gadījumos, Priekules novadā 10 gadījumos (3.3. att.). Katrā parauglaukumā identificēts viens koks ar salīdzinoši daudziem pēcnācējiem – Talsu novadā ar 13, Priekules novadā ar 11 pēcnācējiem.
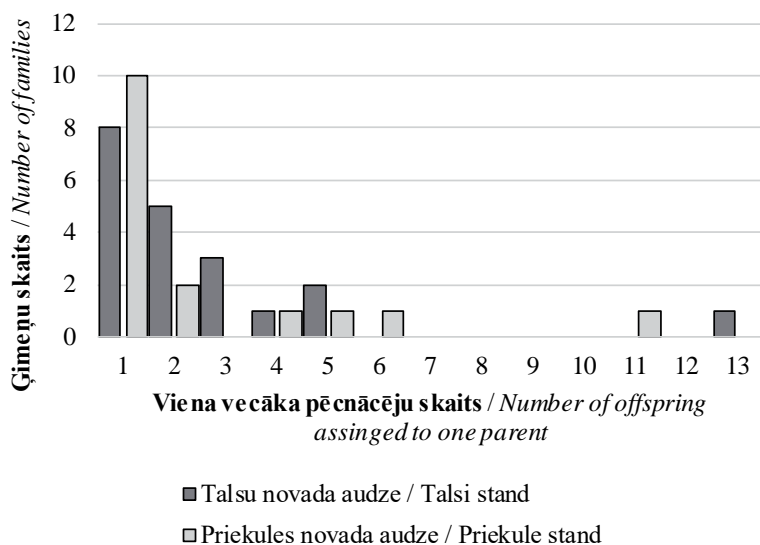
3.3. att. **Koku skaita sadalījums pa ģimenēm dižskābarža dabiskajā atjaunošanā**

Ģenētiskās daudzveidības rādītāji liecina, ka Priekules novada audzē vecāku paaudze ir savstarpēji radniecīgāka nekā Talsu novada audzē (3.2. tab.).

Ģenētiskās daudzveidības rādītāju vidējās vērtības (±standartkļūda)

Populācija	Priekules nov. vecāku koki	Priekules nov. otrā paaudze	Talsu nov. vecāku koki	Talsu nov. otrā paaudze
Alēļu skaits	4.4 ±0.26	4.9 ±0.37	9.6 ±1.01	8.6 ±0.88
Alēļu ar īpatsvaru ≥ 5% skaits	3.6 ±0.22	3.5 ±0.22	4.4 ±0.36	4.8 ±0.41
Efektīvo alēļu skaits	3.0 ±0.19	2.6 ±0.19	4.2 ±0.45	4.3 ±0.42
Šenona daudzveidības indekss	1.2 ±0.06	1.1 ±0.06	1.6 ±0.11	1.6 ±0.10
Sagaidāmā heterozigotāte	0.6 ±0.03	0.6 ±0.03	0.7 ±0.03	0.7 ±0.03

Tas varētu būt izskaidrojams ar sēklu izcelsmi mežaudžu ierīkošanai. Tomēr daudzveidības rādītāji būtiski neatšķīrās starp paaudzēm nevienā no audzēm, ģenētiskā daudzveidība nākamajā paaudzē nesamazinās.

3.2. Dižskābarža otrās paaudzes stādījumu saglabāšanās un augšana Latvijas centrālajā daļā

Mistrotā dižskābaržu – egļu audzē Tērvetes novadā 12 gadus pēc iestādīšanas dižskābaržu saglabāšanās bija apmierinoša un līdzīga kā eglēm (attiecīgi 73% un 78%). Dižskābardim augstums un caurmērs bija statistiski būtiski lielāks nekā eglei (augstums attiecīgi 7.4 ±0.30 m un 3.1 ±0.30 m, caurmērs 8.9 ±0.68 cm un 3.0 ±0.41 cm). Ikgadējais radiālais pieaugums dižskābardim bija ievērojami lielāks nekā eglei (3.4. att.), atšķirības starp koku sugām bija statistiski būtiskas un pieaugošas līdz ar vecumu.
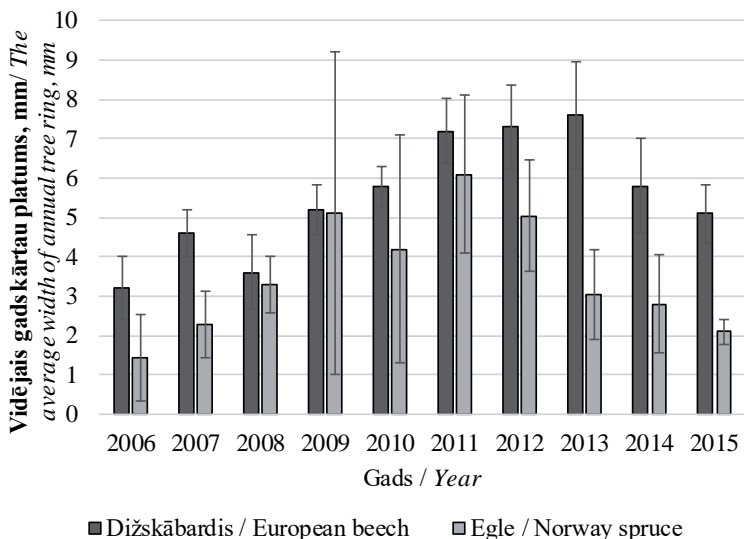
3.4. att. **Dižskābarža un egles vidējais gadskārtu platums**
(±95% ticamības intervāls)

Audzē novērota izteikta konkurence starp abu sugu kokiem. Maksimālais dižskābarža vainaga rādiuss bija vidēji 2.4 ±0.16 m, kas ir līdzvērtīgs ar attālumu starp rindām un starp stādvietām rindās. Dižskābaržu augšanu būtiski ietekmējis fotosintezējošās virsmas laukums, kas raksturots ar vainaga maksimālo rādiusu. Vainaga maksimālajam rādiusam konstatēta cieša un būtiska korelācija gan ar koka augstumu, gan ar caurmēru krūšaugstumā (attiecīgi $r = 0.71$ un $r = 0.87$). Pirmajos augšanas gados dižskābardis izmanto telpu daudz efektīvāk nekā egle, izveidojot plašu vainagu un izmantojot visus pieejamos gaismas resursus.

Aptuveni 80% dižskābaržu bija saglabājušies 33 gadus pēc iestādīšanas zem audzes vainagu klāja Madonas novadā, Kalsnavas apkārtnē. Platībā konstatēta arī atjaunošanās ar atvasēm. Dižskābaržu augstums variēja no 0.30 līdz 13 m, caurmērs krūšaugstumā – no 0.2 līdz 14.9 cm. Koku sadalījumam pēc dimensijām ir apvērsta J forma (3.5. att.), kas ir tipiski ēncietīgām sugām un apliecina dižskābarža paaugas normālu augšanu. Šādā veidā koku sugas pielāgojas ilgstoši saglabāties paaugā, līdz kāda traucējuma rezultātā vainagu klājā izveidosies atvērums un radīsies iespēja straujākai augšanai (Wagner *et al*., 2010).
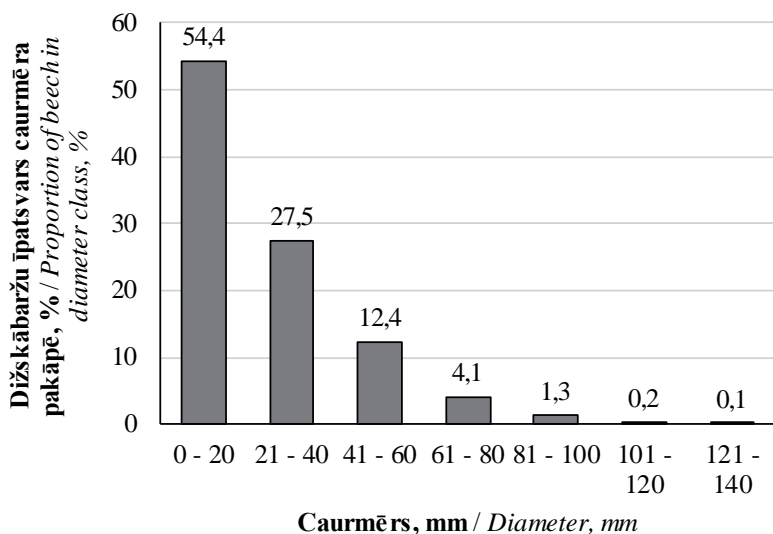
3.5. att. **Dižskābaržu sadalījums pa caurmēra pakāpēm**

Šo dižskābaržu augšanas laikā (1983. līdz 2016. gadam) ziemās bijuši arī ļoti auksti periodi ar gaisa temperatūru -30°C un zemāku, tomēr klimatiskie apstākļi Latvijas centrālajā daļā izrādījušies piemēroti dižskābaržu atjaunošanai zem audzes vainagu klāja (gaisa temperatūra šajā gadījumā nebija limitējošais faktors) (Fang & Lechowicz, 2006; Kramer *et al.*, 2010). Tik augsta saglabāšanās Latvijas centrālajā daļā varētu būt saistīta ne tikai ar koku atrašanos zem audzes vainagu klāja, bet arī ar sēklu izcelsmi – šie ir otrās paaudzes dižskābarži no Latvijas rietumu daļā augošu koku sēklām, kuriem jāspēj adaptēties tikai nedaudz skarbākiem apstākļiem nekā to vecāku kokiem (Yakovlev *et al.*, 2011).

3.3. Dižskābarža augšanas gaita

Paraugkoku augstuma pieauguma dinamiku ilgstošā laika posmā visprecīzāk raksturot bija iespējams ar Chapman-Richards un Sloboda modeļiem. Šo vienādojumu koeficienti būs izmantojami LVMI Silava izveidotajā augšanas gaitas modelēšanas rīkā. Iegūtie dati liecina, ka dižskābarži Latvijas rietumu daļā ir ātraudzīgāki nekā Zviedrijas dienvidu daļā, tātad augšanas apstākļi šeit ir sugai piemēroti. Otrās paaudzes koki ir veiksmīgi adaptējušies vietējiem apstākļiem un uzrāda lielāku ātraudzību, apsteidzot pirmās paaudzes kokus (3.6. att.).
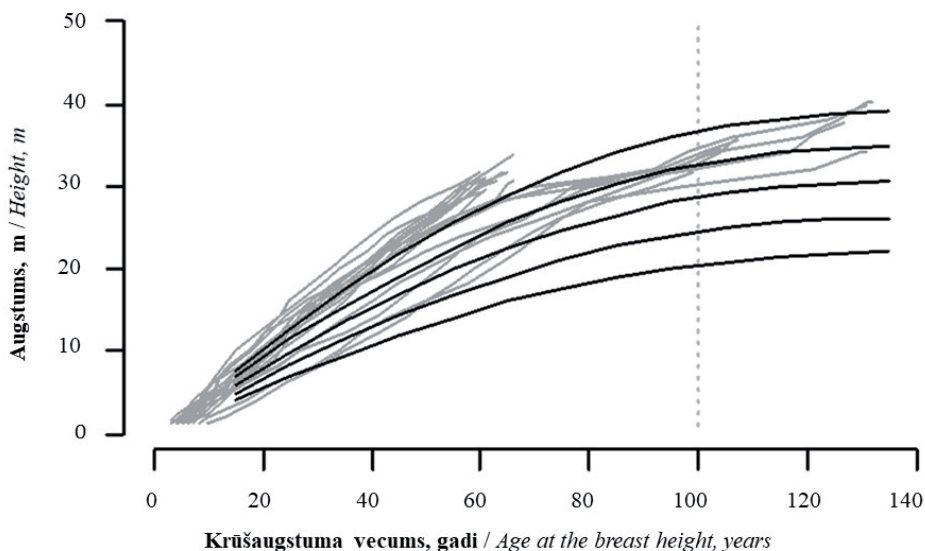
3.6. att. **Nelineārs augšanas gaitas modelis (melnās līnijas, Dienvidzviedrija, Carbonier, 1971), salīdzināts ar mērījumu datiem Latvijas rietumu daļā (pelēkās līnijas, katra līnija attēlo vienu koku)**

3.4. Meteoroloģisko faktoru ietekme uz dažādu dimensiju dižskābaržu caurmēra pieaugumu

Analizējot meteoroloģisko faktoru ietekmi uz stumbra caurmēra pieaugumu sezonas ietvaros, konstatēta dižskābarža jutība pret ūdens deficītu (3.7. att.). Dižskābarža radiālais pieaugums pozitīvi korelēja ar nokrišņiem. Ja kādu laika posmu nokrišņu nebija vispār, šajā laikā gadskārta neauga. Pēc periodiem ar nozīmīgiem nokrišņiem notika stumbra ūdens rezervju atjaunošanās un tai sekojoša gadskārtas augšana. Limitējošais faktors veģetācijas sezonā bija pieejamais ūdens, bet ne gaisa temperatūra.

Otrās paaudzes kokam novērots būtiski lielāks relatīvais radiālais pieaugums nekā pirmās paaudzes kokam veģetācijas sezonas ietvaros (attiecīgi 0.93% un 0.38% no caurmēra). Visstraujākais radiālais pieaugums novērots no veģetācijas perioda sākuma līdz jūlija sākumam.
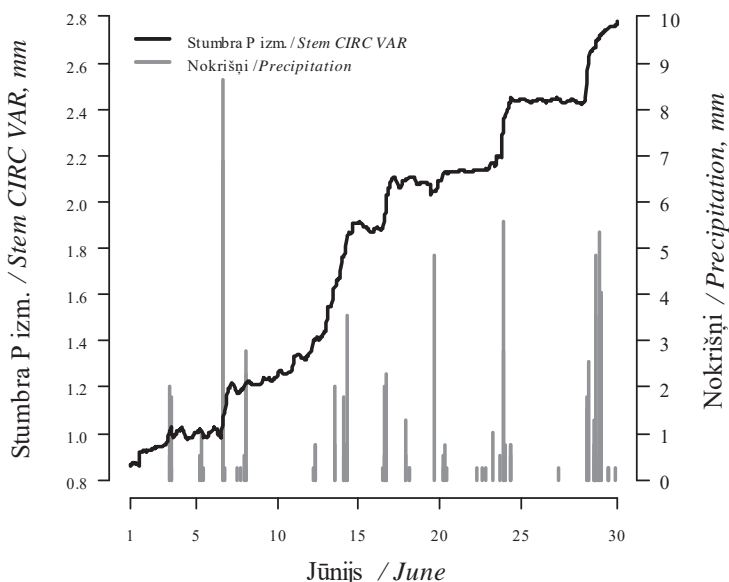
3.7. att. Stumbra apkārtmēra (*P*) izmaiņas pirmās paaudzes dižskābardim jūnijā un nokrišņu daudzums šajā periodā

Novērtējot meteoroloģisko faktoru ietekmi uz stumbra caurmēra pieaugumu ilgākā laika posmā, Latvijas rietumu daļā pētītajiem dižskābaržiem netika konstatētas ekstrēmi šauras gadskārtas (nomākta augšana), liecinot par augšanas apstākļu piemērotību šai koku sugai. Analizējot radiālā pieauguma saistību ar meteoroloģiskajiem apstākļiem, konstatēts, ka pirmās paaudzes koki ir jutīgāki nekā otrās paaudzes koki (3.8. att.).

Pirmās paaudzes valdaudzes koki bija īpaši jutīgi uz nokrišņu apjomu jūnijā, kas saistīts ar ūdens deficītu vasarā. Šīs paaudzes nomāktie koki galvenokārt bija jutīgi pret temperatūru ziemas periodā. Savukārt otrās paaudzes kokus mazāk ietekmēja ziemas perioda temperatūra, tas liecina par adaptāciju Latvijas apstākļiem.
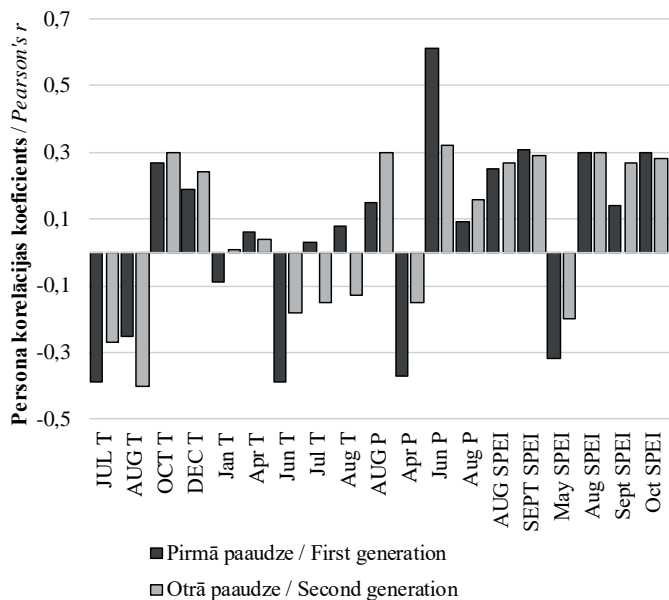
3.8. att. Statistiski būtiskie Pīrsona korelācijas koeficienti (*r*) starp dažādas paaudzes valdaudzē esošu dižskābaržu gadskārtu vidējo platumu un klimatiskajiem (meteoroloģiskajiem) faktoriem: mēneša vidējā temperatūra (*T*), nokrišņi (*P*), standartizēts nokrišņu-iztvaikošanas indekss (SPEI) laika intervālam no 1972. līdz 2015. gadam

Mēnešu nosaukumi ar lielajiem burtiem – Pīrsona korelācijas koeficienti gadā pirms gadskārtas veidošanās

Ātraudzīgākajiem otrās paaudzes kokiem novērota ciešāka pieauguma saistība ar mitruma apstākļiem vasaras periodā, par ko liecināja gan ikgadējā, gan vienas augšanas sezonas pieauguma veidošanās dinamika.

SECINĀJUMI

1. Notikusi sekmīga dižskābarža adaptācija Latvijā: tā otrajai paaudzei nav konstatēta zemāka ģenētiskā daudzveidība, bet ir konstatēts lielāks augstuma pieaugums nekā pirmajai paaudzei. Otrās paaudzes koki labi saglabājas (> 80%) zem citu koku sugu vainagu klāja arī Latvijas centrālajā daļā.

2. Latvijas rietumu daļā dižskābarža dabiskā atjaunošanās ir sekmīga gan pēc vienlaidus atjaunošanas cirtes, līdz 50 m no meža malas, gan zem audzes vainagu klāja arī tādos gaismas apstākļos, kas nav piemēroti citām koku sugām. Dižskābarža paaugas koku augstums vidēji cieši, statistiski būtiski, korelē ar gaismas apstākļiem zem vainagu klāja.

3. Izveidotie dižskābarža augšanas gaitas vienādojumi un dati no paraug-laukumiem mežaudzēs liecina, ka šīs koku sugas otrās paaudzes koku ātraudzība Latvijā ir lielāka nekā Zviedrijas dienvidu daļā un – atsevišķos stādījumos jaunaudzes vecumā – arī salīdzinājumā ar egli, norādot uz iespējām izveidot augstražīgas dižskābarža mežaudzes.

4. Latvijas rietumu daļā pētītajiem dižskābaržiem gadskārtas nebija šauras, liecinot par augšanas apstākļu piemērotību šai koku sugai. Koku jutība pret klimatiskajiem apstākļiem (īpaši – ziemas perioda temperatūru) bija atšķirīga pirmajai un otrajai paaudzei, norādot uz dabiskās un cilvēku veiktās izlases pozitīvo ietekmi.

5. Mitruma deficīts nosaka dižskābarža radiālā pieauguma samazināšanos vai pat īslaicīgu apstāšanos, līdz pilnībā atjaunojas koka stumbra ūdens uzkrājums. Gadskārtu platumu ietekmē galvenokārt ar mitruma deficītu saistīti klimatiskie rādītāji (temperatūra, nokrišņi) vasarā un rudens sākumā. Ņemot vērā klimata izmaiņu prognozes, dižskābarža audžu ierīkošanai būtiski izvēlēties teritorijas ar stabilu un pietiekamu augsnes mitruma nodrošinājumu.

.

REKOMENDĀCIJAS

Latvijas rietumu daļā iespējams izveidot ražīgas dižskābarža audzes. Stādāmo materiālu to ierīkošanai rekomendējams ievākt Latvijā esošajās audzēs. Piemērotākais sēklu avots ir šī promocijas darba izstrādes ietvaros atlasītie pluskoki.

Rekomendējams izveidot sēklu plantācijas stabilas sēklu bāzes nodrošināšanai. Tāpat rekomendējama plašāku provenienču izmēģinājumu ierīkošana, ietverot tajos materiālu arī no areāla daļām, kur raksturīgs augstāks mitruma deficīts vasaras periodā nekā Latvijā šobrīd.

Kontrolētos apstākļos (salcietības testi) un eksperimentālajos stādījumos rekomendējams turpināt pārbaudīt dižskābarža adaptāciju Latvijas austrumu daļas klimatiskajiem apstākļiem.

PATEICĪBAS

Autore izsaka vislielāko pateicību darba vadītājam Dr.silv. Ārim Jansonam un konsultantam Dr.biol. Robertam Matisonam par atbalstu, praktisku un morālu palīdzību un padomu visos darba izstrādes posmos.

Pateicos visiem kolēģiem no LVMI Silava Meža selekcijas un kokaugu adaptācijas radošās grupas, Ģenētisko resursu centra, kā arī no citām radošajām grupām, kuri iesaistījās pētījuma plānošanā, lauka un kamerālajos darbos, datu apstrādē un interpretācijā, kā arī publikāciju tapšanā. Paldies Oskaram Krišānam, Jānim Donim, Unai Neimanei, Dainim Ruņģim un citiem kolēģiem par nenovērtējamu atbalstu. Pateicos publikāciju līdzautoriem par palīdzību publikāciju veidošanā un par atļauju kopīgās publikācijas izmantot disertācijā.

1. GENERAL DESRIPTION

1.1. Topicality of the theme

European beech (*Fagus sylvatica* L.) is the most common deciduous tree species in the central Europe. Eastern border of its distribution areal reaches Ukraine, Moldavia, Bulgaria. The southern border goes through Balkan Peninsula, Apennine Mountains, Sicily and Spain (Leugnerová, 2007). Currently the northern border of natural distribution range reaches northern part of Germany, Denmark, Poland and southern part of Sweden. Latvia is outside of the distribution areal of European beech, and we have only isolated stands of this tree species. However due to climate change, notable shifts of distribution areal of tree species are predicted even during this century (Hickler *et al*., 2012). In Europe increase of the areas northwards due to warmer climate in this region and more frequent and severe droughts in south are expected (Walther *et al.*, 2002; Kullman, 2008). According to the prognosis, in the middle of 21st century, climate in all territory of Latvia and Estonia will be suitable for European beech (Kramer et al., 2010). However, the actual expansion of beech will depend from human intervention, planting this tree species. Natural dispersal of beech is slow due to heavy seeds – most of them end up in a distance of up to 30 m around the seed tree. Only very tiny fraction of seed amount reaches further, transported by birds and small rodents (Dobrovolný, & Tesař, 2010). Study in western part of Latvia indicates that speed of beech natural distributing is 3.4 m per year (Sabule L., 2009). Rich seed years (mast years) for European beech are rare and irregular: intervals between them range from six to nine years (Giesecke *et al*., 2007; Peňa *et al*., 2010; Vanders, 1960a). Part of the reason for this characteristics is necessity of very rich blooming to ensure high proportion of pollinated (viable) seeds, since beech pollen are heavy and typically fly only short distances (Vanders, 1960a). After rich seed year there are 350 000 and more seedlings per hectare in next spring, but only half of them survives to the next year (Vanders, 1957). Spread of European beech around seed sources (existing stands) is affected also by management of young stands – it can only occur, if beech is recognized as target species and retained in precommercial thinning.

Studies have shown, that European beech is resistant to wind damages, shade-tolerant, in many countries commercially significant and it rarely affected by cervids. Due to these properties and also predicted climate changes, that in most part of Baltic See region will have positive influence on this tree species (Hanewinkel *et al*., 2013), in some countries wider use of beech in forest regeneration is already promoted. Timber of beech is valuable, ornamental, it has been used for production of furniture, doors, parquet, also veneer and paper

(von Wühlisch, 2008; Born, 2011). The quality of timber depends from stem quality that, in turn, is affected by genetics, damages by abiotic factors and management regime (Poljanec, & Kadunc, 2013). Therefore it is important to assess factors affecting regeneration and growth of European beech in Latvia, creating information basis and sound recommendation for tree breeding and wider use of this tree species in practical forestry for high-quality timber production.

Literature survey suggests, that European beech have been planted in Latvia territory already in the middle of 18th century, mostly in parks of manors and cities (Freibe, 1805). The first known forest stands were established at the end of 18th century (Vanders, 1960b). European beech is introduced species in Latvia; however already in the middle of 20th century, according to K. Vander's, has been fully naturalized in western part of Latvia, Kurland (Vanders, 1957). This opinion is supported by the multi-layer beech stand structures, forming via successful natural regeneration in the initially planted areas. Natural regeneration of European beech under canopy has been observed also in the areas adjacent to mature stands of this tree species (Bolte *et al*., 2007; Laiviņš, 2010). Yield in beech stands is not inferior to that observed by most of native tree species in Latvia (Dreimanis, 2006), suggesting a successful adaptation of beech. The central and eastern part of Latvia currently is considered inappropriate for beech because of the infrequent extremely low air temperature in winters, that this tree species cannot tolerate (Bolte *et al*., 2007). Nevertheless, taking into account ongoing and predicted increase of average temperature that is partly due to the increase of temperature during winter (Lizuma *et al*., 2007), the growing conditions in this area are gradually becoming become more suitable for European beech, and it is worthwhile to establish experimental plantations and select families (genotypes) that are most adapted for the local conditions.

Selection of such material might be possible, as suggested by the location of current stands or individual trees, mapped by Dr.habil. Maris Laivins. He also has established two long-term sample plots in second generation beech stands (progenies of the first generation with the origin from Germany). In those sample plots tree and stand parameters, dead wood amount and projective cover of crowns has been measured and health condition of crowns has been described (Laiviņš, 2010). Larger set of sample plots for characterization of dynamic of tree and stand development were repeatedly measured by prof. Andrejs Dreimanis (Dreimanis, 2005, 2006). It revealed mostly information on diameter increment and yield, but information on height growth of beech is still missing. Influence of meteorological conditions on the tree-ring width have been analysed, using limited group of samples, and negative impact of summer drought to radial increment indicated (Sabule I., 2009). However, differences in reaction to meteorological conditions between generations of beech has not been analysed and radial increment dynamic during vegetation season, revealing insides and potential causes for the determined impacts, has not been studied.

1.2. Aim of the thesis

To assess the growth potential of European beech in Latvia in context of climate change.

1.3. Research tasks of the thesis

1. To characterize factors affecting natural regeneration of European beech after clearcut and under the canopy and to describe genetic diversity of its second generation.
2. To characterize survival and growth of European beech second generation in relatively harsh climatic conditions in central part of Latvia.
3. To assess the growth dynamics of European beech.
4. To characterize influence of meteorological factors on radial increment of different dimension European beech.

1.4. The thesis

1. Natural regeneration of European beech in Latvia is successful both under the canopy and after clearcut.
2. Growth and sensitivity to meteorological factors of second generation European beech differs from that of first generation.

1.5. Scientific novelty

Differences in reaction to climatic factors of two generations of European beech in its stands northeast form its natural distribution range had been compared for the first time. For the first time in Baltic countries survival of European beech under canopy several decades after planting, genetic diversity of two generations, and height growth had been characterized.

1.6. Approbation of research results

The research results have been summarized in eight publications and have been presented in seven scientific conferences.

2. MATERIAL AND METHODS

Data for the research were collected in the biggest European beech stands in Latvia: in Talsi, Madona, Tērvete, Aizpute and Priekule districts (Fig. 2.1.).

● - atjaunošanos ietekmējošie faktori / *factors affecting regeneration*
▲ - otrās paaudzes ģenētiskā daudzveidība / *genetic diversity of second generation*
★ - otrās paaudzes saglabāšanās un augšana / *survival and growth of second generation*
✚ - augstuma pieauguma veidošanās / *formation of cumulative primary growth*
✘ - caurmēra pieaugumu ietekmējošie meteoroloģiskie faktori / *meteorologic factors affecting secondary growth*

Fig. 2.1. **Distribution of beech in Latvia (with grey dots, data: Latvijas dendrofloras atlants) and sites selected for specific of research tasks**

Trees from two generations were analyzed. First generation in Latvia are represented by stands, established from seed sources, collected in northern part of Germany, age of these stands range from approximately 100 to 140 years. The second generation consists of progenies of these introductions, mostly established via natural regeneration, the age of from approximately 60 to 80 years.

2.1. Influence of light conditions on natural regeneration of European beech

In Talsi district 11 transects were established in pure beech stand, in silver fir stand with birch, oak, spruce and beech admixture, and in mixed stand of different deciduous trees. The aim was to characterize influence of light conditions to natural regeneration of beech under canopy. Forest type – *Oxalydosa* (loamy soil). Age of stands – approximately 120 years. Transects were made through

beech regeneration groups, those were splited in 2×2 m square sample plots without any spaces between. In each sample plot regeneration of all tree species were counted and height of each undergrowth tree was measured. In the center of each sample plot canopy image was taken by a digital camera (Nikon Coolpix E8400) equipped with a fish-eye lens (DSLR 4.9 mm-203) (Regent Instruments Inc., Quebec, Canada), placed at 1.4 m height. In silver fir stand additional data were collected: in every 4 meters of transect distance to the furthest (from the transects central line) undergrowth beach tree was measured to determine shape and area of the beech undergrowth group. Also the closest adult tree, affecting light conditions, was identified and the distance to it, as well as its parameters (height, diameter, species) measured. All dominant and suppressed beech trees (potential seed source) in 30 m radius around the transect were identified, the height, diameter and distance from the transect were measured.

Light conditions in the sample plots were assessed from the images using the WinScanopy 2006a software (Regent Instruments Inc., Quebec, Canada). Direct, diffuse and total radiation (mol m^{-2} day^{-1}) was calculated in pure beech stand and mixed deciduous trees stand. In silver fir stand gap fraction, openness, direct and total radiation were calculated.

In Aizpute district sample plots in clearcut areas were established to assess natural regeneration of beech. Three young stands after clearcut next to stands with adult beech trees (as seed source) were selected. In total 79 sample plots were established with area 25 m^2 each. Distance from nearest stand with adult beech trees for each sample plot was measured. All regeneration of beech and other species was counted, height and diameter of regeneration was measured, herb species were identified, individual and total projective cover of herbs was assessed, Ellenberg's values of herb species were marked.

2.2. Genetic diversity of the second generation

In Priekule and Talsi district genetic diversity of the first and the second generation beech trees were analysed. From two beech stands (age 112–118 years) in *Oxalidosa* forest type (loamy soil) wood samples from the first generation trees were collected. In the centre of stand from the area 20×20 m leaf samples from all second generation beech trees were collected. In total 45 beech trees from the first generation and 106 beech trees from the second generation were analysed from stand in Priekule district, and 63 and 101 beech trees from stand in Talsi district, respectively. Genetic analysis was carried out in LSFRI Silava Genetic Resource Centre.

2.3. Survival and growth of European beech second generation in central part of Latvia

In central part of Latvia, Madona district survival of second generation European beech under canopy was assessed. Beech were planted in 1983, in 90-years old pine stand with birch and spruce admixture. *Hylocomiosa* forest type, fresh, fertile, loamy soil with acidic reaction. The area of stand was 3.5 ha. Seeds from beech stands in western part of Latvia, Talsi district were used. Seedlings were raised in a local nursery and planted in rows in the stand after commercial thinning, average distance between seedlings was 0.8 m, distance between rows were various – from 3.5 m to 8.5 m. Altogether approximately 5000 seedlings were planted. After 33 years 3975 beech seedlings remained. Stand was mapped in winter of 2016: position (in local coordinates), diameter, height and length of the longest branch (to estimate maximum crown radius) was measured for every beech tree as well as positions of trees of other species marked.

Survival of second generation beech seedlings were assessed also in Tervete district twelve years after planting beech-spruce single-row mixture in clearcut area. The young stand was established in fertile, loamy, fresh mineral-soil, forest type – *Oxalidosa*. Two years old spruce seedlings from nursery and beech wildlings from natural regeneration under canopy in western part of Latvia, Talsi district were used. The soil was scarified in rows before planting. Distance between seedlings was 2.5 m, and distance between rows was approximately 2–3 m. All spruce and beech trees were counted in the stand, height and diameter for each tree was measured. For beech trees also the maximum crown radius was estimated. Increment cores from several trees, both beech and spruce, were taken with Pressler borer as close to ground as possible. Increment cores in air-dry condition were polished, then tree-ring width was measured using LINTAB 5 (RinnTECH) system with the precision of 0.01 mm.

2.4. Height increment

Reconstruction of height growth dynamics was based on the sample trees. For this purpose ten stands were selected in Talsi district. Distance between the stands were not larger than 5 kilometers; all stands were with similar soil conditions: fresh fertile mineral soil. Age of the stands approximately 70 to 140 years. Healthy dominant trees with one stem, without serious injuries were selected. The dominant trees were taken to avoid the effect of competition (Brunner & Nigh, 2000). Trees were cut and stem disks (cross-cut samples) collected from the whole stem at 0.2 m, 1.3 m and every 2 m above the base heights. Stem disks were dried, polished and the annual rings were counted under microscope to detect the age of the trees at each height.

2.5. Influence of meteorological factors on radial growth of different dimension beech

To assess influence of meteorological factors on radial growth, sample trees were selected in European beech – Scots pine mixed stand on fresh mineral soil, forest type *Hylocomiosa* in Talsi district. Two trees from different generations were used for the study, located nearby (distance between the trees 8 m). The height of first generation tree (dominant tree in the stand) was 34 m, diameter at breast height 55 cm, age 127 years. The height of second generation tree (suppressed tree in the stand) was 12.6 m, diameter at breast height 16 cm, age 43 years. Monitoring of stem diameter variation was carried out with dendrometer DRL26C (EMS Brno, Czech Republic) at breast height, measurement interval – ten minutes. Measurements were carried out during the whole vegetation season. Meteorological data used in research were obtained from a mobile weather station (Vantage Pro2, Davis Instruments, USA), located directly in site. Also soil water potential was measured in the site by tensiometers T8 (UMS GmbH, Germany).

Dendroclimatological analysis – accessing long term influence of the meteorological parameters on width of annual ring – was carried out, based on data from three European beech stands. Altogether 45 sample trees from each stand in Talsi district and 9 sample trees from stand in Priekule district were selected. All three stands were placed in flat relief, on loamy, fresh mineral soil. The sample trees from different positions in the canopy layer were cored – two cores with the Presler borer were taken at the breast height from opposite directions. Three-ring width of dried, polished cores was measured manually, using Lintab 5 system (Rinntech, Heidelberg, Germany) with the precision of 0.01 mm. The measured time series of tree-ring width were crossdated and their quality was verified by a graphical inspection and statistically, using the program COFECHA (Grissino-Mayer, 2001).

3. RESULTS AND DISCUSSION

3.1. Factors affecting natural regeneration of European beech in clearcut areas and under canopy, and genetic diversity of second generation

Undergrowth below the canopies of the large trees receives less than 20% from the total radiation (Fig. 3.1.). Height of beech undergrowth had medium correlation with light conditions under canopy.
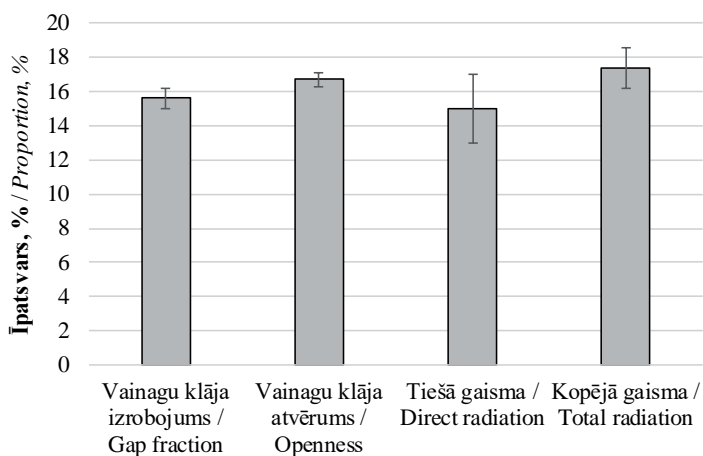
Fig. 3.1. **Average values (± 95% confidence interval) for the parameters characterizing light conditions in sample plots**

In both pure European beech stands all calculated radiation parameters were significantly intercorrelated and had similar variation (variation coefficient was ~0.40). Diffuse and total radiation were the main limiting factors for most of undergrowth species except Norway spruce. The lowest estimated threshold for diffuse radiation was observed for beech (0.37 mol m^{-2} day^{-1}). Also the observed threshold value for total radiation for beech (0.66 mol m^{-2} day^{-1}) was the lowest among the assessed tree species, except for ash which had the same value (Tab. 3.1.). In contrast, the highest threshold values of the diffuse radiation were estimated and observed for silver fir and rowan (ca 0.75 and 1.05 mol m^{-2} day^{-1}, respectively). Density of beech regeneration under the canopy ranged from 2500 to 13 000 seedlings ha^{-1}. This number exceeds the minimum density of regeneration required by legislation in Latvia (1500 seedlings ha^{-1}).

Table 3.1.

Calculated and measured values of light parameters

Species	Radiation (mol m^{-2} per day)			
	Calculated		Measured	
	Diffused	Total	Diffused	Total
Beech	0.37 (2.48%)	0.19 (0.42%)	0.28 (1.9%)	0.66 (1.45%)
Norway spruce	-	-	0.68 (4.61%)	1.45 (3.19%)
Silver fir	0.79 (5.32%)	2.42 (5.31%)	0.70 (4.74%)	1.89 (4.15%)

In open areas (after the clearcut) average density of beech seedlings was 2520 ±720 per hectare (ranging from 400 to 11 200 seedlings ha^{-1}). Pearson correlation analysis showed significant ($p < 0.05$) negative correlation between the density of beech seedlings and density of other species in regeneration ($r = -0.32$), projective cover of mosses ($r = -0.31$) and distance to the forest edge ($r = -0.38$) (Fig. 3.2.). Distance to forest edge was an indicator only of the potential abundance of seeds, since relief in the sites was flat and there were no trends in Ellenberg's values of herbs depending on distance from forest edge. European beech regeneration in open area (clearcut) was successful (at least 1500 seedlings ha^{-1}), if seed source was close enough (distance not bigger than 50 m).
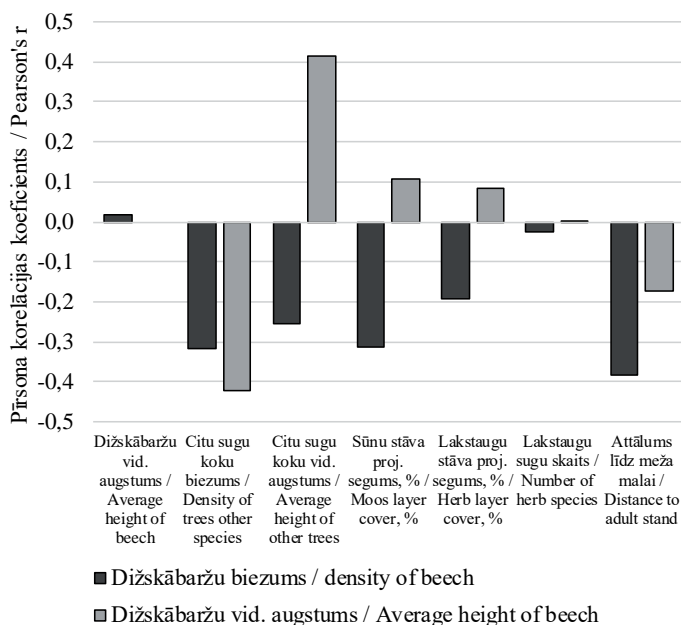
Fig. 3.2. **Factors affecting density and height of beech**

Multiple linear regression (including all traits and then gradually excluding the non-significant ones) indicated, that density and height of seedlings of other tree species and distance from the forest edge significantly ($p < 0.05$) affects density of beech seedlings ($R^2 = 0.34$).

Density and mean height of beech seedlings did not correlate significantly ($p = 0.92$), thus both traits were assessed separately. Density of regeneration was similar (no significant differences found, $p = 0.30$) in all clearcut areas, but there were significant differences of height of beech seedlings ($p < 0.001$).

Average height of beech seedlings was 201 ±25.8 cm and it had significant ($p < 0.01$) negative correlation with density of seedlings of other tree species

(r = -0.42) and significant positive correlation with height of seedlings of other tree species (r = 0.57). Multiple linear regression results demonstrated that only site (specific clearcut) had significant influence on height of beech seedlings (for other traits $p > 0.23$). Therefore each clearcut was analyzed separately. Only in one clearcut area multiple regression model was significant and, after gradually excluding non-significant factors, influence of density of seedlings of other tree species and height of seedlings of other trees species was confirmed (model $R^2 = 0.57$).

Genetic analysis of undegrowth reveal, that in stand in the Talsi district 53% sampled seedlings could be assigned to at least one parent ($p < 0.05$) from the same sample plot, while in the stand in Priekule district corresponding figure was 42%. Mostly one offspring per parent tree was found in the sample plot (Fig. 3.3.). In both stands dominance of a single parent-tree was noted – in Talsi district one parent tree had 13 offsprings, in Priekule district – 11 offsprings.
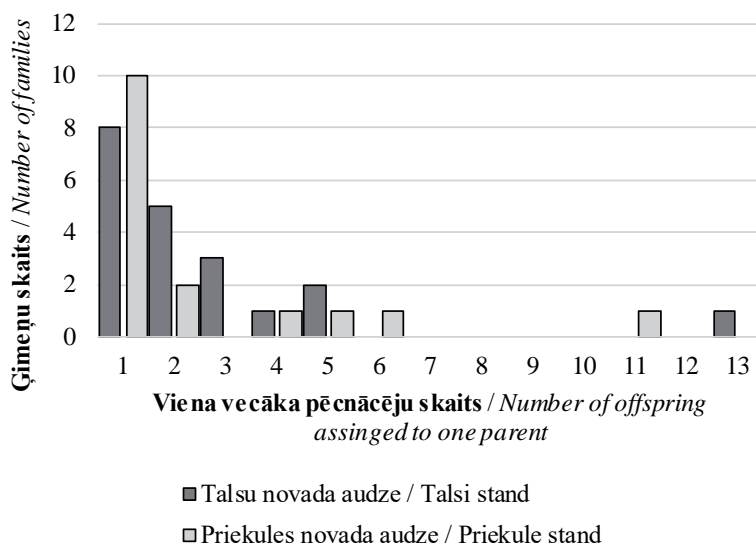
Fig. 3.3. **Distribution of trees in families in natural regeneration of beech**

The genetic diversity was not significantly different between stands and generations. While the origin of the reproductive material, used to establish these stands is not known, kinship and pairwise relatedness analysis indicated a higher degree of relatedness between the parental trees sampled from the Priekule district stand (Tab. 3.2.). There was no reduction of genetic diversity in the offspring generation.

Table 3.2.

Mean values of genetic diversity parameters (±standart error)

Population	Priekule district parents	Priekule district offsprings	Talsi district parents	Talsi district offsprings
Number of alleles	4.4 ±0.26	4.9 ±0.37	9.6 ±1.01	8.6 ±0.88
Number of alleles with frequency ≥ 5%	3.6 ±0.22	3.5 ±0.22	4.4 ±0.36	4.8 ±0.41
Number of effective alleles	3.0 ±0.19	2.6 ±0.19	4.2 ±0.45	4.3 ±0.42
Shannon's Information Index	1.2 ±0.06	1.1 ±0.06	1.6 ±0.11	1.6 ±0.10
Expected heterozygosity	0.6 ±0.03	0.6 ±0.03	0.7 ±0.03	0.7 ±0.03

3.2. Survival and growth of European beech second generation stands in central part of Latvia

Survival of beech and spruce twelve years after planting of mixed stand was high and similar: 73% and 78%, respectively. The height and diameter at breast height of beech was significantly larger than that of spruce (height 7.4 ±0.30 m and 3.1 ±0.30 m, respectively, and diameter 8.9 ±0.68 cm and 3.0 ±0.41 cm, respectively). Annual radial increment of beech notably and significantly exceeded annual radial increment of spruce (Fig. 3.4.), differences between both species were increasing with age. This trend was clearly linked to increasing competition between species in the stand. The maximum radius of beech crowns was similar than the distance between rows and between trees in rows, reaching on average 2.4 ±0.16 m. The growth of beech was notably affected by photosynthesis surface, characterized by maximum radius of crown – it had strong, significant correlation with height of the tree and with its diameter at breast height ($r = 0.71$ and $r = 0.87$, respectively). Results indicated, that during first years after planting beech occupies the space more efficiently than spruce, by developing large crown and using all the light resources available.
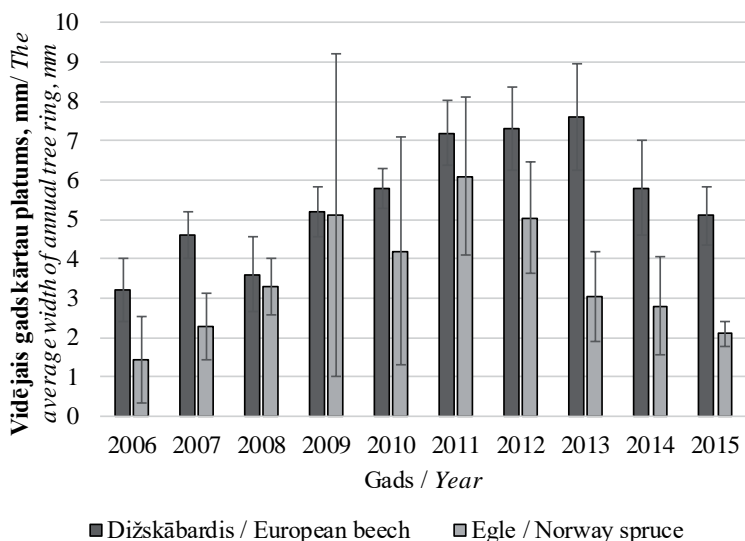
Fig. 3.4. **The average annual ring width (±95% confidence interval) for European beech and Norway spruce**

Survival of European beech 33 years after planting under canopy in Madona district (eastern Latvia) was high and reached ~80%, yet the minimum air temperature in the area during this period had been below -30°C (in 1983), suggested to be limiting for this tree species (Fang & Lechowicz; 2006; Kramer *et al*., 2010). Such high survival of beech in central part of Latvia might be related not only to shelter under canopy, but also to the origin of seeds – those were second generation beech trees from seeds collected in beech stands in western part of Latvia. So those beech had to adapt for only slightly harder climate than the one at the location of the first generation trees (Yakovlev *et al*., 2011).

Trees were generally small: height of beech ranged from 0.30 to 13 m, diameter at breast height – from 0.2 to 14.9 cm: most likely due to insufficient light to realize its growth potential. In the stand also some self-regeneration with sprouting had occurred, affecting the mean size of the trees. The diameter distribution had reverse J shape (Fig. 3.5.), that is typically for shade-tolerant species in such conditions. Results clearly demonstrate, that this tree species have adapted to survive under canopy for a long time, until some disturbance will make a gap in the crown cover and beech will have an opportunity for faster growth (Wagner *et al.*, 2010).
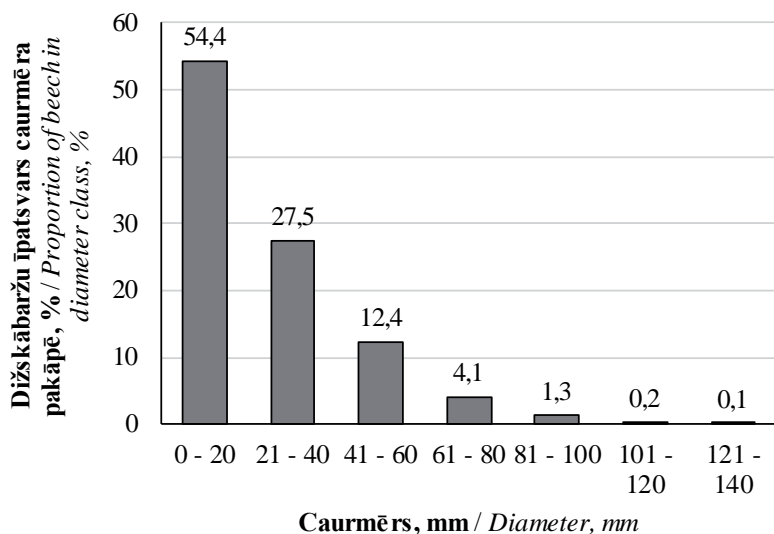
Fig. 3.5. **Proportion of beech in different diameter classes**

3.3. Height increment of European beech

Long-term height increment dynamics of beech in western part of Latvia was best described, using Chapman-Richards and Sloboda models. Coefficients of these models, obtained from sample-tree analysis, will be usable for the growth modelling tool, created in LSFRI Silava. It was found, that European beech in western part of Latvia is faster growing than in southern part of Sweden (considered to be within its natural distribution range). Hence the growth conditions in western Latvia are suitable for this tree species already in current (and past) climate. Additionally, adaptation had occurred also as the generations of beech changed: the second generation beech trees had larger height increment than the first generation beech trees (Fig. 3.6).
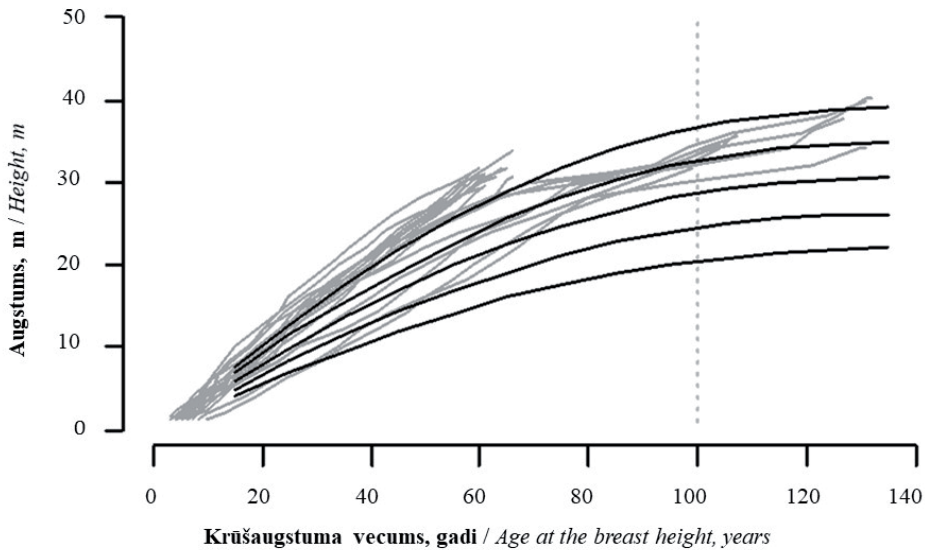
Fig. 3.6. **The non-linear dominant height model (black lines, Southern Sweden, Carbonnier, 1971) fitted to the observed data (grey lines, each line represents single tree)**

3.4. Influence of meteorological factors on radial growth of different dimension beech

Intra-seasonal growth assessment demonstrated, that the most intensive radial growth of European beech occurred from the beginning of vegetation season to the beginning of July. Radial growth was sensitive to water deficit. In period without rain development of the tree-ring stopped. After periods with notable precipitation, stem restored the water storage and afterwards resumed the increment (Fig. 3.7.). No limitations of growth related to temperature during vegetation season were found. Overall, the second generation beech tree had notably higher relative radial increment during the vegetation season than the first generation beech tree (0.93% and 0.38% from diameter at breast height, respectively).

Inter-seasonal analysis of radial increment also demonstrated a clear difference between generations of beech after introduction in Latvia. The first generation beech trees were more sensitive to meteorological conditions than the second generation beech trees (Fig. 3.8.).
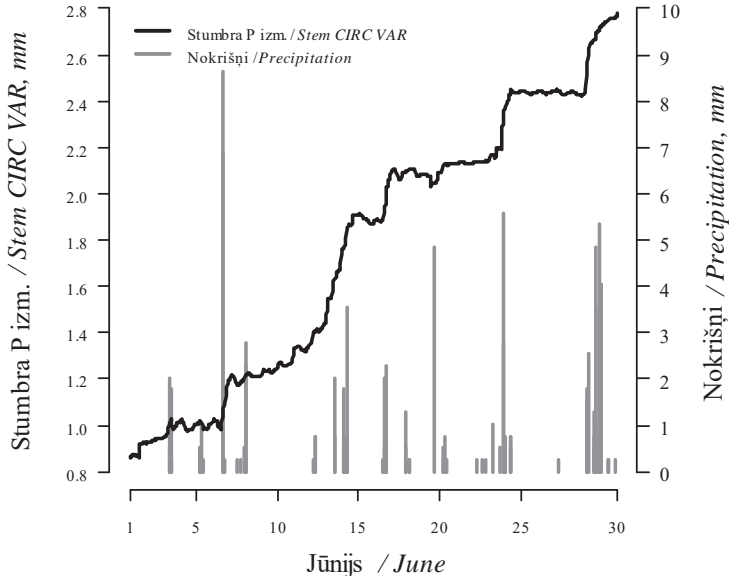
Fig. 3.7. **Changes in total stem circumference (*P*) for first generation beech in June and precipitation in the same period**
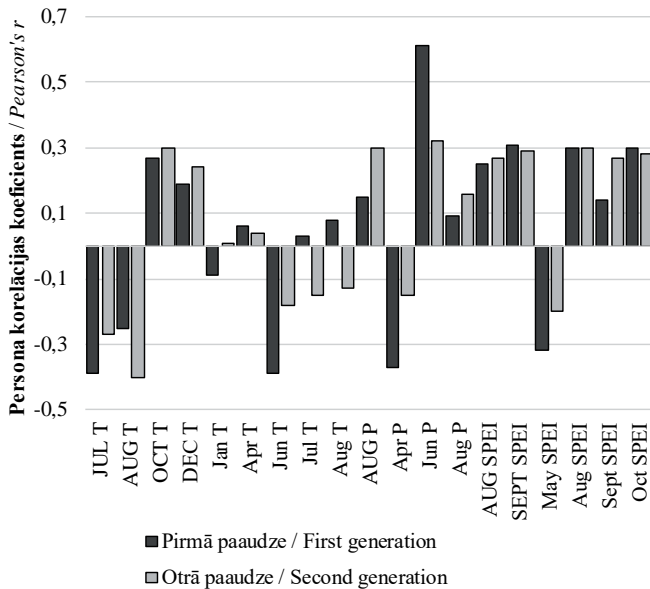
Fig. 3.8. **Pearson correlation coefficients (*r*) calculated between the residual chronologies of tree-ring width of beech of different age/generation and climatic (meteorological) factors: monthly mean temperature (*T*), precipitation (*P*) and standardized precipitation-evapotranspiration index (SPEI) for the common interval 1972–2015**

Months with capital letters – in the year before tree-ring was forming

The dominant beech trees of the first generation were especially sensitive to the sum of precipitation in June, characterizing water deficit in summer. Suppressed trees of the first generation were mostly sensitive to air temperature during winter period. Trees of the second generation were less affected by air temperature during winter period, indicating successful adaptation to conditions in Latvia. Both annual and seasonal growth dynamic suggested that faster growing trees of the second generation had stronger correlation between the radial increment and water availability.

Long increment chronologies from beech trees in western part of Latvia did not contain extremely narrow or missing tree-rings, indicating a suitability of the growing conditions in Latvia for this tree species.

CONCLUSIONS

1. Adaptation of European beech in Latvia has been successful: genetic diversity of its second generation in our country is not reduced, but height increment is larger in comparison to the first generation. Survival of the second generation beech trees under canopy is very high (>80%) also in the central part of Latvia.

2. Regeneration of European beech is successful in western part of Latvia both in open area (clearcut) up to 50 m from edge of mature stand and under canopy, even in light conditions that are not suitable for regeneration of other tree species. The average height of young European beech trees under the canopy significantly correlates with light conditions.

3. Growth models of European beech, developed as part of this thesis work, and data from sample plots in forest stands, indicate that increment of second generation of this tree species in Latvia is higher than that in southern Sweden and, in several plantations in young age – also higher than that of Norway spruce, suggesting strong potential to establish highly productive European beech stands.

4. The studied European beech from western part of Latvia do not have very narrow tree-rings, indicating suitability of current growing conditions for this tree species. Sensitivity to climatic conditions (especially to air temperature during winter period) was different for the first and the second generation of European beech, suggesting a positive effect of natural and human-made selection on adaptation.

5. Width of annual rings for European beech are mainly affected by climatic factors related to water deficit (temperature, precipitation) during summer and beginning of autumn. It causes reduction or even briefly stops radial increment until a complete replenishment of stem water storage. Considering predicted climate change it is important to plant European beech only in areas with sufficient soil moisture availability.

RECOMMENDATIONS

Productive European beech stands can be stablished in western part of Latvia. For this purpose use of seeds from local seed sources, specifically – from plus-trees selected as part of research for this thesis, are recommended. Establishment of seed orchard of European beech to provide secure seed supply is recommended.

Establishment of comprehensive provenance trials, including reproductive material also from the parts within distribution range of European beech with higher water deficit during summer period, than currently in Latvia, is sensible.

Continuous testing of adaptation of European beech to climate in eastern part of Latvia in controlled conditions (freezing tests) and experimental plantations is recommended.

LITERATŪRAS SARAKSTS / *REFERENCES*

1. Bolte A., Czajkowski T., & Kompa T. (2007). The north-eastern distribution range of European beech – a review. Forestry, 80, 413–429. doi: 10.1093/forestry/cpm028.

2. Born, A. (2011). Timber Feature – European Beech. Lejupielādēts no / *Retrieved from* http:// timberhub.com.au/timber-feature-european-beech.

3. Brunner A., & Nigh G. (2000). Light absorption and bole volume growth of individual Douglas-fir trees. Tree Physiology, 20, 323–332. doi: 10.1093/treephys/20.5-6.323.

4. Dreimanis, A. (2005). Mežsaimniecības vēsturiskā mantojuma zinātniska izpēte un izvērtējums Šķēdes mežu novadā – atskaite [Scientific research and assessment of silvicultural heritage in Skede forest district – A report]. Jelgava, 87 lpp. (in Latvian).

5. Dreimanis, A. (2006). Dižskābaržu audžu ražība Šķēdes mežu novadā [Productivity of European beech stands in Skede forest district]. LLU Raksti, 16(311), 97–100. (in Latvian).

6. Dobrovolný L., & Tesař V. (2010). Extent and distribution of beech (*Fagus sylvatica* L.) regeneration by adult trees individually dispersed over a spruce monoculture. Journal of Forest Science, 56(12), 589–599. doi: 10.17221/12/2010-JFS.

7. Fang J., & Lechowicz M. J. (2006). Climatic limits for the present distribution of beech (*Fagus* L.) species in the world. Journal of Biogeography, 33, 1804–1819. doi: 10.1111/j.1365-2699.2006.01533.x.

8. Giesecke T., Hickler T., Kunkel T., Martin T., & Richard H. W. (2007) Towards an understanding of the holocene distibution of *Fagus sylvatica* L. Journal of Biogeography, 34, 118–131.

9. Hanewinkel M., Cullmann D. A., Schelhaas M. J., Nabuurs G. J., & Zimmermann N. E. (2013). Climate change may cause severe loss in the economic value of European forest land. Nature Climate Change, 3(3), 203–207. doi: 10.1038/nclimate1687.

10. Hickler T., Vohland K., Feehan J., Miller P. A., Smith B., Costa L., Giesecke T., Fronzek S., Carter T. R., Cramer W., Kuhn I., & Sykes M. T. (2012). Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. Global Ecology & Biogeography, 21, 50–63. doi: 10.1111/j.1466-8238.2010.00613.x.

11. Kramer K., Degen B., Buschbom J., Hickler T., Thuiller W., Sykes M., & de Winter W. (2010). Modelling exploration of the future of European beech (*Fagus sylvatica* L.) under climate change – Range, abundance, genetic diversity and adaptive response. Forest Ecology and Management, 259,

2213–2222. doi: 10.1016/j.foreco.2009.12.023.

12. Kullman L. (2008). Thermophilic tree species reinvade subalpine Sweden – early responses to anomalous late Holocene climate warming. Arctic Antarctic and Alpine Research, 40, 104–110. doi: 10.1657/1523-0430(06-120).

13. Dobrovolný L., & Tesař V. (2010). Extent and distribution of beech (*Fagus sylvatica* L.) regeneration by adult trees individually dispersed over a spruce monoculture. Journal of forest science, 56 (12), 589–599.

14. Laiviņš M. (2010) Svešzemju platlapu sugu (*Fagus sylvatica, Quercus rubra, Juglans ailanthifolia*) augu sabiedrības Latvijā [Introduced broadleaf plant societies (*Fagus sylvatica, Quercus rubra, Juglans ailanthifolia*) in Latvia]. Latvijas veģetācija, 21, 41–71. (in Latvian).

15. Leugnerová G. (2007). *Fagus sylvatica* L. – European beech. Lejupielādēts no / *Retrieved from* https://botany.cz/en/fagus-sylvatica/.

16. Lizuma L., Klavins M., Briede A., & Rodinovs V. (2007). Long-term changes of air temperature in Latvia. In Kļavins M. (ed.) *Climate change in Latvia*. Riga, University of Latvia, pp. 11–20.

17. Peña J. F. B., Remeš J., & Bílek L. (2010) Dynamics of natural regeneration of even-aged beech (*Fagus sylvatica* L.) stands at different shelterwood densities. Journal of forest science, 56(12), 580–588.

18. Poljanec A., & Kadunc A. (2013). Quality and timber value of European beech (*Fagus sylvatica* L.) trees in the Karavanke Region. Croatian Journal of Forest Engineering, 34(1), 151–165.

19. Sabule L. (2009). Eiropas dižskābarža *Fagus sylvatica* (L.) izplatība Šķēdes mežu novadā [Distribution of European beech *Fagus sylvatica* (L.) in Skede forest district]. Maģistra darbs, Rīga. (in Latvian).

20. Sabule I. (2009). Klimatisko faktoru ietekme uz Eiropas dižskābarža *Fagus sylvatica* (L.) radiālo augšanu Šķēdes novadā [Impact of climatic factors to radial growth of European beech *Fagus sylvatica* (L.)]. Bakalaura darbs, Rīga (in Latvian).

21. Vanders K. (1957). Dižskabārža dabiskā atjaunošanās Latvijas PSR mežos [Natural regeneration of European beech in Latvian forests]. Latvijas Lauksaimniecības Akadēmijas Raksti, 7, 421–434. (in Latvian).

22. Vanders K. (1960a). Dižskābārža sēklu raža LLA Mācību un pētījumu mežsaimniecībā [Seed harvest of European beech in Research forests in Latvia]. Latvijas Lauksaimniecības Akadēmijas Raksti, 9, 511–525. (in Latvian).

23. Vanders K. (1960b). Eiropas dižskabāržu (*Fagus sylvatica* L.) introdukcijas sākums un gaita Latvijas PSR [Beginning and process of European beech (*Fagus sylvatica* L.) introduction in Latvia]. Latvijas Lauksaimniecības Akadēmijas Raksti, 10, 503–512. (in Latvian).

24. Von Wühlisch G. (2008). EUFORGEN Technical Guidelines for genetic conservation and use for European beech (*Fagus sylvatica*). Rome, Italy, 6 p.

25. Wagner S., Collet C., Madsen P., Nakashizuka T., Nyland R. D. & Sagheb-Talebi K. (2010). Beech regeneration research: From ecological to sylvi-cultural aspects. Forest Ecology and Management, 259, 2172–2182. doi: 10.1016/j.foreco.2010.02.029.

26. Walther G. R., Post E., Convey P., Menzel A., Parmesan C., Beebee T. J. C., Fromentin J.-M., Hoegh-Guldberg O., & Bairlein F. (2002). Ecological response to recent climate change. Nature, 416, 389–395. doi: 10.1038/416389a.

27. Yakovlev I. A., Asante D. K., Fossdal C. G., Junttila O., & Johnsen Ø. (2011). Differential gene expression related to an epigenetic memory affecting climatic adaptation in Norway spruce. Plant Science, 180, 132–139. doi: 10.1016/j.plantsci.2010.07.004.

Eiropas dižskābarža (*Fagus sylvatica* L.) atjaunošanos ietekmējošie faktori

Līga Puriņa [1], Una Neimane [1], Baiba Džeriņa [1], Āris Jansons [1]*

Kopsavilkums. Eiropas dižskābardis ir izteikti ēncietīga koku suga, kas salīdzinoši mazāk nekā egle cieš no vēja un trupes sēņu ietekmes. Ņemot vērā šīs īpašības un klimata izmaiņu prognozes, šī suga potenciāli varētu būt perspektīva plašākai izmantošanai Latvijā, īpaši platībās, kur iespējami un/vai lietderīgi izmantot nekailciršu meža apsaimniekošanu. Pētījuma mērķis ir iegūt sākotnējo informāciju par dižskābarža dabisko atjaunošanos Latvijas ziemeļrietumu daļā, ārpus tā dabiskās izplatības areāla. Pilotprojekta ietvaros Šķēdes mežu novadā, Eiropas baltegļu audzē, ar dižskābaržu piemistrojumu, ierīkoti divi parauglaukumi, kur izmērīts jauno koku augstums, novērtēti tuvākie sēklu koki, kā arī noteikti gaismas apstākļi zem vainagu klāja. Dižskābaržu paaugas grupās, kurās ierīkoti parauglaukumi, nav konstatēta citu koku sugu paauga. Jauno koku skaits uz hektāra, kuru augstums ir vismaz 0,2 m, vairākas reizes pārsniedz normatīvajos aktos par meža atjaunošanu prasīto skaitu. Tiešā parauglaukumu tuvumā (30 m rādiusā) konstatēti vairāki pirmā un otrā stāva dižskābarži – potenciālie sēklu avoti. Paaugas koku vidējais augstums vidēji cieši, statistiski būtiski, negatīvi korelē ar gaismas apstākļiem zem vainagu klāja. Kopumā secināms, ka šādi gaismas apstākļi vainagu klāja atvērumos un pirmā stāva sēklu koku skaits un attālums ir pilnīgi pietiekams, lai dižskābardis spētu sekmīgi dabiski atjaunoties ar sēklām. Tas norāda uz jau esošo mikroklimatisko apstākļu piemērotību šīs koku sugas izdzīvošanai un potenciālu tās plašākai izmantošanai nākotnē.

Nozīmīgākie vārdi: dabiskā atjaunošanās, izplatības areāls, nekailciršu meža apsaimniekošana.

<div style="text-align:center">•••</div>

Puriņa, L. [2], Neimane, U. [2], Džeriņa, B. [2], Jansons, Ā. [2]* **European beech (*Fagus sylvatica* L.) regeneration affecting factors.**

Abstract. European beech is a shade tolerant tree species that has higher resistance against root rot and wind damages than Norway spruce and could expand its area in future as the predicted climatic changes are favorable for its establishment and growth. Therefore European beech has a considerable potential for use in forest management, especially in areas

[1] LVMI Silava, Rīgas iela 111, Salaspils, LV-2169, Latvija; *e-pasts: aris.jansons@silava.lv

[2] Latvian State Forest Research Institute "Silava", 111 Riga str., Salaspils, LV-2169, Latvia,

*e-mail: aris.jansons@silava.lv

where shelterwood system can or shall be used.

Aim of the study was to assess natural regeneration of *Fagus sylvatic*a outside its natural distribution range: in north-eastern part of Latvia. Material for the pilot-study has been gathered in two sample plots, established in silver fir (*Abies alba* Mill.) stand with beech admixture. Height of beech seedlings and distance to nearest seed source has been measured and light conditions under the canopy assessed.

Measured natural regeneration consisted only of beech seedling; no other species were detected in the sample area, probably due to very limited light availability. Also mean height of beech seedlings has a strong, statistically significant negative correlation with light conditions under the canopy.

Density of beech seedlings with height at least 0.2 m several times exceeded the threshold for successful regeneration stated in the normative acts on forest regeneration (1500 trees ha^{-1}). Sufficient seed supply was ensured from several adult trees located in the vicinity (distance below 30 m) of the sample plot.

It can be concluded, that microclimatic conditions under the canopy as in the stands used for the study are suitable for successful natural regeneration of beech and therefore it can be expected to spread outside its instruction area in future. It also indicates the need for detailed study to determine the limitations of wider use of this species already in present climatic conditions.

Key words: natural regeneration, species distribution areal, selection cuts, shelterwood management.

• • •

Пуриня, Л. [3], Неймане, У. [3], Джериня, Б. [3], Янсонс, А. [3]* **Факторы влияющие на восстановление бука европейского (*Fagus sylvatica* L.).**

Резюме. Бук европейский очень тенелюбивая порода деревьев, которая сравнительно меньше чем ель подвергнута влиянию ветра и гнилевых грибов. Учитывая эти качества данной породы и прогнозы изменений климата, расширенное использование бука в Латвии потенциально перспективное, особенно на площадях, где возможно и/или целесообразно в ведении лесного хозяйства не прменять сплошные рубки. Цель исследования – получить изначальную информацию о естественном восстановлении бука в северо-западной части республики, вне ареала его естественного распространения. В рамках проекта в лесной области Шкеде (*Šķēde*) заложены две пробные площади в насаждении пихты европейской, с примесью бука, где измерена высота молодых деревьев, оценены ближайшие семенные деревья и условия освещённости под покровом крон. В группах букового подроста на пробных площадях не констатировано присутствие подроста других пород. Количество молодых деревьев на 1 га, высота которых достигает минимум 0,2 м, несколько раз превосходит численность таковых в нормативных актах по восстановлению леса. В прямой близости от пробных

[3] ЛГИЛ «Силава», ул. Ригас 111, Саласпилс, LV-2169, Латвия; *эл. почта: aris.jansons@silava.lv

площадей (в радиусе 30 м) выявлено несколько буков 1-ого и 2-ого ярусов, которые являются потенциальным источником семян. Средняя высота деревьев подроста статистически существенно, средне тесно и негативно коррелирует с условиями освещения под покровом крон. В общем итоге можно сделать вывод, что подобные условия в пробелах полога крон и число семенных деревьев на первом ярусе, а также расстояние вполне достаточные, чтобы бук смог успешно естественно восстанавливаться семенами. Это указывает на пригодность существующих условий микроклимата для выживания данной породы и на потенциал для расширенного выращивания бука в будущем.

Ключевые слова: естественное восстановление, ареал распространённости, ведение лесного хозяйства без сплошных рубок.

Ievads

Eiropas dižskābardis (*Fagus sylvatica*) ir izplatītākā koku suga lapu koku mežos Centrāleiropā. Tā koksne ir cieta un dekoratīva, un tiek plaši izmantota gan iekštelpu apdarei, gan durvju, mēbeļu, parketa, papīra un finiera ražošanā (Born, 2011), kā arī kuģu būvniecībā (Fagus sylvatica..., 2007). Dižskābarža augšanai piemērotākās ir vidēji mitras, vidēji skābas augsnes (Bolte *et al.*, 2007). Plaši izplatīts Centrāl-, Rietum- un Dienvideiropā. Tā areāls ziemeļos plešas līdz Vācijas ziemeļiem, Dānijai, Zviedrijas dienvidu daļai, Polijai; izolētas platības ārpus areāla sastopamas Latvijā. Austrumu robeža sasniedz Ukrainu, Moldāviju, Bulgāriju. Areāla dienvidu daļa ietver Balkānu pussalu, Apenīnu kalnus, Sicīliju, Spāniju (Leugnerová, 2007).

Latvijā Eiropas dižskābardis introducēts 18. gs. vidū (Mangalis, 2004), bet pirmās kultūras ierīkotas 1885. gadā Šķēdes novadā. Ierīkotas gan tīraudzes, gan mistraudzes, kopumā 11,1 ha platībā (Dreimanis, 2005). Vidzemē un Zemgalē dižskābarža stādījumi izsaluši 1939./1940. un 1955./1956. gada bargajās ziemās (Mangalis, 2004).

Dižskābaržu audzes Rietumlatvijā uzrāda labu ražību. Jau 40 gadu vecumā audzes krāja sasniedz 320 m³ ha⁻¹ (Mangalis, 2004). Dreimaņa (2006) pētījumā par dižskābaržu audžu ražīgumu Šķēdes novadā minēts, ka 115 gadus vecas, stādītas tīraudzes koksnes krāja sasniedz 818 m³ ha⁻¹: audzes vidējais šķērslaukums ir 50,5 m² ha⁻¹, vidējais valdaudzes koka augstums 34,8 m, vidējais valdaudzes koka caurmērs 41,7 cm. No sākotnēji iestādītajiem 5000 kokiem ha⁻¹ 115 gadu vecumā valdaudzē saglabājušies 352 un starpaudzē – 88 koki.

Dižskābarža augšanas periods ir samērā ilgs – sākas aprīlī un var turpināties līdz pat oktobrim. Augšanai nepieciešamā gaisa temperatūra ir virs 13°C (Sabule, 2009a). Pirmajos attīstības gados bieži cieš no pavasara salnām pat tad, ja citi klimatiskie faktori ir augšanai piemēroti. Sevišķi labi aug siltos un pietiekami mitros apstākļos. Augšanu veicina ne tikai pietiekams barības vielu un mitruma daudzums, bet arī tas, ka dižskābarža nobiras sadalās relatīvi ātri, tādējādi nodrošinot barības elementu strauju apriti (Dreimanis, 2005). Dižskābarža izplatību limitē galvenokārt klimatiskie faktori. Lai dižskābarži spētu sekmīgi augt

un atjaunoties, nepieciešamais nokrišņu daudzums ir ~500 mm gadā vai ~250 mm no maija līdz septembrim, jūlija vidējā gaisa temperatūra – zemāka par 19°C, sala periods – īsāks par 141 dienu, janvāra vidējā gaisa temperatūra – virs –3°C, vidējā gaisa temperatūra – vismaz 7°C (ne mazāk kā 213 dienas gadā) vai vidējā gaisa temperatūra vismaz 5°C (ne mazāk kā 245 dienas gadā) (Bolte, 2007).

Laika periodā no 1960. līdz 1990. gadam tikai Kurzemes rietumu piekrastē janvāra vidējā gaisa temperatūra pārsniedza –3°C (kas tiek uzskatīts par vienu no kritērijiem šīs sugas areāla ziemeļu robežas noteikšanai), tādēļ pārējā Latvijas teritorija dižskābarža audzēšanai līdz tam nebija piemērota. Tomēr prognozes par gaidāmajām klimata izmaiņām liecina, ka līdz 21. gadsimta vidum vidējā gaisa temperatūra janvārī visā valsts teritorijā varētu paaugstināties par aptuveni 2,7-3°C (Jansons, 2010). Tas nozīmē, ka dižskābarža augšanai atbilstoša temperatūra šajā mēnesī būtu visā Kurzemē, Vidzemes jūrmalā, Rīgas apkārtnē un daļā Zemgales (aptuvenā reģiona robeža – joslā Sigulda–Aizkraukle–Nereta).

Šķēdes mežu novadā veiktajā pētījumā konstatēts, ka aprīļa nokrišņu daudzums negatīvi korelē ar koku radiālo pieaugumu, savukārt vasaras mēnešu un septembra nokrišņu daudzuma korelācija ir pozitīva. Nav noteikta būtiska sakarība starp koku radiālo pieaugumu un vidējo gaisa temperatūru (Sabule, 2009b).

Mežsaimniecībā arvien vairāk pievēršas jautājumam par nepieciešamību plašāk izmantot nekailciršu metodi. Līdz šim Latvijā pieejama tikai viena ēncietīga koku suga – parastā egle, kas piemērota šādam apsaimniekošanas veidam. Eiropas dižskābardis ir izteikti ēncietīgs visā augšanas laikā, kā arī mazāk nekā egle cieš no vēja un trupes sēņu nodarītiem bojājumiem, tādēļ šī suga būtu perspektīva platībās, kur pielietota nekailciršu metode.

Pētījuma *mērķis* ir iegūt sākotnējo informāciju par dižskābarža dabisko atjaunošanos Latvijas ziemeļrietumu daļā, ārpus tā izplatības areāla.

Materiāli un metodes

Pētījums veikts Meža pētīšanas stacijas Šķēdes mežu novada 23. kvartāla 14. nogabalā, Eiropas baltegļu audzē ar atsevišķu bērzu, ozolu, egļu un dižskābaržu piemistrojumu. Audze ierīkota 1897. gadā. Meža tips – vēris.

Šajā audzē 2012. gada rudenī ierīkoti 2 parauglaukumi dižskābaržu paaugas grupās. Katrai grupai apzināta forma un izmērs, tās garenvirzienā novilkts transekts, kas sadalīts 4 m garos posmos. Katrā posmā atsevišķi uzskaitīta dižskābaržu paauga: 2 m platā joslā (1 m uz katru pusi no transekta), ar precizitāti līdz 10 cm uzmērīts pilnīgi visu jauno dižskābaržu augstums, un 4 m platā joslā (papildus vēl metrs uz katru pusi no ass līnijas) izmērīts to jauno dižskābaržu augstums, kas pārsniedz 1,3 m (līdz 4 m augstumam ar precizitāti līdz 10 cm, augstākiem ar precizitāti 0,5 m). Katrā transekta posmā noteikts tālākā pie paaugas grupas piederošā jaunā dižskābarža attālums no transekta abās tā pusēs (lai iegūtu priekšstatu par paaugas grupas aizņemto platību un formu). Katrā 4 m posmā abās transekta pusēs uzskaitīts tuvākais pirmā stāva koks, kas ietekmē gaismas apstākļus paaugas

grupai, noteikta arī tā suga un diametrs. Visos virzienos, 30 m attālumā no transekta, atrasti visi pirmā un otrā stāva dižskābarži, izmērīts to augstums, diametrs un attālums no transekta, kā arī noteikta piederība tuvākajam parauglaukuma 4 m posmam.

Lai raksturotu gaismas apstākļus paaugas grupās, katra transekta posma viduspunktā uzņemts vainagu klājs, izmantojot fotoaparātu *Nikon Coolpix* 8400, ar platleņķa (*fish-eye*) objektīvu (FC-E9) un komplektējošu aprīkojumu (WinSCANOPY O-Mount). Attēlu fiksēšanas brīdī fotoaparāts novietots 1,3 m augstumā, nolīmeņots un noorientēts pret ziemeļiem. Fotografēšana veikta ne vēlāk kā stundu pēc saules lēkta, lai novērstu tiešo saules staru ietekmi. Katrā punktā iegūti 3 attēli ar dažādu ekspozīcijas laiku.

Tālākai audzes gaismas režīma parametru noteikšanai attēli apstrādāti ar *WinSCANOPY 2006a Pro* datorprogrammu. Analīzei izmantoti attēli ar vidēju ekspozīcijas laiku (0,034 s).

Analizējot gaismas apstākļus zem vainagu klāja, ņemti vērā šādi parametri: vainagu klāja izrobojums (*gap fraction*), vainagu klāja atvērums (*openness*), tiešās gaismas īpatsvars (*direct site factor*) un kopējās gaismas īpatsvars (*total site factor*). Visi šie rādītāji ir relatīvas vērtības un tiek izteikti procentos. Vainagu klāja izrobojums ir attēlā redzamo debesu laukumu īpatsvars no kopējās attēla platības. Vainagu klāja atvērums ir vainagu klāja izrobojums, kas transformēts kā projekcija uz zemes virsmas. Tiešās gaismas īpatsvars ir attiecība starp vidējo dienas tiešo radiāciju zem vainagu klāja un vidējo dienas tiešo radiāciju virs vainagu klāja veģetācijas

periodā. Kopējās gaismas īpatsvars ir attiecība starp kopējo (tiešo un izkliedēto) vidējo dienas radiāciju zem vainagu klāja un kopējo vidējo dienas radiāciju virs vainagu klāja veģetācijas periodā.

Rezultāti

Pirmā parauglaukuma transekta garums ir 48 m, uzskaitīto jauno dižskābaržu vidējais skaits uz hektāra ir 3906 un vidējais augstums 1,2 m, no tiem 3593 kokiem ha^{-1} augstums ir vismaz 0,2 m. Otrā parauglaukuma transekta garums ir 16 m, uzskaitīti vidēji 9375 koki ha^{-1} ar vidējo augstumu 2,1 m, no tiem 8281 kokiem ha^{-1} augstums ir vismaz 0,2 m.

Abos parauglaukumos, 30 metru rādiusā ap transektu, konstatēti pirmā un otrā stāva dižskābarži, kas varētu būt potenciālie sēklu avoti paaugas grupām. Pirmajā parauglaukumā (transekta garums 48 m) uzmērīti 7 dižskābarži (no tiem divi otrā stāva), kuru attālums no transekta variē no 1 līdz 17 metriem. Pirmā stāva dižskābaržu vidējais augstums ir 31,2 m (variē no 28,4 līdz 33,4 m), vidējais caurmērs 35,2 cm (variē no 26,9 līdz 47,9 cm). Otrajā parauglaukumā uzmērīti 4 dižskābarži 5-25,5 m attālumā no transekta, no kuriem tikai 1 ir pirmā stāva koks, kam augstums 33,4 m un caurmērs 48,5 cm. Pirmajā stāvā augošo dižskābaržu skaits un attālums līdz konkrētajam transekta posmam nekorelē ar katrā posmā uzskaitīto paaugas dižskābaržu skaitu, augstumu vai paaugas grupas platumu. No tā secināms, ka esošo pirmā stāva dižskābaržu, kā sēklu avotu skaits un attālums, ir pietiekams, lai sekmīgi norisētu dižskābaržu dabiskā atjaunošanās.

Visos 15 punktos, kuros uzņemti

fotoattēli, gaismas apstākļi ir samērā līdzīgi. Audzes vainagu klāja izrobojums variē no 14-19,5 %, vidēji 15,5 % (1. att.). Audzes vainagu klāja atvēruma vērtības ir līdzīgas – no 15,1-20,6 %, vidēji 16,7 %. Vidējais tiešās gaismas īpatsvars ir 15 %, tas variē no 8-20,6 %, bet kopējās gaismas īpatsvars ir vidēji 17,4 %, variē no 13,2-22,4 %.

Nevienam no minētajiem gaismas apstākļus raksturojošiem parametriem nav būtiskas korelācijas ar paaugas koku skaitu katrā konkrētā transekta 4 m posmā, paaugas grupas platumu, attālumu no transekta līdz tuvākajam gaismas apstākļus ietekmējošam pirmā vai otrā stāva kokam, kā arī ar attālumu starp tuvākajiem gaismas apstākļus ietekmējošiem pirmā vai otrā stāva kokiem abās transekta pusēs. Vienīgā pazīme, kas uzrāda vidēji ciešu, negatīvu korelāciju ar

gaismas apstākļus raksturojošiem parametriem, ir vidējais paaugas koku augstums. Vidējā paaugas koku augstuma korelācijas koeficients ar vainagu klāja izrobojumu $r = -0,48$ (p = 0,07), ar vainagu klāja atvērumu $r = -0,47$ (p = 0,07), ar tiešās gaismas īpatsvaru $r = -0,60$ (p = 0,02), ar kopējās gaismas īpatsvaru $r = -0,62$ (p = 0,012). Tajos transekta posmos, kur zem vainagu klāja nonāk vairāk gaismas, vidējais paaugas dižskābaržu augstums ir mazāks.

Diskusija

Dižskābaržu dabisko atjaunošanos ar sēklām ietekmē ne tikai klimats, gaismas apstākļi, bet arī citi faktori, piemēram, sēklu izplatīšanās ātrums un attālums no sēklu avota (dižskābaržu audzes vai atsevišķi koki reproduktīvā vecumā). Dižskābaržu sēklas ir
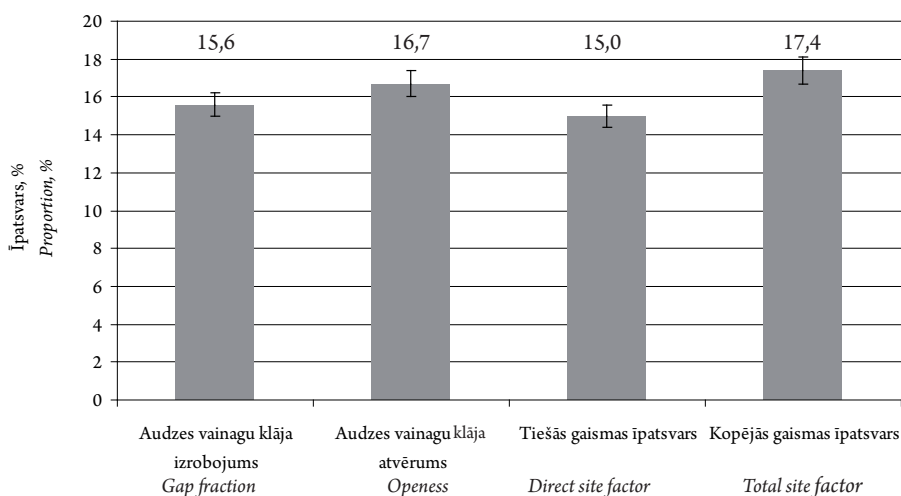
1. attēls. Gaismas apstākļus raksturojošo parametru vidējās vērtības un ticamības intervāls.
Figure 1. Average values and confidence interval for the parameters characterizing light conditions in sample plots.

salīdzinoši smagas (ap 250 mg), tādēļ ar vēju tās praktiski neizplatās. Sēklu izplatīšanos veicina putni un ūdensteces (Götmark *et al.*, 2005), kā arī peļveidīgie grauzēji. Izpētīts, ka pēdējie ozolzīles izplata 10-20 m attālumā, savukārt sīļi – līdz pat 4 km, tomēr parasti dažus simtus metru no sēklu avota (Kollmann, Schill, 1996). Par dzīvnieku ietekmi uz dižskābaržu sēklu izplatību ir salīdzinoši maz pētījumu. Noskaidrots, ka ar šīm sēklām barojas 26 sugu putni un 17 sugu zīdītāji. No putniem galvenais sēklu izplatītājs ir sīlis, bet to dara arī riekstroži, baloži, zīlītes un žubītes (Dobrovolný, Tesař, 2010). Sīļi spēj aiznest sēklas pat līdz 4 km tālu (Johnson, Adkisson, 1985). Peļveidīgie grauzēji dižskābarža riekstiņus parasti pārnēsā ne vairāk kā 30 metru attālumā (Kunstler, 2004).

Čehijā, izpētot dižskābaržu dabisko atjaunošanos ap individuāliem kokiem egļu tīraudzēs, konstatēts, ka lielākais sējeņu blīvums ir tieši zem koka vainaga, bet salīdzinoši augsts blīvums ir arī 15-30 metru rādiusā ap koku. Tālākie sējeņi ir atrasti pat 150-250 m attālumā no koka, atkarībā no reljefa. Arī citos pētījumos iegūti līdzīgi rezultāti – vidējais rādiuss, kura ietvaros sējeņi sastopami lielā blīvumā, variē no 13 līdz 30 metriem, bet maksimālais sējeņu izplatīšanās attālums – līdz pat 250 metriem (Dobrovolný, Tesař, 2010).

No pētījuma rezultātiem secināms, ka parauglaukumos sēklu avotu apjoms, ražība un attālums ir pietiekami, lai nodrošinātu nepieciešamo sēklu daudzumu dabiskās atjaunošanās sekmīgai norisei.

Dižskābardis sāk ziedēt un ražot sēklas apmēram 40-50 gadu vecumā atklātās platībās un 60-80 gadu vecumā – blīvās mežaudzēs (Mauriņš, Zvirgzds, 2006), vai arī gadījumos, kad koku caurmērs pārsniedz 20 cm (Leak, Graber, 1993). Dati par bagātīgu sēklu ražas gadu biežumu dažādos pētījumos ir atšķirīgi: ik pēc trijiem (Leak, Graber, 1993), pieciem (Mauriņš, Zvirgzds, 2006) vai ik pēc 4-6 gadiem (Peña *et al.*, 2010).

Dižskābarža sēklu daudzumu samazina dažādi dzīvnieki, kuri tās lieto uzturā. Visvairāk sēklas iznīcina peles, strupastes un citi grauzēji, kā arī putni (Giesecke *et al.*, 2007). No fizioloģisko gatavību sasniegušajām sēklām 40 %, pirms nokrīt zemē, ir kukaiņu, grauzēju vai putnu bojātas (Leak, Graber, 1993). Daļa no sēklām nav dzīvotspējīgas dažādu apputeksnēšanās un attīstības traucējumu dēļ (Graber, Leak, 1992). Šādu neattīstīto sēklu procents dažādos pētījumos svārstās no 13 % (Leak, Graber, 1993) līdz 27,9 % (Graber, Leak, 1992). K. Vandera (1957) konstatējis, ka atsevišķos gados tukšo sēklu daudzums sasniedz pat 30-80 %, un sēklu dīdzība variē no 70 % līdz 90 %. Sēklas dīgst pavasarī. Jauno sējeņu izdzīvošanu limitējošie faktori ir vēlās pavasara salnas un mitruma trūkums (Aranda *et al.*, 2002). Giesecke un citi (2007) aprakstīja, ka jaunos kokus bojā briežu dzimtas pārnadži, kā arī kukaiņi, grauzēji, gliemji un sēnes. Tomēr, pretēji šai atziņai, mūsu apsekotajos parauglaukumos jaunajiem dižskābaržiem pārnadžu bojājumi netika novēroti.

Lai dižskābaržu pauga varētu sekmīgi augt un attīstīties, pirmajos gados jaunajiem sējeņiem ir nepieciešama segaudze, kas tos pasargā no vēlajām pavasara salnām, sausuma un augstas gaisa temperatūras (Huss,

2004). Segaudze jaunajiem dižskābaržiem samazina arī lakstaugu un saulmīļu koku sugu paaugas konkurenci. Dižskābaržu audzē viengadīgu sējeņu skaits var sasniegt pat 300 000 koku ha⁻¹, pirmajos trīs dzīves gados augsta ir to iznīkšana, koku skaits var samazināties vairākas reizes, un arī pēc 5 gadu vecuma sasniegšanas paauga nav uzskatāma par stabilu, jo koku daudzums joprojām turpina samazināties (Peña *et al.*, 2010).

Pētījuma laikā ierīkotajos parauglaukumos dižskābaržu paaugas grupās netika konstatēta citu koku un krūmu sugu klātbūtne. Tā kā pieaugušo audzi ap parauglaukumiem veido galvenokārt Eiropas baltegles, ar nelielu bērzu, ozolu un dižskābaržu piemistrojumu, bija gaidāms, ka paaugā tiks atrastas arī šīs koku sugas. Bet, acīmredzot, bērzu augšanai zem audzes vainagu klāja pietrūkst gaismas, savukārt ozolu un balteglu atjaunošanos ierobežo lielais pārnadžu blīvums.

Meža atjaunošanas, meža ieaudzēšanas un plantāciju meža noteikumi paredz (Meža atjaunošanas..., 2012), ka dižskābardis izmantojams meža atjaunošanai vai ieaudzēšanai šādos meža tipos: damaksnī, vērī, gāršā, slapjajā damaksnī, slapjajā vērī, slapjajā gāršā, šaurlapju un platlapju ārenī un kūdrenī, kā arī purvaiņos. Mežaudzes koku minimālajam augstumam jāsasniedz 0,2 m, un koku skaitam uz hektāra jābūt vismaz 1500, maksimālais koku skaits uz hektāra netiek ierobežots. Abos ierīkotajos parauglaukumos uzskaitīto paaugas dižskābaržu skaits uz hektāra vairākas reizes pārsniedza normatīvajos aktos prasīto. Jāņem vērā, ka netika uzskaitīti pilnīgi visi paaugas koki, tātad reālais koku skaits uz hektāra bija pat vēl lielāks.

Dižskābardis ir izteikti ēncietīga koku suga, kas ēncietību saglabā visa mūža garumā. Ja jaunie koki saņem tikai 20 % no pilna apgaismojuma, to dzinumu garums nesamazinās, bet samazinās caurmērs, pumpuru garums un stādu svars (Dreimanis, 2005). Tomēr, neskatoties uz to, vainagu klājā ir nepieciešams atvērums, zem kura sekmīgi varētu veidoties pietiekami blīva paaugas grupa (Szwagrzyk *et al.*, 2001). Atvērumi vainagu klājā pieaugušā dižskābaržu tīraudzē parasti sastāda 3-20 %. Vidējais atvēruma lielums ir 50 m², kas sakrīt ar viena koka vainaga platību. Šādi atvērumi parasti rodas, ejot bojā vienam kokam (Nakashizuka, 1987). Augot vidējā vai stiprā apēnojumā, jaunie koki ir garāki un ar labāku stumbra formu nekā pilna apgaismojuma apstākļos (Leonhardt, Wagner, 2006). Citā pētījumā secināts, ka, palielinoties atvērumam vainagu klājā, pieaug paaugas koku augstuma izkliede (Madsen, Larsen, 1997).

Paaugas koku vidējā augstuma negatīvā korelācija ar gaismas apstākļiem zem vainagu klāja varētu būt skaidrojama ar to, ka pietiekamas gaismas apstākļos jaunie dižskābarži neizstīdz, kā arī, ka labāk apgaismotajos transekta posmos pēdējo dažu gadu laikā ir iesējušies papildus jaunie kociņi zem jau iepriekš ieaugušās paaugas, kas nenotiek sliktāk apgaismotajos posmos, kur tiem pietrūkst gaismas.

Kopumā varam secināt, ka pētījumā konstatētie gaismas apstākļi vainagu klāja atvērumos un pirmā stāva sēklu koku skaits un attālums ir pilnīgi pietiekami, lai dižskābardis spētu sekmīgi dabiski atjaunoties ar sēklām. Paredzam, ka sakarā ar prognozētajām klimata

izmaiņām nākotnē, dižskābardim augšanas apstākļi Latvijā tuvināsies optimālajiem, un tas varētu sekmīgi augt un atjaunoties ne tikai Kurzemes rietumu piekrastē, bet jau aptuveni pusē Latvijas teritorijas.

Literatūra

Aranda, I., Gil, L., Pardos, J.A. (2002). Physiological responses of *Fagus sylvatica* L. seedlings under *Pinus sylvestris* L. and *Quercus pyrenaica* Willd. overstories. Forest Ecology and Management, 162(2-3), 153-164. DOI: 10.1016/S0378-1127(01)00502-3.

Bolte, A., Czajkowski, T. & Kompa, T. (2007). The north-eastern distribution range of European beech – a review. Forestry, 80(4), 413-429. DOI: 10.1093/forestry/cpm028.

Born, A. (2011). Timber Feature – European Beech. [WWW dokuments]. – URL http://timberhub.com.au/timber-feature-european-beech [izdrukāts 2013. gada 12. martā].

Dobrovolný, L. & Tesař, V. (2010). Extent and distribution of beech (*Fagus sylvatica* L.) regeneration by adult trees individually dispersed over a spruce monoculture. Journal of Forest Science, 56(12), 589-599.

Dreimanis, A. (2005). Mežsaimniecības vēsturiskā mantojuma zinātniska izpēte un izvēr-tējums Šķēdes mežu novadā – atskaite. Jelgava, 87 lpp.

Dreimanis, A. (2006). Dižskābaržu audžu ražība Šķēdes mežu novadā. LLU Raksti, 16(311): 97-100.

Fagus sylvatica ssp. sylvatica (2007). [WWW dokuments]. – URL http://ecocrop.fao.org/ecocrop/srv/en/cropView?id=6080 [izdrukāts 2013. gada 4. martā].

Giesecke, T., Hickler, T., Kunkel, T., Sykes, M. & Bradshaw, R.H.W. (2007). Towards an understanding of the Holocene distribution of *Fagus sylvatica* L. Journal of Biogeo-graphy, 34(1): 118-131. DOI: 10.1111/j.1365-2699.2006.01580.x.

Götmark, F., Fridman, J., Kempe, G. & Norden, B. (2005). Broadleaved tree species in conifer-dominated forestry: Regeneration and limitation of saplings in southern Sweden. Forest Ecology and Management, 214(1-3): 142-157. DOI: 10.1016/j.foreco.2005.04.001.

Graber, R.E. & Leak, W.B. (1992). Seed fall in an old-growth northern hardwood forest. Forest Expariment Station. Research Paper NE-663, 1-15.

Huss, J. (2004). Stand establishment, treatment and promotion – European experience. In Eciclopedia of forest sciences. Spain. 14-26 pp.

Jansons, Ā. (2010). Mežsaimniecības pielāgošana klimata izmaiņām – zinātniskā pētījuma atskaite. [WWW dokuments]. – URL http://www.lvm.lv/lat/lvm/zinatniskie_petijumi/jaunumi/?doc=12872 [izdrukāts 2012. gada 8. novembrī].

Johnson, V.C. & Adkisson, C.S. (1985). Dispersal of beech nuts by blue jays in fragmented landscapes. American Midland Naturalist, 113: 319-324.

Kollmann, J. & Schill, H.P. (1996). Spatial patterns of dispersal, seed predation and germination during colonization of abandoned grassland by *Quercus petraea* and *Corylus avellana*. Vegetatio, 125: 193-205. DOI: 10.1007/BF00044651.

Kunstler, G., Curt, T. & Jacques, L. (2004). Spatial pattern of beech (*Fagus sylvatica* L.) and oak (*Quercus pubescens* Mill.) seedlings in natural pine (*Pinus sylvestris* L.) woodlands. European Journal of Forest Research, 123: 331-337. DOI: 10.1007/s10342-004-0048-0.

Leak, W.B. & Graber, R.E. (1993). Six-year beechnut production in New Hampshire. Northeastern Forest Expariment Statlon. Research Paper NE-677: 1-10.

Leonhardt, B. & Wagner, S. (2006). Quality aspects of advanced-planted beech under spruce shelter. Forst und Holz, 61 (11): 454-457.

Leugnerová, G. (2007). *Fagus sylvatica* L. – European beech (27.12.2007.). [WWW dokuments]. – URL http://botany.cz/en/fagus-sylvatica/ [izdrukāts 2013. gada 12. martā].

Madsen, P. & Larsen, J.B. (1997). Natural regeneration of beech (*Fagus sylvatica* L.) with respect to canopy density, soil moisture and soil carbon content. Forest Ecology and Management, 97: 95-105. DOI: 10.1016/S0378-1127(97)00091-1.

Mangalis, I. (2004). Meža atjaunošana un ieaudzēšana. Rīga, SIA „Et Cetera". 455 lpp.

Mauriņš, A., Zvirgzds, A. (2006). Dendroloģija. Rīga, LU Akadēmiskais apgāds. 447 lpp.

Meža atjaunošanas, meža ieaudzēšanas un plantāciju meža noteikumi (2012). LR Ministru kabineta noteikumi Nr. 308. Rīga.

Nakashizuka, T. (1987). Regeneration dynamics of beech forests in Japan. Vegetetio, 69(1-3): 169-175.

Peña, J.F.B., Remeš, J. & Bílek, L. (2010). Dynamics of natural regeneration of even-aged beech (*Fagus sylvatica* L.) stands at different shelterwood densities. Journal of Forest Science, 56(12): 580-588.

Sabule, I. (2009b). Klimatisko faktoru ietekme uz Eiropas dižskābarža *Fagus sylvatica* (L.) radiālo augšanu Šķēdes novadā. Bakalaura darbs, Rīga.

Sabule, L. (2009a). Eiropas dižskābarža *Fagus sylvatica* (L.) izplatība Šķēdes mežu novadā. Maģistra darbs, Rīga.

Szwagrzyk, J., Szewczyk, J. & Bodziarczyk, J. (2001). Dynamics of seedling banks in beech forest: results of a 10-year study on germination, growth and survival. Forest Ecology and Management, 141: 237-250. DOI: 10.1016/S0378-1127(00)00332-7.

Vanders, K. (1957). Dižskābarža dabiskā atjaunošanās Latvijas PSR mežos. LLA Raksti, 6. sēj.

Light requirements of regeneration of European beech at its northeasternmost stand in Europe—a case study in Latvia

Āris Jansons[1], Roberts Matisons*[1], Līga Jansone[1] and Andis Adamovičs[1]

* - corresponding author, robism@inbox.lv, +371 29789581

Authors's address: [1] LSFRI "Silava", Rigas str. 111, Salaspils, LV2169, Latvia, aris.jansons@silava.lv

Abstract

Light requirements of European beech and other species regeneration in the northeasternmost beech stand in Europe (western part of Latvia) were assessed by the logarithmic regression analysis between the total height of samplings and light parameters (direct, diffuse and total radiation below crowns). Amongst the accounted ten regenerating tree species, beech and ash had the lowest requirements for light, which were also lower than the minimum light parameters observed in the neighbouring mixed stands, suggesting conditions for a successful spread. Although ash might be competing with beech, lately its regeneration has been strongly limited by the dieback. Additionally, the minimum requirements of the other accoutred species were higher, suggesting that beech would outcompete them for light in a longer term. Amongst the studied light parameters, the diffuse and total radiation below crown appeared to mainly influence the regeneration.

Keywords: *Fagus sylvatica*; canopy opening; radiation; natural regeneration; sapling growth.

Introduction

A norther shift of the vegetation zones, hence, the species distribution is expected in Europe due to climate change and the northern limit of European beech (*Fagus sylvatica* L.) might occur in The Baltic States even by the end of the 21st century (Kramer *et al.*, 2010). Consequently, the economic importance of beech could increase there. The spread of the tree species is determined by the speed of seed dispersal, which, in a modern landscape, is largely affected by human activity e.g. introduction (Petit *et al.*, 2004), and the success of the establishment and growth (Bradshaw & Lindbladh, 2005). The establishment of the alien species is largely affected by the competition with the native ones (Sebert-Cuvillier *et al.*, 2008).

European beech is a shade tolerant species (Minotta & Pinzauti, 1996), which can dominate in the understory in different site types (Madsen & Larsen, 1997). For a successful regeneration, beech requires shelterwood (Ritter *et al.*, 2005), and openings in the canopy are the main source of light (Wagner *et al.,* 2010; Runkle, 2013). Nevertheless, in such gaps, beech might be competing with other shade tolerant species, e.g. maples (*Acer* L.), which might burden beech regeneration (Galbraith-Kent & Handel, 2008; Wagner *et al.*, 2010). The requirements for light are important factor shaping the understory and affecting the development of stand (Poulson & Platt, 1989; Modry *et al.*, 2004) and such information might be useful for the assessment of the potential of the novel species to spread. Hence, the aim of this study was to assess the

1

requirements for light of regeneration of European beech and the native species growing in the northeasternmost beech stand in Europe in Latvia (Bolte *et al.*, 2007).

Material and methods

Study area

The study area is an experimental plantation of alien tree species in the western part of Latvia (57°15′ N, 22°41′ E, elevation ca. 90 m a.s.l.). The topography is flat and the soil is loamy (*Oxalidosa* forest type). The climate is moderately continental (the mean annual temperature is +6.2 °C and precipitation is ca. 600 mm). The studied stand is a plantation (ca. 9 ha) of European beech, established around 1890s (Dreimanis, 2004). At present, the studied stand is mainly formed by beech, although some alien and local species occur in the undergrowth and canopy. The density of stand is ca 700 trees ha^{-1}, mean height is ca. 33 m and the basal area is ca. 35 m^2 ha^{-1}. Beech regeneration is successful and several generations co-occur within the same territory and also in the neighbouring stands. Beech saplings are scattered over the territory of plantation and surrounding it, forming groups in the canopy openings. Soil surface is frequently disturbed by wild boars; the herbal vegetation is scarce.

Sampling

Within the beech plantation, nine transects, from 34 to 80 m long, were placed to cross the canopy openings occupied by regeneration of different height (0.05–6 m). Additionally, one transect was placed in the neighbouring mixed broadleaved stand with scattered beech individuals in the understorey.

Along each transect, sampling plots (2 × 2 m) were placed, leaving no space between them. Within each sampling plot, height of all regeneration was measured with the accuracy of 5 cm, and a canopy image was obtained for the description of the light conditions. The images were acquired by a digital camera (Nikon Coolpix E8400) equipped with a fish-eye lens (DSLR 4.9 mm-203) (Regent Instruments Inc., Quebec, Canada), placed at 1.4 m height; the interfering undergrowth trees were bent aside. The automatic adjustment function of camera (focus, exposition time, aperture etc.) was used. Sampling was done in August 2013.

Data analysis

For the description of light conditions in the plots, the direct, diffuse and total radiation (mean photon flux density, mol m^{-2} day^{-1}) for the vegetation period extending from April 20 to October 25, was calculated from the images using the WinScanopy 2006a software (Regent Instruments Inc., Quebec, Canada). The colour-based pixel classification was used. "Standard overcast sky" model was used for the calculation of the diffuse radiation, which was considered as 48 % of the total radiation.

The relationships of the light parameters was estimated by a Pearson correlation analysis. The light parameters between stands were compared by a t-test. The minimum values of the light parameters, necessary for the presence of regeneration, were estimated by the non-linear regression analysis. Total height of regeneration of each species within a plot, which represents both height and number of seedlings/samplings, was used as the dependent variable. Logarithmic model, $y = a \cdot \ln(E) + b$, where E – light estimate, and a and b – model parameters, was fit using the "nls" function in the program R (R Core Team 2013). In case of a negative parameter "a", the tested light parameter was considered non-limiting. The analysis was conducted for the species present in ≥ 12 plots.

Results

In the studied stands, ten species were accounted in the regeneration, but only seven species were present in more than 12 plots (Table 1). Beech and ash were the most common species, present in 178 and 46 plots, respectively. The density of beech and ash regeneration ranged from 0.25 to 13.5 and from 0.25 to 5.5 individuals m^{-2} and the total height of regeneration within a plot varied from 2.5 to 1505 and from 2.5 to 159 $cm^1\ m^{-2}$, respectively (Fig. 1). The tallest understory trees were common hazel, Norway spruce and European beech (Table 1).

All light parameters were significantly (p-value <0.001) intercorrelated, with the weakest correlation between the direct and diffuse radiation (r = 0.52, n = 205). In both stands, light parameters had similar variation (variation coefficients was ca. 0.40) (Table 2). The crowns absorbed the largest part of the radiation and only ca. 10 % reached the understorey. The diffuse radiation formed ca. 33% of the total radiation below the crowns. Light parameters were slightly lower in the beech stand compared to the mixed stand, but the differences were significant only for the direct radiation (p-value = 0.04).

The estimated and the observed threshold (minimum) values of light parameters differed among the species. The diffuse and total radiation appeared the main limiting factors, as for most of the species (except Norway spruce), as the parameters "a" were positive (Fig. 1) and/or threshold valued were not close to zero (more than 1 % of radiation above the crown) (Table 3). The lowest estimated threshold of the diffuse radiation was observed for beech and ash (0.37 mol m^{-2} day^{-1}) although the observed values were even lower (Fig. 1, Table 3). In contrast, the highest threshold values of the diffuse radiation were estimated and observed for silver fir and rowan (ca 0.75 and 1.05 mol m^{-2} day^{-1}, respectively) (Table 3). The modelled threshold value of the total radiation for beech (0.19 mol m^{-2} day^{-1}) appeared underestimated, but the observed value (0.66 mol m^{-2} day^{-1}) was the lowest amongst the species except ash, which had the same value. The highest threshold value of the total radiation was found for

silver fir and rowan (ca. 2.20 and 3.20 mol m^{-2} day^{-1}, respectively). The amount of the direct radiation appeared related to the occurrence of the silver fir, trembling aspen and European rowan (Fig. 1, Table 3), as the estimated threshold values of the direct and diffuse radiation were similar. The threshold values of beech and ash (Table 3) were lower than the minimum values in the plots in the neighbouring mixed stand (Table 2), while this was true in ≤ 80 % of the plots for other species.

Discussion

The abundance of beech regeneration in the plantation and in the neighbouring stand (Table 1) suggested the success of its acclimation and preconditions for a wider spread (Bradshaw & Lindbladh, 2005), surrounding the northeasternmost stand in Europe. Hence, the microclimatic conditions (e.g. light) increase importance, affecting the dispersion of the species (Poulson & Platt, 1989; Ritter *et al.*, 2005; Rozenbergar *et al.*, 2007). The comparison of the estimated threshold values (Table 3) showed, that amongst the light parameters, the amount of the diffuse and total radiation appeared the main factors affecting regeneration, similarly as observed in other studies (Emborg, 1998; Rozenbergar *et al.*, 2007). Beech had the lowest threshold values of light parameters amongst the accounted species (Table 3), suggesting high shade tolerance (Wagner *et al.*, 2010) also outside its distribution area (Bolte *et al.*, 2007). The threshold values (ca. 2 % of the radiation above crown) (Table 3) were similar to those observed in Denmark, suggesting that the studied beech has not been more subjected to the environmental stresses (Emborg, 1998).

Common ash also had low requirements for light (Table 3), hence it might be competing with beech under closed canopy conditions (Emborg, 1998; Modry *et al.*, 2004). However, the competitiveness of ash, at present, is severely diminished by its decline (Kowalski & Holdenrieder, 2009), thus favouring beech. Although Norway spruce, which can persist in understory for a long time, is also considered as a competitor of beech for light (Bolte *et al.*, 2007), our results showed that spruce had a higher observed minimum value of the radiation parameters (Table 3), suggesting that both species might co-occur, at least in fertile sites (Madsen & Larsen, 1997; Bolte *et al.*, 2007). Considering the ability of beech to persist in understorey for a long period, until a disturbance crates canopy opening and releases its growth (Wagner *et al.*, 2010), and higher requirements for light observed for other species (Table 3), beech is expected to continue the dispersion into the neighbouring territories. Nevertheless, higher light parameters observed in the neighbouring stands (Table 2) might have a dual effect. On one hand, higher radiation might facilitate spread and development of beech, but on other hand it might increase the competition with other species. Though, the light conditions are one

4

of the main factors shaping the regeneration, other factors e.g. browsing, root competition and the availability of seed source should be taken into account for a more comprehensive assessment of the further spread of beech (Rozenbergar *et al.*, 2007).

Conclusions

Successful regeneration and spread of beech was observed at its northeasternmost stand in Europe; threshold values of radiation parameters for regeneration of beech were similar as observed within its distribution area; radiation parameters appeared non-limiting for the further spread of beech into the surrounding stands. Amongst the accounted ten regenerating tree species, beech and ash had the lowest requirements for light. Amongst the studied light parameters, the diffuse and total radiation below crown appeared to mainly influence the regeneration.

Acknowledgements

References

Bolte A., Czajkowski T., Kompa T. 2007. The north-eastern distribution range of European beech – a review. – Forestry, 80, 413–429.

Bradshaw R.H.W., Lindbladh M. 2005. Regional spread and stand-scale establishment of *Fagus sylvatica* and *Picea abies* in Scandinavia. – Ecology, 86, 1679–1686.

Dreimanis A. 2004. Europäische Wurzeln der Forstwirtschaft in Lettland [European beginnings of forestry in Latvia]. – AFZ/Der Wald, 59, 514–515. (in German).

Emborg J. 1998. Understorey light conditions and regeneration with respect to the structural dynamics of a near-natural temperate deciduous forest in Denmark. – Forest Ecology and Management, 106, 83–95.

Galbraith-Kent S.L., Handel S.N. 2008. Invasive *Acer platanoides* inhibits native sapling growth in forest understorey communities. – Journal of Ecology, 96, 293–302.

Kowalski T., Holdenrieder O. 2009. The teleomorph of *Chalara fraxinea*, the causal agent of ash dieback. – Forest Pathology, 39, 304–308.

Kramer K., Degen B., Buschbom J., Hickler T., Thuiller W., Sykes M., de Winter W. 2010. Modelling exploration of the future of European beech (*Fagus sylvatica* L.) under climate change – Range, abundance, genetic diversity and adaptive response. – Forest Ecology and Management, 259, 2213–2222.

Madsen P., Larsen J.B. 1997. Natural regeneration of beech (*Fagus sylvatica* L.) with respect to canopy density, soil moisture and soil carbon content. – Forest Ecology and Management 97, 95–105.

Minotta G., Pinzauti S. 1996. Effects of light and soil fertility on growth, leaf chlorophyll content and nutrient use efficiency of beech (*Fagus sylvatica* L.) seedlings. – Forest Ecology and Management, 86, 61–71.

Modry M., Hubeny D., Rejšek K. 2004. Differential response of naturally regenerated European shade tolerant tree species to soil type and light availability. – Forest Ecology and Management, 188, 185–195.

Petit R.J., Bialozyt R., Garnier-Gere P., Hampe A. 2004. Ecology and genetics of tree invasions: from recent introductions to quaternary migrations. – Forest Ecology and Management, 197, 117–137.

Poulson T., Platt W.J. 1989. Gap light regimes influences canopy tree diversity. – Ecology, 70, 553–555.

R Core Team 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/. [Cited 01 Aug 2015].

Ritter E., Dalsgaard L., Einhorn K.S. 2005. Light, temperature and soil moisture regimes following gap formation in a semi-natural beech-dominated forest in Denmark. – Forest Ecology and Management, 206, 15–33.

Rozenbergar D., Mikac S., Anic I., Diaci J. 2007. Gap regeneration patterns in relationship to light heterogeneity in two old-growth beech-fir forest reserves in South East Europe. – Forestry, 80, 431–443.

Runkle J.R. 2013. Disturbance regimes in temperate forests. – Pickett S.T.A., White P.S. (eds.). The ecology of natural disturbance and patch dynamics. Amsterdam, Elsevier, 17–35.

Sebert-Cuvillier E., Simon-Goyheneche V., Paccaut F., Chabererie O., Goubet O., Decocq G. 2008. Spatial spread of an alien tree species in a heterogeneous forest landscape: a spatially realistic simulation model. – Landscape Ecology, 23, 787–801.

Wagner S., Collet C., Madsen P., Nakashizuka T., Nyland R.D., Sagheb-Talebi K. 2010. Beech regeneration research: From ecological to sylvicultural aspects. – Forest Ecology and Management, 259, 2172–2182.
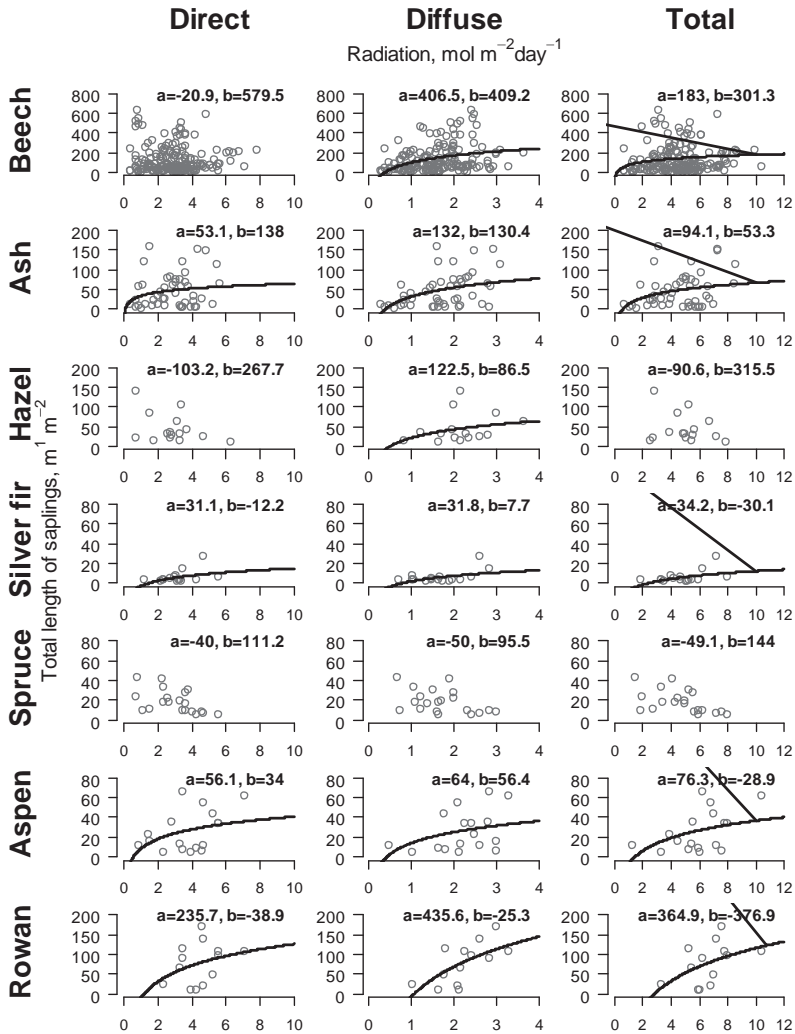
Fig. 1. The total height of regeneration of European beech and other species in relation to the light parameters (direct, diffuse and total radiation) under the crowns in the studied beech and neighbouring stands. Lines represent the logarithmic models. Parameters of the fitted logarithmic models ($y = a \cdot \ln(x) + b$) are shown. Note that the axes differ.

Tables

Species	Occurrence	N	Regeneration density, ind. m^{-2}	Regeneration mean height, cm
European beech (*Fagus sylvatica* L.)	178	1631	2.3 (0.25-13.50)	62.1 (6.7-253.8)
European ash (*Fraxinus excelsior* L.)	47	325	1.7 (0.25-5.50)	25.9 (5.1-50.5)
Common hazel (*Corylus avellana* L.)	15	23	0.4 (0.25-0.75)	137.8 (27.5-550.0)
Silver fir (*Abies alba* Mill.)	16	28	0.4 (0.25-1.75)	11.1 (5.0-18.3)
Norway maple (*Acer platanoides* L.)	6	9	1.5 (0.25-0.75)	12.1 (5.0-32)
Norway spruce (*Picea abies* Karst.)	20	23	0.3 (0.25-0.50)	63.8 (17.5-170.0)
Pedunculate oak (*Quercus robur* L.)	3	4	1.3 (0.25-0.50)	20.8 (16.2-26.3)
Trembling aspen (*Populus tremula* L.)	17	49	0.7 (0.25-1.75)	35.2 (15.0-60.0)
European rowan (*Sorbus aucuparia* L.)	13	87	1.7 (0.25-3.25)	43.6 (17.5-75.0)
Sweet sherry (*Prunus avium* L.)	6	18	3.0 (0.50-1.25)	25.4 (15.3-46.7)

Table 1. The number of sampling plots were species were present in understorey (occurrence), the total number of the measured saplings (N) and the mean density and height of the saplings in the sampling plots. The numbers in parenthesis show the range of the measurements.

	Beech stand, 190 sampling plots			Neighbouring broadleaved stand, 15 sampling plots		
	Direct	Diffuse	Total	Direct	Diffuse	Total
Mean	2.88	1.54	4.41	3.85	1.91	5.76
Minimum	0.36	0.28	0.66	0.73	0.36	1.09
Maximum	7.85	3.64	9.96	7.10	3.29	10.39
Standard dev.	1.33	0.62	1.71	1.76	0.88	2.55
Coefficient of variation	0.46	0.41	0.39	0.46	0.46	0.44

Table 2. The general statistics of the estimated light parameters: direct, diffuse and total radiation below the crowns (mol m^{-2} day^{-1}) in the sampling plots in the beech and the neighbouring mixed broadleaved stands.

Species	Estimated			Observed			DF
	Direct	Diffuse	Total	Direct	Diffuse	Total	
European beech	NA	0.37 (2.48 %)	0.19 (0.42 %)	0.36 (1.17 %)	0.28 (1.9 %)	0.66 (1.45 %)	176
European ash	0.07 (0.24 %)	0.37 (2.52 %)	0.57 (1.25 %)	0.38 (1.24 %)	0.28 (1.9 %)	0.66 (1.45 %)	45
Common hazel	NA	0.49 (3.34 %)	NA	0.70 (2.28 %)	0.82 (5.56 %)	2.58 (5.67 %)	13
Silver fir	1.48 (4.81 %)	0.79 (5.32 %)	2.42 (5.31 %)	1.20 (3.9 %)	0.70 (4.74 %)	1.89 (4.15 %)	14
Norway spruce	NA	NA	NA	0.74 (2.41 %)	0.68 (4.61 %)	1.45 (3.19 %)	18
Trembling aspen	0.55 (1.77 %)	0.41 (2.81 %)	1.46 (3.21 %)	0.84 (2.73 %)	0.46 (3.12 %)	1.30 (2.86 %)	15
European rowan	1.18 (3.83 %)	1.06 (7.18 %)	2.81 (6.17 %)	2.30 (7.48 %)	1.01 (6.84 %)	3.31 (7.27 %)	11

Table 3. Estimated and observed minimum values of light parameters: direct, diffuse and total radiation (mol m^{-2} day^{-1}) necessary for the presence of regeneration. Estimates are based on the total height of regeneration in the sampling plots. DF – degree of freedom of the estimates. The numbers in parentheses show the threshold values as the proportion of the light parameters above the crown.

Līga Puriņa, Roberts Matisons, Āris Jansons and Silva Šēnhofa

Survival of European beech in the central part of Latvia 33 years since the plantation

Highlights

- Beech saplings growing in the central part of Latvia had ca. 80% survival during the recent three decades.
- The dimensions of saplings varied greatly likely due to canopy conditions.
- Some beech self-regeneration was observed.
- Mainly saplings had narrow crowns.
- The distribution of sapling dimensions had the reverse-J shape, suggesting successful development of beech.

Abstract

The projections of vegetation zones suggest increasing growth potential of European beech (*Fagus sylvatica* L.) in Northern Europe. Such changes usually are most apparent in the marginal populations. In this study, survival of young beech growing in an experimental plantation under canopy of a mixed coniferous stand in the central part of Latvia was assessed after 33 years since the establishment. The planting material originated from an older experimental stand in the western part of Latvia. Although, at present, the studied plantation could be considered as the northeasternmost beech stand in Europe, a good survival was observed – ca. 80% of the seedlings have survived, despite several cold spells of ca. –30 °C that occurred during the recent three decades. Additionally, some self-regeneration i.e. branch sprouting was observed. The saplings were rather low, as their mean height was ca. 4 m. Still, some individuals, which were growing under canopy openings, reached considerable dimensions; their height and stem diameter exceeded 10 m and 9 cm, respectively. The distribution of sapling dimensions had the reverse-J shape that is typical for shade tolerant species, indicating normal development of the beech regrowth. The crowns of saplings were narrow and the stems were spindly, suggesting that trees with a good stem quality might be bred. Hence, our results suggest that environmental conditions in the central part of Latvia have been satisfactory for beech, thus encouraging establishment of more extensive trials within the region.

1　Introduction

Northward expansion of nemoral tree species is predicted in Northern Europe due to changes in climate (Hickler et al. 2012). The distribution model of European beech (*Fagus sylvatica* L.) suggests that conditions for its growth in the Baltic States might be suitable by the end of the 21st century (Kramer et al. 2010). Nevertheless, already at present, successful growth and regeneration of beech is observed in the western part of Latvia (Bolte et al. 2007; Jansons et al. 2015), suggesting adaptation of the species. In the central and eastern regions of Latvia, conditions, however, are considered unsuitable due to cold spells in winter, which the species have not been able to tolerate (Mangalis 2004; Bolte et al. 2007). Nevertheless, considering the observed warming (by ca. 2 °C during the last century), particularly due to increase of temperature in the dormant period (Lizuma et al. 2007), growth potential of beech already might be improved.

　　Mortality of planting material is a crucial parameter that influences profitability of forest management (Burton 2011). Regarding the species, which are planted outside their natural distribution area, increased mortality can be expected due to unfavourable climatic conditions (Fang and Lechowicz 2006; Burton 2011) or browsing by wildlife (Hansson 1985), while the risks related to pathogens might be lower (Hansson 1985). The climate-induced mortality of alien (introduced) species is often caused by weather extremes rather than mean values of weather parameters (Bolte et al. 2007), hence long term surveys are necessary to evaluate such effects. The aim of this study was to evaluate survival and growth of beech saplings in an experimental plantation in the central part of Latvia after 33 years since the establishment. We hypothesised that irrespectively of harsher climate, beech had a high survival, hence that the meteorological conditions were satisfactory for the existence of the species.

2　Material and methods

2.1 Study site and sampling

Study site was located in the central part of Latvia (56°42´N, 25°56´E). The climate in study area was moist continental; the mean (±SD) annual temperature calculated for the period 1983–2015 was +6.2±0.9 °C. February and July were the coldest and warmest months with the mean temperature of –4.6±4.2 and +17.8±1.7 °C, respectively. During that period, the bottom-six six-hour mean temperatures were recorded in January 1987 (–31.1 °C), 2003 (–31.7 °C) and 2006 (–28.7 °C), and in February 1985 (–31.2 °C), 2007 (–29.6 °C) and 2012 (–28.9 °C). The mean (±SD) annual sum of precipitation was 683±73 mm. The highest monthly precipitation occurred in summer months (ca. 75 mm per month), but the lowest in spring (ca. 37 mm per month).

　　The study site was an experimental plantation of beech, established under the canopy of Scots pine (*Pinus sylvestris* L.) stand with Norway spruce (*Picea abies* (L.) H. Karst.) and silver birch (*Betula pendula* Roth.) admixture. The age of the stand was ca. 90 years; it was growing on moderately dry, fertile loamy soil with acidic reaction (*Hylocomiosa* type). The area of the plantation was ca. 3.5 ha. Beech was planted in summer of 1983 along the strip roads with the spacing of 0.75–0.95 m (mean 0.83 m) forming curved planting lines. The distance between the lines mainly ranged from 3.5 to 8.5 m. Seedlings were raised in a local nursery. The seed material was obtained from a stand located in the western part of Latvia (57°15´N, 22°41´E) (Bolte et al. 2007) where beech from northeastern Germany was introduced in 1890s. Unfortunately, no information about the total number of planted seedlings was available.

In the winter 2016, each beech sapling within the plantation was mapped. For this purpose, the territory was divided into regular 25×25 m plots. Within each plot, polar coordinates of beech saplings were fixed using theodolite with the precision of 20″ and 0.15 m for azimuth and radius, respectively. For each beech, height (±0.10 m) and, for those above 1.6 m, also stem diameter at 1.3 m height (DBH, ±0.5 mm) was measured. Additionally, length of the longest branch was estimated (±0.10 m).

2.2 Data analysis

For each beech sapling, Cartesian coordinates relative to the plantation were calculated. Further, spatial data were processed using the QGIS v.1.8.0 software. For the estimation of the number of initially planted seedlings, the total length of planting lines was assessed by means of remote sensing. The number of planted seedlings was estimated according to the total length of planting lines and the mean initial spacing between the seedlings. The survival of beech was estimated as the fraction of accounted trees from the number of initially planted seedlings. For the description of crown form, length of the longest branch was expressed as the fraction of tree height. Additionally, stem taper was calculated where possible.

3 Results

From the estimated ca. 5000 beech seedlings planted in 1983, 3975 were alive in autumn of 2015, resulting in the overall survival of 79.5%. Additionally, some self-regeneration (branch sprouting) was observed. The dimensions of beech varied considerably; the mean (±SD) height of saplings was 3.85 ± 2.30 m and the mean DBH (±SD) was 24 ± 20 mm; nevertheless, some individuals reached >10 m in height and >9 cm in DBH (Table 1). The median value of both variables was below the mean, suggesting that the smaller beeches were more frequent; hence, the distributions of height and DBH were positively skewed and had positive kurtosis (Fig. 1). The distribution of sapling height peaked in the second height class, i.e. 2–4 m, while nearly half of the saplings had DBH ≤ 20 mm, hence the distribution of DBH followed the reverse-J shape. The mean (±SD) relative length of the longest branch was ca. $26 \pm 11\%$ of tree height (Table 1), suggesting formation of narrow crown for the understory beech. The distribution of this parameter was positively skewed, implying that the relatively narrow crowns were prevailing (Fig. 1). Still, trees with considerably wider (>50%) crowns were also observed, particularly in the lowest height classes. The mean (±SD) stem taper of saplings was 0.29 ± 0.20.

Table 1. Main statistics of beech sapling height, stem diameter at 1.3 m height and relative length of the longest branch.

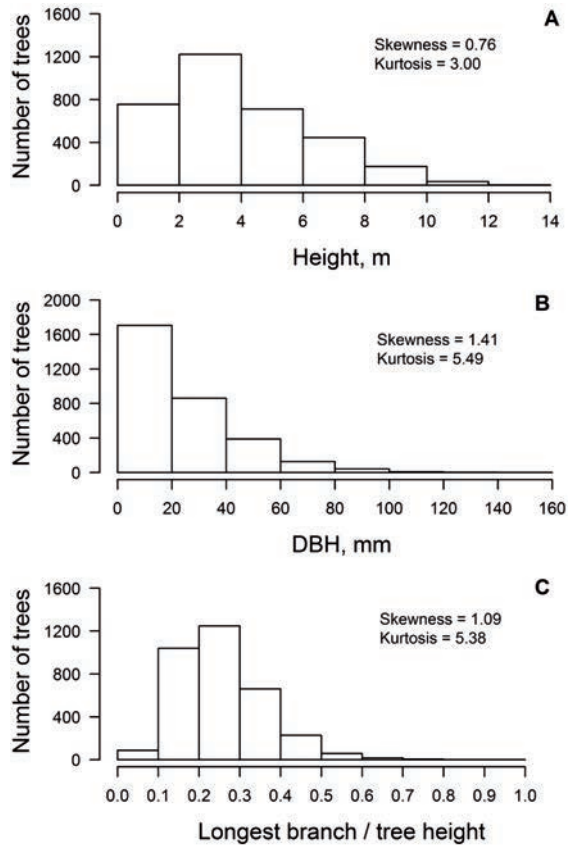|	Height, m	Stem diameter at 1.3 m height, mm	Relative length of the longest branch, %
Minimum	0.30	2	2.6
Maximum	13.00	149	150.0
Mean	3.95	24	25.9
Median	3.50	18	24.2
Standard deviation	2.30	20	11.1
Coeff. of variation	0.59	0.83	0.43

Fig. 1. Distribution of height (A), stem diameter at 1.3 m height (DBH, B) and the relative length of the longest branch (C) of the beech saplings.

4 Discussion

Although the studied site at present could be considered as the northeasternmost plantation (stand) of beech in Europe (Bolte et al. 2007), good survival (ca. 80%) of saplings and evidence of self-regeneration during the period 1983–2015 suggested high growth potential of the species. Despite several cold spells (when temperature was ca. –30 °C) that occurred during the recent three decades, the climatic conditions in the central part of Latvia appeared non-limiting (suitable) for the existence of the species within a stand under shelterwood (Fang and Lechowicz 2006; Kramer et al. 2010). Alternatively, such a high survival of beech in the central part of Latvia might be related to the origin of seeds, which came from the trees adapted only to a slightly milder climate (Yakovlev et al. 2011), i.e. from the western part of Latvia.

The dimensions of beech saplings were rather low (Table 1) that might be explained by the closed canopy conditions, hence by the deficit of light (Modry et al. 2004; Wagner et al. 2010). Also stem form, low stem taper and narrow crowns (Table 1) contributed to limited growth, rendering the saplings spindly. Nevertheless, several individuals, which were growing under canopy openings, had reached considerable dimensions (>10 m height), suggesting favourable growing conditions (Wagner et al. 2010). The distribution of sapling height and particularly DBH had the reverse-J shape (Fig. 1), typical for shade tolerant species (Angelstam and Kuuluvainen 2004), thus the development of beech followed the pattern similar to the native species (e.g. Norway spruce), which have successful self-regeneration. Hence, to promote further development of beech, openings in the canopy, e.g. from the selective or group cutting, appear necessary (Modry et al. 2004; Wagner et al. 2010). The prevailing saplings with low relative width of crown (Fig. 1) also implied potential formation of beech with stems of a good form (Wagner et al. 2010).

5   Conclusions

The high survival and evidence of self-regeneration of beech in the central part of Latvia during the recent three decades are promising, suggesting successful adaptation, hence potentially increasing economic importance of the species already in the near future. Nevertheless, more information about the influence of stand structure and light conditions on the development of beech saplings is necessary. Our results also suggest that more trials i.e. in different growing conditions and regions can be established for more comprehensive assessment of the potential of the species in forestry in the Baltics.

Acknowledgements

References

Angelstam P., Kuuluvainen T. (2004). Boreal forest disturbance regimes, successional dynamics and landscape structures: a European perspective. Ecological Bulletins 51: 117–136. http://www.jstor.org/stable/20113303.

Bolte A., Czajkowski T., Kompa T. (2007). The north-eastern distribution range of European beech – a review. Forestry 80: 413–429. http://dx.doi.org/10.1093/forestry/cpm028.

Burton L.D. (2011). Introduction to forestry science, 3rd ed. Delmar, Clifton park. 544 p.

Fang J., Lechowicz M.J. (2006). Climatic limits for the present distribution of beech (*Fagus* L.) species in the world. Journal of Biogeography 33: 1804–1819. http://dx.doi.org/10.1111/j.1365-2699.2006.01533.x.

Hansson L. (1985). Damage by wildlife, especially small rodents, to North American *Pinus contorta* provenances introduced into Sweden. Canadian Journal of Forest Research 15: 1167–1171. http://dx.doi.org/10.1139/x85-189.

Hickler T., Vohland K., Feehan J., Miller P.A., Smith B., Costa L., Giesecke T., Fronzek S., Carter

T.R., Cramer W., Kuhn I., Sykes M.T. (2012). Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. Global Ecology and Biogeography 21: 60–63. http://dx.doi.org/10.1111/j.1466-8238.2010.00613.x.

Jansons Ā., Matisons R., Puriņa L., Neimane U., Jansons J. (2015). Relationships between climatic variables and tree-ring width of European beech and European larch growing outside of their natural distribution area. Silva Fennica 49(1) article 1255. 8 p. http://dx.doi.org/10.14214/sf.1255.

Kramer K., Degen B., Buschbom J., Hickler T., Thuiller W., Sykes M., de Winter W. (2010). Modelling exploration of the future of European beech (*Fagus sylvatica* L.) under climate change – range, abundance, genetic diversity and adaptive response. Forest Ecology and Management 259: 2213–2222. http://dx.doi.org/10.1016/j.foreco.2009.12.023.

Lizuma L., Kļaviņš M., Briede A., Rodinovs V. (2007). Long-term changes of air temperature in Latvia. In: Kļaviņš M. (ed.). Climate change in Latvia. University of Latvia, Riga. p. 11–20.

Mangalis I. (2004). Forest regeneration and re-establishment. "Et Cetera," Riga. 445 p. [In Latvian].

Modry M., Hubeny D., Rejšek K. (2004). Differential response of naturally regenerated European shade tolerant tree species to soil type and light availability. Forest Ecology and Management 188: 185–195. http://dx.doi.org/10.1016/j.foreco.2003.07.029.

Wagner S., Collet C., Madsen P., Nakashizuka T., Nyland R.D., Sagheb-Talebi K. (2010). Beech regeneration research: from ecological to silvicultural aspects. Forest Ecology and Management 259: 2172–2182. http://dx.doi.org/10.1016/j.foreco.2010.02.029.

Yakovlev I.A., Asante D.K., Fossdal C.G., Junttila O., Johnsen Ø. (2011). Differential gene expression related to an epigenetic memory affecting climatic adaptation in Norway spruce. Plant Science 180: 132–139. http://dx.doi.org/10.1016/j.plantsci.2010.07.004.

Total of 13 references.

GROWTH OF *FAGUS SYLVATICA* IN YOUNG MIXED STAND: CASE STUDY IN CENTRAL LATVIA

Liga Purina, **Andis Adamovics**, **Juris Katrevics**, **Zaiga Katrevica**, **Baiba Dzerina**
Latvian State Forest Research Institute 'Silava'
liga.purina@silava.lv

Abstract
Climatic changes are shifting the potential tree distribution limits of many tree species northwards. One of such species is *Fagus sylvatica*, currently represented in Latvia only by a few stands. In order to increase knowledge on its potential use in the forest management, the aim of our study was to characterize the growth of beech in a young stand in the central part of Latvia. The stand of beech and spruce, mixed in rows with an initial spacing of 2.5 x 2.5 m in *Oxalidosa* forest type was assessed. Survival of European beech in clearcut was similar to that observed for the native Norway spruce (73% and 79%, respectively), but both height and diameter were notably and significantly superior for wildlings at the mean age of 15 ± 2 years, reaching on average 7.4 ± 0.30 m and 8.9 ± 0.69 cm, respectively. Increasing ring width with increasing tree age for both tree species was observed until the last four years, when large and increasing superiority of beech over spruce, coinciding with reduction of ring width of spruce, was noted. It was most likely caused by intensified competition due to very wide crowns formed by young beech trees in the plantation with wide spacing: average crown radius reached 2.4 ± 0.16 m, for few trees exceeding even 4 m.
Key words: introduced tree species, mixed stand, adaptability, survival, European beech.

Introduction

Climate envelop models are used to predict changes of species distribution due to climatic changes. Generally, northward shift of the vegetation zones, therefore also the species distribution is expected in Europe (Walther *et al*., 2002; Kullman, 2008). However, the actual natural changes of the borders of tree species areals are much slower, since the spread is determined by the distance of seed dispersion, affected by numerous factors including forest fragmentation. To ensure that the expected improvement in forest productivity due to warmer climate (Lindner *et al*., 2010) is realized, the adjustments in forest management practice and introduction of potentially suitable tree species, in this way altering the predicted natural changes in forest composition (Hickler *et al*., 2012), are crucial (Petit *et al*., 2004). Increasing the number of tree species used in forestry also allows forest managers to diversify risks as well as find the most suitable alternative for any particular site, considering not only growth but also increasing probability of damages by abiotic factors (Seidl *et al*., 2014). It is predicted, that northeastern limit of European beech (*Fagus sylvatica* L.) might occur in the Baltic States by the end of the 21st century (Kramer *et al*., 2010), since the already occurring climatic changes in Latvia are reflected as an increase of temperature in the dormant period and spring (Lizuma *et al*., 2007), making the conditions more suitable for the requirements of this species (Bolte, 2007). However, it is not advisable to rely on the theoretical considerations, therefore ecological demands, i.e. climatic limitation of growth of this tree species should be comprehensively evaluated. Detailed information on climate-growth relationships can be obtained via dendrochronological analysis.

This technique was applied for the assessment of relationships between tree ring width (TRW) and climatic variables for beech in Latvia. Chronologies of TRW, which covered the periods 1949 – 2012 were produced. Variation of TRW was affected by drought-related climatic variables, temperature in the previous July and August, as well as an effect of spring and autumn temperature was observed. It was found that during the recent decades July precipitation also has become significant (Jansons *et al*., 2015a). The latter might have a negative effect on beech growth since intensification of heat and drought events are expected (Avotniece *et al*., 2010).

Successful natural regeneration is the first indication of species to thrive in the particular conditions. Abundant regeneration has been found in canopy openings of the few existing beech stands in Latvia (Purina *et al*., 2013), limited mainly by light conditions (Jansons *et al*., 2016). Even so, the results proved very high shade tolerance of this tree species in comparison to other common trees species in Latvia (Jansons *et al*., 2016) as well as broadleaved tree species with northernmost point of distribution limit being in the territory of our country – European hornbeam (*Carpinus betulus* L.). Hornbeam understory distribution and abundance was significantly linked to light parameters, particularly – diffuse radiation (Purina *et al*., 2015). Growth of beech under shelterwood, as recommended for its regeneration (Ritter *et al*., 2005), mainly due to high spring frost risk (Aranda *et al*., 2002), was similar to that found for other shade-tolerant species – Norway spruce: the mean height in particular study plots was 62 and 64 cm, respectively (Jansons *et al*., 2016). However, the growth of young beech seedlings planted in clearcut (with higher temperature amplitude) has

not been assessed previously in Latvia. Productivity of old beech trees, assessed in several permanent sample plots in the western part of Latvia, was high in comparison to native tree species (Dreimanis, 1995). However, only middle-aged and mature stands were assessed in this study, but not young stands. Due to already occurring changes in climatic conditions, meteorological factors (and periods) notably affecting increment of trees are changing (Jansons *et al.*, 2015b), therefore gathering of information about early growth from currently mature trees (using sample tree cutting) is not advisable. In order to improve the knowledge on the potential of beech use in Latvia, the aim of our study was to characterize growth of this tree species in young stands in the central part of our country.

Materials and Methods

A planted stand of European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*) has been established in the entral part of Latvia on a flat terrain on fertile, well-drained clayey soil *Oxalidosa* forest type. Climate in the study area is mild, the mean annual temperature is ~ +6.1 °C, July is the warmest month, with mean temperature ~ +16 °C, and January is the coldest month, with mean temperature ~ -3.6 °C. The period when the mean daily temperature exceeds 5 °C is ~185 days. Annual precipitation sum is ~ 560. Most of the precipitation falls during summer.

Planting was carried out in spring of 2004 in clearcut using two-year old spruce plants and beech wildlings from natural regeneration under the canopy of beech stand in the western part of Latvia.

The ground was scarified in rows and single-row mixture of beech and spruce was used (one row of beech, adjacent – spruce etc.). Distance between rows varied from 2 to 3 meters (average 2.5 m) and distance between saplings in row was 2.5 meters.

The height and the diameter of breast height (DBH) of each tree on January 2016 were measured for altogether 116 beeches and 124 spruces. For beech the largest radius of crown (as defined by the longest branch) was measured. For spruce height increment of last three years was measured. Increment cores from several trees as close to ground as possible were taken with Pressler borer. In the laboratory, air-dried cores were fixed and gradually grinded (sandpaper roughness 100, 150, 250 and 400 grains per inch). Tree-ring width was measured using LINTAB 5 (RinnTECH) measurement system with the precision of 0.01 mm. There were no signs (like old stumps of young trees) that any pre-commercial thinning has been carried out before.

Significance of differences was calculated using ANOVA.

Results and Discussion

Density of trees was relative, similar to that expected at the particular height in young stands in Latvia for broadleaved trees: 580 ha^{-1} of beech and 620 ha^{-1} of spruce. The survival of beech was 73% and it was similar to that of Norway spruce (78%). A higher survival might be expected as a result of successful plantation; however, this level is also not uncommon in the plantation of native tree species, as reported, for example, for Silver birch in Finland, where survival was on average 82% after 6th growing season and 79% after 11th, and notable and significant effect of timely (and effective) weed control in the first years on this parameter was found (Hytönen & Jylhä, 2005). There was no information on the tending carried out in the studied area, therefore, the impact of it can't be analysed. Even a higher survival (94%) at the age of 8 years had been found in beech provenance trial in Croatia, noting general adaptedness and phenotypic stability of the material (most of the provenances) based on this information (Ivanković, Bogdan, & Božič, 2008).

The average DBH of beech was 8.9 ± 0.68 cm and it significantly exceeded the average DBH of spruce (3.0 ± 0.41 cm) (Fig. 1). Also, the average height of
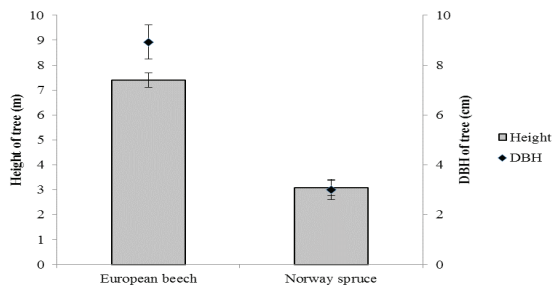

Figure 1. The average height and diameter of breast height (DBH) of European
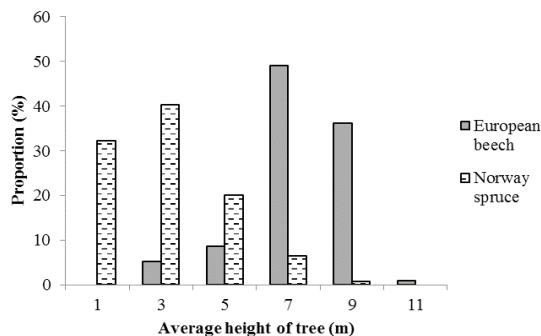beech and Norway spruce (± confidence interval).

Figure 2. Tree distribution in the height groups.

beech was superior to the average height of spruce (7.4 ± 0.30 and 3.1 ± 0.30 m, respectively). Comparison of height curves of both tree species revealed that spruce with height under 7.5 m had greater DBH than beech. It was in accordance to the expected, since largest (dominant) spruces were compared to suppressed beeches. DBH of beech with height over 7.5 m become notably larger but there were no spruces so high to compare with.

The average values did not reflect the differences between species clearly enough, therefore trees were arranged into height groups (Fig. 2). At the moment in the area dominated beech; most of those had the height of 6.1 to 8 m (49%) and of 8.1 to 10 m (36%) and there was no beech with the height under 2 m. Meanwhile, the majority of spruce had the height of 2.1 to 4 m and of 0.1 to 2 m. Also there were no spruce trees higher than 10 m. Superiority of beech was even more pronounced in diameter the greatest proportion (28%) of beech had DBH from 10.1 to 12 cm while 66% of spruce had DBH less or equal 4 cm. The height of beech varied from 2.5 m to 10.5 m, DBH from 1.1 cm to 15.0 cm, for spruce the height of tree was from 0.5 m to 7.1 m and DBH was from 0.5 cm to 9.2 cm. In the analysis of natural regeneration in canopy opening in beech stand in Latvia Jansons *et al.* (2016) found a notably wider range of heights for beech than for spruce (from 7 to 254 cm *vs.* from 18 to 170 cm, respectively), even so the mean height of both tree species was similar (62 and 64 cm, respectively). Also, in our study the distribution was wider of beech, but presumably due to differences in spacing or competition, the interspecies differences were more pronounced for diameter of trees, than for height.

Annual increment depends both on growth intensity (mm day^{-1}) as well as on the length of the growing period. Notable differences between spruce and beech in the timing of height growth had been observed in Slovakia: height increment

of beech trees started earlier than that of spruce, but lasted a shorter time (~45 days vs. ~70 days, respectively); however, the total length of the annual shoot of both species was similar (Konôpka, 2014). In contrast, high importance of determination of the total length of height increment (and therefore growth superiority over other tree species) due to a very long growth period had been found for hybrid aspen (*Populus tremuloides* × *P. tremula*) in Latvia (Jansons *et al.*, 2014). Radial and height growth of different tree species often is affected by contrasting meteorological factors, as demonstrated in numerous dendrochronological analyses (Senhofa *et al.*, 2016; Matisons *et al.*, 2015; Jansons *et al.*, 2013a; Jansons *et al.*, 2013b). Therefore, the increment might be larger for one species at a particular year and for another – in the next year and it is important to evaluate the total increment over longer time. Overall, a faster growth in young stands, especially after the initial years of establishment, had been found for Norway spruce than for beech, even so beech might outcompete other shade-tolerant species in the situation with limited light availability (Galbraith-Kent & Handel, 2008; Wagner *et al.*, 2010). In older stands the productivity of beech might be similar or higher than that of spruce trees in appropriate soil conditions, as found also in the sample plots in beech stands in western Latvia at the age of 115 years, where the height of dominant trees was 34.8 m, basal area 50.5 m² and yield 818 m³ (Dreimanis, 2006).

Since our study site was a mixed stand with not a very high density, it is important to notice the results of meta-analysis of data from beech-spruce mixed stands in Europe: in these stands maximum productivity is reached in lower density than in pure beech or spruce stands (Pretzsch, 2003). Growth of beech can be promoted by admixture of spruce, particularly on fertile sites (Pretzsch *et al.*, 2010), but overyielding of mixed stands occurs less frequently on rich sites
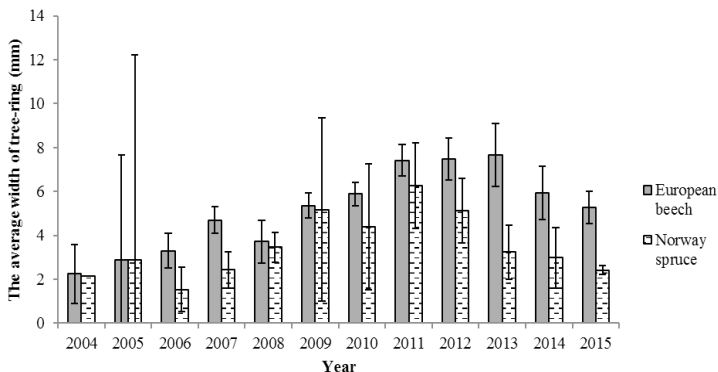
Figure 3. The average width of annual tree ring (± confidence interval) for
European beech and Norway spruce.

than on poor and appears to be based on an admixture effect, with spruce reducing the severe intra-specific competition common in pure beech stands (mostly naturally regenerated with high density, that is not the case in our study site).

Differences in growth might be part of the explanation of observed height and diameter superiority of beech in our site. Another potential source is unknown differences in initial tree parameters. Based on analysis of increment cores, the age of beech wildlings varied from 12 to 19 years (on average 15 ± 1.9 years), while the age of planted spruce was 12 years. It means that beech wildlings could be higher and with a larger root system at the start that could have caused greater increment in the first years (even so the growth could have been affected by re-planting stress, possible root damages). Nevertheless, due to large initial spacing, the effect of size differences on

spruce due to competition most likely was negligible during the first 3-6 years, but might have affected it during later years. It was in line with findings of radial increment analysis (Fig. 3), demonstrating large and increasing superiority of beech over spruce during the last four years (coinciding with the reduction of ring width of spruce) and some growth reduction also of beech during the last two years, most likely due to further intensified competition, since the overall trend of increasing radial increment with increasing age of plantation can be observed and was disrupted. The ring width of the largest cored beech trees also was marginally reduced during the last two years. The width of tree ring for spruce was more varying. The maximal tree ring width for beech was 7.7 ± 1.2 mm, for spruce – 6.3 ± 1.9 mm.

The tendency of height increment of spruce in the last three years was similar to the tendency of
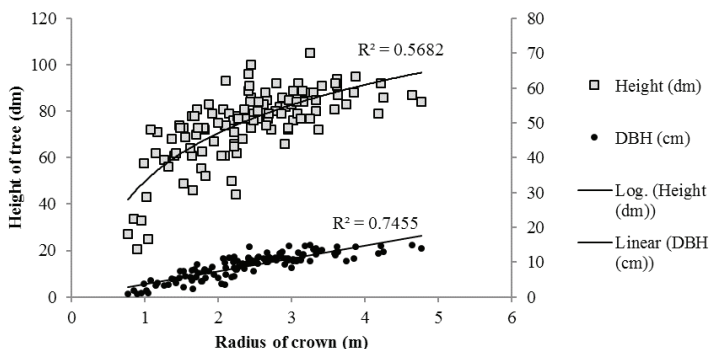

Figure 4. The correlation of beech crown radius with DBH and height of tree.

radial increment – it was slightly, but not significantly decreasing. Presumably, the relatively smaller spruce trees invested most resources into the height increment (retaining it on average 38 ± 2.7 cm – not large for spruce at that age comparing to those which have been measured in tree breeding trials) to catch up with beech and get better light conditions. On average, beech were higher and less affected by competition in the dense stand.

Very intense competition in the stand was demonstrated also by the largest crown radius of beech, reaching on average 2.4 ± 0.16 m, i.e. the distance between the trees in row and between rows. In fact, the number of trees value of this parameter even exceeded 4 m (Fig. 4). The growth of beech trees was notably affected by the length of branches - used as an indicator of crown size, i.e. the total production of organic matter. This parameter had a strong and significant correlation with both the height of the tree and DBH ($r = 0.71$ and $r = 0.87$, respectively).

Our results are in line with findings of other studies, suggesting that both species might co-occur, at least in fertile sites (Madsen & Larsen, 1997; Bolte *et al*., 2007). However, with low initial density beech occupies the area more efficiently, relating long branches and using all the light resources available.

The tree species in natural stands adapt in such a way and persist in understorey with limited light for a long period, until a disturbance creates canopy opening and releases its growth (Wagner *et al*., 2010).

Conclusions
1. Survival of European beech in clearcut in mixed stand was similar to that observed for the native tree species. At the age of 15 ± 2 years the average height of beech trees was 7.4 ± 0.30 m, the average DBH was 8.9 ± 0.69 cm.
2. European beech wildings exceeded the height and diameter of Norway spruce saplings 12 years after planting significantly and notably: by 140% and 196%, respectively.
3. The mean annual radial increment of European beech almost three times exceeded the increment of Norway spruce in the same conditions (0.74 and 0.25 cm per year, respectively).

References
1. Aranda, I., Gil, L., & Pardos, J.A. (2002). Physiological responses of *Fagus sylvatica* L. seedlings under *Pinus sylvestris* L. and *Quercus pyrenaica* Willd. overstories. *Forest Ecology and Management*, 162(2-3), 153-164. DOI: 10.1016/S0378-1127(01)00502-3.
2. Avotniece, Z., Rodinov, V., Lizuma, L., Briede, A., & Kļavins, M. (2010). Trends in frequency of extreme climate events in Latvia. *Baltica*, 23, 135-148.
3. Barbaroux, C., & Breda, N. (2002). Contrasting distribution and seasonal dynamics of carbohydrate reserves in stem wood of adult ring-porous sessile oak and diffuse-porous beech trees. *Tree Physiology*, 22, 1201-1210. DOI: 10.1093/treephys/22.17.1201.
4. Bolte, A., Czajkowski, T., & Kompa, T. (2007). The north-eastern distribution range of European beech-a review. *Forestry*, 80, 413-429. DOI: 10.1093/forestry/cpm028.
5. Dreimanis, A. (1995). Dižskābardis un lapegle Šķēdes mežniecībā (The beech and the larch-tree in Shkede forestry) In: Forestry education 75th anniversary conference proceedings of Latvia University of Agriculture. (94-97). (in Latvian).
6. Dreimanis, A. (2006). Dižskābaržu audžu ražība Šķēdes mežu novadā (Productivity of European beech in Shkede forest district). *LLU Raksti*, 16(311), 97-100. (in Latvian).
7. Galbraith-Kent, S.L., & Handel, S.N. (2008). Invasive *Acer platanoides* inhibits native sapling growth in forest understorey communities. *Journal of Ecology*, 96, 293-302. DOI: 10.1111/j.1365-2745.2007.01337.x.
8. Hickler, T., Vohland, K., Feehan, J., Miller, P., Smith, B., Costa, L., Giesecke, T., Fronzek, S., Carter, T.R., Cramer, W., Kühn, I., & Sykes, M.T. (2012). Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. *Global Ecology and Biogeography*, 21, 50-63. DOI: 10.1111/j.1466-8238.2010.00613.x.
9. Hytönen, J., & Jylhä, P. (2005). Effects of competing vegetation and post-planting weed control on the mortality, growth and vole damages to *Betula pendula* planted on former agricultural land. *Silva Fennica*, 39(3), 365-380. DOI:10.14214/sf.374.
10. Ivanković, M., Bogdan, S., & Božič, G. (2008). European beech (*Fagus sylvatica* L.) height growth variability in Croatian and Slovenian provenance trials. Journal of Forestry Society of Croatia, 132 (11-12), 529-541.

11. Jansons, A., Matisons, R., Purina, L., Neimane, U., & Jansons, J. (2015a). Relationships between climatic variables and tree-ring width of European beech and European larch growing outside of their natural distribution area. *Silva Fennica*. 49 (1), 1-8. DOI: 10.14214/sf.1262.

12. Jansons, A., Matisons, R., Baumanis, I., & Purina, L. (2013). Effect of climatic factors on height increment of Scots pine in experimental plantation in Kalsnava, Latvia. *Forest Ecology and Management*, 306, 185-191. DOI: 10.1016/j.foreco.2013.06.039.

13. Jansons, A., Matisons, R., Libiete-Zalite, Z., Baders, E., & Rieksts-Riekstins, J. (2013a). Relationships of Height Growth of Lodgepole Pine (*Pinus contorta* var. *latifolia*) and Scots Pine (*Pinus sylvestris*) with Climatic Factors in Zvirgzde, Latvia. *Baltic Forestry*, 19(2), 236-244.

14. Jansons, A., Matisons, R., Purina, L., & Adamovics, A. (2016). Light requirements of regeneration of European beech at its northeasternmost stand in Europe-a case study in Latvia (submitted) *Silva Fennica*.

15. Jansons, A., Matisons, R., Zadiņa, M., Sisenis, L., & Jansons, J. (2015b). The effect of climatic factors on height increment of Scots pine in sites differing by continentality in Latvia. *Silva Fennica*, 49 (3), 14p. DOI: 10.14214/sf.1262.

16. Jansons, A., Zeps, M., Rieksts-Riekstins, J., Matisons, R., & Krisans, O. (2014). Height increment of hybrid aspen *Populus tremuloides* × *P. tremula* as a function of weather conditions in south-western part of Latvia. *Silva Fennica*, 48 (5), id 1124, 13p.

17. Konôpka, B., Pajtík, J., Bošeľa, M., Hlásny, T., & Sitková, Z. (2014). Inter- and intra-annual dynamics of height increment in young beech and spruce stands in relation to tree size and weatherconditions. *Lesnícky Časopis – Forestry Journal*, 60, 51-59.

18. Kramer, K., Degen, B., Buschbom, J., Hickler, T., Thuiller, W., Sykes, M., & de Winter, W. (2010). Modelling exploration of the future of European beech (*Fagus sylvatica* L.) under climate change-Range, abundance, genetic diversity and adaptive response. *Forest Ecology and Management*, 259, 2213-2222. DOI: 10.1016/j.foreco.2009.12.023.

19. Kullman, L. (2008). Thermophilic tree species reinvade subalpine Sweden-early responses to anomalous late Holocene climate warming. *Arctic Antarctic and Alpine Research*, 40,104-110. DOI: 10.1657/1523-0430(06-120).

20. Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Grazia-Gonzalo, J., Seidl, R., Delzon, S., Corona, P., Kolström, M., Lexer, M.J., & Marchetti, M. (2010). Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *Forest Ecology and Management*, 259, 698-709. DOI: 10.1016/j.foreco.2009.09.023.

21. Lizuma, L., Klavins, M., Briede, A., & Rodinovs, V. (2007). Long-term changes of air temperature in Latvia. In: Kļaviņš M. (ed.) *Climate change in Latvia* (pp. 11-20). Riga: University of Latvia.

22. Madsen, P., & Larsen, J.B. (1997). Natural regeneration of beech (*Fagus sylvatica* L.) with respect to canopy density, soil moisture and soil carbon content. *Forest Ecology and Management*, 97, 95-105.

23. Matisons, R., Jansons, J., Katrevics, J., & Jansons, A. (2015). Relation of tree-ring width and earlywood vessel size of alien *Quercus rubra* L. with climatic factors in Latvia. *Silva Fennica*, 49 (4), id 1391, 14 p. DOI: 10.14214/sf.1391.

24. Petit, R.J., Bialozyt, R., Garnier-Gere, P., & Hampe, A. (2004). Ecology and genetics of tree invasions: from recent introductions to quaternary migrations. *Forest Ecology and Management*, 197, 117-137. DOI: 10.1016/j.foreco.2004.05.009.

25. Pretzsch, H. (2003). The elasticity of growth in pure and mixed stands of Norway spruce (*Picea abies* [L.] Karst.) and common beech (*Fagus sylvatica* L.). *Journal of Forest Science*, 49 (11), 491-501.

26. Pretzsch, H., Block, J., Dieler, J., Dong, P.H., Kohnle, U., Nagel, J., Spellmann, H., & Zingg, A. (2010). Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. Annals of Forest Science, 67 (7), 712-712.

27. Puriņa, L., Džeriņa, B., Neimane, U., & Jansons, Ā. (2013). Eiropas dižskābarža (*Fagus sylvatica* L.) atjaunošanos ietekmējošie faktori Factors affecting regeneration of European beech (*Fagus sylvatica* L.)). Mežzinātne, 27(60), 67-76. (in Latvian).

28. Purina, L., Matisons, R., Katrevics, J., & Jansons, A. (2015). Regeneration and sapling growth of European hornbeam at its northern limit in Latvia. In: Research for Rural Development, 13 – 15 May 2015 (29-36). Jelgava: Latvia University of Agriculture.

29. Ritter, E., Dalsgaard, L., & Einhorn, K.S. (2005). Light, temperature and soil moisture regimes following gap formation in a semi-natural beech-dominated forest in Denmark. *Forest Ecology and Management*, 206, 15-33. DOI: 10.1016/j.foreco.2004.08.011.

30. Senhofa, S., Zeps, M., Matisons, R., Smilga, J., Lazdina, D., & Jansons, A. (2016). Effect of climatic factors on treering width of *Populus* hybrids in Latvia. *Silva Fennica*, 50 (1), id 1442, 12 p. DOI: 10.14214/sf.1442.

31. Sudachkova, N.E., Milyutina, I.L., Romanova, L.I., & Semenova, G.P. (2004). The annual dynamics of reserve compounds and hydrolytic enzymes activity in the tissues of *Pinus sylvestris* L. and *Larix sibirica* Ledeb. *Eurasian Journal of Forest Research*, 7, 1-10.

32. Wagner, S., Collet, C., Madsen, P., Nakashizuka, T., Nyland, R.D., & Sagheb-Talebi, K. (2010). Beech regeneration research: From ecological to sylvicultural aspects. *Forest Ecology and Management*, 259, 2172-2182. DOI: 10.1016/j.foreco.2010.02.029.

33. Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O., & Bairlein, F. (2002). Ecological response to recent climate change. *Nature*, 416, 389-395. DOI: 10.1038/416389a.

SILVA FENNICA

Roberts Matisons, Guntars Šņepsts, Līga Puriņa, Jānis Donis and Āris Jansons

Dominant height growth of European beech at the northeasternmost stands in Europe

Highlights

- The dominant height growth of the introduced European beech was modelled using the generalised algebraic difference approach.
- The Chapman-Richards and Sloboda models showed the best fit to the data.
- Height growth of the second generation trees exceeded the first generation trees.
- In the western part of Latvia, height growth of beech exceeded that in southern Sweden.

Abstract

The height growth of trees influences the productivity of stands and the competitiveness of species, shaping the range of their distribution. Dominant height growth was assessed for European beech (*Fagus sylvatica* L.), growing outside of its natural distribution range in the western part of Latvia. In 10 neighbouring experimental stands, 20 dominant trees were felled for stem analysis. Height growth was modelled using the generalised algebraic difference approach, applying several non-linear equations and mixed procedures. The Chapman-Richards and Sloboda models showed the best fit to the data. Height growth of the second generation (younger) trees exceeded that of the first generation, and followed curve for a higher site index, suggesting sufficient adaptation and improving conditions. Height growth of the studied beech exceeded predictions for beech in southern Sweden, which is considered to be the northern limit of the species range, yet the growth pattern differed. In Latvia, slower height growth was estimated for site indices <32 m (in 100 years) during the first 60 years, yet larger maximal height was predicted, suggesting a longer establishment period. Nevertheless, the improving height growth indicated increasing potential for the application of the species in commercial forestry, and an expansion of the species within the region even during the 21th century.

1   Introduction

Bioclimatic models predict that conditions in the Baltic States would become suitable for European beech (*Fagus sylvatica* L.) by the end of the 21st century; accordingly, shifts in the geographic distribution of the species are expected (Kramer et al. 2010; Hickler et al. 2012). Improved growth of beech has been observed in southern Sweden (cf. Falkengren-Grerup and Eriksson 1990). The distribution limits of trees have been related to primary growth rate (Loehle 1998); hence, the spread of a species is influenced by the success of height increment and competition (Seynave et al. 2008). Height increment is also among the main parameters that influence the productivity of stands (Burton 2012); and such information is valuable for the prediction of growth under current and future climates. In this regard, experimental plantations outside the natural range serve as useful indicators for the adaptive capacity of the species, particularly in the context of climatic change (Seynave et al. 2008; Kreyling et al. 2014).

At present, the northeasternmost stands of beech occur in the western part of Latvia (Bolte et al. 2007), providing an opportunity to study their growth under a harsher climate, outside of its natural range (Kramer et al. 2010). Nevertheless, good survival (Puriņa et al. 2016) and productivity (Dreimanis 1995) indicate that conditions in Latvia are already satisfactory for growth of the introduced beech. Still, height growth of beech near its northern distribution limit has been scarcely studied (cf. Carbonnier 1971). The aim of this study was to assess dominant height growth of beech in the western part of Latvia. We hypothesised that, due to climate warming, height growth of beech in the western part of Latvia is comparable to the northern parts of its natural distribution.

2   Material and methods

2.1 Study site and sampling

The studied stands were located in the western part of Latvia (57°15′N, 22°38′E), within 5 km distance of each other. The stands were growing in similar lowland conditions (80–105 m a.s.l.), in a flat topography. The soil was fertile and silty, yet well drained. The climate was mild; the mean annual temperature ± standard deviation during 1914–2014 was 6.1 ± 1.0 °C; the mean monthly temperature ranged from -3.8 ± 3.7 in February to 16.6 ± 1.5 °C in July (Harris et al. 2014). The mean annual precipitation was 658 ± 102 mm; the highest monthly precipitation occurred during the summer months (June–August; 72 ± 36 mm). Climatic changes were expressed as a warming of winters and springs (Lizuma et al. 2007) and an extension of precipitation-free periods in the summers (Avotniece et al. 2010).

In 2017, 20 dominant sample trees, growing in 10 unthinned stands of different ages (ca. 70, 110 and 140 years), were felled for stem analysis. The dominant trees were selected to avoid the effects of competition (Brunner and Nigh 2000). Stem disks were taken at 0.2 (stump), 1.3, and every 2 m above the base heights. The surface of the stem disks was grinded and the number of tree-rings was counted under a microscope. The cambial age of the trees at each height was determined. Tree height was corrected for 'hidden tops' using the Carmean (1972) correction. The oldest trees (age > 100 years) originated from seed material transferred from northern Germany (exact provenance unknown); the younger trees were propagated from local seed material, representing the second generation. The initial spacing of the plantations was 2×2 m.

2.2 Data analysis

Dominant height growth was modelled using non-linear Chapman-Richards, Hossfeld, King-Prodan, log-logistic, Sloboda, and Strand equations (Table 1), transformed according to the generalised algebraic difference approach (Cieszewski and Baily 2000; Sharma et al. 2011). Such models have been applied for height growth modelling (Sharma et al. 2011), as they are polymorphic, allowing site-specific parameters, e.g., multiple asymptotes, and are base-age invariant (Cieszewski and Baily 2000). The models were developed for dominant heights above 1.3 m. Time-series of tree heights were reorganised to height difference for each observation period, where h_0 was the height at age t_0, and h_1 was the height at age t_1 (in metres and years, respectively). The mean±standard error age, when the studied beech had reached breast height, was $4.7±0.4$ years.

As several measurements originated from a single tree, mixed models were applied to solve the independence problem (Bates et al. 2015), accounting for random effects of tree and stand. The models were evaluated by fit statistics, graphical analysis of residuals, and biological realism (Goelz and Burk 1992). Statistically, model fit was estimated by mean residual (MR), McNemar's adjusted R^2, root mean squared error (RMSE), and the Akaike information criterion (AIC). Yield tables for beech in southern Sweden were used for comparison (Carbonnier 1971). Data analysis was conducted in the program R v. 3.3.3, using the "lme4" package (Bates et al. 2015).

3   Results

The developed dominant height models showed a slightly differing fit to the measurements (Table 2) and conformance with the biological realism principle (Fig. 1). For most of the models, errors were similar (MR ≤ 0.53 m and RMSE ≤ 0.66, except for Hossfeld I, which showed higher errors), and the R^2-values were high (>0.99, Table 2). The t-values of the parameter estimates mostly exceeded 2.0, except for the single parameters in the Chapman-Richards and log-logistic models. According to the AIC, the Sloboda and Chapman-Richards models showed the best fit, while the Hossfeld's and log-logistic models showed the weakest fit to the data. The variance of random effects was < 2.50.

The Sloboda and Chapman-Richards models appeared to be the most realistic, as the modelled curves followed, and encompassed, the measured time-series throughout the reference period (Fig. 1). These models (particularly the Sloboda model) predicted slow height growth in the initial stage of stand (first 20 years) for site indices ≤27 m in 100 years. In addition, these models showed the best conformity with the improving height growth of the younger trees (ca. 70 years old). The Strand model showed similar tendencies, yet was more optimistic regarding the highest site indices. The log-logistic model was the most conservative, predicting the lowest maximum tree heights, yet it showed lower conformance with measurements at a younger age (<20 years). The Hossfeld and King-Prodan models overestimated height increment for the site indices > 36 m during the first 60–70 years, obviously exceeding the biologically possible growth.

The dominant height models (yield tables) developed in southern Sweden (cf. Carbonnier 1971) showed weak conformity with the observed height growth of the studied beech, particularly regarding the younger trees (ca. 70 years old) and the lower site indices (Fig. 1). In addition, height growth of the younger trees exceeded the range of the yield table (cf. Carbonnier 1971) predictions. The predictions of the yield table also showed high bias, compared to the best of the developed modes (Chapman-Richards, and particularly Sloboda): overestimation at younger age (<100 years) and underestimation at the older age (Fig. 2). The bias was stronger for the lower site indices.

Table 1. The generalized algebraic difference approach models fitted to dominant height time series of beech according to Sharma et al. (2011).

| Base model	Generalized algebraic difference approach model
Chapman-Richards: $h = a_1 \left[1 - \exp(-a_2 t) \right]^{a_3}$, Site specific parameters: a_1, a_3	$h_1 = h_0 \left(\dfrac{1 - \exp(-b_1 t_1)}{1 - \exp(-b_1 t_0)} \right)^X$, where : $X = b_2 + \dfrac{b_3}{(0.5(\psi + \sqrt{\psi^2 + 4 b_3 \phi}))}$, with $\phi = \ln(h_0) - b_2 \phi$, and $\phi = \ln(1 - \exp(-b_1 t_0))$
Hossfeld: $h = \dfrac{a_1}{1 + a_2 t^{-a_3}}$, Site specific parameters: a_1, a_2	$h_1 = \dfrac{b_1 + \dfrac{h_0 - b_1}{1 - b_2 h_0 t_0^{-b_3}}}{1 + \dfrac{t_1^{-b_3} b_2 (h_0 - b_1)}{1 - b_2 h_0 t_0^{-b_3}}}$
Hossfeld I: $h = \dfrac{t^2}{a_1 + a_2 t + a_3 t^2}$, Site specific parameters: a_2, a_3	$h_1 = \dfrac{t_1^2}{b_1 (1 + t_1^2 + \dfrac{t_1 (1 + b_2 t_1)(t_0^2 (1 - b_1 h_0) - b_1 h_0)}{t_0 h_0 (1 + b_2 t_0)}}$
King-Prodan: $h = \dfrac{t^{a_1}}{a_2 + a_3 t^{a_1}}$, Site specific parameters: a_2, a_3	$h_1 = \dfrac{t_1^{b_1}}{b_2 + b_3 \left(\dfrac{\dfrac{t_0^{b_1}}{h_0} - b_2}{b_3 + t_0^{b_1}} \right) + \left(\dfrac{\dfrac{t_0^{b_1}}{h_0} - b_2}{b_3 + t_0^{b_1}} \right) t_1^{b_1}}$
Log-logistic: $h = \dfrac{a_1}{1 + a_2 \exp(-a_3 \log(t))}$, Site specific parameters: a_1, a_3	$h_1 = \dfrac{b_1 + X}{1 + \dfrac{b_2}{X \exp(b_3 \log(t_1))}}$, where $X = 0.5(h_0 - b_1 + ((h_0 - b_1)^2 + 4 b_2 \exp(b_3 \log(t_0)) h_0)^{0.5})$
Sloboda: $h = a_1 \exp\left[-a_2 \exp\left(\dfrac{a_3}{(a_4 - 1) t^{(a_4 - 1)}} \right) \right]$, Site specific parameters: a_2	$h_1 = b_1 \left(\dfrac{h_0}{b_1} \right)^{\exp\left(\dfrac{b_2}{(b_3 - 1) t_1^{b_3 - 1}} - \dfrac{b_2}{(b_3 - 1) t_0^{b_3 - 1}} \right)}$
Strand: $h = \left(\dfrac{t}{a_1 + a_2 t} \right)^{a_3}$, Site specific parameters: a_1, a_2	$h_1 = \left[\dfrac{t_1}{\left(\dfrac{t_0 (h_0^{-\frac{1}{b_3}} - b_1)}{1 + b_2 t_0} \right) + t_1 \left(b_1 + b_2 \left(\dfrac{t_0 (h_0^{-\frac{1}{b_3}} - b_1)}{1 + b_2 t_0} \right) \right)} \right]^{b_3}$
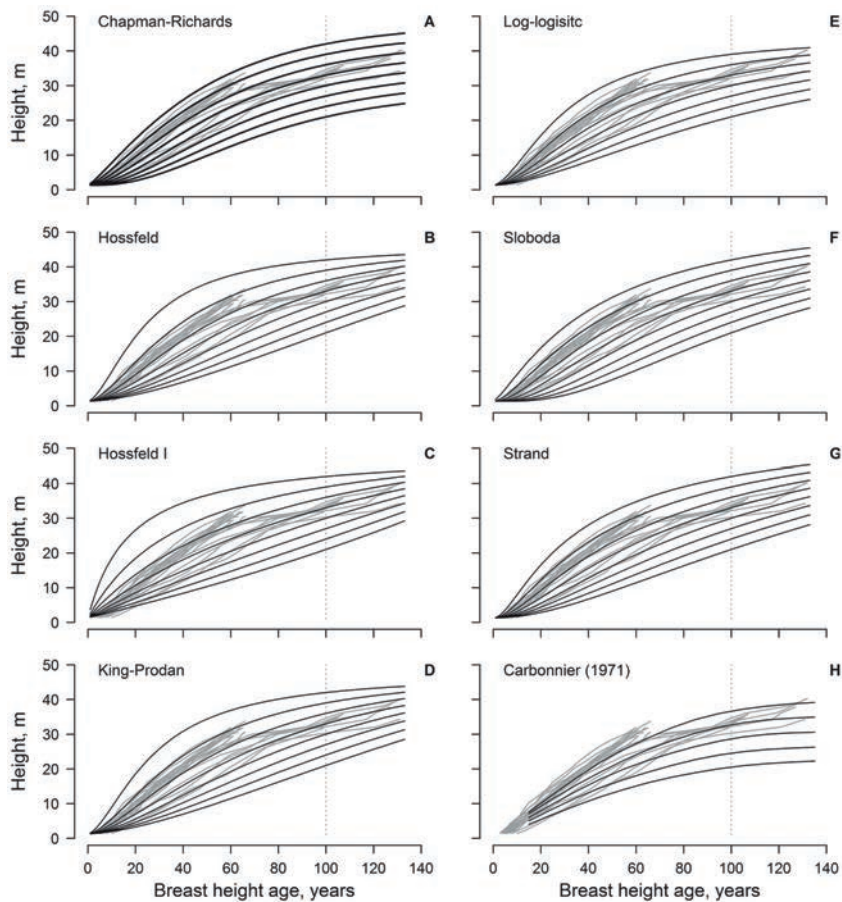
Fig. 1. The non-linear dominant height models (black lines) fitted to the observed data (grey lines, each line represent single tree); model predictions are for 3 m site index intervals for the range 21–42 m (A–G). Panel H show the height growth of beech in southern Sweden according to Carbonnier (1971); black line show site indices in 4 m intervals for the range 20–36 m.

Table 2. Parameter estimates and their *t*-values of the fitted models. Models fit statistics: mean absolute residual (MR), residual standard error (RSE), root mean squared error (RMSE), Akaike information criterion (AIC), adjusted R^2-value (McNemar's method), and variance components of the random effects (VAR).

|	Chapman-Richards	Hossfeld	Hossfeld I	King-Prodan	Log-logistic	Sloboda	Strand
Parameter estimates							
b1	0.0227	43.7466	0.0228	1.576	43.803	52.9402	0.1789
b2	–9.8636	121.078	–0.0054	118.678	–104.29	0.2502	–0.0034
b3	42.6561	1.5954		–5281.7	–1.6153	0.6489	2.2777
Estimate t-values							
b1	16.88	10.36	11.47	37.15	11.83	7.8	8.48
b2	1.91	2.65	4.7	2.17	0.06	7.57	2.03
b3	2.23	37.81		2.03	38.12	12.98	15.7
Model statistics							
MR (m)	0.48	0.51	0.72	0.52	0.53	0.49	0.51
RSE (m)	0.6	0.65	0.83	0.65	0.67	0.63	0.64
RMSE (m)	0.6	0.64	0.82	0.65	0.66	0.62	0.64
AIC	660.3	685.3	835	686.9	694.3	656.8	677.7
Adj. R^2	0.9963	0.9956	0.9958	0.9956	0.9954	0.9959	0.9958
VAR (tree)	0.317	1.125	0.133	0.013	0.432	0.721	0.009
VAR (stand)	0.011	1.965	2.231	2.023	0.414	0.168	0.377
VAR (residual)	0.367	0.418	0.553	0.422	0.441	0.384	0.409
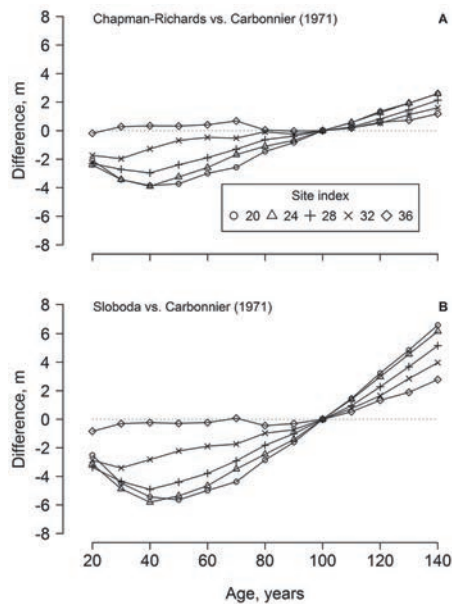
Fig. 2. The differences between beech dominant height predicted by the developed Chapman-Richards (A) and Sloboda (B) models in the western part of Latvia and yield tables for southern Sweden (cf. Carbonnier 1971) according to stand age and site index.

4   Discussion

The fit statistics (Table 2) and biological realism (Fig. 1) indicated the Chapman-Richards and, particularly, Sloboda model, which showed higher t-values of the parameters, as the best for estimating the dominant height of beech in the western part of Latvia. The differences in precision of the parameter estimates of these models (Table 2) were likely caused by the limited dataset (Sharma et al. 2011). Although the dominant height models are often region-specific (Sharma et al. 2011), wider verification of the developed models within the region was impossible, due to an absence of beech stands. The models were developed based on even-aged plantation (Fig. 1), and their predictions might be biased for stands with extreme density (Brunner and Nigh 2000; Sharma et al. 2011).

Considering that climatic changes appear beneficial for beech growth in the Northern Europe (Falkengren-Grerup and Eriksson 1990; Kramer et al. 2010), improved height growth, following the curve for a better site, was observed for the younger (second generation) trees (Fig. 1). This relates to the climatic component of site quality for species growing in marginal populations (Sharma et al. 2012; Kreyling et al. 2014). Improved tree growth has also been related to eutrophication (Pretzsch et al. 2014). Alternatively, improved growth of the second generation trees might be related to the natural and anthropogenic selection of the best adapted genotypes (Matisons et al. 2017).

The dominant height models from southern Sweden (Carbonnier 1971) showed rather poor conformity with the height growth of beech in the western part of Latvia, particularly for site indices <32 m (Fig. 2), which, however, were not represented by the measurements (Fig. 1). Under harsher climatic conditions in Latvia (compared to southern Sweden), a longer time appeared necessary for beech to establish, explaining the deviations from the yield tables (Fig. 2). Slower establishment (extended "lag" phase of growth), which is ordinarily for shade-tolerant species (Seynave et al. 2008; Sharma et al. 2011), was predicted by the Chapman-Richards and, particularly, the Sloboda models (Fig. 1). The yield tables (cf. Carbonnier 1971) also underestimated height growth in longer term (>100 years, Fig. 2), indicating improving growing conditions for beech in the western part of Latvia. Still, the Carbonnier (1971) model might be outdated, due to warming and eutrophication (Falkengren-Grerup and Eriksson 1990; Sharma et al. 2012). Nevertheless, height growth of the younger trees exceeded the predictions of the yield table (Fig. 1 H), indicating improving growing conditions (cf. Carbonnier 1971) and, hence, a rising potential for wider distribution of beech in the Baltics.

5   Conclusions

The developed dominant height models indicated high forestry potential of European beech in the western part of Latvia, particularly for the planting material propagated from local plantations. Accordingly, beech could be approbated for wider application in commercial forestry within the region in the near future. Still, verification of these models on a larger dataset, containing a wider spectrum of site indices, would be necessary to increase the accuracy of the estimates.

Acknowledgements

References

Avotniece Z., Rodinov V., Lizuma L., Briede A., Kļaviņš M. (2010). Trends in the frequency of extreme climate events in Latvia. Baltica 23: 135–148.

Bates D., Maechler M., Bolker B., Walker S. (2015). Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67(1): 1–48. https://doi.org/10.18637/jss.v067.i01.

Bolte A., Czajkowski T., Kompa T. (2007). The north-eastern distribution range of European beech – a review. Forestry 80(4): 413–429. https://doi.org/10.1093/forestry/cpm028.

Brunner A., Nigh G. (2000). Light absorption and bole volume growth of individual Douglas-fir trees. Tree Physiology 20(5–6): 323–332. https://doi.org/10.1093/treephys/20.5-6.323.

Burton L. (2012). Introduction to Forestry Science, 3rd edition. Cengage Learning, New York. 554 p.

Carbonnier C. (1971). Yield of beech in southern Sweden. Studia Forestalia Suecica 91: 1–89.

Carmean W.H. (1972). Site index curves for upland oaks in the Central States. Forest Science 18: 109–120.

Cieszewski C., Bailey R.L. (2000). Generalized algebraic difference approach: theory based derivation of dynamic site q with polymorphism and variable asymptotes. Forest Science 46: 116–126.

Dreimanis A. (1995). The beech and the larch-tree in Shkede forestry. Proceedings of 75th Conference of Latvia University of Agriculture 5: 94–97.

Falkengren-Grerup U., Eriksson H. (1990). Changes in soil, vegetation and forest yield between 1947 and 1988 in beech and oak sites of southern Sweden. Forest Ecology and Management 38(1–2): 37–53. https://doi.org/10.1016/0378-1127(90)90084-O.

Goelz J.C.G., Burk T.E. (1992). Development of a well-behaved site index equation – jack pine in North-central Ontario. Canadian Journal of Forest Research 22(6): 776–784. https://doi.org/10.1139/x92-106.

Harris I.P., Jones P.D., Osborn T.J., Lister D.H. (2014). Updated high-resolution grids of monthly climatic observations – the CRU TS3. 10 dataset. International Journal of Climatology 34: 623–642. https://doi.org/10.1002/joc.3711.

Hickler T., Vohland K., Feehan J., Miller P., Smith B., Costa L., Giesecke T., Fronzek S., Carter T., Cramer W., Kühn I., Sykes M. (2012). Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. Global Ecology and Biogeography 21(1): 50–63. https://doi.org/10.1111/j.1466-8238.2010.00613.x.

Kramer K., Degen B., Buschbom J., Hickler T., Thuiller W., Sykes M., de Winter W. (2010). Modelling exploration of the future of European beech (*Fagus sylvatica* L.) under climate change – range, abundance, genetic diversity and adaptive response. Forest Ecology and Management 259(11): 2213–2222. https://doi.org/10.1016/j.foreco.2009.12.023.

Kreyling J., Buhk C., Backhaus S., Hallinger M., Huber G., Huber L., Jentsch A., Konnert M., Thiel., Wilmking M., Beierkuhnlein C. (2014). Local adaptations to frost in marginal and central populations of the dominant forest tree *Fagus sylvatica* L. as affected by temperature and extreme drought in common garden experiments. Ecology and Evolution 4: 594–605. https://doi.org/10.1002/ece3.971.

Lizuma L., Kļaviņš M., Briede A., Rodinovs V. (2007). Long-term changes of air temperature in Latvia. In: Kļaviņš M. (ed.). Climate change in Latvia. University of Latvia, Riga, Latvia. p. 11–20.

Loehle C. (1998). Height growth rate tradeoffs determine northern and southern range limits for trees. Journal of Biogeography 25: 735–742. https://doi.org/10.1046/j.1365-2699.1998.2540735.x.

Matisons R., Puriņa L., Adamovičs A., Robalte L., Jansons A. (2017). European beech in its northeasternmost stands in Europe: varying climate-growth relationships among gen-

erations and diameter classes. Dendrochronologia 45: 123–133. https://doi.org/10.1016/j.dendro.2017.08.004.

Pretzsch H., Biber P., Schütze G., Bielak K. (2014). Changes of forest stand dynamics in Europe. Facts from long-term observational plots and their relevance for forest ecology and management. Forest Ecology and Management 316: 65–77. https://doi.org/10.1016/j.foreco.2013.07.050.

Puriņa L., Matisons R., Jansons Ā., Šēnhofa S. (2016). Survival of European beech in the central part of Latvia 33 years since the plantation. Silva Fennica 50(4) article 1656. https://doi.org/10.14214/sf.1656.

Seynave I., Gegout J.C., Herve J.C., Dhote J.F. (2008). Is the spatial distribution of European beech (*Fagus sylvatica* L.) limited by its potential height growth? Journal of Biogeography 35: 1851–1862. https://doi.org/10.1111/j.1365-2699.2008.01930.x.

Sharma R.P., Brunner A., Eid T., Øyen B.H. (2011). Modelling dominant height growth from national forest inventory individual tree data with short time series and large age errors. Forest Ecology and Management 262(12): 2162–2175. https://doi.org/10.1016/j.foreco.2011.07.037.

Sharma R.P., Brunner A., Eid T. (2012). Site index prediction from site and climate variables for Norway spruce and Scots pine in Norway. Scandinavian Journal of Forest Research 27(7): 619–636. https://doi.org/10.1080/02827581.2012.685749.

Total of 23 references.

Intra-annual radial growth of European beech – a case study in north easternmost stand in Europe

Oskars Krišāns[1], Līga Puriņa[1], Dāvis Mesters[2], Rolands Kāpostiņš[1], Juris Rieksts-Riekstiņš[1] and Āris Jansons[1,*]

Abstract. *Fagus sylvatica* L. is one of the most important commercial tree species in Europe and its natural distribution range is expected to shift northwards due to climatic changes. Detailed information of factors affecting its growth is crucial as a basis for recommendations of wider use of this tree species. Aim of the study was to characterize the changes of radial growth intensity of European beech during a vegetation season. In mature beech stand in northwest Latvia two sample trees (dominant (DT) and suppressed (ST)) were selected in *Hylocomiosa* forest type. Continuous measurements of changes of stem diameter and xylem sap flow as well as meteorological parameters were carried out. Stem cycle approach was applied to distinguish the duration of contraction, expansion and increment of the stem. Onset and cessation of growth of the ST tree was observed several days later compared with DT and mean growth intensity during the entire observation period was considerably lower (0.014 mm/day^{-1} for ST and 0.022 mm/day^{-1} for DT, respectively). Most intensive growth increment diurnally was observed in the early morning before sunrise, and seasonally till beginning of July. Positive effect of precipitation and low water pressure deficit (VPD) on growth was observed, while high VPD coincided with stem contraction. Results indicate the sensitivity of radial growth of European beech to water deficit and high atmospheric transpirational demand; therefore, future potential of cultivation of beech in Latvia depends on changes in moisture regime.

Key words: *Fagus sylvatica* L., climate change, radial growth, dendrometer, soil water potential.

Authors' addresses: [1]Latvian State Forest Research Institute "Silava", 111 Rigas st., Salaspils, LV2169, Latvia; [2]Society of Annas Tree School, "Annas koku skola", Klīves, Babītes pag., Babītes nov., LV2107, Latvia; *e-mail: aris.jansons@silava.lv

VI

Introduction

European beech (*Fagus sylvatica* L.) is one of the most important commercial tree species in Europe, its distribution range currently stretches from the southern part of the Scandinavian Peninsula in the North till Sicily in the South and from the Iberian Peninsula in the West till Western Ukraine in the East (Ellenberg, 1988, 1996; Fang & Lechowicz, 2006). Continentality, which can be characterized by high summer temperatures, summer droughts (Betsch *et al.*, 2011) and late spring frosts (Augustaitis *et al.*, 2015), is considered as one of the limiting factors of the distribution of European beech (Fang & Lechowicz, 2006). Modelled occurrence and severity of drought occasions (Rasztovits *et al.*, 2014) and decrease of probability of extreme cold events in the

southern and northern parts of its distribution range, respectively, coincide with forecasted effects of global climate change (IPCC, 2014) and therefore with the natural distribution range of beech, which is expected to shift northwards (Hickler *et al.*, 2012). Currently, in several forest stands (established at the end of 19th century) in Western Latvia, beech have shown high level of acclimatization (Jansons *et al.*, 2015), successful natural regeneration (Puriņa *et al.*, 2016) and productivity similar to that of common tree species, like Norway spruce and silver birch (Dreimanis, 2006).

Detailed understanding of tree short term response to environmental conditions is important for predictions of tree growth in changing climate and subsequent development of forest management strategy. Data on short term responses based on stem diameter variation (SDV) can be conveniently gathered by means of dendrometry. Several studies (Ceschia *et al.*, 2002; Knott, 2004; Charru *et al.*, 2010; Šimpraga *et al.*, 2011; Michelot *et al.*, 2012) have used it to assess intra-annual growth of European beech. Fluctuations of stem diameter are result of contraction and expansion caused by irreversible increment of xylem, changes in tissue water storage, wood thermal properties and internal tensions of conducting elements (Daudet *et al.*, 2005). Therefore, SDV can indicate the level of tissue hydration and potential drought stress (De Swaef *et al.*, 2015).

As demonstrated by Steppe & Lemeur (2004) and Michelot *et al.* (2012), growth of both juvenile and mature beech trees was drought sensitive. Sufficient water uptake ensures cell turgor pressure which is the main force providing cell expansion and division (Lockhart, 1967). Thereofre, minimized cell expansion in drought stressed trees is related to insuficient xylem hydration (Hsiao, 1973; Abe *et al.*, 2003). Due to water deficit, newly-formed vessels are reduced in size (Sass & Eckstein, 1995) which, in combination with reduction of xylem conductance (Barigah *et al.*, 2013) hinders further water supply and hence assimilation.

So far such studies have not been carried out for European beech on the edge of its current distribution. Significant differences in water use have been found between dominant and suppressed beech trees, suggesting suppressed trees being under a higher drought stress risk beneath a closed canopy compared with dominant trees (Dalsgaard, 2008). Therefore, the aim of the study was to assess the intra-annual radial growth dynamics between dominant and suppressed European beech trees growing in northwest Latvia. We hypothesized that the intra-annual radial growth dynamics of beech in northwest Latvia is sensitive to water deficit.

Material and Methods

Study area and study period

The study area is located in north west Latvia (57°14´ N, 22°41´ E) in the central part of Ziemeļkursas upland which is situated in a hemiboreal mixed forest of the temperate climatic zone where annual air temperature and the sum of precipitation is + 6.3 °C and 750 mm, respectively (Latvian Environment, Geology and Meteorology Centre). Movement of North Atlantic air masses generally determines climatic conditions in Latvia; however, a gradient of small scale continentality in the territory of Latvia increases in direction from the coast in south west to inland in north east (Laiviņš & Melecis, 2003; Draveniece, 2007). Therefore, regional differences in the duration of the vegetation period (in the western part of Latvia the vegetation period is 2 to 3 weeks longer than in the eastern part) are observed (Klavins & Rodinov, 2010). According to the data from the closest meteorological observation station in Stende (about 20 km from the study site), both mean daily air temperature (14.9 °C) and sum of precipitation (327 mm) of the studied period (May–August, 2014) exceeded 30-year means of the cor-

responding period (14.5 °C and 271 mm, respectively).

Two nearby trees located 8 m from each other (DT–34.0 m high, diameter at breast height (DBH) 55 cm, 127 years old and ST–12.6 m high, DBH 16 cm, 43 years old) were sampled in a mixed Scots pine and European beech stand on well drained loamy soil in *Hylocomiosa* forest type. Sample trees were selected according to differences in dominance (DT formed the emergent layer of the stand while ST was located in the understory).

Measurements of SDV, sap flow and weather parameters

Monitoring of SDV was done at the breast height once per 10 minutes by automated band dendrometers DRL26C (EMS Brno, Czech Republic). Simultaneously, at the same height (4 m) of the trunk, xylem sap flow was measured every 10 minutes by applying the heat ratio method integrated in a SFM1 sap flow meter (ICT International, Australia). Probes of SFM1 have two measurement points with 15 mm spacing in between, and, to avoid the influence of ambient temperature on sap flow data, outer measurement point was placed in the depth of 5 mm below cambium layer within the sapwood (Burgess *et al.*, 2001). Accordingly, inner measurement point was located in the sapwood in the depth of 20 mm. Raw sap flow data were arranged by Sap Flow Tool software (ICT International, Australia) removing logging errors and applying correction factors (bark thickness, sapwood depth and tree size) for calculating the sap flow rate for the whole tree. Meteorological data used in study were obtained from a mobile weather station (Vantage Pro2, Davis Instruments, USA) located near the forest stand. Soil water potential was measured in the study site by using tensiometers (T8, UMS GmbH, Germany) and obtained data were stored in the DL6 logger (Delta-T Devices, UK).

Data analysis

Dendrometer data were analysed according to the methodology of stem cycle approach by Deslauriers *et al.* (2007) and Deslauriers *et al.* (2011). This method is based on division of daily pattern of stem shrinking/swelling cycles into different phases. Accordingly, phases of contraction (period between the daily maximum and next minimum), expansion (period between the end of contraction and next maximum) and increment (part of the expansion phase from the time the stem radius exceeds the previous maximum until the next maximum) were distinguished (Deslauriers *et al.*, 2007) using DendrometeR package (van der Maaten *et al.*, 2016) in R v.3.0.2. (R Core Team, 2016) software.

In order to characterize the relationship between sap flow rate and vapour pressure deficit (VPD), Gompertz function was fitted in analysis of nonlinear least squares:

$$f(VPD) = \alpha^{-\beta^{-\gamma * VPD}}$$

where α = asymptote, β = shape parameter, γ = scale parameter. Coefficient of determination (R^2) of the nonlinear model was obtained by the formula:

$$R^2 = (1 - \sum r_i^2) / (\sum (y - \bar{x}y)^2),$$

where $\sum r_i^2$ is residual sum of squares and $\sum (y - \bar{x}y)^2$ is total sum of squares. Statistical analysis was done in R v.3.0.2. (R Core Team, 2016) software.

Results and Discussion

The sum of precipitation and average air temperature of the studied period were 285 mm and 17.2 °C, respectively, but the mean value of VPD reached 1.2 kPa (Figure 1C). Maximum air temperature was 33.4 °C, recorded in the beginning of August during a no rain period. Groundwater remained very low – between 19.48 and 19.41 m (Figure 1B), which, due to the geomorphological properties of the study site, is located in
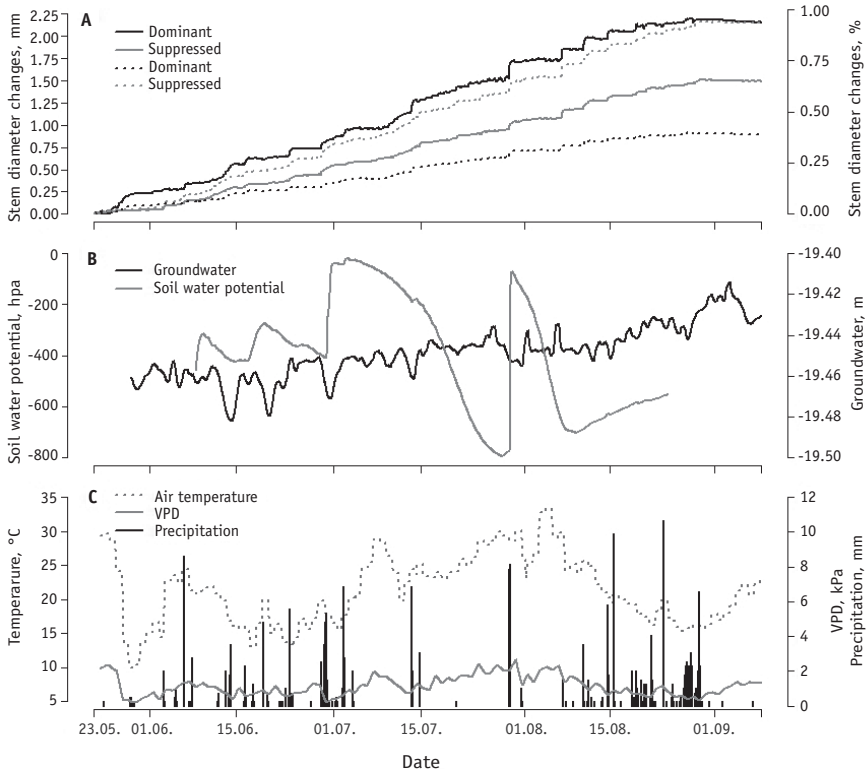
Figure 1. Seasonal course of changes in total (solid lines) and relative (dashed lines, secondary axis) radial increment (A), soil water potential and groundwater level (secondary axis) (B), and air temperature, vapour pressure deficit (VPD) and hourly sums of precipitation (secondary axis) (C).

the aquifer under a confining layer formed by fat clay. Therefore, capillary rise of water is excluded and soil moisture available for trees is supplied by precipitation only. Values of soil water potential fluctuated between drought conditions during the longest no rain periods with high VPD in the end of July/beginning of August and saturation right after intense rainfall along with decrease of VPD (Figure 1C).

Total radial increment for DT and ST tree was 2.2 and 1.5 mm, respectively (Figure 1A). Nevertheless, ST had larger relative increment from the initial DBH compared to DT (0.93 and 0.38%, respectively). At the end of dormancy, tissue rehydration and translocation of growth stimulants occur (Mäkinen *et al.*, 2008), explaining the onset of fluctuations of stem diameter for both trees observed several weeks before the first record of increment phase. Following winter dehydration, restoration of sufficient xylem water content is one of preconditions for initiation of division of vascular cambium cells (Yamashita *et al.*, 2006; Mäkinen *et al.*, 2008); therefore, a rapid increase of stem diameter as it was observed for DT in the last decade of May (Figure 1) can be explained by reduced transpirational water loss due to a decrease of VPD (Steppe &
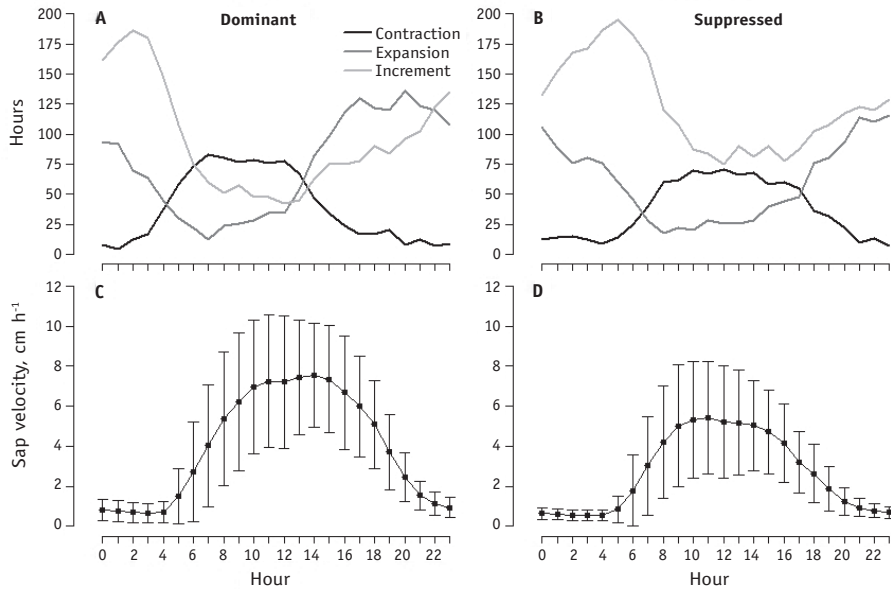
Figure 2. Hourly sums of duration of distinct phases of SDV (A; B) and mean hourly sap velocity (C; D).

Lemeur, 2004).

Notable increase of stem diameter for ST started 2 weeks after DT during the period with rain events (Figure 1A). Earlier growth onset for DT can be explained by higher root competitiveness of dominant trees which are very competitive, ensuring better water absorption (Le Goff & Ottorini, 2001). During the observation period, cumulative changes of stem diameter formed a sawblade shaped curve with fluctuations caused by daily variations of wood hydration (Steppe & Lemeur, 2004; Michelot *et al.*, 2012). Pronounced leaps, corresponding to rain events and/or a decrease in VPD and air temperature, are distinguished as phases of increment. During such conditions, water absorbed from the soil is not being transpired completely but integrated into formation of xylem cells (Pallardy, 2008). Subsequently, for both trees the highest values of single increment phases were recorded just after rain events during periods when both

air temperature and VPD decreased (Figure 1). Cumulative radial growth was completed in 98 and 101 days for DT and ST, respectively, which corresponds to results of the study from Slovenia by Čufar *et al.* (2008) showing that the average time of cambial activity for beech is 100 days. The timing of growth cessation generally is controlled by shortening of the photoperiod; however, age, vigour as well as environmental conditions influence the control of development of dormancy (Kozlowski & Pallardy, 1997).

On the diurnal cycle, a period of the most intensive growth was observed in early morning, just before sunrise and subsequent start of daily sap flow; it was especially pronounced after stem rehydration following the rain events (Figure 2). Contraction of stems coincided with the increase of sap flow due to intensification of transpiration.

In the afternoon, sap flow decreased and expansion of stems due to restoration
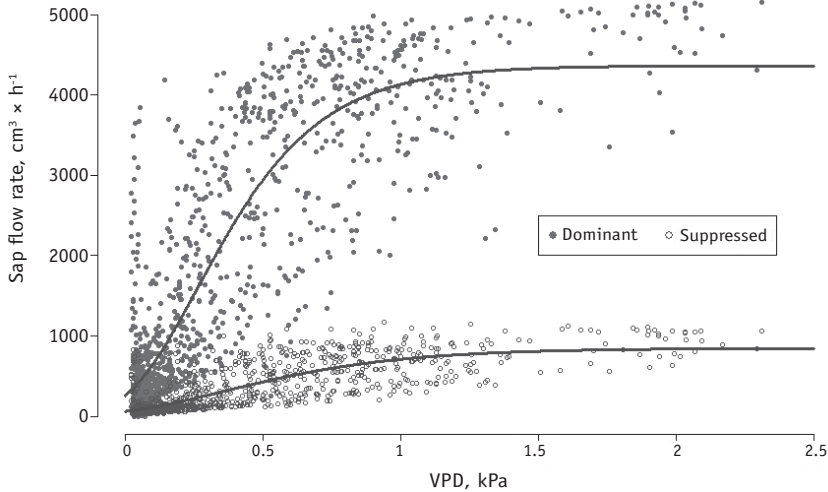
Figure 3.   Relationship between sap flow rate and VPD in dominant (A) suppressed (B) tree.

of xylem water storage (Čermák *et al.*, 2007) followed. Diurnal distribution of stem cycle phases between both trees was similar. However, during the diurnal cycle, total duration of increment phase for ST exceeded the duration of expansion and was longer compared with DT. Earlier onset of daily sap flow and following stem contraction for DT is caused by both higher root competitiveness and canopy exposure to direct solar radiation and wind compared with ST. In the understory layer, in the morning, air temperature increase and subsequent onset of transpiration is delayed in comparison with emergent layer of the stand (Granier, 1987). A diurnal peak of increment phase duration for ST was observed on average 3 hours later compared with DT, and subsequent start of contraction for ST was 1 hour later. Additionally, this phase lasted longer in the afternoon. Therefore, diurnal course of radial growth of ST showed less xylem water loss resulting in less sensitivity to weather conditions.

Since the success of tree growth is related to water availability (Pallardy, 2008),

sap flow measurements can be used to trace tissue hydration and changes in vigour (Čermák *et al.*, 2007). Čermák *et al.* (2007) showed that an increase of sap flow rate and depletion of internal water storage of the stem coincides. Comparing both sample trees, higher sap flow rates were observed for DT (up to 5000 cm^3 ha^{-1}) than for ST (up to 1000 cm^3 ha^{-1}). For both trees, high sap flow rates during very low VPD indicates rehydration during nights (Daley & Phillips, 2006) or rainy/cloudy and cool days when formation of radial increment was observed (Figures 2, 3). High sap flow rates during high VPD indicates water movement through xylem driven by transpiration during sunny, warm days coinciding with contraction of the stem or very low radial increment (Figure 1). An increase of VPD above 1.5 kPa indicates upper limits of sap flow capacity for both trees. A high transpiration in combination with insufficient water supply causes stomata closure and cavitation leading to cessation of xylem sap flow (Jones, 1998; Tyree & Sperry, 1989). Therefore, hydration of xylem tissue is hindered

Table 1. Values of parameters (*α*, *β* and *γ*) and performance of nonlinear model.

Parameter ± SD	Dominant	Suppressed	*p*-value
α	4364.03 ± 76.82	847.48 ± 25.16	< 0.001
β	2.84 ± 0.1	2.64 ± 0.1	< 0.001
γ	3.94 ± 0.18	2.69 ± 0.16	< 0.001
R^2	0.76	0.66	

(Zeppel *et al.*, 2004). Turgor pressure is considered to be the main driving factor of vessel enlargement (Ray *et al.*, 1972). Therefore, vessel growth is negatively affected by the water deficit (Sass & Eckstein, 1995). Since larger vessels in diameter have higher water conducting capacity (Tyree & Zimmermann, 2013), insufficient tissue hydration can have negative effect on growth during next vegetation period (Sass & Eckstein, 1995).

Analysis of nonlinear least squares (Figure 3 and Table 1) resulted in a sigmoidal relationship between sap flow rate and VPD for both trees.

Differences in explained variances by the model for DT (R^2 = 0.76) and ST (R^2 = 0.66) and more rapid increase of sap flow rate (determined by differences in scale parameter (*γ*)) of DT at low values of VPD compared with ST, as already mentioned, can be explained by exposure of the canopy of DT to direct sunlight and wind favoring transpiration, thus providing large amounts of water for transpiration (Le Goff & Ottorini, 2001).

Conclusions

Due to water deficit, formation of radial increment is very slow or completely interrupted until the restoration of stem water storage is completed facilitating the expansion of xylem cells. Thus, confirming our hypothesis that radial growth of European beech in northwest Latvia is sensitive to water deficit. Therefore, according to the predicted increase in mean annual air temperature, the future cultivation potential of beech in Latvia depends on the precipitation regime.

References

Abe, H., Nakai, T., Utsumi, Y., Kagawa, A. 2003. Temporal water deficit and wood formation in *Cryptomeria japonica*. – Tree Physiology, 23(12), 859–863.

Augustaitis, A., Kliučius, A., Marozas, V., Pilkauskas, M., Augustaitiene, I., Vitas, A., Staszewski, T., Jansons, A., Dreimanis, A. 2015. Sensitivity of European beech trees to unfavorable environmental factors on the edge and outside of their distribution range in northeastern Europe. – iForest, 9, 259–269.

Barigah, T.S., Charrier, O., Douris, M., Bonhomme, M., Herbette, S., Améglio, T., Fichot, R., Brignolas, F., Cochard, H. 2013. Water stress-induced xylem hydraulic failure is a causal factor of tree mortality in beech and poplar. – Annals of Botany, 10(23), 1–7.

Betsch, P., Bonal, D., Breda, N., Montpied, P., Peiffer, M., Tuzet, A., Granier, A. 2011. Drought effects on water relations in beech: the contribution of exchangeable water reservoirs. – Agricultural and Forest Meteorology, 151(5), 531–543.

Burgess, S.S., Adams, M.A., Turner, N.C., Beverly, C.R., Ong, C.K., Khan, A.A., Bleby, T.M. 2001. An improved heat pulse method to measure low and reverse rates of sap flow in woody plants. – Tree Physiology, 21(9), 589–598.

Čermák, J., Kučera, J., Bauerle, W.L., Phillips, N., Hinckley, T.M. 2007. Tree water storage and its diurnal dynamics related to sap flow and changes in stem volume in old-growth Douglas-fir trees. – Tree Physiology, 27(2), 181–198.

Ceschia, É., Damesin, C., Lebaube, S., Pontailler, J.Y., Dufrêne, É. 2002. Spatial and seasonal variations in stem respiration of beech trees (*Fagus sylvatica*). – Annals of Forest Science, 59(8), 801–812.

Charru, M., Seynave, I., Morneau, F., Bontemps, J. D. 2010. Recent changes in forest productivity: an analysis of national forest inventory data for common beech (*Fagus sylvatica* L.) in north-eastern France. – Forest Ecology and Management, 260(5), 864–874.

Čufar, K., Prislan, P., de Luis, M., Gričar, J. 2008. Tree-ring variation, wood formation and phenology of

beech (*Fagus sylvatica*) from a representative site in Slovenia, SE Central Europe. – Trees, 22(6), 749–758.

Daley, M.J., Phillips, N.G. 2006. Interspecific variation in nighttime transpiration and stomatal conductance in a mixed New England deciduous forest. – Tree Physiology, 26, 411–419.

Dalsgaard, M.L. 2008. Transpiration and water budgets of European beech (*Fagus sylvatica* L.) dominated stands in relation to canopy structure. – Trees, 9(5), 247–252.

Daudet, F.A., Améglio, T., Cochard, H., Archilla, O., Lacointe, A. 2005. Experimental analysis of the role of water and carbon in tree stem diameter variations. – Journal of Experimental Botany, 56, 135–144.

De Swaef, T., De Schepper, V., Vandegehuchte, M.W., Steppe, K. 2015. Stem diameter variations as a versatile research tool in ecophysiology. – Tree Physiology, 35(10), 1047–1061.

Deslauriers, A., Rossi, S., Anfodillo, T. 2007. Dendrometer and intra-annual tree growth: What kind of information can be inferred? – Dendrochronologia, 25, 113–124.

Deslauriers, A., Rossi, S., Turcotte, A., Morin, H., Krause, C. 2011. A three-step procedure in SAS to analyze the time series from automatic dendrometers. – Dendrochronologia, 29, 151–161.

Draveniece, A. 2007. Oceanic and continental air masses over Latvia Riga. – Latvijas Veģetācija, 14, 135 pp. (In Latvian with English abstract).

Dreimanis, A. 2006. Productivity of beech stands in Skede forest district. – Latvijas Lauksaimniecības Universitātes Raksti, 16, 94–100. (In Latvian with English abstract).

Ellenberg, H. 1988. Vegetation ecology of central Europe. Cambridge, Cambridge University Press. 735 pp.

Ellenberg, H. 1996. Vegetation of Central Europe with the Alps in ecological, dynamic and historical view. (Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht). Stuttgart, Verlag Eugen Ulmer. 1095 pp. (In German).

Fang, J., Lechowicz, M.J. 2006. Climatic limits for the present distribution of beech (*Fagus sylvatica* L.) species in the world. – Journal of Biogeography, 33(10), 1804–1819.

Granier, A. 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. – Tree Physiology, 3(4), 309–320.

Hickler, T., Vohland, K., Feehan, J., Miller, P.A., Smith, B., Costa, L., Giesecke, T., Fronzek, S., Carter, T.R., Cramer, W., Kühn, I., Sykes, M.T. 2012. Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. – Global Ecology and Biogeography, 21(1), 50–63.

Hsiao, T.C. 1973. Plant responses to water stress. – Annual Review of Plant Physiology, 24(1), 519–570.

IPCC. 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [WWW document]. – URL https://www.ipcc.ch/report/ar5/syr/ [Accessed 3 September 2016].

Jansons, Ā., Matisons, R., Puriņa, L., Neimane, U., Jansons, J. 2015. Relationships between climatic variables and tree-ring width of European beech and European larch growing outside of their natural distribution area. – Silva Fennica, 49(1) article id 1255.

Jones, H.G. 1998. Stomatal control of photosynthesis and transpiration. – Journal of Experimental Botany, 49, 387–398.

Klavins, M., Rodinov, V. 2010. Influence of large-scale atmospheric circulation on climate in Latvia. – Boreal Environment Research, 15, 533–543.

Knott, R. 2004. Seasonal dynamics of the diameter increment of fir (*Abies alba* Mill.) and beech (*Fagus sylvatica* L.) in a mixed stand. – Journal of Forest Science, 50(4), 149–160.

Kozlowski, T.T., Pallardy, S.G. 1997. Physiological regulation of vegetative growth. – Kozlowski, T.T., Pallardy, S.G. (eds.). Growth control in woody plants. San Diego, Elsevier, 73–165.

Laiviņš, M., Melecis, V. 2003. Bio-geographical interpretation of climate data in Latvia: multidimensional analysis. – Acta Universitatis Latviensis, 654, 7–22.

Le Goff, N., Ottorini, J.M. 2001. Root biomass and biomass increment in a beech (*Fagus sylvatica* L.) stand in North-East France. – Annals of Forest Science, 58(1), 1–13.

Lockhart J.A. 1967. Physical nature of irreversible deformation of plant cells. – Plant Physiology, 42, 1545–1552.

van der Maaten, E., van der Maaten-Theunissen, M., Smiljanić, M., Rossi, S., Simard, S., Wilmking, M., Deslauriers A., Fontie, P., von Arxe, G. Bouriaud, O. 2016. dendrometeR: analyzing the pulse of trees in R. – Dendrochronologia, 40, 12–16.

Mäkinen, H., Seo, J.W., Nöjd, P., Schmitt, U., Jalkanen, R. 2008. Seasonal dynamics of wood formation: a comparison between pinning, microcoring and dendrometer measurements. – European Journal of Forest Research, 127(3), 235–245.

Michelot, A., Simard, S., Rathgeber, C., Dufrêne, E., Damesin, C. 2012. Comparing the intra-annual wood formation of three European species (*Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris*) as related to leaf phenology and non-structural carbohydrate dynamics. – Tree Physiology, 32(8), 1033–1045.

Pallardy, S.G. 2008. Physiology of Woody Plants (Third Edition). San Diego, Academic Press. 454 pp.

Puriņa, L., Neimane, U., Džeriņa, B., Jansons, Ā. 2016. European beech (*Fagus sylvatica* L.) regeneration affecting factors. – Mežinātne, 27(60), 67–76. (In Latvian with English abstract).

R Core Team. 2016. R: A language and environment for statistical computing. Vienna, R Foundation for Statistical Computing. 13 pp.

Rasztovits, E., Berki, I., Mátyás, C., Czimber, K., Pötzelsberger, E., Móricz, N. 2014. The incorporation of extreme drought events improves models for beech persistence at its distribution limit. – Annals of Forest Science, 71(2), 201–210.

Ray, P.M., Green, P.B., Cleland, R. 1972. Role of turgor in plant cell growth. – Nature, 239, 163–164

Sass, U., Eckstein, D. 1995. The variability of vessel size in beech (*Fagus sylvatica* L.) and its ecophysiological interpretation. – Trees, 9(5), 247–252.

Šimpraga, M., Verbeeck, H., Demarcke, M., Joó, É., Pokorska, O., Amelynck, C., Schoon, N., Dewulf, J., Van Langenhove, H., Heinesch, B., Aubinet, M., Laffineur, Q., Müller, J.-F., Steppe K. 2011. Clear link between drought stress, photosynthesis and biogenic volatile organic compounds in *Fagus sylvatica* L. – Atmospheric Environment, 45(30), 5254–5259.

Steppe, K., Lemeur, R. 2004. An experimental system for analysis of the dynamic sap-flow characteristics in young trees: results of a beech tree. – Functional Plant Biology, 31(1), 83–92.

Tyree, M.T., Sperry, J.S. 1989. Vulnerability of xylem to cavitation and embolism. – Annual Review of Plant Biology, 40(1), 19–36.

Tyree, M.T., Zimmermann, M.H. 2013. Xylem structure and the ascent of sap. Berlin, Springer Science & Business Media. 146 pp.

Yamashita, K., Okada, N., Kamo, K. 2006. Application of the wire dendrometer for monitoring the radial growth of trees: a comparison with the conventional band dendrometer and the pinning method. – Mokuzai Gakkaishi, 52, 8–18. (In Japanese with English abstract and legends).

Zeppel, M.J., Murray, B.R., Barton, C., Eamus, D. 2004. Seasonal responses of xylem sap velocity to VPD and solar radiation during drought in a stand of native trees in temperate Australia. – Functional Plant Biology, 31(5), 461–470.

Original Article

European beech in its northeasternmost stands in Europe: Varying climate-growth relationships among generations and diameter classes

Roberts Matisons[*], Līga Puriņa, Andis Adamovičs, Linda Robalte, Āris Jansons

LSFRI "Silava", Rigas str. 111, Salaspils, LV2169, Latvia

A B S T R A C T

Age, genetics and social status of trees affect their sensitivity to environmental factors, and information about such effects is needed for comprehensive assessment of growth potential. Climatic sensitivity of radial increment (i.e., tree-ring width) of introduced European beech (*Fagus sylvatica* L.) of different generations and social status, growing in its northeasternmost stands in Europe, was studied by dendroclimatological methods. At present, the studied stands occur outside of the natural distribution area of the species, providing opportunity to study adaptability and potential growth of beech in novel environments under changing climate. The sensitivity of radial growth to climatic factors was modulated by the generation and social status (size) of trees. The first generation trees, which were propagated from the material transferred from the northern Germany, were highly sensitive to climatic factors and showed wide spectrum of responses. The dominant trees were particularly sensitive to June precipitation, indicating sensitivity to water deficit in summer. The suppressed trees were mainly sensitive to temperature in the dormant period. Tree-ring width of the second generation trees, which were propagated from the first generation stands, was mainly affected by water deficit in summer, yet the local factors, modulated the mechanisms of response. In one stand, tree-ring width was affected by conditions during the formation of tree-ring, indicating direct influence of weather conditions on xylogenesis. In the other stand, tree-ring width was correlated to weather conditions in the preceding year, suggesting influence via carbohydrate reserves. The effect of social status on climatic sensitivity in the second generation stands was considerably weaker, likely due to the natural and anthropogenic selection of the material best adapted for local conditions. The effect of climatic factors on radial growth of beech has shifted during the 20th century. The effect of autumn temperature has weakened, likely due to warming; the effect of factors related to water deficit in summer has intensified that could be related to both, changes in climate and ageing. The observed climate-growth relationships suggested that conditions in winter have become suitable for beech, yet careful selection of sites/regions with appropriate hydrological conditions appear necessary to counteract the increasing effect of water deficit, hence to ensure productivity of future beech sites in Latvia.

1. Introduction

In Europe, northward expansion of European beech (*Fagus sylvatica* L.) is expected by the end of the 21st century in response to climatic changes (Hickler and Vohland, 2012; Kramer et al., 2010); however, considering slow dispersion of propagules (Saltre et al., 2013), assisted migration appears important issue for wider spread of the species (Björkman and Bradshaw, 1996; Vitt et al., 2010). Introduction of forest reproductive material suitable for warmer climates has been advised as one of the means for mitigation of the effects of warming climate on forestry (Winder et al., 2011), thus broadening perspectives for a wider (commercial) application of beech in the hemiboreal zone. Such introductions would require adjustments in forest management practices

that creates necessity for comprehensive information about the benefits and environmental risks of the novel species (Burton, 2012).

Sensitivity of populations growing near the species distribution limits to environmental factors is largely determined by the genetics (provenance) (Peuke et al., 2002), which affects the adaptive capacity (Aitken et al., 2008; Kreyling et al., 2014). In this regard, experimental plantations, particularly near or outside the natural range of the species, serve as good indictors of adaptability and potential growth of species in novel environments under changing climate (Isaac-Renton et al., 2014; Kreyling et al., 2014; Vetaas, 2002). At present, the northeasternmost experimental stands of beech, which are located outside of its natural distribution range and have reached maturity, occur in the western part of Latvia (Augustaitis et al., 2015; Bolte et al.,

Table 1

Description of the studied stands of European beech and descriptive statistics (mean value, range, and standard deviation) of stem diameter at breast height (DBH) and number of measured tree-rings for sampled trees. CI—confidence interval.

	Young 1	Young 2	Mature
Location	57.2505° N, 22.6993° E	57.2464° N, 22.6264° E	57.2504° N, 22.7209° E
Area, ha	1.7	2.2	2.0
Year established (stand age at sampling, years)	1956 (60)	1951 (65)	1889 (127)
Initial density, ind. ha^{-1}	4000	4000	3800
Admixture	Pure beech	Oak, 20%	Birch, 20%
Mean DBH ± CI, cm	25.86 ± 3.03	26.85 ± 3.12	28.95 ± 3.26
Range DBH, cm	10.4–46.3	12.4–48.5	14.1–49.6
St. dev. DBH, cm	9.9	9.8	10.5
Mean length of series ± St. dev., number of tree-rings	44.4 ± 9.7	56.2 ± 4.7	106.6 ± 14.0

2007), where the species has been planted on ca. 40 ha of forest land. Good survival, productivity and self-regeneration of these stands suggest that conditions in the western part of Latvia have been suitable for beech (Bolte et al., 2007; Dreimanis, 1995), yet little information is available about its growth variation (Augustaitis et al., 2015; Jansons et al., 2015).

Climate is one of the main factors that affects tree increment (Fritts, 2001), hence information about its climatic sensitivity is essential for assessment of future growth potential and necessary adjustments in management (Burton, 2012). Detailed information about the effect of climatic factors on tree growth can be obtained by retrospective analysis of tree-ring proxies (e.g., width), which act as a natural archive of the environment-growth interactions (Cook, 1985; Fritts, 2001). Trees growing close or even outside their natural distribution area have been considered as highly informative for such analysis due to pronounced effect of limiting factor(s) (Speer, 2010; Vetaas, 2002). The effect of climatic factors on tree growth is usually complex, modulated by regional, site and internal factors, which have to be considered when extrapolating the obtained relationships (Cook, 1985; Friedrichs et al., 2009; Fritts, 2001). Hence, the selection of empirical material (sample trees) influences the detectable climate-growth relationships (Carrer and Urbinati, 2004; Piutti and Cescatti, 1997).

Size and social status of trees within a stand, which depends on age, genetics, and micro-site factors, affects assimilation, maintenance costs, water transport (Peuke et al., 2002; Ryan et al., 1997) and carbon allocation (Genet et al., 2010). The synergy of these processes alters growth responses, hence sensitivity to particular environmental factors, resulting in a spectrum of growth patterns (Carrer and Urbinati, 2004; Piutti and Cescatti, 1997). Trees of different canopy status also have diverse water use efficiency (Granier et al., 2000; et al., 1997; Orwig and Abrams, 1997), implying varying sensitivity to the factors related to water deficit.

Besides the age- and size-related alterations in climatic sensitivity (Carrer and Urbinati, 2004), the sets of limiting factors can shift over time due to the changes in climate (Jansons et al., 2015; Lloyd and Fastie, 2002; Wilmking et al., 2004), as certain thresholds of environmental factors are exceeded (Speer, 2010). For example, improved growth of thermophilic species has been observed under warming climate (Kullman, 2008; Walther et al., 2002), while increasing temperature during the vegetation period might cause the opposite reaction, intensifying evapotranspiration and water deficit (Lindner et al., 2010; Wilmking et al., 2004). In addition, changing climate can cause diversification of growth patterns at a fine geographic scale, increasing the effect of micro-site conditions and competition (Briffa et al., 1998; Piutti and Cescatti, 1997; Wilmking et al., 2004).

Considering these factors, pooling of data from trees of different age/size might cause biased results, as environmental signals captured by xylogenesis might interfere (Fritts, 2001); nevertheless, only several studies have analysed the size- and age-related differences in sensitivity of tree growth (Carrer and Urbinati, 2004). Current studies from the eastern Baltic region, which have analysed pooled data from randomly

selected trees, showed that radial increment of beech has been sensitive to both temperature in winter and water deficit in summer (Augustaitis et al., 2015; Jansons et al., 2015). However, there is still poor information about the diversity of growth responses within a stand and locality, as well as about the temporal changes in climatic sensitivity of growth. Hence, the aim of this study was to assess the sensitivity of tree-ring width (TRW) of beech of different generations (age) and stem diameter at breast height (DBH) classes to climatic (meteorological) factors at its northeasternmost experimental plantations (stands) in Europe. Regarding age (generation), we hypothesised that the older trees have been more sensitive to climatic factors than the younger ones. Additionally, we assumed that sensitivity has been affected by the social status within a stand (DBH class); accordingly, the dominant (larger) trees were more sensitive to drought related factors due to higher demand for water, while trees of smaller DBH (suppressed) were more sensitive to winter temperature due to lesser carbohydrate reserves and vigour (Gerard and Breda, 2014; Guy, 1990). We also assumed that, beside the age-related changes, the sets of the significant climatic factors have shifted during the 20th century due to warming of climate.

2. Material and methods

2.1. Study area

Study site was located in the northwestern part of Latvia (Table 1), representing lowland conditions; the elevation was ca. 100 m a.s.l. and the topography was flat. Soil was silty and well drained. The climate could be classified as moist continental, yet it was largely determined by the westerlies, which brought air masses from the Baltic Sea and the Atlantic. The mean annual temperature (± standard deviation) in the period 1940–2015 was +6.2 ± 1.0 °C; the mean monthly temperature ranged from −3.7 ± 3.6 in February to +16.5 ± 1.5 °C in July. Vegetation period, when the mean diurnal temperature exceeds +5 °C, mostly extended from mid-April to October. The mean annual precipitation sum was 667 ± 106 mm; the highest monthly precipitation occurred in summer months (June–August; 75 ± 30 mm). Climatic changes were mainly expressed as increase of the mean temperature, particularly during the dormant period and spring, and as extension of the vegetation period (Lizuma et al., 2007), while summer temperature and precipitation regimes were becoming more heterogeneous (Avotniece et al., 2010).

Three plantations (stands) of beech located within 5 km distance from each other, growing on rich sites (*Myrtilloso-polytrichosa-Oxalidosa*) were selected (Table 1). The age of the plantations differed; two stands (Young 1 and Young 2) were ca. 60 years old, and the third stand (Mature) was twice older; however, the DBH ranges were similar. The initial density of the plantations was ca. 4000 trees ha^{-1}. The older (Mature) beech stand was established by the reproductive material originating from wild stands in the northern Germany, yet the exact area of provenance was unknown. Two younger stands were established

by the reproductive material collected in the older stand, representing the second generation of trees.

2.2. Sampling and data preparation

In each stand, 45 trees representing the DBH distribution of the plantations (according to inventory) were sampled. Tilted trees and trees with wood rot were avoided. From each tree, two samples at breast height from the opposite sides of stem were taken by a 5-mm Pressler increment borer. The collected samples had < 2 cm offset from the pith.

In the laboratory, increment cores were dried, mounted, and their surface was grinded by a sandpaper of four roughness grits (120–800). The TRWs were measured manually, using the Lintab 5 measurement system (Rinntech, Heidelberg, Germany) with the precision of 0.01 mm. The measured time series of TRW were crossdated and their quality was verified by a graphical inspection and statistically, using the program COFECHA (Grissino-Mayer, 2001). The number of tree-rings measured per tree was by 9–21 lower than the stand age (Table 1).

Climatic data (CRU TS v. 3.24.01) were obtained from the Climatic Research Unit of University of East Anglia (Harris et al., 2014). Data from the nearest grid entry (< 7 km) were used. The tested climatic variables were monthly mean temperature, precipitation sum, and standardized precipitation-evapotranspiration index (SPEI) (Vicente-Serrano et al., 2010), calculated with the respect of the preceding three months. The climatic year from the July of the year preceding tree-ring formation to October of the year of tree-ring formation was used.

2.3. Data analysis

For each tree, a mean TRW times series was calculated based on the crossdated samples. To assess the high-frequency (annual) variation of TRW, these series were detrended. Double detrending by a modified negative exponential curve and flexible cubic spline with the wavelength of 40 years preserving 50% of variation was used. Autoregressive modelling ('AR', first order) was applied to remove autocorrelation, which interferes with the climatic signal (Cook, 1985).

A principal component analysis (Jolliffe, 1986) based on the detrended series of TRW was used to assess grouping of the studied trees according to their growth patterns. The analysis was based on the common interval of 1972–2015. Trees were used as samples, and years (TRW indices) were used as variables. Correlation was used for calculation of the cross-product matrix. The significance of the principal components (PCs) was determined by the randomization test ('broken stick'), performing 10^4 iterations.

To assess the effect of social status on high-frequency variation of TRW, datasets of each stand were divided in three equal groups according to DBH (dominant, intermediate and suppressed, respectively; Table 2). For the description of the datasets, mean interseries correlation (r-bar), expressed population signal (EPS), signal to noise ratio (SNR), first order autocorrelation in detrended series (AC), and Gleichläufigkeit (GLK) coefficients (Wigley et al., 1984) were calculated. Chronologies of TRW for each group were established by averaging the detrended series of trees; biweight robust mean was used (Cook, 1985). The similarity of chronologies was described by a Pearson correlation coefficient *r*.

The relationships of TRW chronologies and PCs with climatic variables (factors) were assessed by a bootstrapped Pearson correlation analysis, performing 10^4 iterations. For all chronologies (groups), the analysis was conducted for the common interval (1972–2015). Additionally, for the older trees (from the Mature stand), the analysis was conducted for 30-year moving intervals, to assess the temporal changes in climatic sensitivity; data for 1903–2015 were used for this. Data analysis was conducted in the program R v. 3.3.2 (R Core Team, 2016), using packages "dplR" (Bunn, 2008), "treeclim" (Zang and Biondi, 2015), and "SPEI" (Beguería and Vicente-Serrano, 2013).

3. Results

3.1. Variation of tree-ring width

After the quality verification and crossdating, time series of TRW from 126 of the 135 initially sampled trees, which showed good agreement and substantial dating (e.g. matching signature years), were used for further analysis (Table 2). The number of crossdated series (trees) for the distinguished groups ranged from 13 to 15. The synchrony of high-frequency variation of TRW, as indicated by GLK, was comparable for most of the groups (GLK ≥ 0.57), although it was slightly lower for trees from the Mature stand at the younger age (1900–1960, mean GLK was 0.59). Nevertheless, GLK tended to be slightly higher for the dominant trees. The r-bar value of the datasets differed according to stands; it was higher for the younger stands (mean r-bar was 0.49) compared to the older one during the common as well as earlier interval (mean r-bar was 0.25 and 0.26 during 1900–1960 and 1961–2015, respectively). Differences among the DBH classes were observed. In the younger stands, higher r-bar was observed for the suppressed trees, while in the older stand, higher r-bar was observed among the dominant trees. The r-bar values calculated for stands and for the entire dataset where generally lower than calculated for individual groups. The EPS values of the groups were mostly below 0.85 (cf. Wigley et al., 1984), yet for the stands and the entire dataset, they exceeded this threshold. The SNR of the groups ranged from 1.55–7.88 (except the suppressed trees from the Mature stands during 1900–1960), yet it was considerably higher for the stands and the entire dataset as well (≥ 9.97). The AC for groups was rather high (≥ 0.49) and the mean sensitivity was intermediate (0.20–0.32).

The first two PCs were significant (p-value < 0.001) and corresponded for 15 and 11% of the high-frequency variation of TRW, respectively (Fig. 1). The ordination of trees by the first two PCs displayed partly overlapping grouping according to generation (stand age) and DBH class (Fig. 1). The first PC might be associated with generation of trees, as the scores of the younger trees (Young 1 and Young 2 stands) generally exceeded those of the older ones (Mature stand); still, this was not distinct for the suppressed trees. For trees from the Young 2 and Mature stand, the first PC also captured variation of TRW related to DBH, as indicated by higher scores for trees with lower social status. The second PC might be associated with size of trees, as the PC scores of trees within each stand increased with DBH. Additionally, the second PC could be associated with stand specifics properties, as suggested by the differences in the mean scores of the stands.

Residual chronologies of TRW were successfully produced for each group (Fig. 2). The range of TRW indices was higher for the older trees (Mature stand); nevertheless, within stands, higher range of indices was observed for the suppressed trees. Chronologies from the same stand showed rather high similarity, as the mean *r* between the chronologies from each stand was 0.65 (Table 3), while the mean *r* among the stands was 0.33. When the chronologies were compared according to social status, the *r* increased with DBH; the chronologies of the dominant trees were rather similar (mean *r* = 0.61), while correlation among the intermediate and suppressed trees was considerably lower (mean *r* = 0.35 and 0.15, respectively). No similarity (|*r*| ≤ 0.06) was observed between the chronologies produced for the intermediate and suppressed trees from the Mature and Young 2 stands, respectively.

3.2. Sensitivity of tree-ring width to climatic variables during 1972–2015

The main components of variation of TRW captured by the first two PCs were associated with climatic factors. The scores of the first PC significantly (at α = 0.05) correlated with temperature in the preceding summer (r = 0.36), temperature in January (r = 0.32), and winter precipitation (r = 0.32). The scores of the second PC showed significant correlation with temperature in April (r = −0.37) and precipitation in July (r = −0.34).

Table 2
Statistics for the datasets of beech tree-ring width for the distinguished groups: mean tree-ring width, first order autocorrelation in detrended series (AC), mean sensitivity (MS), mean Gleichläufigkeit index among series (GLK), interseries correlation (r-bar), expressed population signal (EPS), signal to noise ratio (SNR), and number of crossdated trees (N). Statistics for the Mature stand are calculated for split intervals as well as for the entire period. The range of diameter at breast height for each group is shown in brackets.

	Mean tree-ring width ± st. dev., mm	AC	MS	GLK	r-bar	EPS	SNR	N
Young 1								
Dominant (30.8–46.3 cm)	3.6 ± 1.4	0.69	0.21	0.68	0.45	0.82	4.46	15
Intermediate (20.0–28.7 cm)	2.8 ± 1.2	0.63	0.26	0.67	0.37	0.72	2.55	14
Suppressed (10.4–18.4 cm)	2.0 ± 1.0	0.61	0.28	0.63	0.59	0.84	5.38	13
Total	2.9 ± 1.2	0.64	0.24	0.65	0.41	0.91	10.52	42
Young 2								
Dominant (32.8–48.5 cm)	3.2 ± 1.1	0.69	0.20	0.67	0.46	0.82	4.53	14
Intermediate (21.1–30.3 cm)	2.1 ± 1.1	0.84	0.20	0.58	0.48	0.81	4.23	13
Suppressed (12.4–19.8 cm)	1.4 ± 0.9	0.82	0.24	0.58	0.58	0.88	7.21	14
Total	2.2 ± 1.0	0.78	0.21	0.59	0.42	0.93	13.75	41
Mature, whole period								
Dominant (32.0–49.6 cm)	1.9 ± 0.7	0.68	0.23	0.66	0.41	0.89	7.88	15
Intermediate (21.7–30.6 cm)	1.2 ± 0.6	0.71	0.25	0.64	0.37	0.8	3.93	15
Suppressed (14.1–19.5 cm)	0.9 ± 0.6	0.78	0.27	0.58	0.25	0.61	1.55	13
Total	1.3 ± 0.6	0.70	0.25	0.62	0.19	0.87	9.97	43
Mature 1900–1960								
Dominant (32.0–49.6 cm)	1.8 ± 0.7	0.65	0.21	0.59	0.39	0.86	6.23	15
Intermediate (21.7–30.6 cm)	1.2 ± 0.5	0.55	0.26	0.60	0.31	0.8	3.91	15
Suppressed (14.1–19.5 cm)	0.9 ± 0.5	0.57	0.32	0.57	0.08	0.37	0.59	11
Total	1.3 ± 0.5	0.56	0.26	0.59	0.2	0.89	7.84	41
Mature 1961–2015								
Dominant (32.0–49.6 cm)	2.0 ± 0.6	0.49	0.23	0.70	0.34	0.87	6.87	15
Intermediate (21.7–30.6 cm)	1.2 ± 0.5	0.63	0.26	0.67	0.24	0.79	3.69	15
Suppressed (14.1–19.5 cm)	0.8 ± 0.5	0.81	0.25	0.57	0.19	0.65	1.86	13
Total	1.3 ± 0.6	0.62	0.25	0.64	0.18	0.9	9.44	43
Total								
	2.1 ± 0.9	0.71	0.24	0.58	0.18	0.94	15.26	126

From the tested 48 climatic variables, 19 showed significant correlation with at least one of the chronologies; the *r* ranged −0.48 to 0.64 (Fig. 3). The TRW of beech was mainly sensitive to factors related to water deficit in summer; however, the sets of significant climatic variables differed among the stands and DBH classes. The younger trees were more sensitive (showed higher correlation coefficients) to SPEI in late summer, as well as to temperature in previous summer. The older trees were more sensitive to temperature and precipitation in June and
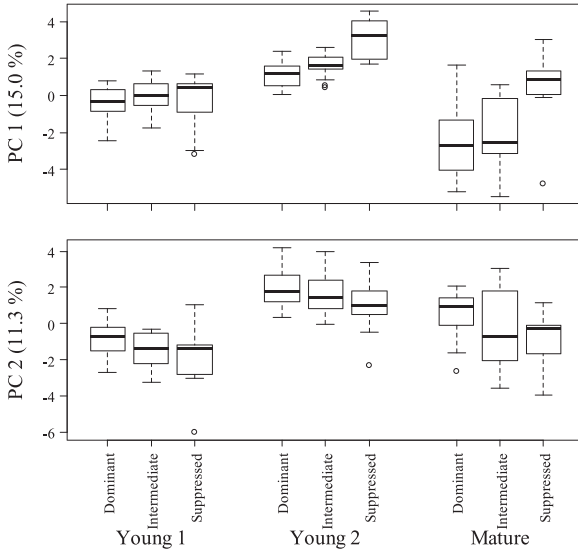

Fig. 1. The first two principal component scores of the high-frequency variation (residual chronologies) of tree-ring width of European beech trees of different age/generation (ca. 60 years for stands Young 1 and Young 2, and ca. 120 years for Mature stand) and diameter at breast height classes (dominant, intermediate, and suppressed, respectively) for the period of 1972–2015. Line shows the median, box represents the 1st and 3rd quartile, whiskers mark the range (not exceeding 150% of interquartile distance) and circles denote the outliers of the datasets.
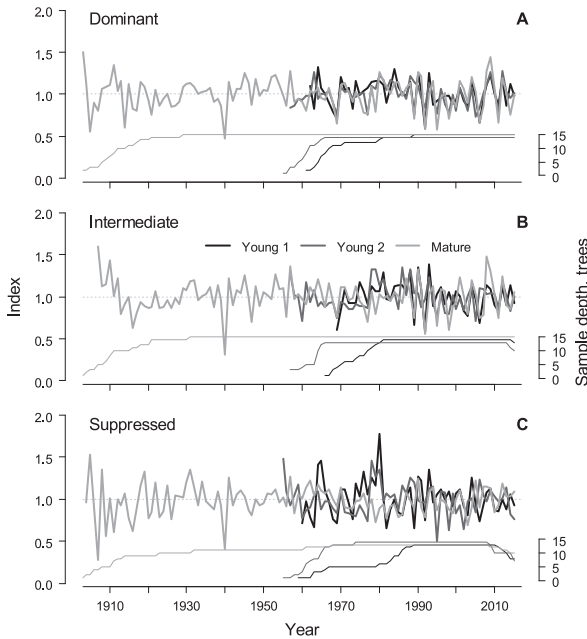
Fig. 2. Residual chronologies (thick lines) of tree-ring width of European beech trees of different age/generation (ca. 60 years for stands Young 1 and Young 2, and ca. 120 years for Mature stand) and diameter at breast height classes (dominant (A), intermediate (B), and suppressed (C), respectively). Thin lines show sample depth.

less sensitive to late summer SPEI, yet they were sensitive to temperature in previous October. Site-specific responses to climatic variables were apparent. The effect of current July and August temperature was significant only in the Young 1 stand. Correlations with temperature and precipitation in previous August, SPEI in previous August and September, as well as with precipitation in current August were specific for the Young 2 stand. In this stand, correlations with June temperature, April precipitation, and SPEI in May were not significant.

The climatic sensitivity of TRW was affected by the DBH class, particularly in the Mature stand (Fig. 3). Specifically, the suppressed trees showed significant positive correlations with temperature in the dormant period and spring (in previous December and current January and April); the dominant trees showed significant correlation with temperature in previous July and SPEI in previous September.

Correlation with precipitation in June and SPEI in October was stronger for the dominant trees and it gradually weakened with decreasing DBH. In the Young 1 stand, correlations with June precipitation and late summer SPEI slightly decreased from the dominant to the suppressed trees. In the Young 2 stand, strength and significance of the correlation with precipitation in August increased with decreasing DBH. Correlation with temperature in previous July was significant only for the suppressed trees.

3.3. Temporal changes in sensitivity of tree-ring width to climatic variables

The sets of climatic variables significant for TRW of beech in the Mature stand have shifted during the 20th century (Fig. 4). All trees, irrespectively of their DBH class, were sensitive to temperature in

Table 3
Pearson correlation coefficients between the residual chronologies of tree-ring width of beech trees of different age/generation (ca. 60 years for stands Young 1 and Young 2, and ca. 120 years for Mature stand) and diameter at breast height classes (dominant, intermediate, and suppressed, respectively) for the common interval of 1972–2015. The significant correlations at $\alpha = 0.05$ are shown in bold.

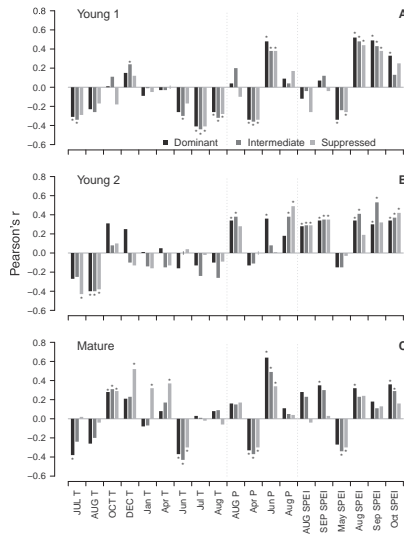|		Young 1			Young 2			Mature	
		Dominant	Intermediate	Suppressed	Dominant	Intermediate	Suppressed	Dominant	Intermediate
Young 1	Intermediate	**0.79**							
	Suppressed	**0.66**	**0.59**						
Young 2	Dominant	**0.57**	**0.47**	**0.32**					
	Intermediate	**0.31**	**0.36**	0.18	**0.65**				
	Suppressed	0.10	0.11	0.15	**0.54**	**0.76**			
Mature	Dominant	**0.61**	**0.50**	**0.36**	**0.65**	**0.30**	**0.31**		
	Intermediate	**0.57**	**0.49**	**0.34**	**0.56**	0.21	0.21	**0.88**	
	Suppressed	**0.33**	**0.36**	**0.30**	0.24	−0.06	−0.01	**0.38**	**0.57**

Fig. 3. Pearson correlation coefficients (*r*) calculated between the residual chronologies of tree-ring width of beech of different age/generation (ca. 60 years for stands Young 1 (A) and Young 2 (B), and ca. 120 years for Mature stand (C)) and diameter at breast height classes (dominant, intermediate, and suppressed, respectively) and climatic (meteorological) factors: monthly mean temperature (T), precipitation (P) and standardized precipitation-evapotranspiration index (SPEI) for the common interval 1972–2015. Months in uppercase correspond to the year prior to formation of tree-ring. Asterisks indicate the significant correlations at α = 0.05. Only the factors showing significant correlations are plotted.

previous October in the intervals ending before 1960s, although for the intermediate trees, this factor was also significant in a few intervals ending after 2000s. Changes in sensitivity to other factors differed by the DBH classes. For the dominant trees, the effect of June precipitation (positive) became significant in the intervals ending after 1980s. The effect of temperature in previous July was significant in the intervals ending before 1970s and also in the intervals ending after 1998. The negative effect of precipitation in April became significant in the intervals ending after 1970s; however, it was again non-significant in the most recent intervals. Similarly, the intermediate trees were sensitive to precipitation in April in the intervals ending between 1970 and 2010. The effect of June precipitation intensified in the intervals ending after 1990, yet it was not constantly significant thereafter. Additionally, the intermediate trees showed increasing effect of June temperature in the intervals ending after 1980s.

The suppressed trees were sensitive to temperature in previous July in the intervals ending before 1980. Then, for ca. 25 intervals, none of the tested factors showed consistent effect (significant correlation in ≥10 intervals), yet the effect of precipitation in September was significant in seven of those intervals (not shown). At the later part of the analysed period (in the intervals ending after 2000), effect of temperature in previous December became significant (Fig. 4). In addition, during the latter eight intervals, the effect of precipitation in previous August intensified and became significant (not shown).

4. Discussion

4.1. Variation of tree-ring width

The studied datasets were sufficient to present the regional and stand level environmental signals in TRW of beech, as the EPS values calculated for the stands as well as all series (Table 2) exceeded 0.85 (Wigley et al., 1984). The EPS values calculated for the groups were lower (Table 2), likely due to lower number of trees (Wigley et al., 1984). The mean sensitivity of TRW in all groups was intermediate (Table 2) that is sufficient for the climate-growth analysis (Speer, 2010). The TRW of beech contained rather high AC (Table 2), suggesting that radial increment has been influenced by previous growth, and hence nutrient reserves (Barbaroux and Breda, 2002; Pallardy, 2008), as observed for other species within the region (Jansons et al., 2016). The GLK values generally exceeded 0.60, suggesting presence of common tendencies in the variation of TRW (Speer, 2010).

As hypothesised, high-frequency variation of TRW of beech was affected by size (DBH class) and generation (age) of trees. Stand specific variation of TRW was indicated by lower r-bar calculated for the entire dataset compared to the stands (Table 2), differences in the PC scores of trees (Fig. 1), and correlation structure between the chronologies (Table 3), supporting the influence of generation and local factors. In each stand, the TRW patterns of trees were more similar (higher r-bar) within rather between the distinguished DBH classes (Table 2), likely due the specifics in physiology of trees of different size and social status (Carrer and Urbinati, 2004; Genet et al., 2010; Ryan et al., 1997). The amount of variance explained by the PCs (Fig. 1) suggested that growth was more affected by generation rather than DBH class, implying rapid adaptation of the introduced beech (Kreyling et al., 2014). Still, the PC scores of groups partly overlapped (Fig. 1), suggesting gradual differences in growth patterns of individual trees within stand/location. This also explains the decreased EPS values (Wigley et al., 1984) calculated for the groups (Table 2).

The similarity of TRW patterns differed among stands and groups, suggesting varying responses to environmental forcing (Lloyd and Fastie, 2002; Wilmking et al., 2004). The highest diversity of TRW patterns in the first generation (Mature) stand, as shown by low r-bar (Table 2) and wide range of PC scores (Fig. 1), might be explained by unconstrained combination of traits in the freshly transferred reproductive material, resulting in a broader spectrum of growth patterns (Aitken et al., 2008). The TRW patterns of the second generation trees showed higher similarity (Table 2, Fig. 1), likely, due to the natural and anthropogenic selection of the most appropriate traits/individuals (Aitken et al., 2008; Kreyling et al., 2014), as hinted by improved productivity (similar DBH was observed for the younger and older stands, Table 1). Nevertheless, the TRW patterns were affected by competition (Piutti and Cescatti, 1997), as r-bar differed by the DBH classes in each stand (Table 2), yet the effect was modulated by the generation. In the first generation stand, the dominant trees showed higher similarity of TRW patterns (Table 2), indicating that the influence of the climatic variables on increment increased when competition is reduced (Fritts, 2001). The opposite was observed in the younger stands (Table 2), presumably due to better adaptation of the second generation trees to the local climate (Kreyling et al., 2014), when effect of micro-site conditions on the dominant trees is pronounced (Speer, 2010).

4.2. Sensitivity of tree-ring width to climatic variables

The correlation of PC with climatic variables (January and July temperature and July precipitation) suggested that sensitivity to water deficit in summer and temperature in winter distinguished the responses of trees. Nevertheless, the similarity of chronologies decreased with DBH class (Table 3), indicating that competition modulated sensitivity of TRW to climatic factors (Fritts, 2001; Piutti and Cescatti,
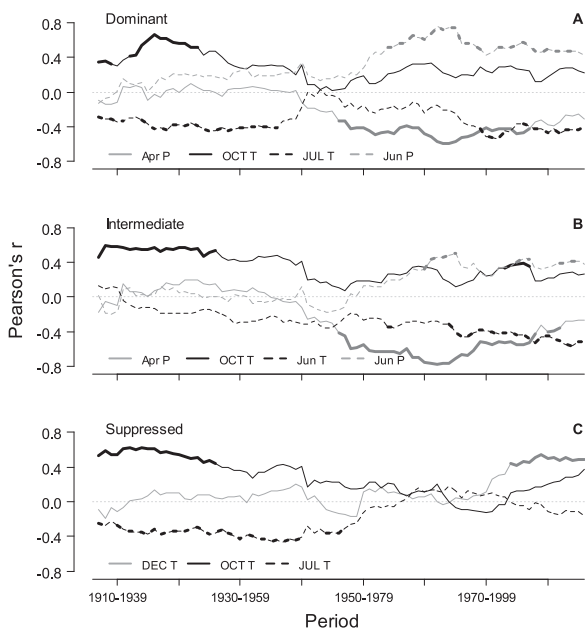
Fig. 4. Pearson correlation coefficients calculated for 30-year moving intervals between the residual chronologies of tree-ring width of beech from the Mature stand (age ca. 120 years) of different diameter classes (dominant (A), intermediate (B), and suppressed (C), respectively) and climatic (meteorological) factors: monthly mean temperature (T) and precipitation (P). Thick line represent the significant correlations at α = 0.05. Months in uppercase correspond to the year prior to formation of tree-ring. Only the factors showing significant correlation in ≥10 intervals are shown. Note that the displayed factors differ among the panels.

1997).

4.2.1. First generation beech

In the first generation (Mature) stand, the differences in sensitivity to weather conditions among the DBH classes were the most pronounced (Fig. 3), likely due to variable adaptation to local climate (Kreyling et al., 2014). The TRW of the dominant trees was mainly influenced by water deficit in June as well as in late summer (Fig. 3). Beech is a drought-sensitive species (Gessler et al., 2007), hence similar relationships have been often observed throughout its range (Čufar et al., 2008; Dittmar et al., 2003; Lebourgeois et al., 2005; Piovesan et al., 2008). The negative effect of temperature in previous July and positive effect of water availability (SPEI) in previous September (Fig. 3) might be explained by the influence of water deficit on formation of nutrient reserves (Barbaroux and Breda, 2002), hence on early growth in the following year (Pallardy, 2008). Nevertheless, the effect of these climatic variables has not been stable (Fig. 4), and shifts over time appear to be primarily caused by changes in climate (Lloyd and Fastie, 2002; Wilmking et al., 2004). The effect of water deficit has intensified during the 20th century (Fig. 4), likely in response to warming, hence increased evapotranspiration and extension of precipitation-free periods during summer (Avotniece et al., 2010). Still, this might be also related to ageing (Carrer and Urbinati, 2004).

The suppressed trees in the first generation (Mature) stand were sensitive to temperature during the dormant period (Fig. 3), as expected for individuals growing northwards from their natural distribution area, where low temperatures are often limiting (Fritts, 2001). Apparently, the suppressed trees had smaller nutrient reserves and lower vigour (Gerard and Breda, 2014), hence decreased resistance to low temperature likely due to limited production of antifreeze compounds (Guy, 1990). The intensification of these correlations during the recent decades (Fig. 4) might imply that the effect was age-related, as the

maintenance costs increase with ageing (Ryan et al., 1997), decreasing the amount of nutrient reserves (Gerard and Breda, 2014) and vigour (Pallardy, 2008). Alternatively, this might be related to warming (Lizuma et al., 2007), when temperature reached certain level to which growth was responsive (Speer, 2010). The decreasing sensitivity of the suppressed trees to temperature in previous July (Fig. 4) might be explained by gradual climate-related shift of limiting factors, when their individual effects weaken (Briffa et al., 1998).

The correlations with climatic variables in October (Fig. 3), which indicated responsiveness of trees to weather conditions in autumn, might be explained by the extension of vegetation period, hence additional assimilation and/or longer xylogenesis (Walther et al., 2002). The weakening of the correlation between TRW and previous October temperature (Fig. 4), likely due to warming (Lizuma et al., 2007), suggested upcoming alteration in sensitivity to conditions (e.g. water deficit) in autumn. Nevertheless, the sensitivity of TRW to weather conditions in autumn (Fig. 4) also suggested susceptibility of growth to damage from late frosts, which is expected to increase with warming (Kreyling et al., 2014; Zeps et al., 2017). The negative correlation with April precipitation and SPEI in May, as observed also in the Young 1 stand (Fig. 3), might be explained by the effect of soil water excess after snowmelt on root aeration (Alaoui-Sosse et al., 2005; Gessler et al., 2007). The analysis of moving intervals (Fig. 4) showed that this effect has intensified since the 1960s, likely due to earlier onset of the active period (Von Wuehlisch et al., 1995), explaining the responsiveness of growth to condition in early spring.

4.2.2. Second generation beech

The second generation trees did not show sensitivity to temperature in the dormant period, but were mainly affected by the water deficit (Fig. 3), similarly as in the native range of the species (Čufar et al., 2008; Dittmar et al., 2003; Lebourgeois et al., 2005). In both second

generation stands, TRW was stronger correlated with conditions in autumn (Fig. 3), indicating sensitivity to length of vegetation season (Gessler et al., 2007). Nevertheless, site-specific correlations were observed, suggesting effect of local factors, likely via mechanisms controlling increment, as the periods of response (i.e., months with significant correlations between TRW and climatic variables) differed. In the Young 1 stand, TRW was sensitive to conditions during the period of formation of tree-ring, indicating direct effect of water deficit on assimilation (Pallardy, 2008) and xylogenesis, as observed in central part of natural distributing area (Lebourgeois et al., 2005). In the Young 2 site, radial increment, apparently, was more influenced by nutrient reserves (Barbaroux and Breda, 2002), as TRW was mainly correlated with climatic variables of preceding summer (Fig. 3).

The effect of DBH on climatic sensitivity of the second generation beech was weaker (similar sets of factors were observed) than in the older stand (Fig. 3), likely due to genetic constants imposed by the selection (Aitken et al., 2008; Kreyling et al., 2014). In both stands the dominant trees were more sensitive to June precipitation, likely due to higher water demand (Genet et al., 2010; Granier et al., 2000; Ryan et al., 1997). In addition, the effect of this factor was age-dependent, as considerably higher correlation was observed in the first generation stand (Fig. 3), as expected for older trees (Carrer and Urbinati, 2004). The dominant trees from the Young 1 stand were also more sensitive to late summer water deficit (Fig. 3). The opposite was observed in Young 2 stand (e.g. suppressed trees were more sensitive to precipitation in August, Fig. 3), suggesting that trees have been competing for water (Orwig and Abrams, 1997).

5. Conclusions

The sensitivity of European beech in the northeasternmost stands was affected by the generation of trees, likely due to the natural and anthropogenic selection. The productivity and prevailing sensitivity of the second generation trees to water deficit in summer rather than winter temperature, indicated adaptation of the population to winter conditions. Hence, cold damage already appear non-limiting for growth, suggesting potential for a wider application of the species within the region. Still, the observed climate-growth relationships suggested that the second generation trees had extended growing period, thus increased risk of damage by early frosts. The sensitivity of growth to weather conditions, particularly to those related to water deficit, was increased by ageing, and was stronger for the dominant (largest) trees, likely due to larger canopy, hence more intensive transpiration. Considering the regional changes of climate and ageing of trees, the effect of water deficit is expected to intensify in future, hence careful selection of sites/regions with appropriate hydrological conditions, apparently, is becoming the main issue for maintaining productivity of future beech stands outside their natural distribution range.

References

Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T., Curtis-McLane, S., 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evol. Appl. 1, 95–111. http://dx.doi.org/10.1111/j.1752-4571.2007.00013.x.
Alaoui-Sosse, B., Gérard, B., Binet, P., Toussaint, M.L., Badot, P.M., 2005. Influence of flooding on growth, nitrogen availability in soil, and nitrate reduction of young oak seedlings (Quercus robur L.). Ann. For. Sci. 62, 593–600. http://dx.doi.org/10.1051/

forest:2005052.
Augustaitis, A., Kliučius, A., Marozas, V., Pilkauskas, M., Augustaitiene, I., Vitas, A., Staszewski, T., Jansons, A., Dreimanis, A., 2015. Sensitivity of European beech trees to unfavorable environmental factors on the edge and outside of their distribution range in northeastern Europe. iForest 9, 259–269. http://dx.doi.org/10.3832/ifor1398-008.
Avotniece, Z., Rodinov, V., Lizuma, L., Briede, A., Kļaviņš, M., 2010. Trends in frequency of extreme climate events in Latvia. Baltica 23, 135–148.
Barbaroux, C., Breda, N., 2002. Contrasting distribution and seasonal dynamics of carbohydrate reserves in stem wood of adult ring-porous sessile oak and diffuse-porous beech trees. Tree Physiol. 22, 1201–1210. http://dx.doi.org/10.1093/treephys/22.17.1201.
Begueria, S., Vicente-Serrano, S.M., 2013. SPEI: Calculation of the Standardised Precipitation-Evapotranspiration Index. R Package Version 1.6. Accessed 29 March 2017. https://CRAN.R-project.org/package=SPEI.
Björkman, L., Bradshaw, R., 1996. The immigration of Fagus sylvatica L. and Picea abies (L.) Karst. into a natural forest stand in southern Sweden during the last 2000 years. J. Biogeogr. 23, 235–244. http://dx.doi.org/10.1046/j.1365-2699.1996.00972.x.
Bolte, A., Czajkowski, T., Kompa, T., 2007. The north-eastern distribution range of European beech—a review. Forestry 80, 413–429. http://dx.doi.org/10.1093/forestry/cpm028.
Briffa, K.R., Schweingruber, F.H., Jones, P.D., Osborn, T.J., Shiyatov, S.G., Vaganov, E.A., 1998. Reduced sensitivity of recent tree-growth to temperature at high northern latitudes. Nature 391, 678–682. http://dx.doi.org/10.1038/35596.
Bunn, A., 2008. A dendrochronology program library in R (dplR). Dendrochronologia 26, 115–124. http://dx.doi.org/10.1016/j.dendro.2008.01.002.
Burton, L., 2012. Introduction to Forestry Science, third edition. Cengage Learning, New York.
Carrer, M., Urbinati, C., 2004. Age-dependent tree-ring growth responses to climate in Larix decidua and Pinus cembra. Ecology 85, 730–740. http://dx.doi.org/10.1890/02-0478.
Cook, E.R., 1985. A Time Series Approach to Tree-Ring Standardization Dissertation. University of Arizona, Tucson.
Čufar, K., Prislan, P., de Luis, M., Gričar, J., 2008. Tree-ring variation, wood formation and phenology of beech (Fagus sylvatica) from a representative site in Slovenia, SE Central Europe. Trees-Struct. Funct. 22, 749–758. http://dx.doi.org/10.1007/s00468-008-0235-6.
Dittmar, C., Zech, W., Elling, W., 2003. Growth variations of common beech (Fagus sylvatica L.) under different climatic and environmental conditions in Europe—a dendroecological study. For. Ecol. Manag. 173, 63–78. http://dx.doi.org/10.1016/S0378-1127(01)00816-7.
Dreimanis, A., 1995. The beech and the larch-tree in Shkede forestry. Proc. For. Edu. 75th Anniv. Conf. Latvia Univ. Agr., vol. 5, 94–97.
Friedrichs, D.A., Büntgen, U., Frank, D.C., Esper, J., Neuwirth, B., Löffler, J., 2009. Complex climate controls on 20th century oak growth in central-west Germany. Tree Physiol. 29, 39–51. http://dx.doi.org/10.1093/treephys/tpn003.
Fritts, H.C., 2001. Tree-Rings and Climate. The Blackburn Press, Caldwell.
Genet, H., Breda, N., Dufrene, E., 2010. Age-related variation in carbon allocation at tree and stand scales in beech (Fagus sylvatica L.) and sessile oak (Quercus petraea (Matt.) Liebl.) using a chronosequence approach. Tree Physiol. 30, 177–192. http://dx.doi.org/10.1093/treephys/tpp105.
Gerard, B., Breda, N., 2014. Radial distribution of carbohydrate reserves in the trunk of declining European beech trees (Fagus sylvatica L.). Ann. For. Sci. 71, 675–682. http://dx.doi.org/10.1007/s13595-012-0240-1.
Gessler, A., Keitel, C., Kreuzwieser, J., Matyssek, R., Seiler, W., Rennenberg, H., 2007. Potential risks for European beech (Fagus sylvatica L.) in a changing climate. Trees-Struct. Funct. 21, 1–11. http://dx.doi.org/10.1007/s00468-006-0107-x.
Granier, A., Biron, P., Lemoine, D., 2000. Water balance, transpiration and canopy conductance in two beech stands. Agr. For. Meteorol. 100, 291–308. http://dx.doi.org/10.1016/S0168-1923(99)00151-3.
Grissino-Mayer, H.D., 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree-Ring Res. 57, 205–221.
Guy, C.L., 1990. Cold acclimation and freezing stress tolerance: role of protein metabolism. Ann. Rev. Plant Physiol. Plant Mol. Biol. 41, 187–223. http://dx.doi.org/10.1146/annurev.pp.41.060190.001155.
Harris, I.P., Jones, P.D., Osborn, T.J., Lister, D.H., 2014. Updated high-resolution grids of monthly climatic observations—the CRU TS3. 10 dataset. Int. J. Climatol. 34, 623–642. http://dx.doi.org/10.1002/joc.3711.
Hickler, T., Vohland, K., et al., 2012. Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. Glob. Ecol. Biogeogr. 21, 50–63. http://dx.doi.org/10.1111/j.1466-8238.2010.00613.x.
Isaac-Renton, M.G., Roberts, D.R., Hamann, A., Spiecker, H., 2014. Douglas-fir plantations in Europe: a retrospective test of assisted migration to address climate change. Glob. Change Biol. 20, 2607–2617. http://dx.doi.org/10.1111/gcb.12604.
Jansons, Ā., Matisons, R., Puriņa, L., Neimane, U., Jansons, J., 2015. Relationships between climatic variables and tree-ring width of European beech and European larch growing outside of their natural distribution area. Silva Fenn. 49. http://dx.doi.org/10.14214/sf.1255.
Jansons, Ā., Matisons, R., Šēnhofa, S., Katrevičs, J., Jansons, J., 2016. High-frequency variation of tree-ring width of some native and alien tree species in Latvia during the period 1965–2009. Dendrochronologia 40, 151–158. http://dx.doi.org/10.1016/j.dendro.2016.10.003.
Jolliffe, I.T., 1986. Principal Component Analysis. Springer-Verlag, Berlin. http://dx.doi.org/10.1007/b98835.
Kramer, K., Degen, B., Buschbom, J., Hickler, T., Thuiller, W., Sykes, M., de Winter, W.,

2010. Modelling exploration of the future of European beech (*Fagus sylvatica* L.) under climate change-range, abundance, genetic diversity and adaptive response. For. Ecol. Manag. 259, 2213–2222. http://dx.doi.org/10.1016/j.foreco.2009.12.023.

Kreyling, J., Buhk, C., Backhaus, S., Hallinger, M., Huber, G., Huber, L., Jentsch, A., Konnert, M., Thiel, D., Wilmking, M., Beierkuhnlein, C., 2014. Local adaptations to frost in marginal and central populations of the dominant forest tree *Fagus sylvatica* L. as affected by temperature and extreme drought in common garden experiments. Ecol. Evol. 4, 594–605. http://dx.doi.org/10.1002/ece3.971.

Kullman, L., 2008. Thermophilic tree species reinvade subalpine Sweden—early responses to anomalous late Holocene climate warming. Arct. Antarct. Alp. Res. 40, 104–110. http://dx.doi.org/10.1657/1523-0430(06-120[KULLMAN]2.0.CO;2.

Lebourgeois, F., Breda, N., Ulrich, E., Granier, A., 2005. Climate-tree-growth relationships of European beech (*Fagus sylvatica* L.) in the french permanent plot network (RENECOFOR). Trees-Struct. Funct. 19, 385–401. http://dx.doi.org/10.1007/s00468-004-0397-9.

Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl, R., Delzon, S., Corona, P., Kolström, M., Lexer, M.J., Marchetti, M., 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. For. Ecol. Manag. 259, 698–709. http://dx.doi.org/10.1016/j.foreco.2009.09.023.

Lizuma, L., Kļaviņš, M., Briede, A., Rodinovs, V., 2007. Long-term changes of air temperature in Latvia. In: Kļaviņš, M. (Ed.), Climate Change in Latvia. University of Latvia, Riga, pp. 11–20.

Lloyd, A.H., Fastie, C.L., 2002. Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. Clim. Change 52, 481–509. http://dx.doi.org/10.1023/A:1014278819094.

Orwig, D.A., Abrams, M.D., 1997. Variation in radial growth responses to drought among species, site, and canopy strata. Trees-Struct. Funct. 11, 474–484. http://dx.doi.org/10.1007/s004680050110.

Pallardy, S.G., 2008. Physiology of Woody Plants, third edition. Elsevier, London.

Peuke, A.D., Schraml, C., Hartung, W., Rennenberg, H., 2002. Identification of drought-sensitive beech ecotypes by physiological parameters. New Phytol. 154, 373–387. http://dx.doi.org/10.1046/j.1469-8137.2002.00400.x.

Piovesan, G., Biondi, F., Filippo, A.D., Alessandrini, A., Maugeri, M., 2008. Drought-driven growth reduction in old beech (*Fagus sylvatica* L.) forests of the central Apennines, Italy. Glob. Change Biol. 14, 1265–1281. http://dx.doi.org/10.1111/j.1365-2486.2008.01570.x.

Piutti, E., Cescatti, A., 1997. A quantitative analysis of the interactions between climatic response and intraspecific competition in European beech. Can. J. For. Res. 27, 277–284. http://dx.doi.org/10.1139/x96-176.

R Core Team, 2016. R: A Language and Environment for Statistical Computing. R

Foundation for Statistical Computing, Vienna, Austria Accessed 01 February 2016. https://www.R-project.org/.

Ryan, M.G., Binkley, D., Fownes, J.H., 1997. Age related decline in forest productivity: pattern and process. Adv. Ecol. Res. 27, 213–262. http://dx.doi.org/10.1016/S0065-2504(08)60009-4.

Saltre, F., Saint-Amant, R., Gritt, E.S., Brewer, S., Gaucherel, C., Davis, B.A.S., Chuine, I., 2013. Climate or migration: what limited European beech post-glacial colonization? Glob. Ecol. Biogeogr. 22, 1217–1227. http://dx.doi.org/10.1111/geb.12085.

Speer, J.H., 2010. Fundamentals of Tree-Ring Research. The University of Arizona Press, Tucson.

Vetaas, O.R., 2002. Realized and potential climate niches: a comparison of four *Rhododendron* tree species. J. Biogeogr. 24, 545–554. http://dx.doi.org/10.1046/j.1365-2699.2002.00694.x.

Vicente-Serrano, S.M., Begueria, S., Lopez-Moreno, J.I., 2010. A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index – SPEI. J. Clim. 23, 1696–1718. http://dx.doi.org/10.1175/2009JCLI2909.1.

Vitt, P., Havens, K., Kramer, A.T., Sollenberger, D., Yates, E., 2010. Assisted migration of plants: changes in latitudes, changes in attitudes. Biol. Conserv. 143, 18–27. http://dx.doi.org/10.1016/j.biocon.2009.08.015.

Von Wuehlisch, G., Krusche, D., Muhs, H.J., 1995. Variation in temperature sum requirement for flushing of beech provenances. Silvae Genet. 44, 343–346.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological response to recent climate change. Nature 416, 389–395. http://dx.doi.org/10.1038/416389a.

Wigley, T.M.L., Briffa, K.R., Jones, P.D., 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. J. Clim. Appl. Meteorol. 23, 201–213. http://dx.doi.org/10.1175/1520-0450(1984) 023<0201:OTAVOC>2.0.CO;2.

Wilmking, M., Juday, G.P., Barber, V.A., Zald, H.J., 2004. Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska trough temperature thresholds. Glob. Change Biol. 10, 1724–1736. http://dx.doi.org/10.1111/j.1365-2486.2004.00826.x.

Winder, R., Nelson, E., Beardmore, T., 2011. Ecological implications for assisted migration in Canadian forests. For. Chron. 87, 731–744. http://dx.doi.org/10.5558/tfc2011-090.

Zang, C., Biondi, F., 2015. Treeclim: an R package for the numerical calibration of proxy-climate relationships. Ecography 38, 431–436. http://dx.doi.org/10.1111/ecog.01335.

Zeps, M., Jansons, Ā., Matisons, R., Stenvall, N., Pulkkinen, P., 2017. Growth and cold hardening of European aspen seedlings in response to an altered temperature and soil moisture regime. Agr. For. Meteorol. 242, 47–54.

SILVA FENNICA

Āris Jansons[1], Roberts Matisons[1], Līga Puriņa[1], Una Neimane[1] and
Jānis Jansons[2]

Relationships between climatic variables and tree-ring width of European beech and European larch growing outside of their natural distribution area

Jansons Ā., Matisons R., Puriņa L., Neimane U., Jansons J. (2015). Relationships between climatic variables and tree-ring width of European beech and European larch growing outside of their natural distribution area. Silva Fennica vol. 49 no. 1 article id 1255. 8 p.

Highlights

- In western Latvia, variation of tree-ring width of European beech and European larch within stands was similar.
- Dry summers and cold winters caused common event years in tree-rings.
- Moisture availability at the end of summer was apparently the main limiting factor for tree-ring width.
- Winter and spring temperature did not have significant and lasting effect on variation of tree-ring width.

Abstract

Relationships between climatic variables and tree-ring width (TRW) of dominant European larch (*Larix decidua* Mill.) and European beech (*Fagus sylvatica* L.) trees growing outside of their natural distribution area in western Latvia were studied. Chronologies of TRW, which covered the periods 1949–2012 and 1911–2012, were produced for beech and larch, respectively. Common signatures in TRW between both species were observed, but their amplitude differed. Correlation analysis showed that variation of TRW of both species was affected by drought related climatic variables. Tree-ring width of beech was affected by temperature in the previous July and August and the effect of spring and autumn temperature was observed. Since the 1980s, the effect of July precipitation has become significant. Summer precipitation was significant for larch in the mid-part of the previous century; however, temperature in the previous September has become a limiting factor since 1970s. The limiting effect of winter and spring temperature apparently lost its significance around the 1950s.

VIII

1   Introduction

Climatic changes cause shifts in distribution of tree species (Walther et al. 2002; Kullman 2008) and affect forest productivity (Lindner et al. 2010). Although warming of climate might increase productivity of boreal forests (Lindner et al. 2010), changes in forest composition are also predicted (Hickler et al. 2012). In this regard, adjustments in forest management practices are crucial to ensure sustainable forestry. One such adjustment may be the introduction of novel species, however, their ecological demands, i.e. climatic limitation of growth, should be comprehensively evaluated. Detailed information on climate-growth relationships can be obtained via dendrochronological analysis, especially for trees growing close to their natural distribution limit or outside of it (Fritts 2001; Vetaas 2002).

In Latvia, European beech (*Fagus sylvatica* L.) and European larch (*Larix decidua* Mill.) occur northwards from their natural distribution area (Bolte et al. 2007; EUFORGEN 2009) and cover 43 and 1139 ha of forestlands, respectively; both of these species are productive (Dreimanis 1995). Although warming of climate appears beneficial for growth of these species in Latvia (Hickler et al. 2012), the effect of climatic variables might still be substantial (Fritts 2001). The aim of this study was to assess the relationships between climatic variables and tree-ring width (TRW) of larch and beech in western Latvia. We hypothesized that winter-spring temperature has been limiting TRW, but that these effects have weakened during the 20th century.

2   Material and methods

2.1 Study area, sampling and measurements

European larch and European beech growing in western Latvia in even-aged plantations near Auce (56°31′N, 22°56′E, 50 m a.s.l.) and Kaleti (56°21′N, 21°29′E, 80 m a.s.l.), respectively, were studied. North-eastern Germany is considered as the area of origin for both species. Mean dimensions of the studied trees are shown in Table 1. Plantations were situated on flat terrain on fertile, well-drained clayey soils. Climate in the study areas is mild: mean annual temperature is ca.+6.1 °C, July is the warmest month with a mean temperature ca. +16 °C, and January is the coldest month with a mean temperature ca. –3.6 °C. The period when the mean daily temperature exceeds + 5 °C is ca. 185 days. Annual precipitation sum is ca. 560 and ca. 750 mm in the Auce and Kaleti sites, respectively. Most of the precipitation falls during summer. Climatic changes are reflected as an increase of temperature in the dormant period and spring, during the 20th century, mean November–April temperature has increased by 0.83 and 1.10 °C in Kaleti and Auce, respectively, and an intensification of heat and drought events (Avotniece et al. 2010).

In the studied sites, visually healthy, dominant trees, 22 larches and 9 beeches, were cored at breast height. Two samples per tree from opposite sides of stem were collected using a Pressler corer. In the laboratory, air-dried cores were fixed and gradually grinded (sandpaper roughness 100, 150, 250 and 400 grains per inch). Tree-ring width was measured using the LINTAB 5 (RinnTECH, Heidelberg, Germany) measurement system with precision of 0.01 mm.

2.2 Data analysis

Time series of TRW were cross-dated and their quality was checked graphically and using the program COFECHA (Grissino-Mayer 2001). Mean time series of TRW for trees were produced and rechecked. Residual chronologies of TRW were produced using the program ARSTAN (Cook

Table 1. Mean dimensions of sampled trees and statistics of TRW (tree-ring width) datasets: number of measured and crossdated time-series; range, agreement (interseries correlation, first order autocorrelation, GLK (Gleichläufigkeit) and EPS (expressed population signal)) and mean sensitivity of crossdated tree time-series of beech and larch.

	Beech	Larch
Studied period	1949–2012	1911–2012
Number of samples	18	44
Number of crossdated samples	18	38
Number of crossdated trees	9	20
Mean tree height, m	28.3	32.2
Standard deviation of tree height, m	4.26	3.17
Mean tree diameter at breast height, cm	41.5	48.7
Standard deviation of diameter at breast height, cm	6.3	10.7
Min TRW, mm	0.30	0.23
Max TRW, mm	6.63	13.22
Mean TRW, mm	2.80	2.40
Standard deviation of TRW, mm	1.01	1.62
Interseries correlation	0.69	0.60
First order autocorrelation	0.61	0.76
Mean sensitivity	0.22	0.29
GLK	0.70	0.64
EPS	0.88	0.91

and Holmes 1986); double detrending with negative exponential curve, cubic-spline with 128-year wavelength and autoregressive modelling were used. Statistics of datasets were calculated using library "dplR" in R (Bunn 2008). Chronologies were compared using the Gleichläufigkeit (GLK) and Pearson correlation coefficients. Gridded climatic data: mean monthly temperature and precipitation sums were obtained from the Climatic Research Unit (Jones et al. 1999) for points closest to the sites. The effect of climatic variables on TRW was assessed by bootstrapped Pearson correlation and response function analysis using the program DendroClim2002 (Biondi and Waikul 2004) for the whole chronologies and by 40-year moving intervals. Time windows from June of the preceding year to October of the current year were used for climatic data.

3 Results

Most of the measured time series of TRW (Fig. 1A,B) were maintained for production of the chronologies. Time series of TRW showed good agreement as EPS were above 0.85 and interseries correlation were above 0.60 (Table 1), thus confirming the validity of datasets. Considering that autocorrelation was high (Table 1), residual chronologies were produced (Fig. 1C). Chronologies were synchronous, as GLK was 0.59, but the correlation coefficient between them was rather low ($r = 0.27$, p-value $= 0.03$). Common decreases of TRW were observed in 1979, 1992, 1995, 1998, 2006 and 2008, and common increases were observed in 1957, 1978 and 1994 (Fig. 2C).

The established chronologies showed significant correlation ($|r| < 0.41$) and/or response function with seven of the tested 34 climatic variables, when the entire periods were analysed (Fig. 2). Tree-ring width of beech was mainly affected by temperature in the previous July and August as suggested by the significance of both coefficients. Temperature in the previous October and current May also showed a significant effect on TRW of beech. The analysis of moving intervals showed (Fig. 3A,B) that temperature in the previous August has had a stable effect throughout
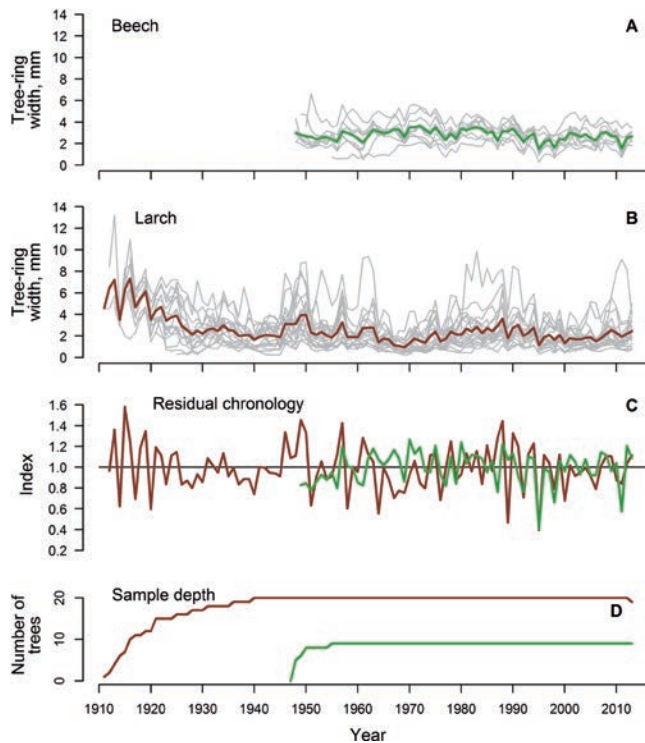
Fig. 1. Crossdated time series of TRW of beech (A) and larch (B), residual chronologies (C) and sample depth (D) (in C and D, green line represents beech and red line represents larch).

the analysed period, while the effect of precipitation in the previous July has become significant in moving intervals after 1960–2000. Precipitation in February and May has been significant for TRW in the mid part of the analysed period (Fig. 3A,B).

When the entire larch chronology was analysed, temperature in the previous September and current June and precipitation in July were the main limiting variables for TRW (Fig. 2 B), as suggested by correlation and response coefficients, although coefficient values were lower compared to beech (Fig. 2A). Nevertheless, TRW of larch was also correlated with temperature in the previous July and August, similarly to beech (Fig. 2A). Changes in the set of the significant climatic variables were observed during the 20th century (Fig. 3C,D). The effect of summer precipitation has been significant for larch until the mid-part of the 20th century. The effect of temperature in the previous July, August and particularly September has become significant or intensified in moving intervals after about 1950–1990. Precipitation in the current May and temperature in April have been significant for TRW in several intervals, when the trees were younger.
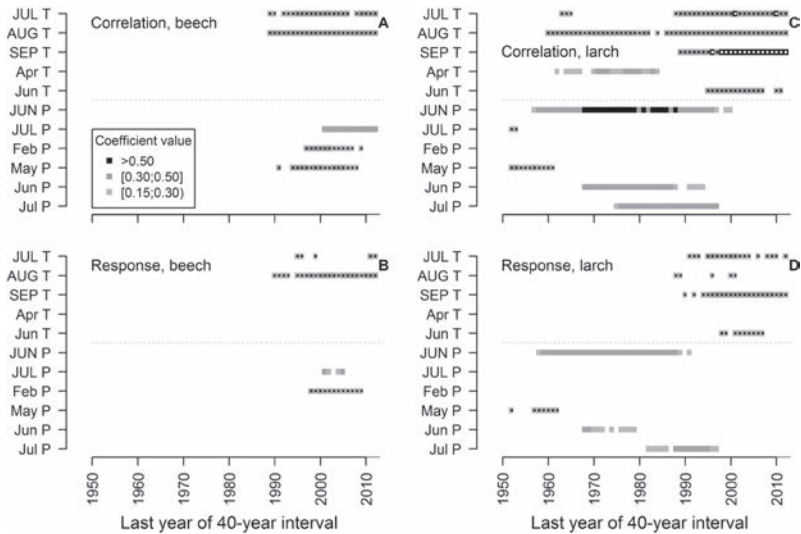
Fig. 2. Significant (p-value < 0.05) Pearson correlation (black bars) and response function (grey bars) coefficients between climatic variables: mean monthly temperature (T) and precipitation sums (P) and residual chronologies of beech (A) and larch (B) TRW, calculated using data for whole period (1911–2012 for larch and 1949–2012 for beech). Months in uppercase correspond to the year prior to tree-ring formation (t–1).
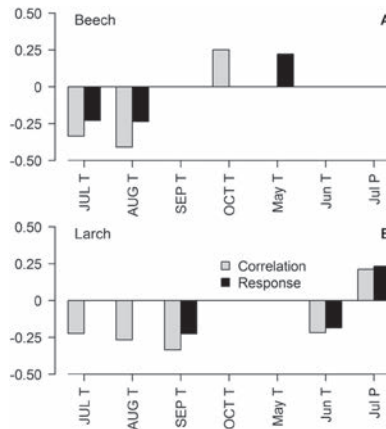

Fig. 3. Significant (p-value < 0.05) Pearson correlation and response function coefficients between climatic variables: mean monthly temperature (T) and precipitation sums (P) and residual chronologies of beech TRW (A and B, respectively) and larch (C and D, respectively) calculated for 40-year moving intervals. Months in uppercase correspond to the year prior to tree-ring formation (t–1). Dots represent negative coefficient values. Note that length of the analysed chronologies differs between species.

4   Discussion

Good agreement of TRW time series, as shown by EPS > 0.85 and interseries correlation > 0.60 (Table 1), suggested presence of environmental signals in TRW of both species (Wigley et al. 1984). The synchrony between chronologies suggested that both species reacted to similar environmental events; however, a different intensity of reaction was suggested by low correlation between chronologies. The observed signature years (Fig. 2C) coincided with climate-related pointer years observed for larch in Lithuania (Vitas and Žeimavičius 2010) or beech in Central Europe (Dittmar et al. 2003). Although both species occurred outside their natural range (Bolte et al. 2007; EUFORGEN 2009), a significant but non-drastic effect of the tested climatic variables on TRW was suggested by intermediate correlation/response coefficients (Fig. 2).

Drought related variables generally controlled TRW of both species, as suggested by the negative effect of summer temperature and positive effect of summer precipitation (Fig. 2), as was previously observed in Central Europe (Oleksyn and Fritts 1991; Dittmar et al. 2003). Growth of deciduous trees is partially dependent on nutrient reserves, which are formed at the end of the vegetative period (Barbaroux and Breda 2002; Sudachkova et al. 2004), thus, explaining the effect of climatic conditions in the preceding year (Fig. 2). However, response function coefficients suggested that climatic conditions in the previous year had stronger effect on beech than on larch. Observed changes in TRW-climate relationships and the intensification of the effect of drought-related variables, (Fig. 3) might be explained by warming or alternatively by aging of trees (Carrer and Urbinati 2004). The positive effect of April/May temperature was also observed (Fig. 2), but apparently, it had likely weakened since the 1950s (Fig. 3).

5   Conclusions

Tree-ring width of larch and beech in western Latvia was not narrow (suppressed), suggesting suitability of growth conditions. Climate-TRW analysis suggested that increment was generally limited by climatic variables related to summer drought; a negative effect of temperature and positive effect of precipitation was observed. The expected effect of winter-spring temperature has lost significance, suggesting successful acclimation of the studied trees in stands growing northwards from their natural distribution.

Acknowledgements

References

Avotniece Z., Rodinov V., Lizuma L., Briede A., Kļaviņš M. (2010). Trends in frequency of extreme climate events in Latvia. Baltica 23: 135–148.

Barbaroux C., Breda N. (2002). Contrasting distribution and seasonal dynamics of carbohydrate reserves in stem wood of adult ring-porous sessile oak and diffuse-porous beech trees. Tree Physiology 22: 1201–1210. http://dx.doi.org/10.1093/treephys/22.17.1201.

Biondi F., Waikul K. (2004). DENDROCLIM2002: a C++ program for statistical calibration of climate signals in tree ring chronologies. Computers and Geosciences 30: 303–311. http://dx.doi.org/10.1016/j.cageo.2003.11.004.

Bolte A., Czajkowski T., Kompa T. (2007). The north-eastern distribution range of European beech – a review. Forestry 80: 413–429. http://dx.doi.org/10.1093/forestry/cpm028.

Bunn A.G. (2008). A dendrochronology program library in R (dplR). Dendrochronologia 26: 115–124. http://dx.doi.org/10.1016/j.dendro.2008.01.002.

Carrer M., Urbinati C. (2004). Age-dependent tree-ring growth response to climate in *Larix decidua* and *Pinus cembra*. Ecology 85: 730–740. http://dx.doi.org/10.1890/02-0478.

Cook E.R., Holmes R.L. (1986). Guide for computer program ARSTAN. In: Holmes R.L., Adams R.K., Fritts H.C. (eds.). Tree-ring chronologies of Western North America: California, eastern Oregon and northern Great Basin. University of Arizona, Tucson. p. 50–65.

Dittmar C., Zech W., Elling W. (2003). Growth variation of common beech (*Fagus sylvatica* L.) under different climatic and environmental conditions in Europe – a dendrochronological study. Forest Ecology and Management 173: 63–78. http://dx.doi.org/10.1016/S0378-1127(01)00816-7.

Dreimanis A. (1995). [The beech and the larch-tree in Shkede forestry]. Dižskābardis un lapegle Šķēdes mežniecībā. In: Forestry education 75th anniversary conference proceedings of Latvia University of Agriculture. p. 94–97.

EUFORGEN (2009). Distribution maps. http://www.euforgen.org/distribution-maps/. [Cited 1 Jan 2014].

Fritts H.C. (2001). Tree-rings and climate. The Blackburn Press, Caldwell. 582 p.

Grissino-Mayer H.D. (2001). Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree-Ring Research 57: 205–221.

Hickler T., Vohland K., Feehan J., Miller P.A., Smith B., Costa L., Giesecke T., Fronzek S., Carter T.R., Cramer W., Kühn I., Sykes M.T. (2012). Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. Global Ecology and Biogeography 21: 50–63. http://dx.doi.org/10.1111/j.1466-8238.2010.00613.x.

Jones P.D., New M., Parker D.E., Martin S., Rigor I.G. (1999). Surface air temperature and its variations over the last 150 years. Reviews of Geophysics 37: 173–199. http://dx.doi.org/10.1029/1999RG900002.

Kullman L. (2008). Thermophilic tree species reinvade subalpine Sweden – early responses to anomalous late Holocene climate warming. Arctic Antarctic and Alpine Research 40: 104–110. http://dx.doi.org/10.1657/1523-0430 (06-120)[KULLMAN]2.0.CO;2.

Lindner M., Maroschek M. et al. (2010). Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. Forest Ecology and Management 259: 698–709. http://dx.doi.org/10.1016/j.foreco.2009.09.023.

Lizuma L., Kļaviņš M., Briede A., Rodinovs V. (2007). Long-term changes of air temperature in Latvia. In: Kļaviņš M. (ed.). Climate change in Latvia. University of Latvia, Riga. p. 11–20.

Oleksyn J., Fritts H.C. (1991). Influence of climatic factors upon tree rings of *Larix decidua* and *L.*

decidua × *L. kaempferi* from Pulawy, Poland. Trees-Structure and Function 5: 75–82. http://dx.doi.org/10.1007/BF00227488.

Sudachkova N.E., Milyutina I.L., Romanova L.I., Semenova G.P. (2004). The annual dynamics of reserve compounds and hydrolytic enzymes activity in the tissues of *Pinus sylvestris* L. and *Larix sibirica* Ledeb. Eurasian Journal of Forest Research 7: 1–10.

Vetaas O.R. (2002). Realized and potential climate niches: a comparison of four *Rhododendron* tree species. Journal of Biogeography 24: 545–554. http://dx.doi.org/10.1046/j.1365-2699.2002.00694.x.

Vitas A., Žeimavičius K. (2010). Regional tree-ring chronology of European larch (*Larix decidua* Mill.) in Lithuania. Baltic Forestry 16: 187–193.

Walther G.R., Post E. et al. (2002). Ecological response to recent climate change. Nature 416: 389–395. http://dx.doi.org/10.1038/416389a.

Wigley T.M.L., Briffa K.R., Jones P.D. (1984). On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. Journal of Climate and Applied Meteorology 23: 201–213. http://dx.doi.org/10.1175/1520-0450(1984)023<0201:OTAVOC>2.0.CO;2.

Total of 23 references