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

METEOROLOĢISKO FAKTORU UN STĀDMATERIĀLA IETEKME UZ PAPEĻU AUGŠANU

Silva Šēnhofa

EFFECT OF METEOROLOGICAL FACTORS AND PLANTING MATERIAL ON POPLAR GROWTH

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

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

LATVIJAS LAUKSAIMNIECĪBAS UNIVERSITĀTE
LATVIA UNIVERSITY OF LIFE SCIENCES AND TECHNOLOGIES

Mg.silv. **SILVA ŠĒNHOFA**

METEOROLOĢISKO FAKTORU UN STĀDMATERIĀLA IETEKME UZ PAPEĻU AUGŠANU

EFFECT OF METEOROLOGICAL FACTORS AND PLANTING MATERIAL ON POPLAR GROWTH

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

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

Salaspils 2021

ANOTĀCIJA

Mežsaimniecība saskaras ar aizvien jauniem izaicinājumiem ilgtspējīgu atjaunojamo dabas resursu nodrošināšanā. Apaļkoksnes produktu un enerģētiskās koksnes ražošana no ātraudzīgo koku sugu kokiem sniedz iespēju palielināt kokrūpniecībai pieejamo resursu apjomu. Ziemeļeiropā augsta ātraudzība raksturīga atsevišķām papeļu sugām (*Populus* spp.) un to hibrīdiem. Papeļu plantāciju produktivitāte galvenokārt atkarīga no tajā izmantotajiem kloniem. Ziemeļeiropas valstīs nenotiek plaša un sistemātiska papeļu selekcija, tādēļ šajā reģionā galvenokārt izmanto citos Eiropas reģionos atlasītus klonus. Kloniem, kas pārvietoti ziemeļu virzienā no to vecāku izcelsmes vietas, jābūt piemērotiem citādiem fotoperioda un meteoroloģiskajiem apstākļiem. Šādas piemērotības pārbaude pirms klonu rekomendēšanas komerciālai izmantošanai ir aktuāla arī Latvijā. Promocijas darba mērķis ir identificēt audzēšanai Latvijā piemērotus papeļu klonus.

Promocijas darbs sastāv no sešām tematiski vienotām zinātniskajām publikācijām, un to rezultāti liecina par būtisku klimata ietekmi uz papeļu augšanu. *Populus* hibrīdu radiālo pieaugumu negatīvi ietekmē sausuma stress vasaras periodā un palielināta gaisa temperatūras amplitūda miera perioda laikā. Augstuma pieaugumu būtiski ietekmē klons un spraudeņa garums, un ātraudzīgākiem kloniem ir mazāka augstuma pieauguma jutība pret sezonas meteoroloģisko faktoru svārstību ietekmi. Rudens salnu izraisīti galotnes bojājumi biežāk novērojami ātraudzīgiem kloniem. Koki ar salnu dēļ nokaltušu virszemes daļu veido atvases, bet to augšana uzsākas novēloti. Ziemas sala bojājumi novērojami augšanā atpaliekošajiem kloniem. Kopumā ir iespējams atlasīt ātraudzīgus klonus ar labu rudens salnu un ziemas sala noturību un saglabāšanos.

ABSTRACT

Forestry is challenged by the global demand for sustainable renewable resources. Fast-growing tree species are highly productive and pose the potential to increase roundwood and energy wood production. In Northern Europe, poplars (*Populus* spp.) and their hybrids are among the most productive tree species. The productivity of poplar plantations is mainly determined by selected clones. Northern European countries lack wide and systematic poplar breeding programs, therefore mainly uses clones that are imported from other European regions. Clones that are transferred northward from their parental species origin should be suitable to an altered length of the vegetation period and low temperatures during the winter season. Clonal testing before recommendation for their commercial use is topical also in Latvia. The thesis aims to identify poplar clones suitable for growing in Latvia.

This thesis summarizes six thematically linked scientific publications, and their results indicate the significant effect of climatic factors on poplar growth. The radial growth of *Populus* clones is negatively affected by drought-related stress during the growing season and increased temperature range during the dormancy. Height growth is determined by clone and length of the cuttings, and faster-growing clones are more robust to the negative effect of meteorological factors during the growing season. The faster-growing clones are more likely to have damaged leading shoots by early autumn frost. Trees that have withered aboveground shoots by autumn frost are sprouting during the next growing season, but the regrowth is delayed. Winter frost damage is more likely for weakly growing clones. Overall, fast-growing clones with sufficient autumn and winter frost resistance and survival could be selected.

SATURS / *CONTENTS*

PUBLIKĀCIJU SARAKSTS / *LIST OF PUBLICATIONS*

Promocijas darba galvenie rezultāti apkopoti sešās publikācijās, uz kurām atsauces tekstā veidotas, izmantojot romiešu ciparus:

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

I **Šēnhofa S.**, Zeps M., Matisons R., Smilga J., Lazdiņa D., Jansons Ā. (2016) Effect of climatic factors on tree ring width of *Populus* hybrids in Latvia. Silva Fennica, 50(1), id 1442, 12 p. 10.14214/sf.1442

II 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. 10.1016/j.dendro.2016.10.003

III **Šēnhofa S.**, Zeps M., Ķēniņa L., Neimane U., Kāpostiņš R., Kārkliņa A., Jansons Ā. (2018) Intra-annual height growth of hybrid poplars in Latvia. Results from the year of establishment. Agronomy Research, 16(1), 254–262. 10.15159/ar.17.073

IV Lazdiņa D., **Šēnhofa S.**, Zeps M., Makovskis K., Bebre I., Jansons Ā. (2016) The early growth and fall frost damage of poplar clones in Latvia. Agronomy Research, 14(1), 109–122.

V **Šēnhofa S.**, Lazdiņa D., Zeps M. (2021) Winter frost damage and its link to early growth and survival in a poplar clone collection. In: Proceedings of 27th International Scientific Conference 'Research for Rural Development 2021', Jelgava, 12–14 May 2021. Jelgava: LUA, Vol. 36, p. 70–76. 10.22616/rrd.27.2021.010

VI **Senhofa S.**, Neimane U., Grava A., Sisenis L., Lazdina D., Jansons A. (2017) Juvenile growth and frost damages of poplar clone OP42 in Latvia. Agronomy Research, 15(5), 2113–2125. 10.15159/ar.17.061

Promocijas darba ietvaros sagatavota recenzēta monogrāfija:
A peer-reviewed monograph was published:

Šēnhofa S., Lazdiņa D., Jansons Ā. (2019) Papeļu (*Populus* spp.) stādījumu ierīkošana un apsaimniekošana. Salaspils: LVMI Silava, DU AA Saule, 84 lpp.

Autoru ieguldījums publikācijās / *The contribution of the authors*

	I	II	III	IV	V	VI
Ideja / *Original idea*	**SŠ**, ĀJ	RM, ĀJ	**SŠ**, ĀJ	DL, ĀJ, **SŠ**	**SŠ**, DL	**SŠ**, ĀJ
Pētījuma plāns / *Study design*	**SŠ**, RM	**SŠ**, RM	**SŠ**, MZ	**SŠ**, DL	**SŠ**	**SŠ**, DL
Datu ievākšana / *Data collection*	MZ, JS, **SŠ**	**SŠ**, JK, JJ, ĀJ	LĶ, UN, RK, AK	MZ, KM, IB	**SŠ**, DL, MZ	UN, AG, **SŠ**
Datu analīze / *Data analysis*	**SŠ**, RM	**SŠ**, RM	**SŠ**, MZ	**SŠ**	**SŠ**	**SŠ**, DL, LS
Manuskripta sagatavošana / *Manuscript preparation*	**SŠ**, RM, ĀJ, DL	RM, **SŠ**	**SŠ**, ĀJ	**SŠ**, DL, ĀJ	**SŠ**, DL, MZ	**SŠ**, ĀJ
Promocijas darba autora ieguldījums, % / *Contribution of author of the thesis, %*	70%	50%	70%	60%	80%	70%

AG – Annija Grava, AK – Annija Kārkliņa, ĀJ – Āris Jansons, DL – Dagnija Lazdiņa, IB – Ieva Bebre, JJ – Jānis Jansons, JK – Juris Katrevičs, JS – Jānis Smilga, KM – Kristaps Makovskis, LĶ – Laura Ķēniņa, LS – Linards Sisenis, MZ – Mārtiņš Zeps, RK – Rolands Kāpostiņš, RM – Roberts Matisons, **SŠ – Silva Šēnhofa**, UN – Una Neimane.

PĒTĪJUMU REZULTĀTU PREZENTĒŠANA KONFERENCĒS / *APPROBATION OF RESEARCH RESULTS*

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

1. **Šēnhofa S.** (2021) Winter frost damage and its link to early growth and survival in a poplar clone collection. 27th Annual International Scientific Conference 'Research for Rural Development 2021', 12–14 May 2021, Jelgava, Latvia, prezentācija.

2. **Šēnhofa S.** (2021) Assessment of poplar clone plantations in Latvia. Konference 'Knowledge Based Forest Sector', 2021. gada 26.–27. janvāris, Rīga, Latvija, prezentācija.

3. **Šēnhofa S.** (2020) Piemērota meža reproduktīvā materiāla izvēle adaptācijas kontekstā: iespējas un riski. Konference "Eiropas zaļais kurss bioekonomikas attīstībai", 2020. gada 17. decembris, Jelgava, Latvija, prezentācija.

4. **Šēnhofa S.** (2019) Cold hardiness of *Populus* spp. clones. 25th Annual International Scientific Conference 'Research for Rural Development 2019', 15–17 May 2019, Jelgava, Latvia, prezentācija.

5. **Šēnhofa S.**, Zeps M., Lazdiņa D., Matisons R., Kāpostiņš R., Jansons Ā. (2019) Climate response and risks for poplar plantations. International conference 'Alders and other fast-growing trees', 29–30 April 2019, Kalsnava, Latvia, prezentācija.

6. Neimane U., **Šēnhofa S.**, Grava A., Lazdiņa D., Jansons Ā. (2016) Juvenile growth and frost damage of poplar clone OP42 in Latvia. 4th International Conference of Dendrochronologists and Dendroecologists from the Baltic Sea Region 'BaltDendro 2016'. 22–25 August, 2016, Annas Tree School, Latvia, prezentācija.

7. Lazdina D., **Senhofa S.**, Zeps M., Makovskis K., Bebre I., Jansons A. (2016) The selection of the commercial poplar clones in Latvia. 7th International conference 'Biosystems Engineering 2016', 12–13 May 2016, Tartu, Estonia, prezentācija.

1. DARBA VISPĀRĪGS RAKSTUROJUMS

1.1. Tēmas aktualitāte

Mežsaimniecība saskaras ar aizvien jauniem izaicinājumiem globālā ilgtspējīgu, atjaunojamu dabas resursu nodrošināšanā. Ātraudzīgās koku sugas sniedz iespēju palielināt ārpus meža izaudzētās koksnes apjomu (Mola-Yudego et al., 2017). Šādā veidā iespējams paaugstināt koksnē uzglabātā CO_2 daudzumu un aizstāt fosilo resursu izmantošanu, tādējādi kavējot klimata pārmaiņas (Sulaiman et al., 2020) un samazinot nepieciešamību izstrādāt koksni dabiskajos mežos (Pawson et al., 2013). Ziemeļeiropas apstākļos pie kokaugu kultūrām ar augstu produktivitāti pieder papeles (*Populus* spp.) un to hibrīdi (Tullus et al., 2013). Šajā reģionā introducēts ievērojams skaits papeļu klonu (Karačić et al., 2003; Christersson, 2006; Karačić & Weih, 2006), ko izmanto gan biomasas, gan apaļkoksnes audzēšanai ar rotācijas periodu attiecīgi no 5 līdz 10 vai no 20 līdz 30 gadiem (Tullus et al., 2012).

Papeļu plantāciju produktivitāte galvenokārt atkarīga no tajā izvēlētajiem kloniem. Papelēm pieejama plaša ģenētiskā materiāla bāze, un klonus ir vienkārši pavairot veģetatīvi, iegūstot precīzas māteskoka "kopijas" ar vēlamajām īpašībām. Tomēr dažādu papeļu klonu izmantošana komerciālajai audzēšanai Eiropā joprojām ir ierobežota, dodot priekšroku plašu plantāciju ierīkošanai ar vienu atsevišķu klonu. Dānijā (Stener & Westin, 2017) un Zviedrijā (Karačić et al., 2021) visbiežāk tiek stādīts klons OP42, Dienvideiropā – klons I-214 (FAO, 2016). Šobrīd papeļu selekcijas programma un 16 komerciālai izmantošanai jau reģistrēti kloni pieejami Zviedrijā (Stener & Westin, 2017), savukārt citās Ziemeļeiropas valstīs izmanto tikai stādmateriālu, kas selekcionēts un importēts no dienvidu reģioniem, galvenokārt no Itālijas un Vācijas (Niemczyk et al., 2018).

Klimats ir viens no galvenajiem koku augšanu ietekmējošajiem faktoriem (Lindner et al., 2010). Būtiska meteoroloģisko faktoru ietekme uz *Populus* klonu augšanu vērojama gan veģetācijas sezonas (*intra-annual*) ietvaros (Yu et al., 2001; Tullus et al., 2012), gan ilgtermiņā (*inter-annual*), ietverot meteoroloģiskos apstākļus arī miera periodā. Sugu un hibrīdu krustošana (hibridizācija) izmaina ģenētiski noteiktās adaptīvās pazīmes (Gudynaitė-Franckevičienė et al., 2020). *Populus* hibrīdu augstā produktivitāte saistīta ar spēju izmantot garāku veģetācijas periodu, salīdzinot ar to vecāku sugām (Yu et al., 2001), turklāt lielu daļu no hibrīdiem iespējams audzēt ārpus to vecāku sugu dabiskā izplatības areāla (Sykes & Prentice, 1996). Kloniem, kas pārvietoti ziemeļu virzienā no to vecāku sugu izcelsmes reģiona, garāks fotoperiods var izraisīt novēlotu augšanas pārtraukšanu (Li et al., 2002; Ingvarsson et al., 2006; Kalcsits et al., 2009), kas savukārt saistīts ar sala bojājumu risku (Ferm et al., 1989; Christersson, 1996, 2006; Ilstedt, 1996; Telenius, 1999; Karačić et al., 2003; Pliura et al., 2014). Lai gan vislielākais sala bojājumu risks ir pārejas periodā no aktīvās augšanas uz miera stāvokli (Charrier et al., 2015), ziemeļu reģionos introducētajiem

kokiem jāpiemērojas ne tikai citādam augšanas sezonas ilgumam, bet arī zemajām miera perioda temperatūrām, kas mijas ar īslaicīgiem atkušņiem (Schreiber et al., 2013). Tieši nepietiekama introducēto sugu un hibrīdu piemērotība klimatam ir viens no būtiskākajiem plašāka mēroga papeļu audzēšanas izaicinājumiem Ziemeļeiropā (Schreiber et al., 2013; Gudynaitė-Franckevičienė et al., 2020; Karačić et al., 2021), aktualizējot introducēto klonu pārbaužu nepieciešamību pirms to rekomendēšanas komerciālai izmantošanai (Pliura et al., 2014).

Sala bojājumu ietekme ir kompleksa – tie samazina koku vitalitāti un paaugstina mirstību (Cunti et al., 1991; Diamandis & Koukos, 1992; Pliura et al., 2014), samazina stumbra kvalitāti, veicinot dubultās galotnes, līkumu un plaisu veidošanos (Verwijst et al., 1996; Christersson, 2006), un nosalušas dzinumu augšējās daļas samazina koka augstumu. Tomēr vairāki pētījumi liecina, ka uz ziemeļiem pārvietoto sugu un hibrīdu ražība atsver potenciālos ar sala bojājumiem saistītos riskus (Schreiber et al., 2013; Pliura et al., 2014).

1.2. Promocijas darba mērķis

Promocijas darba mērķis ir identificēt audzēšanai Latvijā piemērotus papeļu klonus.

1.3. Promocijas darba pētnieciskie uzdevumi

Promocijas darbā izvirzīti trīs uzdevumi:
1. Raksturot papeļu radiālā un augstuma pieauguma jutību pret meteoroloģiskajiem faktoriem.
2. Novērtēt stādmateriāla un klona ietekmi uz papeļu augstuma pieaugumu.
3. Novērtēt salnu un sala bojājumu ietekmi uz papeļu augšanu.

1.4. Promocijas darba tēzes

Promocijas darbā izvirzītas divas tēzes:
1. Sausuma stress vasaras periodā būtiski negatīvi ietekmē papeļu radiālo pieaugumu.
2. Sala bojājumu negatīvās ietekmes uz koku augstuma pieaugumu pakāpe dažādiem papeļu koniem ir atšķirīga.

1.5. Zinātniskā novitāte

Pirmo reizi Eiropas hemiboreālajos mežos veikta retrospektīvā gadskārtu parametru analīze meteoroloģisko faktoru ilgtermiņa ietekmes uz papeļu augšanu vērtēšanai. Pirmo reizi Baltijas valstīs vērtēta rudens salnu un ziemas sala bojājumu ietekme uz papeļu saglabāšanos un augšanu. Latvijas mērogā iegūta jauna informācija par līdz šim plašāko dažādas izcelsmes papeļu klonu skaitu un dažāda garuma spraudeņu piemērotību stādījumiem.

2. MATERIĀLI UN METODES

Pētījumā ievākti un analizēti dati no divām papeļu mežaudzēm Auces un Talsu novada Šķēdes apkārtnē un pieciem stādījumiem iepriekš lauksaimniecībai izmantotā zemē Skrīveru, Vecumnieku un Kalsnavas apkārtnē (2.1. att.). Kopumā stādījumos pārstāvēti 36 dažādas izcelsmes kloni no *Aigeiros* un *Tacamahaca* sekcijām (2.1. tabula). Kloni no Itālijas, Beļģijas, Vācijas, Zviedrijas un Nīderlandes introducēti Latvijā pirms 10–15 gadiem. Kloni ar Latvijas izcelsmi ir pēcnācēji (spraudeņi) papelēm, kas Latvijā saglabājušās no introdukcijas ap 1960. gadu (Saliņš, 1971). Hybride275 un OP42 ir viena klona atšķirīgi nosaukumi, bet dažādās stādmateriāla izcelsmes dēļ tie vērtēti kā atsevišķi kloni.
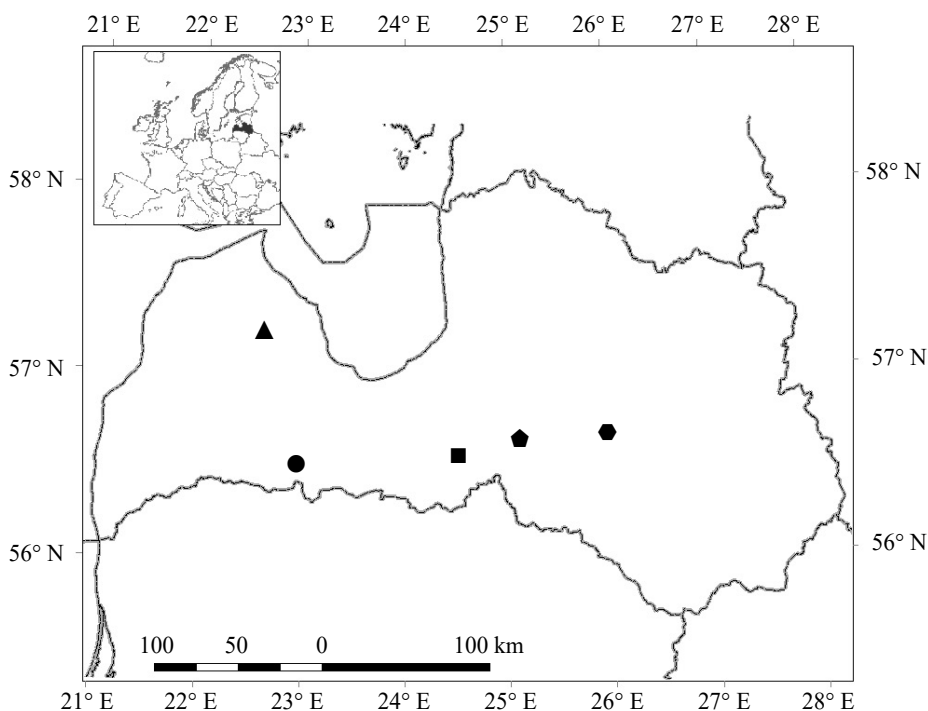
2.1. att. **Pētījuma objektu izvietojums**
● – Auce (I un II), ▲ – Šķēde (I un II), ■ – Vecumnieki (III un VI), ⬠ – Skrīveri (IV) un
⬡ – Kalsnava (IV un V). Vecumniekos un Kalsnavā dati ievākti divos atsevišķos stādījumos.

Publikācijās pārstāvēto klonu izcelsme

Klons	Publikācija						Ražotājs / izstrādātājs / īpašnieks un izcelsmes valsts	Suga / krustojums / sekcija
	I	II	III	IV	V	VI		
AF2				x	x		Franco Alasia, Itālija	*P. × canadensis* [a]
AF6				x	x			*P. nigra × P. × generosa* [b]
AF7				x	x			*P. × generosa* [b] *× P. × canadensis* [a]
AF8				x	x			*P. × generosa* [b] *× P. trichocarpa*
AF16					x			*P. × canadensis* [a]
AF18					x			*P. × canadensis* [a]
Baldo			x		x		Unità di ricerca per le Produzioni Legnose fuori Foresta, Itālija	*P. deltoides*
Oudenberg			x		x		Eigen Vermogen van het Instituut Voor Natuur en Bosonderzoek, Beļģija	*P. × canadensis* [a]
Vesten			x		x			
Matrix11				x	x		Nordwestdeutsche Forstlichen Versuchsanstalt, Vācija	*P. maximowiczii × P. trichocarpa*
Matrix24			x	x	x			
Matrix49			x		x			
Max1			x		x		Vācija	*P. nigra × P. maximowiczii*
Max3			x		x			
Max4					x			
LV1			x	x	x		Swedish Forestry Agency, reģistrācijas Nr. KB-003, Zviedrija	*Tacamahara*
LV3			x	x	x			
LV4			x	x	x			
LV5				x	x			
LV7				x	x			
LV9				x	x			
LV10				x	x			
LV11				x	x			
LV12				x	x			
LV14				x	x			
LVX				x	x			
P0114	x	x		x	x		Latvijā atrastu pieaugušu papeļu pēcnācēji (spraudeņi), introducēti 20. gs. 60. gados (Saliņš, 1971)	*P. balsamifera × P. laurifolia*
Pop1				x	x			nezināms
Pop2				x	x			
Pop3				x				
Pop4				x	x			
Pop5				x	x			
Pop6				x	x			
Pop7				x				

| Hybride275 | | | x | | x | | North West Forest Research Station, Vācija | *P. maximowiczii × P. trichocarpa* |
| OP42 | | | x | x | x | x | Nīderlande, sākotnēji selekcionēts Oxford Paper Company (ASV) | |

[a] *P. × canadensis* ir hibrīds *P. nigra × P. deltoides*;
[b] *P. × generosa* ir hibrīds *P. deltoides × P. trichocarpa*.

2.1. Radiālā pieauguma starpgadu dinamika un tā saistība ar meteoroloģiskajiem faktoriem

2.1.1. Datu ievākšanas metodika

Starpgadu radiālā pieauguma saistība ar meteoroloģiskajiem faktoriem vērtēta divās papeļu hibrīda *Populus balsamifera* L. × *P. laurifolia* Ledeb. audzēs ar normāla mitruma režīma augsnēm (Vr) netālu no Auces (56° 31' N, 22° 56' E) un Šķēdes (57° 14' N, 22° 37' E) (2.1. att.). Audžu vecums pēc taksācijas datiem attiecīgi 62 un 64 gadi, sākotnējais biezums aptuveni 5000 koki ha⁻¹, nav veikta kopšanas cirte.

Aucē atlasīti 12 un Šķēdē atlasīti 10 audzes caurmēra sadalījumu reprezentējoši vizuāli vitāli koki bez bojājumu pazīmēm. No katra koka 2013./2014. gada ziemā 1.3 m augstumā virs sakņu kakla ievākti stumbra šķērsgriezuma diski. Šie diski laboratorijā izžāvēti līdz gaissausas koksnes mitruma līmenim un slīpēti ar slīppapīru, pakāpeniski nomainot tā graudainību no P80 līdz P400. Gadskārtas platuma mērījumi veikti, izmantojot Lintab 5 (RinnTECH, Germany, Heidelberg) sistēmu ar precizitāti līdz 0.01 mm. Mērījumi veikti divos pretējos šķērsgriezuma ripas virzienos.

Meteoroloģisko novērojumi dati iegūti no UEA *Climatic Research Unit* mājaslapas (Harris et al., 2014) tīkla punktiem, kas atrodas iespējami tuvu (<30 km) pētījumos iekļautajām audzēm. Izmantotie meteoroloģiskie rādītāji:
1. minimālā, maksimālā un vidējā mēneša gaisa temperatūra, mēneša temperatūras amplitūda, mēneša nokrišņu summa un potenciālā evapotranspirācija (PET) laika posmam no janvāra gadu pirms gadskārtas veidošanās līdz septembrim gadskārtas veidošanās gadā;
2. mēneša vidējā gaisa temperatūra un nokrišņu summa, un standartizēts nokrišņu evapotranspirācijas indekss (SPEI) (Vicente-Serrano et al., 2010) laika posmam no jūlija gadu pirms gadskārtas veidošanās līdz septembrim gadskārtas veidošanās gadā.

2.1.2. Datu statistiskā apstrāde

Gadskārtu platuma sēriju kvalitāte un to savstarpējā sakritība audzes ietvaros un starp tām vērtēta vizuāli un izmantojot statistisko šķērsdatēšanu programmā COFECHA (Grissino-Mayer, 2001). Atmestas sērijas, kas uzrādīja zemu sakritību (r < 0.40) ar kopējo datu kopu. Gadskārtu sēriju atlikumu hronoloģijas katrai audzei aprēķinātas programmā ARSTAN (Cook & Holmes, 1986). Tām veikta dubultā detrendēšana ar vecumu un konkurenci saistītās datu variācijas daļas noņemšanai.

Vecuma ietekme noņemta, izmantojot modificēto negatīvi eksponenciālo funkciju, un konkurences ietekme noņemta, izmantojot trešās kārtas polinomiālo funkciju (*spline*) ar viļņa garumu 40 gadi vai 48 gadi, saglabājot 50% no sākotnējās datu variācijas. Gadskārtu platuma sēriju variācijas raksturošanai izmantota vidējā jutība (SENS), vidējās starpsēriju korelācijas (*r-bar*), sinhronitāte (*Gleichläufigkeit* (GLK)), populācijas signāla izpausmes (EPS), pirmās pakāpes autokorelācijas (AC) un signāla stipruma (*signal to noise ratio* (SNR)) indeksi (Wigley et al., 1984), kas aprēķināti detrendētām sērijām.

Datu analīze veikta laika periodam no 1965. līdz 2009. gadam. Salīdzināta papeļu hibrīda, kārpainā bērza (*Betula pendula* Roth), parastās egles (*Picea abies* H. Karst.), parastās priedes (*Pinus sylvestris* L.), melnalkšņa (*Alnus glutinosa* Gaertn.), Eiropas lapegles (*Larix decidua* Mill.), Eiropas dižskābarža (*Fagus sylvatica* L.), sarkanā ozola (*Quercus rubra* L.) un hibrīdapses (*Populus tremuloides* Michx. × *P. tremula* L.) augšanu ietekmējošo meteoroloģisko faktoru līdzība attiecīgajai sugai raksturīgos saimnieciskajos mežos. Pieauguma ikgadējā mainība, ko reprezentē hronoloģiju indeksi (ikgadējais radiālais papildpieaugums), starp sugām un audzēm analizēta ar galveno komponentu analīzi (PCA) (Jolliffe, 1986), kur audžu atlikumu hronoloģijas izmantotas kā paraugi, un gadi (gadskārtu sēriju indeksi) – kā mainīgie. Galveno komponentu būtiskums noteikts ar randomizācijas testu (*broken stick*) ar 10^3 atkārtojumiem. Meteoroloģiskie faktori, kas veido galvenās komponentes, noteikti, izmantojot būtstrepa (Johnson, 2001) Pīrsona korelācijas analīzi ar 10^3 atkārtojumiem starp mainīgo (gadu) īpašvērtībām un meteoroloģiskajiem faktoriem Latvijas rietumu un centrālajai daļai. Būtisko meteoroloģisko faktoru ietekmes noteikšanai izmantota būtstrepa Pīrsona korelācijas analīze. Datu statistiskā apstrāde veikta brīvprogrammatūrā R 3.3.1 (R Core Team, 2020), izmantojot paketi *dplR* (Bunn, 2008).

2.2. Augstuma pieauguma dinamika un tā saistība ar meteoroloģiskajiem faktoriem veģetācijas sezonas ietvaros

2.2.1. Datu ievākšanas metodika

Papeļu klonu augšanas dinamika un tās saistība ar meteoroloģiskajiem faktoriem veģetācijas sezonas ietvaros vērtēta stādījumā Vecumnieki-1 (56° 34' N, 24° 31' E; 2.1. att.). Stādījums ierīkots 2016. gada pavasarī auglīgā, nosusinātā kūdras augsnē ar pH reakcijas līmeni 6. Stādīti neapsakņoti spraudeņi ar garumu 30 un 50 cm (tālāk tekstā attiecīgi "īsie" un "garie"), virs zemes atstājot 3–5 cm. Pārstāvēti 12 kloni (2.2. tabula), veidotas viena klona rindas trīs atkārtojumos ar attālumu starp rindām 4 m, un starp kokiem rindā 2 m.

Augstuma mērījumi pirmajā augšanas sezonā veikti katra klona un spraudeņu garuma grupas 20 nejauši izvēlētiem rametiem, vidēji 6 rametiem no viena atkārtojuma. Veikti deviņi augstuma mērījumu atkārtojumi ar vidēji 11 dienu intervālu starp tiem (no 5 līdz 18 dienām). Augstums mērīts no zemes virskārtas

līmeņa. Aptuveni pusei no rametiem bija vērojami briežu dzimtas dzīvnieku un gliemežu radīti bojājumi; tikai nebojāto koku dati izmantoti datu analīzē.

2.2. tabula

Izmantotie papeļu kloni

Klons	Rametu skaits	Spraudeņu garums, cm
OP42	3	30
Max1	6	
Max3	7	
Matrix24	6	
Matrix49	7	
Hybride275	9	
LV1	3	
LV3	6	
LV4	6	
Baldo	7	30
	9	50
Oudenberg	8	30
	10	50
Vesten	7	50

Katram kokam aprēķināta vidējā augšanas intensitāte (mm dienā) periodam starp veiktajiem mērījumiem. Katram klonam un tā spraudeņu garuma grupai aprēķināts gada vidējais augstuma pieaugums, vidējā augšanas intensitāte. Novērojumu perioda beigās "īsie" kloni iedalīti trīs grupās atkarībā no to augstuma pieauguma: (1) "īsie-max" – Hybrid275, Oudenberg, (2) "īsie-average" – Baldo, Max1, Max3, Matrix24, Matrix49, (3) "īsie-min" – OP42, LV1, LV3, LV4. Augšanas gaitas salīdzināšanai no "garo" klonu grupas iekļauti tikai kloni Oudenberg un Vesten, jo klona Baldo koku augstums bija būtiski (p < 0.05) mazāks.

Gaisa temperatūras un nokrišņu summas stundu vidējās vērtības iegūtas no tuvākās Latvijas Vides, ģeoloģijas un meteoroloģijas centra stacijas netālu no Bauskas (56° 22' N, 24° 13' E).

2.2.2. Datu statistiskā apstrāde

Augstuma pieauguma un augšanas intensitātes atšķirību vērtēšanai starp spraudeņu garuma grupām un kloniem izmantota viena faktora dispersijas analīze (ANOVA) un *Tukey HSD* tests. Katram kokam augstuma mērījumi aproksimēti ar Gompertz vienādojumu:

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

kur:

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

β – pārliekuma punkts (*displacement parameter*) – horizontālās nobīdes

koeficients, kas raksturo pieauguma tempa izmaiņu uzsākšanas laiku;

k – pieauguma temps – koeficients, kas raksturo attiecību starp asimptotu un pārliekuma punktu;

A – novērojuma diena.

Atšķirības starp Gompertz parametriem (α, β, *k*) vērtētas, izmantojot ANOVA. Pieauguma tempa koeficienta no jūnija līdz septembrim saistība ar šī perioda meteoroloģiskajiem faktoriem vērtēta, izmantojot Pīrsona korelācijas analīzi. Pieauguma tempa koeficienta un temperatūras atšķirības starp mērījumu periodiem vērtētas ar ANOVA. Visi testi veikti pie būtiskuma līmeņa α = 0.05. Norādītas vidējās vērtības un to ticamības intervāli. Aprēķini veikti brīvprogrammatūrā R 3.3.1 (R Core Team, 2020).

2.3. Augstuma pieauguma starpgadu dinamika

2.3.1. Datu ievākšanas metodika

Augstuma pieauguma starpgadu dinamika vērtēta stādījumos Skrīveros (56° 39' N, 25° 7' E) un Kalsnavā (56° 41' N, 25° 58' E) (2.1. att.). Skrīveru stādījums ierīkots 2011. gadā. Stādījumā pārstāvēti 23 papeļu kloni (2.1. tabula). Katram klonam stādīti vismaz 30 spraudeņi viena klona rindās ar attālumu starp rindām 2.2 m, un starp kokiem rindā 0.7 m.

Klonu sērija AF stādīta trīs atkārtojumos, pārējie kloni vienā līdz divos atkārtojumos, kas vienmērīgi un nejauši izvietoti laukā. Pēc pirmās augšanas sezonas visiem kloniem, izņemot kloniem no AF sērijas, to dzinumus pilnībā līdz zemei nopostīja briežu dzimtas dzīvnieki. Augstuma mērījumi veikti pēc otrās, trešās un piektās augšanas sezonas. Klonu sērijai AF augstuma mērījumi veikti arī pēc pirmās un ceturtās augšanas sezonas.

Kalsnavas stādījums (turpmāk tekstā – Kalsnava-1) ierīkots 2016. gada pavasarī vienlaidus sagatavotā augsnē. Pārstāvēti 34 papeļu kloni, katram klonam stādīti 97 līdz 102 aptuveni 25 cm gari spraudeņi viena klona rindās ar attālumu starp rindām 3.5 m, un starp kokiem rindā 0.5 m. Veikta zāles pļaušana starp rindām, stādījums iežogots. Visiem dzīvajiem kokiem (izņemot klonu OP42) augstums mērīts pēc pirmās (2017. gada pavasarī) un trešās augšanas sezonas (2019. gada pavasarī). Pēc ceturtās augšanas sezonas (2020. gada pavasarī) visiem kloniem augstums mērīts katram otrajam kokam rindā.

2.3.2. Datu statistiskā apstrāde

Datu atbilstības normālajam sadalījumam pārbaude veikta, izmantojot Šapiro-Vilka testu. Augstuma atšķirības starp kloniem vērtētas ar ANOVA vai Kruskala-Vallisa testu, kam būtisko pāru vērtējums veikts, izmantojot Dunna multiplās salīdzināšanas testu. Visi testi veikti pie būtiskuma līmeņa α = 0.05. Norādītas vidējās vērtības un to ticamības intervāli. Aprēķini veikti brīvprogrammatūrā R 4.0.2 (R Core Team, 2020).

2.4. Rudens salnu un ziemas sala bojājumu raksturojums un to saistība ar koku augstuma pieaugumu

2.4.1. Datu ievākšanas metodika

Rudens salnu bojājumi vērtēti abos Kalsnavas stādījumos, savukārt ziemas sala bojājumi vērtēti tikai vienā no Kalsnavas stādījumiem (2.1. att.; turpmāk tekstā – Kalsnava-2). Kalsnava-2 stādījums ierīkots 2014. un 2015. gadā, izmantojot Skrīveru stādījumā ievāktus spraudeņus. Stādījums ierīkots atklātā, līdzenā laukā, viena klona rindās bez atkārtojumiem. Agrās rudens salnas novērotas 2015. gada rudenī (informāciju par meteoroloģiskajiem apstākļiem skatīt 2.5.1. apakšnodaļā). Salnu bojājumi vērtēti 19 viengadīgiem un divgadīgiem kloniem (2.1. tabula). Sakarība starp koku augstumu (dati no Kalsnavas-2 stādījuma) un salnu bojājumiem (dati no Skrīveru stādījuma) vērtēta 16 kloniem, kas atradās abos stādījumos.

Vērtējums, balles

(a)

1_L	2_L	3_L	4_L	5_L
bez vizuāliem bojājumiem	atsevišķas bojātas lapas	bojāta lielākā daļa tekošā gada dzinuma lapu	bojāta lielākā daļa lapu	koki miera stāvoklī, t.i., lapas nobirušas, pumpuri izveidojušies pirms salnas

(b)

1_{ST}	2_{ST}	3_{ST}	4_{ST}	5_{ST}
bez vizuāliem bojājumiem	atsevišķi zaru bojājumi	atsevišķi stumbra bojājumi	bojāta vairāk nekā ⅓ stumbra	pilnībā bojāts stumbrs

2.2. att. **Shematisks (a) lapu un (b) stumbra bojājumu vērtējuma attēlojums**
(D. Lazdiņas zīmējumi)

Kalsnava-1 stādījumā (stādījuma apraksts 2.3.1. apakšnodaļā) rudens salnu vērtējums veikts pēc pirmās augšanas sezonas 2017. gada pavasarī.

Lapu un stumbra salnu bojājumu vizuālā vērtēšana Kalsnava-2 stādījumā veikta piecu ballu skalā (2.2. att.) 15. oktobrī. Koku atbilstība miera vai aktīvās augšanas stāvoklim noteikta pēc pumpuru fenoloģijas. Kalsnava-1 stādījumā veikta rudens salnu bojāto koku uzskaite.

Ziemas sala bojājumi novēroti Kalsnava-1 stādījumā pēc otrās augšanas sezonas (2018. gada pavasarī). Kloni vizuāli vērtēti piecu ballu skalā: 0 – gājis bojā, 1 – stipri bojāts, 2 – vidēji stipri bojāts, 3 – nelieli bojājumi, 4 – vizuāli nebojāts.

2.4.2. Datu statistiskā apstrāde

Klona un vecuma ietekme uz koka fenoloģisko fāzi un rudens salnu lapu un stumbra bojājumiem, kā arī lapu un stumbra bojājumu balles ietekme uz koka augstumu vērtēta, izmantojot vispārīgu lineāru modeli. Koku vecuma ietekme uz salnu bojājumu intensitāti (balli) vērtēta 10 kloniem individuālu koku līmenī. Atšķirības starp koku skaita sadalījumu pa rudens salnu lapu bojājumu ballēm viengadīgiem un divgadīgiem klonu LV4, LV11 un LV12 rametiem vērtētas ar Hī kvadrāta testu.

Bojāto un nebojāto koku augstuma salīdzināšanai klonu līmenī izmantots Manna-Vitnija U-tests. Sakarības starp koku un klonu augšanas parametriem un rudens salnu un ziemas sala bojājumiem vērtētas, izmantojot Spīrmena korelācijas analīzi.

Visi testi veikti pie būtiskuma līmeņa α = 0.05. Norādītas vidējās vērtības un to ticamības intervāli. Aprēķini veikti brīvprogrammatūrā R 3.0.2 un R 4.0.2 (R Core Team, 2020).

2.5. Atvašu veidošana pēc rudens salnu bojājumiem

2.5.1. Datu ievākšanas metodika

Atvašu veidošana pēc rudens salnu bojājumiem vērtēta stādījumā Vecumnieki-2 (2.1. att.). Stādījums ierīkots kūdras augsnē (pH 6) 2015. gada pavasarī, izmantojot 30 cm garus klona OP42 spraudeņus, kas ievākti no māteskokiem Latvijas rietumu daļā. Koki stādīti, ievērojot attālumu starp rindām 4 m, un starp kokiem rindā – 2 m. Nezāļu ierobežošanai rudenī pirms stādīšanas veikta platības aršana un apstrāde ar herbicīdu, bet augšanas sezonas laikā – ravēšana aptuveni 25 cm rādiusā ap koku.

Rudens salnas novērotas 2015. gada rudenī. Meteoroloģiskie dati iegūti uz lauka, reizi stundā veicot temperatūras mērījumus: (1) gaisa temperatūra 20 cm augstumā virs zemes, (2) augsnes temperatūra virskārtas līmenī un (3) 20 cm dziļumā (2.3. att.). Negatīva gaisa temperatūra pirmo reizi reģistrēta 11. septembrī, un līdz 6. oktobrim tā periodiski (deviņās no 22 dienām) atkārtojās. Šajā periodā garākie negatīvas gaisa temperatūras periodi reģistrēti 27. septembrī (deviņas
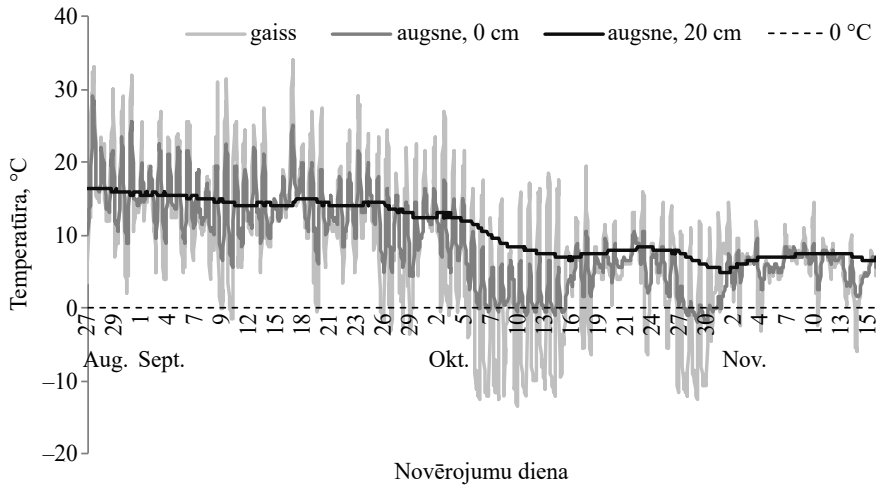
2.3. att. Gaisa (20 cm augstumā virs zemes) un augsnes (virskārtas (0 cm) līmenī un 20 cm dziļumā) temperatūra laika periodā no 27.08.2015. līdz 18.11.2015.
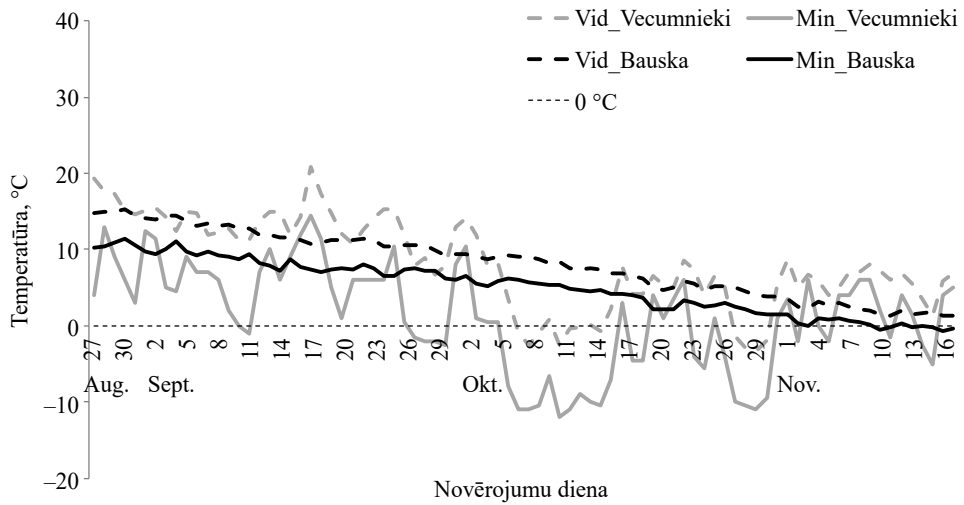
2.4. att. Gaisa temperatūra stādījumā (Vecumnieki) un ilgtermiņa novērojumi tuvākajā LVĢMC stacijā (Bauska) laika periodā no 27.08.2015. līdz 18.11.2015.
Vid_Vecumnieki – vidējā diennakts temperatūra, aprēķināta no stundas mērījumiem;
Min_Vecumnieki – minimālā diennakts temperatūra;
Vid_Bauska – vidējā diennakts temperatūra 30 gadu periodam;
Min_Bauska – vidējā minimālā diennakts temperatūra 30 gadu periodam.

stundas, minimālā temperatūra −2 °C) un 30. septembrī (septiņas stundas, minimālā temperatūra −3 °C). Salna pieņēmās spēkā 7. oktobrī: negatīva gaisa temperatūra saglabājās 14 stundas un sasniedza −12.5 °C. Minimālā gaisa temperatūra no −9.5 līdz −13.5 °C ar ilgumu no 11 līdz 16 stundām saglabājās 10 dienas. Līdzīgi apstākļi atkārtojās periodā no 28. līdz 31. oktobrim. Abos šajos periodos negatīva temperatūra reģistrēta arī augsnes virskārtā. Pirmo reizi negatīva augsnes virskārtas temperatūra reģistrēta 8. oktobrī, un tā saglabājās divas stundas, 13. oktobrī negatīva temperatūra saglabājās septiņas stundas, bet 30. un 31. oktobrī − 15 stundas (minimālā temperatūra −2 °C). Augsnē 20 cm dziļumā negatīva temperatūra novērojumu periodā nav konstatēta.

Ilgtermiņa meteoroloģisko apstākļu dati attiecīgajam laika periodam iegūti no tuvākās LVĢMC novērojumu stacijas netālu no Bauskas (56° 22′ N, 24° 13′ E). Tajos negatīva vidējā minimālā gaisa temperatūra pirmo reizi reģistrēta 11. novembrī (2.4. att.), kas ir ievērojami vēlāk nekā analizētajā augšanas sezonā.

Nākamās augšanas sezonas sākumā (jūnijā) visiem kokiem konstatēti pilnībā nokaltuši pirmā gada dzinumi. Daļa no kokiem veidoja celma atvases. Katram kokam mērīts garākā iepriekšējās sezonas dzinuma augstums un caurmērs pie sakņu kakla, un zaru garums, noteikts iepriekšējās sezonas dzinumu un zaru (garāki par 5 cm) skaits. Katram kokam noteikta dzīvnieku radīto bojājumu un jauno dzinumu sastopamība (0/1). Kopumā dati ievākti 3025 kokiem. Atkārtots atvašu veidošanas vērtējums veikts jūlija vidū daļā no stādījuma (1018 kokiem).

2.5.2. Datu statistiskā apstrāde

Datu atbilstības normālajam sadalījumam pārbaude veikta, izmantojot Šapiro-Vilka testu. Augstuma, caurmēra un zaru garuma atšķirības kokiem, kas bija izveidojuši vienu, divus, trīs un vairāk nekā trīs stumbrus, vērtētas, izmantojot ANOVA. Hī kvadrāta tests izmantots, lai vērtētu (1) zaru skaita, kā arī atvases veidojošo koku īpatsvara un dzīvnieku bojāto koku īpatsvara atšķirības starp kokiem ar dažādu stumbru skaitu, (2) atvases veidojošo koku īpatsvara atšķirības starp dzīvnieku bojātiem un nebojātiem kokiem un (3) atvases veidojošo koku īpatsvara atšķirības starp stādījuma rindām. Pīrsona korelācijas analīze izmantota, lai vērtētu saistību starp atvases veidojošo koku īpatsvaru un vidējo koku augstumu rindā. Spīrmena korelācijas analīze izmantota, lai vērtētu saistības starp (1) koka zaru un stumbru skaitu, (2) zaru garumu un skaitu, un (3) zaru garumu un stumbru skaitu. Telpiskā autokorelācija vērtēta, izmantojot Morana I testu. Visi testi veikti pie būtiskuma līmeņa $α = 0.05$. Norādītas vidējās vērtības un to ticamības intervāli.

3. REZULTĀTI UN DISKUSIJA

3.1. Radiālā pieauguma starpgadu dinamika un tā saistība ar meteoroloģiskajiem faktoriem

Vērtējot starpgadu radiālā pieauguma saistību ar meteoroloģiskajiem faktoriem divās papeļu hibrīda audzēs 62–64 gadu vecumā, šķērsdatētās gadskārtu platuma sērijas uzrādīja augstu sakritību starp koku mērījumiem ar starpsēriju korelācijas koeficientu 0.42–0.51 un sēriju sinhronitātes rādītāju GLK 0.68–0.69, norādot uz izteikti vienotu vides faktoru ietekmi uz papeļu hibrīda radiālo pieaugumu. Par to liecina arī cieša (r > 0.75) sakarība starp audžu hronoloģijām. Abās audzēs papeļu augšanas dinamika bija līdzīga – tekošais vidēji periodiskais
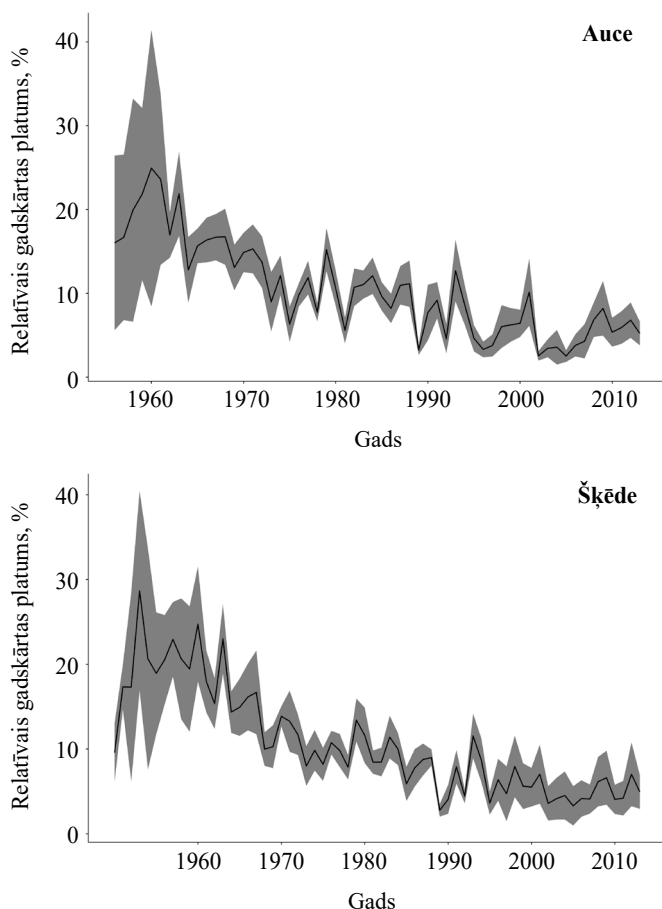
3.1. att. **Papeļu hibrīda relatīvais gadskārtas platums Aucē un Šķēdē**

radiālais pieaugums kulminē 10 līdz 15 gadu vecumā un izlīdzinās, sasniedzot 25 līdz 30 gadu vecumu (3.1. att.).

Augstie signāla intensitātes rādītāji SNR (6.17–10.77) skaidrojami ar homogēniem augšanas apstākļiem audzē un vienveidīgu ģenētisko materiālu (pārstāvēts viens klons). Samērā lielās SNR atšķirības norāda uz klimatiskajām atšķirībām audzēs, kas, iespējams, skaidrojamas ar izteiktāku kontinentalitāti Aucē. Populācijas signāla (EPS) vērtības bija pietiekoši augstas (0.86–0.92), lai raksturotu gadskārtu platumu ietekmējošos faktorus abās analizētajās audzēs (Wigley et al., 1984). Par ārējo faktoru ietekmi liecina izteiktas gadskārtu platuma atšķirības starp gadiem, jutības koeficientam sasniedzot vērtības 0.40–0.42. Vidēji cieša līdz augsta autokorelācija (0.56–0.74) liecina par iepriekšējās augšanas ietekmi uz tekošā gada gadskārtas veidošanos. Sērijām vērojamas arī atsevišķas krasas izmaiņas (gadskārtu platuma samazinājums) 1975., 1989. un 2002. gadā, ko izraisījusi zema gaisa temperatūra rudenī gadu pirms gadskārtas veidošanās, kam sekoja īpaši augsta vidējā mēneša temperatūra laika periodā no decembra pirms gadskārtas veidošanās līdz augustam gadskārtas veidošanās gadā.

Atlikumu sērijas uzrādīja būtisku korelāciju ar 12 no 132 pārbaudītajiem faktoriem, un astoņi no tiem bija būtiski abās audzēs. Ņemot vērā, ka gadskārtas platumu būtiski ietekmē liels skaits faktoru, kas savstarpēji mijiedarbojas, katrs atsevišķs faktors izskaidroja salīdzinoši nelielu daļu no variācijas, un to korelācijas koeficientu vērtības nepārsniedza 0.35. Zemās korelācijas koeficientu vērtības, iespējams, saistītas arī ar faktoru ietekmes stipruma izmaiņām laika gaitā (Cook et al., 1992; Büntgen et al., 2006).

Kopumā papeļu hibrīds *Populus balsamifera* × *P. laurifolia* uzrādīja jutību pret gaisa temperatūru vasaras otrajā pusē (jūlijs–septembris) gan gadskārtas veidošanās gadā, gan gadu pirms tās veidošanās. Šķēdē gadskārtas platumu būtiski ietekmēja arī gaisa temperatūra gadskārtas veidošanās gada februārī, martā un jūnijā, kamēr Aucē – temperatūras amplitūda septembrī. Meteoroloģisko faktoru ietekme gadu pirms gadskārtas veidošanās saistīta ar barības vielu uzkrājuma veidošanu (Barbaroux & Bréda, 2002; Pallardy, 2008), kas noris veģetācijas sezonas beigās un tiek izmantots augšanas uzsākšanai nākamā gada pavasarī (Landhäusser & Lieffers, 2003; Jones et al., 2004; Regier et al., 2010). Paaugstināta gaisa temperatūra veicina evapotranspirāciju (Trajkovic, 2005), kas var izraisīt īslaicīgu ūdens deficītu un radīt sausuma stresu (Pallardy, 2008). Šādos apstākļos tiek traucēta barības vielu veidošana (Regier et al., 2009), iespējams, izskaidrojot arī konstatēto negatīvo saistību starp gadskārtu platumu un augusta PET (3.2. att.). Turklāt karstās vasarās tipiski ir arī samazināts nokrišņu daudzums. Papelēm, līdzīgi kā citām ātraudzīgām lapu koku sugām, raksturīga intensīva evapotranspirācija (Perry et al., 2001), kas palielina ūdens deficītu augsnē, tādējādi nepietiekamas ūdens pieejamības apstākļos pastiprinot sausuma radīto ietekmi.

Tekošā gada meteoroloģisko faktoru ietekme saistīta ar konkrētā brīža barības vielu izmantošanu (Deslauriers et al., 2009), kas ietekmē koksnes veidošanos veģetācijas perioda laikā (Lebourgeois et al., 2005). Paaugstināta gaisa temperatūra
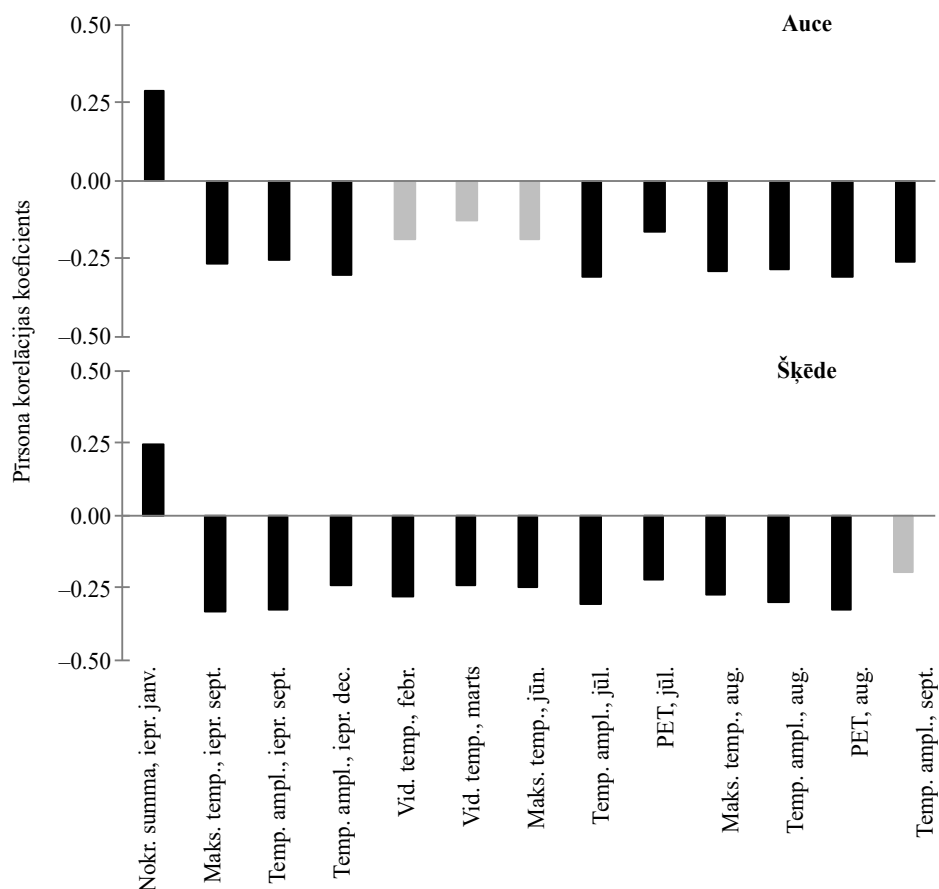
3.2. att. Pīrsona korelācijas koeficienti starp meteoroloģiskajiem faktoriem un gadskārtu platuma atlikuma hronoloģijām Aucē un Šķēdē
Faktori, kas kādā no audzēm nebija būtiski, iekrāsoti pelēki. Parādīti tikai nekolineārie faktori. Nokr. – nokrišņu, iepr. – iepriekšējā gada, Maks. – maksimālā, temp. – temperatūra, ampl. – amplitūda, Vid. – vidējā, PET – potenciālā evapotranspirācija.

var kavēt fotosintēzi (Haldimann & Feller, 2004) un kambija aktivitāti ksiloģenēzes jeb koksnes veidošanās procesā (Oberhuber & Gruber, 2010). Savukārt mēneša gaisa temperatūras amplitūdas negatīvā ietekme augšanas sezonas laikā saistīta ar nepieciešamību mainīgajiem apstākļiem strauji pielāgot koka bioķīmiskos un fizioloģiskos procesus (Pallardy, 2008).

Radiālā pieauguma negatīvā sakarība ar septembra gaisa temperatūru saistīta ar pāreju no aktīvās augšanas uz miera stāvokli, kad papeles ir pakļautas rudens salnu bojājumiem. Savukārt decembrī, kad koki atrodas miera stāvoklī, gaisa temperatūras amplitūdas negatīvā ietekme, visticamāk, saistāma ar salcietības mazināšanās reakciju atkušņu dēļ (Cox & Stushnoff, 2001), pakļaujot kokus spēcīgākai sala ietekmei, temperatūrai atkal krītoties (Hänninen, 2006). Traucēts miera stāvoklis var paātrināt arī barības vielu rezervju izmantošanu intensīvākas elpošanas dēļ (Ögren

et al., 1997). Nokrišņu (parasti – sniega) summa janvārī gadu pirms gadskārtas veidošanās bija vienīgais faktors, kas pozitīvi ietekmēja gadskārtas platumu. Biezāka sniega sega nodrošina labāku termoizolāciju, samazinot augsnes sasalšanas dziļumu un augsnes temperatūras svārstības (Hardy et al., 2001), tādējādi samazinot sakņu mirstību (Tierney et al., 2001) un labvēlīgi ietekmējot ūdens uzņemšanu.

Galveno komponentu analīzē pirmie trīs komponenti bija būtiski (p < 0.01) un kopā izskaidroja 32.1% no kopējās datu variācijas (3.3. att.). Pirmais komponents (PC1) atspoguļoja koku reakciju uz veģetācijas perioda garumu un ūdens pieejamību aktīvās augšanas laikā, kas izpaudās kā būtiskas korelācijas ar gaisa temperatūru septembrī gadu pirms gadskārtas veidošanās (r = 0.36) un nokrišņu summu jūnijā (r = −0.33). Otrais galvenais komponents (PC2) norādīja uz temperatūras ietekmi un korelēja ar gaisa temperatūru tekošā gada februārī un martā (attiecīgi r = 0.38 un r = 0.55), un iepriekšējā gada jūlijā (r = 0.33). Trešais galvenais komponents (PC3) bija saistīts ar koku reakciju uz ūdens deficītu vasaras vidū, korelējot ar gaisa temperatūru, nokrišņu summu un SPEI jūlijā gadu pirms gadskārtas veidošanās (attiecīgi r = 0.32, r = −0.39 un r = −0.30).

Gadskārtu platumu atlikumu hronoloģiju izvietojums pēc pirmā un otrā komponenta veidoja izteiktu sugu grupēšanos koordinātu plaknē (3.3. att.) un norādīja uz dažādu sugu atšķirīgu jutību pret dažādiem klimatiskajiem faktoriem. Arī izvietojums pēc otrā un trešā komponenta vairumam vietējo un introducēto koku sugu veidoja salīdzinoši ciešu punktu mākoni, daļai sugu pārklājoties. Papeļu hibrīdu hronoloģijas abos gadījumos atradās izteikti nomaļus no citu sugu hronoloģijām,
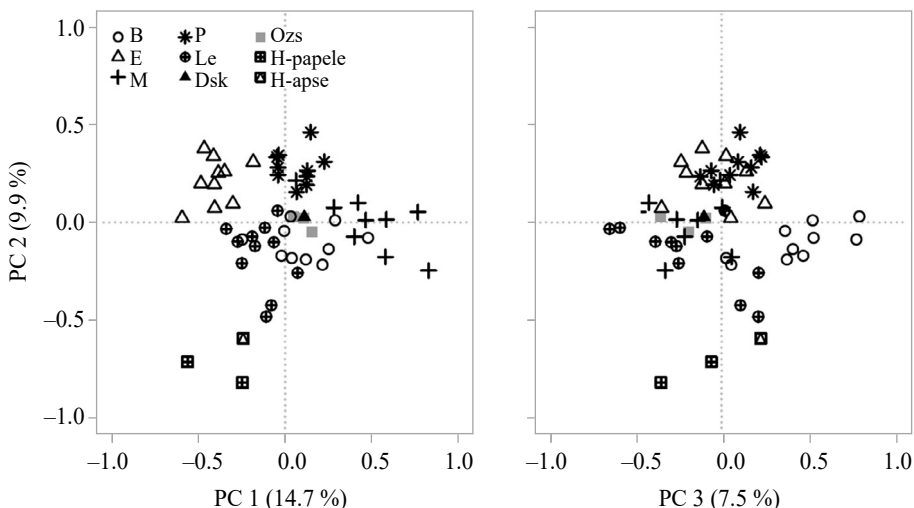
3.3. att. **Gadskārtu platumu atlikumu hronoloģiju (1965–2009) izkārtojums atkarībā no trim galvenajiem komponentiem (PC1, PC2 un PC3)**
Iekavās norādīta katra komponenta izskaidrotā variācijas daļa (%). B – *Betula pendula* Roth, E – *Picea abies* H. Karst., M – *Alnus glutinosa* Gaertn., P – *Pinus sylvestris* L., Le – *Larix decidua* Mill., Dsk – *Fagus sylvatica* L., Ozs – *Quercus rubra* L., H-papele – *Populus balsamifera* L. × *P. laurifolia* Ledeb., H-apse – *Populus tremuloides* Michx. × *P. tremula* L.

norādot uz atšķirīgām gadskārtu platuma variācijas iezīmēm. Iespējams, tas saistīts ar hibridizāciju, kas vecākkoku īpašību kombinācijas dēļ var izraisīt specifisku pēcnācēja – hibrīda – reakciju uz vides apstākļiem (Li et al., 1998).

3.2. Augstuma pieauguma dinamika un tā saistība ar meteoroloģiskajiem faktoriem veģetācijas sezonas laikā

Dažādu papeļu klonu stādījumā Vecumnieki-1 pirmajā augšanas sezonā augstuma mērījumu uzsākšanas brīdī vidējais galotnes dzinumu garums bija sasniedzis 4.0 ± 1.6 cm. Klonam OP42 un "īsajam" klonam Baldo galotnes dzinums bija būtiski (p < 0.05) īsāks (attiecīgi 1.6 un 1.8 cm), savukārt "īsajam" klonam Oudenberg un "garajiem" kloniem Vesten un Oudenberg – būtiski garāks (attiecīgi 11.8, 12.1 un 14.2 cm) nekā vidēji stādījumā.

Vidējais koku augstums pirmās augšanas sezonas beigās bija 81.0 ± 6.8 cm. Tas būtiski (p < 0.001) atšķīrās starp kloniem, un bija no 32 līdz 132 cm (3.4. att.). Vidējais augstums "īsajiem" kloniem bija 69.2 ± 6.9 cm. Kloni Hybride275, Oudenberg un Matrix49 bija būtiski (p < 0.05) augstāki, bet kloni OP42 un LV1 būtiski zemāki par stādījuma vidējo augstumu. Vidējais augstums kloniem, kam izmantoti "garie" spraudeņi, bija 107.9 ± 13.4 cm. Kloni Oudenberg un Vesten bija būtiski (p < 0.05) garāki nekā klons Baldo: augstums pirmās sezonas beigās attiecīgi 131.8, 118.3 un 73.3 cm.

Kloniem Oudenberg un Baldo koku augstumu būtiski (p < 0.001) ietekmēja gan klons, gan spraudeņu garums, bet ne šo faktoru mijiedarbība (p = 0.74; R^2 = 0.75). Klonam Oudenberg augstums rametiem no "garajiem" spraudeņiem bija par 31% lielāks nekā "īsajiem" spraudeņiem: attiecīgi 132 ± 12.0 cm un 101 ± 17.1 cm.
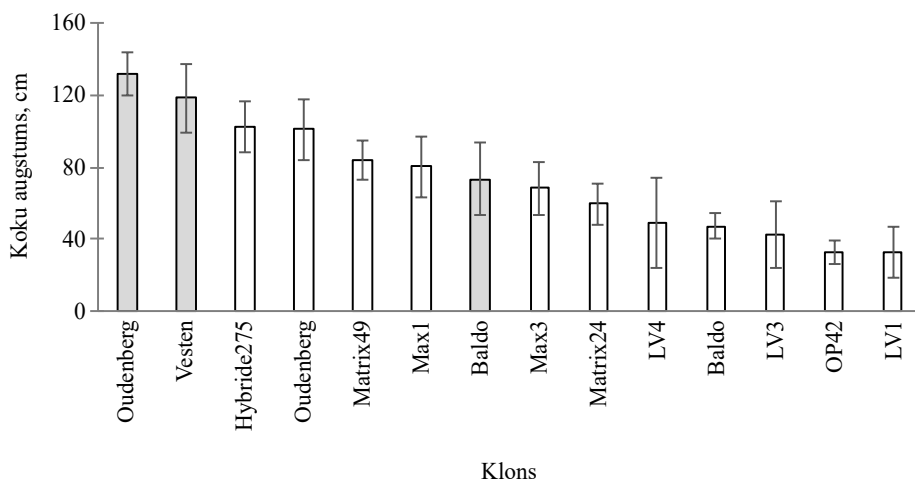

3.4. att. **Papeļu klonu augstums pirmās augšanas sezonas beigās (± ticamības intervāls)**
Baltie stabiņi norāda klonus, kam izmantoti "īsie" (30 cm) spraudeņi, pelēkie stabiņi norāda klonus, kam izmantoti "garie" (50 cm) spraudeņi.

Savukārt klonam Baldo augstums rametiem no "garajiem" spraudeņiem bija par 55% lielāks nekā "īsajiem" spraudeņiem: attiecīgi 73 ± 20.0 cm un 47 ± 7.0 cm. Rezultāti norāda uz garāku spraudeņu pārākumu augstuma veidošanā, kas sakrīt ar citu pētījumu rezultātiem (Burgess et al., 1990; Rossi, 1999; Camp et al., 2012) un, iespējams, saistīts ar lielākām barības vielu rezervēm (Buhler et al., 1998; Marino & Gross, 1998), nodrošinot priekšrocības to augšanai. Piemēram, salīdzinot 20 un 40 cm garu klona Max4 spraudeņu biomasu pēc vienas augšanas sezonas, stumbra un lapu biomasa garo spraudeņu rametiem bija attiecīgi 46.6 ± 3.2 un 47.7 ± 3.3 g sausnes, savukārt īso spraudeņu rametiem attiecīgi 39.5 ± 2.8 un 33.1 ± 1.6 g sausnes (Vigl & Rewald, 2014). Konstatēts, ka kopējā biomasa pēc vienas augšanas sezonas būtiski pozitīvi korelē ar spraudeņa sākotnējo masu (Vigl & Rewald, 2014).

Vidējā augšanas intensitāte visos starpmērījumu posmos bija no 10 līdz 15 mm dienā. Atsevišķiem kloniem (piemēram, OP42, LV1, LV3) augšanas intensitāte nepārsniedza 10 mm dienā, kamēr kloni "garais" Vesten, "īsais" Oudenberg un Hybride275 pārsniedza augstuma pieaugumu 15 mm dienā vismaz divos no starpmērījumu posmiem, norādot uz atšķirīgām augšanas dinamikas stratēģijām (Devine et al., 2010).

Gompertz modeļa asimptotas (maksimālās vērtības) parametrs būtiski (p < 0.05) atšķīrās starp "īso" klonu grupām, lai gan to pieauguma tempa izmaiņu uzsākšanas laiks būtiski neatšķīrās (3.5. att.). Līdz ar to vērojamas būtiskas (p < 0.05) atšķirības pieauguma tempa koeficientam *k* starp klonu grupām "īsie-min" un "īsie-max". Šīs atšķirības liecina, ka kloniem, kas augšanas sezonas beigās sasniedza lielāku augstumu, bija straujāka augšana jūlija sākumā, un tas daļēji varētu būt saistīts ar ģenētiski noteiktām lapu plaukšanas laika atšķirībām (Jansons et al., 2014). Kloniem
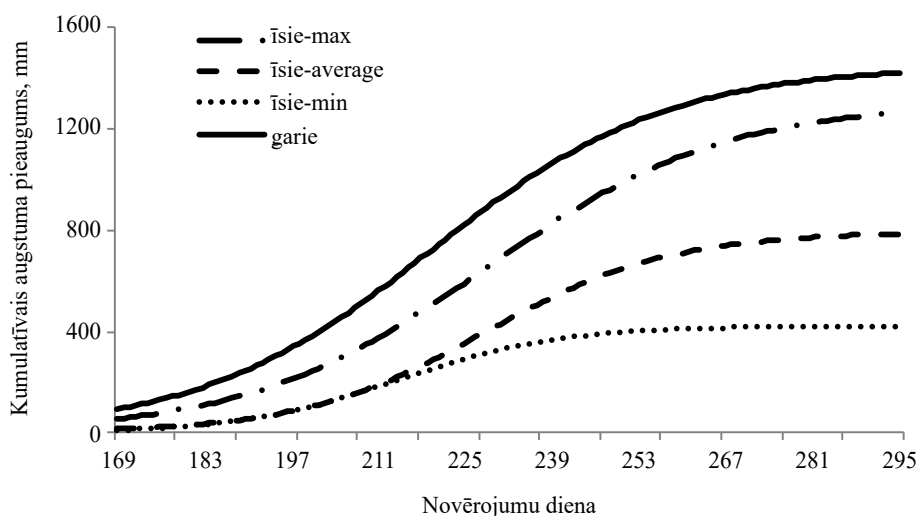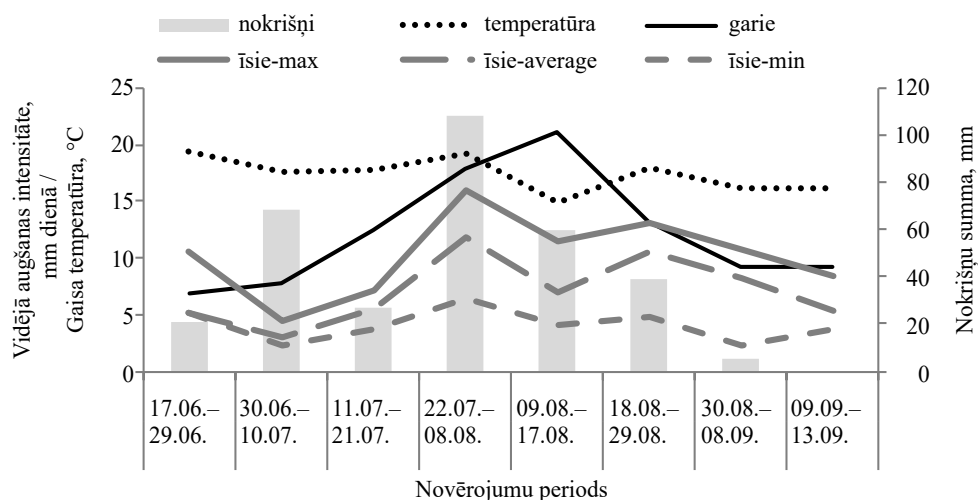

3.5. att. **Aproksimētās Gompertz vienādojuma līknes vidējam augstuma pieaugumam klonu grupām "īsie-max", "īsie-average", "īsie-min" (spraudeņu garums 30 cm) un "garie" (spraudeņu garums 50 cm)**

no grupas "īsie-max" un "garie" atšķirības starp visiem modeļa parametriem (α, β, k) nebija statistiski būtiskas.

Augšanas intensitāte uzrādīja vidēji ciešu (p > 0.05, r = 0.60) pozitīvu korelāciju ar nokrišņu daudzumu, bet vāju (p > 0.05, r = 0.17) korelāciju ar gaisa temperatūru (3.6. att.). Līdzīgi, arī Chhin (2010) konstatējis izteiktāku nokrišņu ietekmi uz papeļu pieaugumu, salīdzinot ar dažādiem gaisa temperatūras rādītājiem. Otrajā novērojumu periodā (30.06.–10.07.) vidējā gaisa temperatūra pazeminājās no 19.3 uz 17.6 °C, izraisot augšanas intensitātes samazināšanos vidēji par 2.2 mm dienā. Maksimālā augstuma pieauguma intensitāte bija 12.7 mm dienā, un tā sasniegta jūlija beigās (22.07.–08.08.), periodā ar lielāko nokrišņu daudzumu (108 mm). Augšanas intensitāte ceturtajā novērojumu periodā uzrādīja ievērojamas atšķirības starp kloniem, un bija no 4.6 mm dienā klonam LV1 līdz 18.5 mm dienā "garajam" klonam Oudenberg. Netipiskas gaisa temperatūras un nokrišņu daudzuma izmaiņas konstatētas augusta vidū (09.08.–17.08.), kad šie rādītāji saruka attiecīgi līdz 14.9 °C un 60 mm, izraisot augšanas intensitātes samazināšanos līdz vidēji 10.2 mm dienā. Kloni, kas novērojumu perioda beigās bija sasnieguši lielāko augstuma pieaugumu ("garie" Vesten un Oudenberg), turpināja augšanu arī šajā (09.08.–17.08.) periodā, kamēr pārējie kloni to samazināja (3.6. att.). Līdzīga ātraudzīgo klonu noturība pret meteoroloģisko faktoru izmaiņām novērota hibrīdam *Populus tremuloides* × *P. tremula* (Jansons et al., 2014). Nākamajā novērojumu periodā (18.08.–29.08.) gaisa temperatūra atkal pieauga, tomēr augšanas intensitāte palika gandrīz nemainīga (10.3 mm dienā). Turpmākajos novērojumu periodos gan gaisa temperatūra un nokrišņu daudzums, gan augšanas intensitāte pakāpeniski samazinājās.

Lai gan korelācijas starp augšanas intensitāti un vērtētajiem meteoroloģiskajiem faktoriem nebija statistiski būtiskas, temperatūras ietekme uz augšanu

3.6. att. **Vidējā augšanas intensitāte klonu grupām "īsie-max", "īsie-average", "īsie-min" (spraudeņu garums 30 cm) un "garie" (spraudeņu garums 50 cm) atkarībā no perioda vidējās gaisa temperatūras un nokrišņu summas**

izpaudās kā ievērojamas augšanas intensitātes izmaiņas starp periodiem ar straujām temperatūras izmaiņām (3.6. att.), t.i., starp trešo un ceturto, ceturto un piekto, kā arī sesto un septīto novērojumu periodu, kas saistītas ar papeļu spēju strauji reaģēt uz vides signāliem (Rohde et al., 2011).

3.3. Augstuma pieauguma starpgadu dinamika

Skrīveru stādījumā divu gadu vecumā lielāko augstumu uzrādīja kloni AF6, LV3 un LV12: attiecīgi 159.5 ± 10.5, 154.3 ± 14.2 un 143.9 ± 8.5 cm (3.7. att.). Konstatētas būtiskas atšķirības starp dažādu klonu augstumu (p < 0.01); būtiski lielāks koku augstums bija klonam AF6, bet būtiski mazāks – kloniem POP1, POP2 un POP6. Kaut arī pēc pirmās augšanas sezonas daudziem kloniem to dzinumus pilnībā bija nopostījuši briežu dzimtas dzīvnieki, tomēr vairumam no tiem divu gadu vecumā netika konstatētas būtiskas augstuma atšķirības no kloniem AF2, AF8 un AF7, ko dzīvnieki nebija bojājuši. Straujā ataugšana, iespējams, saistīta ar jau izveidotu sakņu sistēmu (Christersson, 1986), un attiecīgi veicina lielāku otrās rotācijas ražību, salīdzinot ar ražību stādījumu ierīkošanas gadā (Dillen et al., 2013).

Kalsnava-1 stādījumā klonu augstums viena gada vecumā bija no 51 ± 8 līdz 124 ± 5 cm dzīvajiem kokiem (V; 3.8. att.) un no 37 ± 9 līdz 159 ± 25 cm nebojātajiem kokiem. Konstatēta cieša, būtiska korelācija starp dzīvo un nebojāto koku augstumu (rho = 0.82, p < 0.001). Atsevišķiem kloniem bojājumi ievērojami ietekmēja to augstumu: klonam AF16 nebojātie koki bija par 28% īsāki nekā dzīvie koki, savukārt klonam LV3 nebojātie koki bija par 39% garāki nekā dzīvie koki.

Abos stādījumos visos salīdzinātajos vecumos augstuma atšķirības starp kloniem bija būtiskas (visi p < 0.001; 3.7. un 3.8. att.), un tās palielinājās līdz ar vecumu. Skrīveru stādījumā divu gadu vecumā konstatēti 80 būtisko atšķirību pāri, trīs gadu vecumā šis skaits pieauga līdz 124, un četru gadu vecumā līdz 169, savukārt
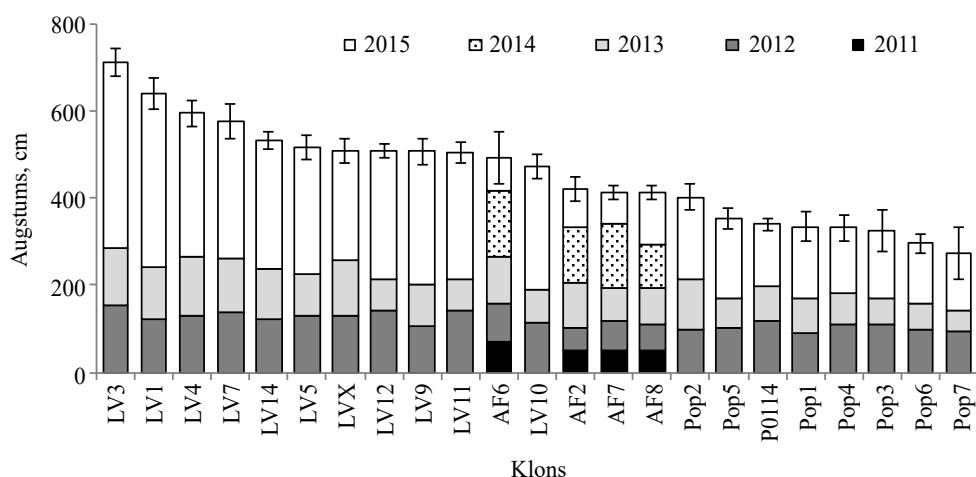
3.7. att. **Klonu augstums viena (2011), divu (2012), trīs (2013), četru (2014) un piecu (2015; ± 95% ticamības intervāls) gadu vecumā**

Kalsnava-1 stādījumā augstuma atšķirība starp augstāko un zemāko klonu pieauga no 2.4 reizēm viena gada vecumā līdz 2.9 reizēm trīs gadu vecumā. Kaut arī Kalsnava-1 stādījumā konstatēta būtiska korelācija starp klona augstuma mērījumiem viena un trīs gadu vecumā (rho = 0.61, p < 0.001), tomēr ir kloni, kas ievērojami mainījuši savu rangu (3.9.a. att.). Tas saistīts ar atšķirīgu augšanas dinamiku, ko ietekmē klonu
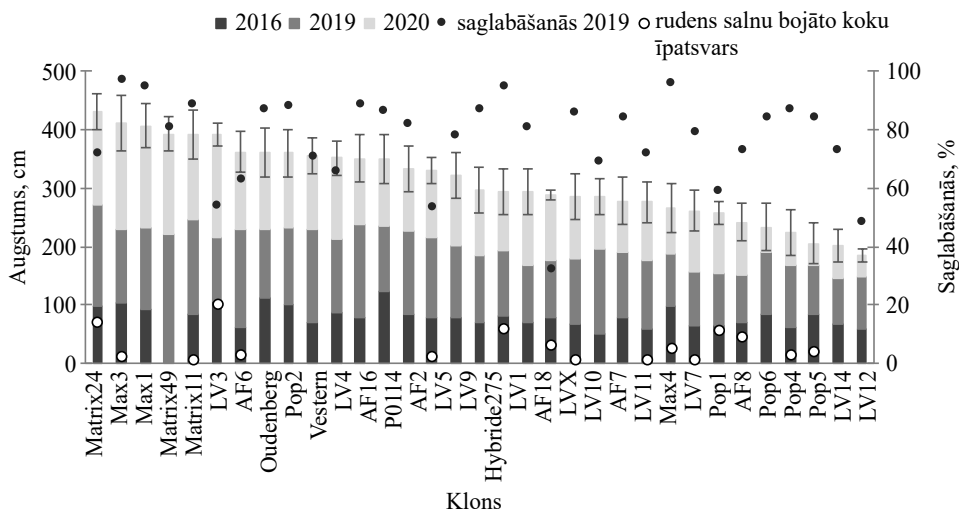
3.8. att. Klonu augstums viena (2016), trīs (2019) un četru (2020; ± 95% ticamības intervāls) gadu vecumā un saglabāšanās (2019) trīs gadu vecumā
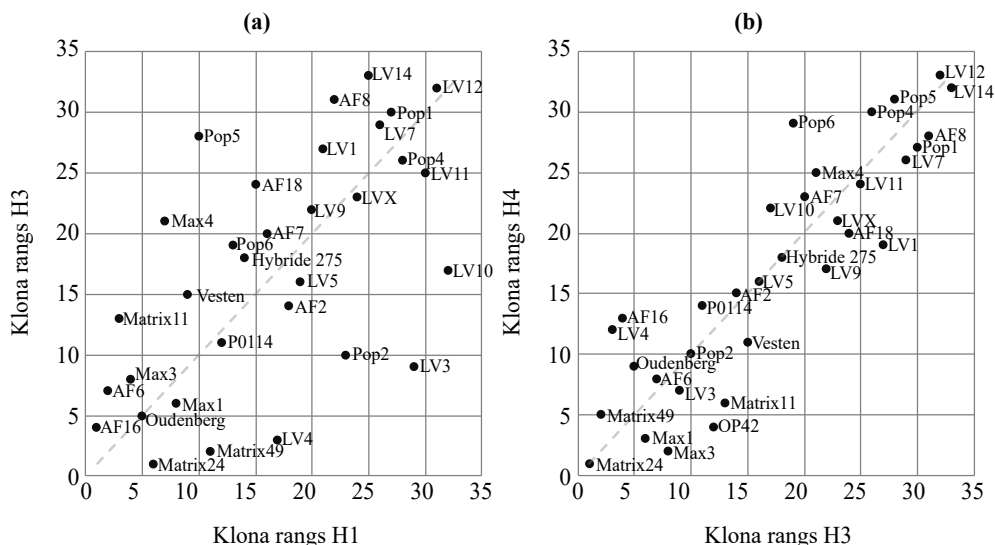
3.9. att. Klonu augstuma rangu atšķirības starp (a) viena (H1) un trīs (H3) gadu vecumu un (b) trīs (H3) un četru (H4) gadu vecumu
Pārtrauktā līnija norāda nemainīgu ranga pozīciju. Kloni virs pārtrauktās līnijas ir ieguvuši zemāku rangu, un kloni zem pārtrauktās līnijas ir ieguvuši augstāku rangu.

alometrija (Karačić et al., 2021) un spēja apsakņoties (Zalesny et al., 2005; Zhao et al., 2014). Četru gadu vecumā atšķirība starp augstāko un zemāko klonu bija nedaudz mazāka, un korelācija starp klona augstumu trīs un četru gadu vecumā – ciešāka nekā iepriekšējā periodā (rho = 0.90, p < 0.001). Turklāt klonu rangi starp trīs un četru gadu vecumu (maksimālā atšķirība: 10 pozīcijas klonam Pop6; 3.9.b att.) bija mainījušies mazāk nekā starp viena un trīs gadu vecumu (maksimālā atšķirība: 20 pozīcijas klonam LV3; 3.9.a att.).

3.4. Rudens salnu un ziemas sala bojājumu raksturojums un to saistība ar koku augstuma pieaugumu

Kalsnava-2 stādījumā 65.4% koku rudens salnu bojājumu vērtēšanas brīdī bija aktīvās augšanas fenoloģiskajā fāzē. Trim kloniem visi rameti atradās miera stāvoklī, 10 kloniem visi rameti bija aktīvās augšanas stāvoklī, bet sešiem kloniem rameti bija gan miera, gan aktīvās augšanas stāvoklī (3.10.a att.). Būtiskās (p < 0.01) fenoloģiskā stāvokļa atšķirības starp kloniem skaidrojamas ar vidēju līdz stipru ģenētikas ietekmi uz papeļu pumpuru veidošanu (Howe et al., 2000; Christersson, 2006; Hall et al., 2007; Friedman et al., 2008; Rohde et al., 2011).

Starp kloniem, kas atradās aktīvās augšanas stāvoklī, lapu bojājumi konstatēti 81% koku (3.10.b att.). Četriem kloniem (LV3, LV7, LVX un OP42) bija vairāk nekā 80% rametu ar bojātu lielāko daļu lapu (balle 4_L). Klons LV4 uzrādīja visaugstāko sala noturību ar 76% rametu bez salnu bojājuma pazīmēm (balle 1_L).

Stumbram salnu bojājumi konstatēti retāk nekā lapām (3.10.c att.). Starp miera stāvoklī esošajiem kokiem tikai klonam LV3 bija viens ramets ar atsevišķiem zaru bojājumiem (balle 2_{ST}), savukārt starp aktīvās augšanas stāvoklī esošajiem kokiem kloniem Matrix24 un LV14 bija attiecīgi 87% un 100% rametu ar atsevišķiem zaru bojājumiem (balle 2_{ST}). Tikai vienam kokam (klons LV3) konstatēti bojājumi vairāk nekā ⅓ daļai stumbra (balle 4_{ST}). Iegūtie rezultāti apstiprina, ka koki, kas pumpurus veido vēlāk rudenī, ir uzņēmīgāki pret salnu bojājumiem (Junttila & Kaurin, 1990; Howe et al., 2000).

Kalsnava-1 stādījumā pēc 2016. gada rudens salnām (otrās augšanas sezonas sākumā) rudens salnu bojājumi novēroti 16 no 33 kloniem (3.11. att.). Vairumam klonu bojāti tikai atsevišķi rameti (bojāto koku īpatsvara mediāna bija 4%), bet kloni no krustojuma *P. maximowiczii × P. trichocarpa* bija jutīgāki pret rudens salnām nekā citi: klonam Hybride275 bojāti 12%, klonam Matrix24 – 14%, un klonam Matrix11 – 20% rametu.

Kalsnava-2 stādījumā individuālu koku līmenī koku vecums būtiski (p < 0.01) ietekmēja salnu bojājumus lapām, bet ne stumbram (p > 0.05). Būtiskas (p < 0.01) atšķirības konstatētas arī starp kloniem vienādā vecumā. Kloniem LV4 un LV11 visi rameti atradās aktīvās augšanas stāvoklī neatkarīgi no vecuma. Arī klonam LV12 visi divgadīgie un vairums (87%) viengadīgo rametu bija aktīvās augšanas stāvoklī. Šiem trim kloniem konstatētas būtiskas (p < 0.01) lapu bojājumu atšķirības dažāda vecuma rametiem. Kloniem LV4 un LV11 visi divgadīgie rameti bija bez bojājumiem (balle 1_L), kamēr starp viengadīgajiem rametiem konstatēti gan koki ar bojātām
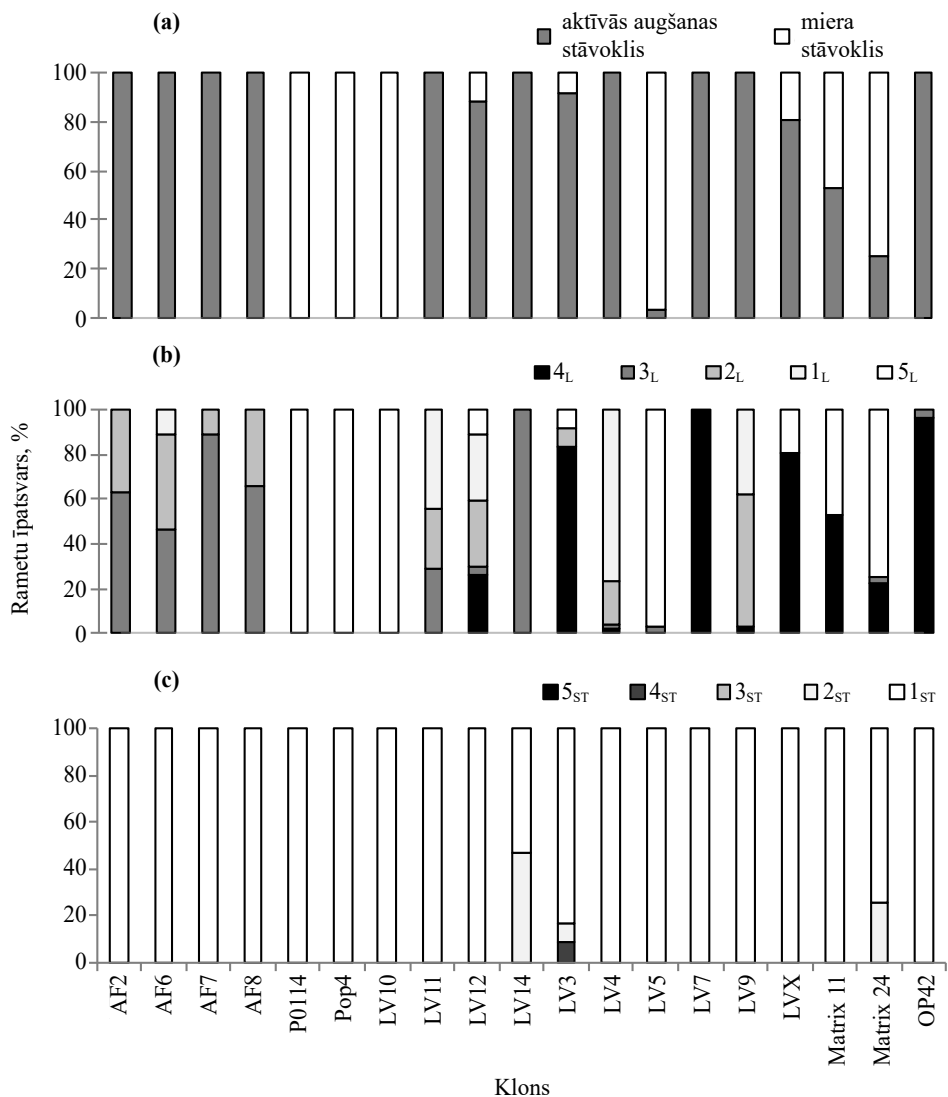
3.10. att. **Rametu īpatsvars (a) fenoloģiskā stāvokļa, (b) lapu un (c) stumbra bojājumu vērtējuma ballēs**

Lapu salnu bojājumu vērtējums: 1_L – bez vizuāliem bojājumiem, 2_L – atsevišķas bojātas lapas, 3_L – bojāta lielākā daļa tekošā gada dzinuma lapu, 4_L – bojāta lielākā daļa lapu, 5_L – koki miera stāvoklī. Stumbra salnu bojājumu vērtējums: 1_{ST} – bez vizuāliem bojājumiem, 2_{ST} – atsevišķi zaru bojājumi, 3_{ST} – atsevišķi stumbra bojājumi, 4_{ST} – bojāta vairāk nekā ⅓ daļa stumbra, 5_{ST} – pilnībā bojāts stumbrs.
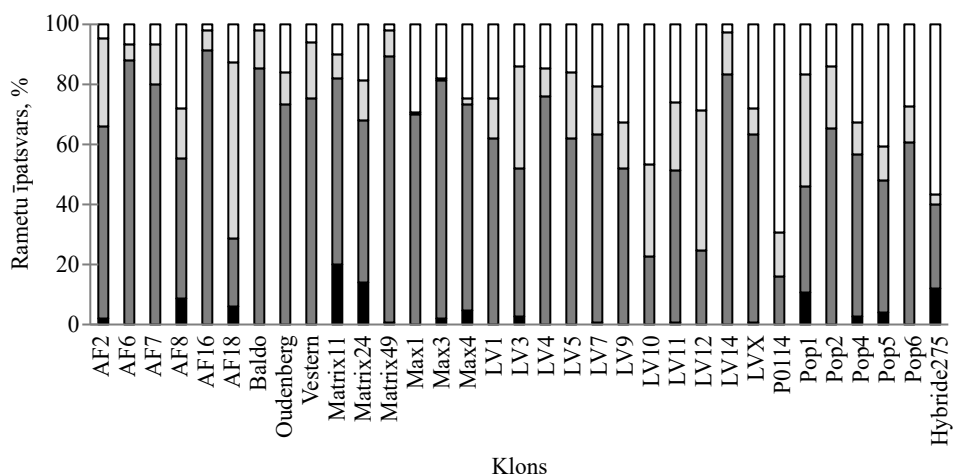
3.11. att. Bojāto rametu īpatsvars pēc pirmās augšanas sezonas
Salikto stabiņu krāsa: melns – rudens salnu bojātie koki, tumši pelēks –
dzīvnieku bojātie koki, gaiši pelēks – bojā gājušie koki, balts – nebojātie koki.

atsevišķām lapām, gan ar bojātu lielāko daļu no tekošā dzinuma lapām (balles
2_L un 3_L). Savukārt klonam LV12 vairums divgadīgo rametu bija bojāta lielākā
daļa lapu (balle 4_L), bet viengadīgajiem rametiem konstatēti mazāki bojājumi
(balles 3_L un 4_L).

Rudens salnu bojājumiem nav konstatēta negatīva ietekme uz saglabāšanos
(rho = 0.53, p < 0.001). Koka augstumam nebija saistības ar salnu izraisītiem lapu
bojājumiem (p > 0.05), bet abos Kalsnavas stādījumos novērota saistība starp
koku augstumu un salnu izraisītiem stumbra bojājumiem. Kalsnava-2 stādījumā šī
sakarība galvenokārt skaidrojama ar klonu LV14 un LV3 rādītājiem: relatīvi augsti
kloni, kam stumbra bojājumi konstatēti attiecīgi 46.5% un 16.6% koku. Kalsnava-1
stādījumā augstums klonu līmenī nebija saistīts ar rudens salnu bojāto koku
īpatsvaru (rho = 0.42, p > 0.05), bet salnu bojātie koki bija būtiski (p < 0.001)
augstāki nekā nebojātie koki: attiecīgi 105.3 ± 7.9 un 72.0 ± 2.5 cm. Ievērojamās
augstuma atšķirības liecina, ka ātraudzīgāki koki ir jutīgāki pret salnām augšanas
sezonas beigās, jo, izmantojot garāku veģetācijas periodu, neuzsāk laicīgi gatavoties
miera periodam, t.sk. pazeminātai gaisa temperatūrai (Pliura et al., 2014).

Rudens salnu bojāto koku īpatsvaram nav konstatēta sakarība ar ziemas
sala vērtējumu (3.12. att.). Pretēji novērotajam rudens salnu bojājumu gadījumā,
kloniem ar ziemas sala bojājumiem bija mazāks augstums (3.13. att.) un zemāka
saglabāšanās (rho = 0.47, p < 0.01) nekā ziemas sala nebojātiem kokiem. Kloniem
ar stipriem ziemas sala bojājumiem (vērtējuma balle 1) saglabāšanās trīs gadu
vecumā bija 32%, vidēji stipri bojātiem kloniem (vērtējuma balle 2) – 72%, kloniem
ar nelieliem bojājumiem (vērtējuma balle 3) – 78%, un vizuāli nebojātiem kloniem
(vērtējuma balle 4) – 85%. Šī sakarība saistīta ar koksnes parametriem – ksilēmas
vadaudu izmērs ir atkarīgs no koka dimensijām, un tas ietekmē koka sala noturību
(Schreiber et al., 2013).
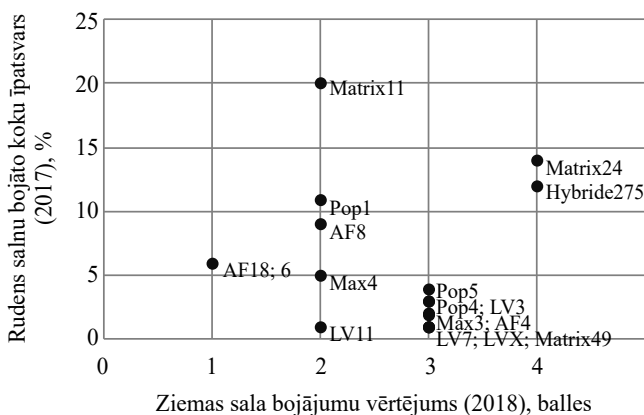
3.12. att. Rudens salnu (vērtēti 2017. gada pavasarī) bojāto koku īpatsvars un ziemas sala bojājumu vērtējums (vērtēti 2018. gada pavasarī)
Ziemas sala bojājumi vizuāli vērtēti piecu ballu skalā: 0 – gājis bojā, 1 – stipri bojāts,
2 – vidēji stipri bojāts, 3 – nelieli bojājumi, 4 – vizuāli nebojāts.
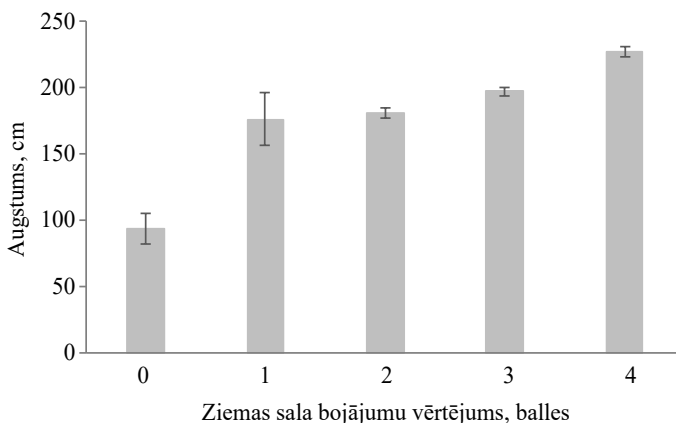
3.13. att. Koku augstums trīs gadu vecumā atkarībā no ziemas sala bojājumu vērtējuma
Ziemas sala bojājumi vizuāli vērtēti piecu ballu skalā: 0 – gājis bojā, 1 – stipri bojāts,
2 – vidēji stipri bojāts, 3 – nelieli bojājumi, 4 – vizuāli nebojāts.

Rezultāti liecina par iespēju atlasīt ātraudzīgus klonus ar labu sala noturību (piemēram, kloni Max1, Max3 un Matrix49; 3.8. att.). Savukārt, citi kloni (piemēram, Matrix24 un Matrix11), kaut arī cietuši no rudens salnu izraisītiem bojājumiem, tomēr bija starp augstākajiem, t.i., to ātraudzība kompensēja nepietiekamo noturību pret salnām. Kloni no sugu krustojuma *P. maximowiczii* × *P. trichocarpa* arī citos pētījumos saglabājuši pozīciju starp augstākajiem kokiem, neskatoties uz ievērojamu galvenā dzinuma augstuma samazinājumu salnu dēļ (Gudynaitė-Franckevičienė et al., 2020). Kopumā vietēji atlasīto papeļu klonu sala noturība nenodrošina lielāku augstumu, salīdzinot ar salnās bojātajiem ātraudzīgākajiem introducētajiem kloniem.

3.5. Atvašu veidošana pēc rudens salnu bojājumiem

Pirms rudens salnu bojājumiem (pirmās augšanas sezonas beigās) stādījumā Vecumnieki-2 (2.1. att.) 49% koku bija izveidojuši vienu stumbru, 31% – divus, 10% – trīs un 10% – četrus vai vairāk stumbrus. Koku augstums bija no 10 līdz 251 cm (vidēji 118 ± 1.18 cm). Koki ar vienu stumbru bija būtiski (p < 0.001) augstāki nekā koki, kas bija veidojuši vairāk nekā vienu stumbru, vidējais garākā stumbra augstums attiecīgi 121 ± 2.5 un 114 ± 2.6 cm (3.14. att.). Vidējais caurmērs pie saknu kakla bija 6.6 ± 0.32 mm, un koki ar lielāku stumbru skaitu bija tievāki (3.14. att.). Vidējais caurmērs kokiem ar vienu un diviem stumbriem bija līdzīgs (p > 0.05, attiecīgi 7.1 ± 0.48 un 7.0 ± 0.49 mm), un tie bija būtiski resnāki nekā koki ar trim vai vairāk stumbriem (attiecīgi 4.9 ± 1.0 un 4.0 ± 0.73 cm).

Pēc 2015. gada rudens salnām visiem kokiem konstatēta pilnībā nokaltusi virszemes daļa. Novērtējot atvašu veidošanos jūnijā, jaunu dzinumu augšana no augsnes virskārtas līmeņa konstatēta 19.6% koku. Pētījumi liecina, ka papeles labi veido atvases, un otrās rotācijas biomasa tipiski pārsniedz pirmās (ierīkošanas) rotācijas ražību, un virszemes daļas nogriešana neatstāj negatīvu ietekmi uz spraudeņu saglabāšanos (Laureysens et al., 2003, 2005; Dillen et al., 2013; Verlinden et al., 2015). Tomēr jāņem vērā, ka šajā gadījumā virszemes biomasa nevis nogriezta, bet nokaltusi sala radītu bojājumu dēļ, kas, iespējams, ietekmējis arī saknu sistēmas vitalitāti.

Neatkarīgi no iepriekšējās sezonas stumbru skaita koki, kas veidoja atvases, iepriekšējā augšanas sezonā bijuši nedaudz, tomēr statistiski būtiski (p < 0.001)
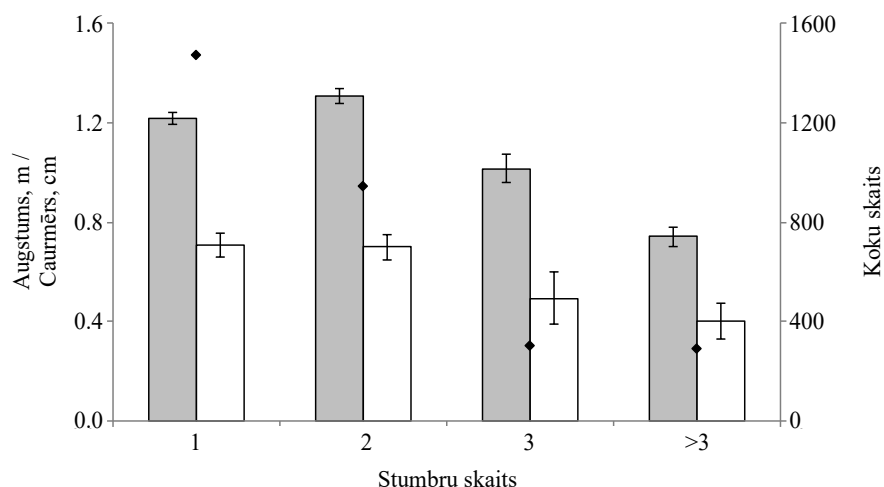
3.14. att. Vidējais augstums (pelēkie stabiņi), caurmērs (baltie stabiņi) pie saknu kakla (± 95% ticamības intervāls) un koku skaits (punkti) atkarībā no koka stumbru skaita pēc vērtēšanas pirmās sezonas beigās
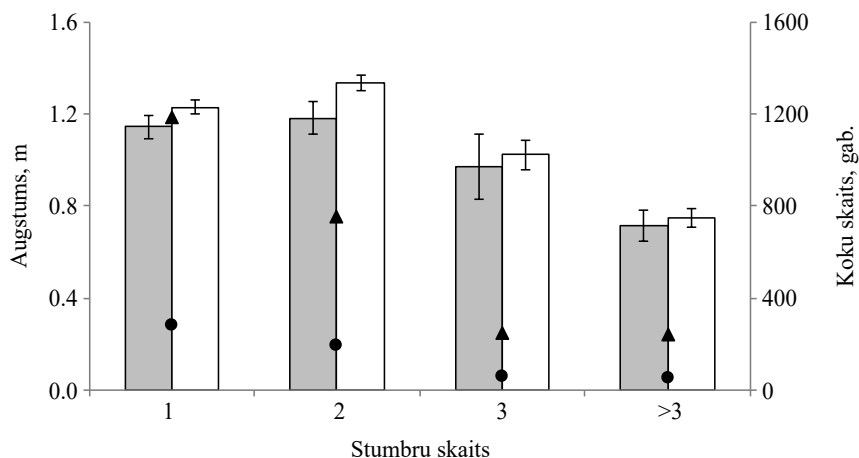
3.15. att. **Vidējais augstums (stabiņi; ± 95% ticamības intervāls) un skaits (simboli) kokiem ar atvasēm (pelēkie stabiņi un punkti) un bez atvasēm (baltie stabiņi un trijstūri) atkarībā no stumbru skaita iepriekšējā sezonā pēc pirmās vērtēšanas**

zemāki nekā koki, kas neveidoja atvases, attiecīgi 110 ± 3.9 un 119 ± 2.0 cm (3.15. att.). Pētījumi liecina, ka tas saistāms ar koksnes strukturālajām īpašībām – koku augstums ir pozitīvi saistīts ar vadaudu diametru (Martínez-Cabrera et al., 2011), kas ir galvenais parametrs, kas nosaka koka jutību pret embolismu (Sperry & Sullivan, 1992). Augi visefektīvāk nodrošina vadītspēju, veidojot nelielu skaitu platu un garu vadaudu (Sperry et al., 2008), kamēr pret embolismu noturīgāki ir koki ar daudz smalkiem vadaudiem (Davis et al., 1999).

Atvases veidojošo koku īpatsvars kokiem ar iepriekšējā sezonā novērotu vienu, diviem, trim vai vairāk stumbriem nebija būtiski atšķirīgs ($p = 0.89$), attiecīgi 19.4%, 20.1%, 20.0% un 18.2%. Būtiskas ($p = 0.006$) atvases veidojošo koku īpatsvara atšķirības konstatētas starp kokiem ar dzīvnieku radītiem bojājumiem (12.6%) un kokiem bez šādiem bojājumiem (20.1%). Lai gan atvases veidojošo koku īpatsvars būtiski ($p < 0.001$) atšķīrās starp rindām, nav konstatēta sakarība ($p > 0.90$) starp atvases veidojošo koku īpatsvaru rindā un vidējo augstumu tajā. Arī telpiskais atvases veidojošo koku izkārtojums bija nejaušs ($p > 0.05$).

Atkārtotajā novērtējumā jūlijā atvases veidojošo koku īpatsvars bija pieaudzis līdz 44.0%. Saistība ar iepriekšējā gada augstumu neatkarīgi no stumbru skaita saglabājās līdzīga kā jūnijā veiktajā novērtējumā: atvases veidojošie koki iepriekšējā sezonā bijuši būtiski ($p < 0.001$) zemāki nekā koki, kas atvases neveidoja, attiecīgi 111 ± 4.6 un 123 ± 4.5 cm.

SECINĀJUMI

1. Papeļu radiālo pieaugumu negatīvi ietekmē sausuma stress vasaras periodā, ko raksturo paaugstināta gaisa temperatūra un samazināts standartizētais nokrišņu evapotranspirācijas indekss. Tāpat to negatīvi ietekmē gaisa temperatūras amplitūda decembrī, ietekmējot/traucējot koka fizioloģiskos procesus miera stāvoklī. Klimata pārmaiņu kontekstā piemērotu klonu atlasē nepieciešams iekļaut klonus ar mazāku jutību pret šiem meteoroloģiskajiem faktoriem.

2. Augstuma pieaugumu būtiski ietekmē gan klons, gan spraudeņa garums. Garāki spraudeņi nodrošina straujāku sākotnējo augšanu: izmantojot 50 cm garus spraudeņus, koku augstums pirmā veģetācijas perioda beigās bija par 31–55% lielāks nekā izmantojot 30 cm garus spraudeņus. Ātraudzīgākajiem kloniem raksturīgs augstāks fenotipiskais plastiskums, t.i., mazāka jutība pret sezonas meteoroloģisko faktoru svārstībām.

3. Rudens salnu izraisīti galotnes bojājumi novēroti ātraudzīgākajiem kokiem (kokiem ar salnu bojājumiem augstums bija būtiski lielāks nekā kokiem bez šādiem bojājumiem). Ziemas sala bojājumi novēroti augšanā atpaliekošajiem kloniem, un saglabāšanās trīs gadu vecumā bija no 32% kloniem ar nozīmīgiem ziemas sala bojājumiem līdz 85% vizuāli nebojātiem kloniem.

4. Izšķiroši ir izmantot Latvijas klimatam piemērotus klonus. Koki ar salnu dēļ nokaltušu virszemes daļu var veidot atvases, bet to augšana uzsākas novēloti: jūnija sākumā atvases konstatētas 20% koku, un jūlija vidū – 44% koku.

5. Ir iespējams atlasīt ātraudzīgus klonus ar labu rudens salnu un ziemas sala noturību un saglabāšanos. Par to liecina no selekcija viedokļa pozitīvas vai nebūtiskas klonu vidējo vērtību (ģenētiskās) korelācijas starp ātraudzību un pārējām pazīmēm.

PRIEKŠLIKUMI

Stādījumu ierīkošanai rekomendējams izmantot klonus Matrix49, Max1 un Max3, kam raksturīga laba augšana un saglabāšanās, kā arī zems salnu un sala bojājumu risks. Papeļu stādījumus ieteicams ierīkot rudens salnu maz apdraudētās platībās.

Populus balsamifera × *P. laurifolia* klona tekošais vidēji periodiskais radiālais pieaugums kulminē 10 līdz 15 gadu vecumā un izlīdzinās pēc 25 līdz 30 gadu vecuma. Rekomendējams turpināt pētījumus optimāla aprites cikla garuma noteikšanai.

Atziņas par papeļu jutību pret sausuma stresu vasaras periodā, rudens salnām un ziemas salu izmantojamas sākotnējās klonu piemērotības pārbaudēs kontrolētos apstākļos.

PATEICĪBAS

1. GENERAL DESCRIPTION

1.1. The topicality of the theme

Forestry is challenged by the global demand for sustainable renewable resources. Fast-growing tree species are highly productive and pose the potential to increase roundwood and energy wood production outside the forest land (Mola-Yudego et al., 2017). This helps to increase the sequestrated CO_2 within the wood and replace the use of fossil resources, hence mitigating the climate change (Sulaiman et al., 2020) and reducing wood extraction pressure on natural forests (Pawson et al., 2013). In Northern Europe, poplars (*Populus* spp.) and their hybrids are among the most productive tree species (Tullus et al., 2013). In this region, a vast number of clones are introduced (Karačić et al., 2003; Christersson, 2006; Karačić & Weih, 2006) for biomass and roundwood production at the rotation length of 5 to 10 or 20 to 30 years, respectively (Tullus et al., 2012).

The productivity of poplar plantations is mainly determined by selected clones. The productivity of poplar plantations is mainly determined by the selected clones. Poplars have a wide genetic material basis and are easily propagated vegetatively, obtaining precise 'copies' of the mother tree with the desired characteristics. However, a limited number of clones are commercially used in Europe, mostly establishing monoclonal plantations. In Denmark (Stener & Westin, 2017) and Sweden (Karačić et al., 2021), the most popular clone is OP42, in Southern Europe— clone I-214 (FAO, 2016). Currently, an active poplar breeding program and 16 clones for commercial use are registered in Sweden (Stener & Westin, 2017), while other Northern European countries rely on planting material that is imported from more southern regions, mainly from Italy and Germany (Niemczyk et al., 2018).

Climate is among the main factors that determined tree growth (Lindner et al., 2010). Significant effect of meteorological factors on the growth of *Populus* clones is observed during the vegetation period (intra-annual) (Yu et al., 2001; Tullus et al., 2012) as well as in long term (inter-annual), including meteorological factors during dormancy. Crossing (hybridization) of species and hybrids alters genetically set adaptive traits (Gudynaitė-Franckevičienė et al., 2020). The high productivity of *Populus* hybrids is linked to their ability to use longer vegetation periods compared to their parental species (Yu et al., 2001), and most of the hybrids could be grown outside the natural range of their parental species (Sykes & Prentice, 1996). Clones that are transferred northward from their parental species origin should be suitable to an altered length of the vegetation period that can delay growth cessation (Li et al., 2002; Ingvarsson et al., 2006; Kalcsits et al., 2009), hence posing risk to frost damage (Ferm et al., 1989; Christersson, 1996, 2006; Ilstedt, 1996; Telenius, 1999; Karačić et al., 2003; Pliura et al., 2014). Although the highest risk of frost damage occurs during the transition from active growth to dormancy (Charrier et al., 2015),

clones that are transferred northward should be also adapted to low temperatures and freeze-thaw cycles during the winter season (Schreiber et al., 2013). The insufficient suitability of the introduced species and hybrids to climate is among the main challenges for the wider use of poplars in Northern Europe (Schreiber et al., 2013; Gudynaitė-Franckevičienė et al., 2020; Karačić et al., 2021), underlying the importance of the clonal testing before their recommendations for commercial use (Pliura et al., 2014).

The effect of frost damage is complex—they decrease tree vitality and increase mortality (Cunti et al., 1991; Diamandis & Koukos, 1992; Pliura et al., 2014), reduces stem quality by increased formation of double leaders, crooks, and cracks (Verwijst et al., 1996; Christersson, 2006), and the dead tops reduce tree height. However, studies have shown that the productivity of the northward transferred species and hybrids outweighs potential frost-related risks (Schreiber et al., 2013; Pliura et al., 2014).

1.2. Aim of the thesis

The thesis aimed to identify poplar clones suitable for growing in Latvia.

1.3. Thesis objectives

Three research objectives have been advanced:
1. To characterize the sensitivity of poplar radial and height growth on meteorological factors.
2. To assess the effect of planting material and clone on poplar height growth.
3. To assess the effect of autumn and winter frost damage on poplar growth.

1.4. Thesis statements

Thesis statements:
1. The drought stress during the growing season negatively affects poplar radial growth.
2. The negative relation between tree height growth and frost damage differs for various clones.

1.5. Scientific novelty

For the first time, the retrospective analysis of the meteorological factors affecting the long-term growth of the poplar clones was analyzed in the European hemiboreal forest zone. For the first time in the Baltic States, the effect of autumn and winter frost damage on poplar survival and growth was assessed. For the first time in Latvia, new information of the largest set of poplar clones with different origins and the suitability of different lengths of the poplar cuttings were obtained.

2. MATERIALS AND METHODS

The study was done in two poplar stands near Auce and Šķēde, and five plantations on former agricultural land near Skrīveri, Vecumnieki, and Kalsnava (Fig. 2.1). In total, 36 clones with different origins from the sections *Aigeiros* and *Tacamahaca* are represented (Table 2.1). Clones from Italy, Belgium, Germany, Sweden, and the Netherlands were introduced into Latvia 10–15 years ago. Clones originating in Latvia are progenies (cuttings) from poplars that have remained from introduction around the 1960s (Saliņš, 1971). Hybride275 and OP42 are different synonyms for a single clone but are assessed as separate clones due to their different origins.
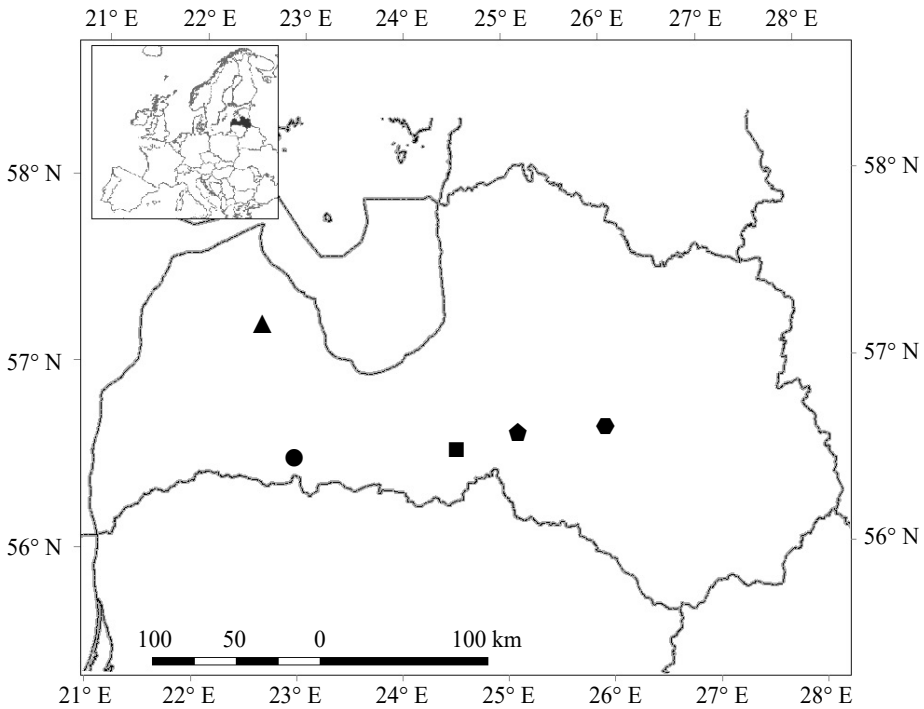
Fig. 2.1. **Location of the study objects**
●—Auce (I and II), ▲—Šķēde (I and II), ■—Vecumnieki (III and VI), ⬠—Skrīveri (IV), and ⬡—Kalsnava (IV and V). In Vecumnieki and Kalsnava, two separate plantations are studied.

Table 2.1

Origin of the poplar clones

Clone	I	II	III	IV	V	VI	Breeder / owner and country of origin	Species / hybrid / section
AF2				x	x		Franco Alasia, Italy	*P. × canadensis ᵃ*
AF6				x	x			*P. nigra × P. × generosa ᵇ*
AF7				x	x			*P. × generosa ᵇ × P. × canadensis ᵃ*
AF8				x	x			*P. × generosa ᵇ × P. trichocarpa*
AF16					x			*P. × canadensis ᵃ*
AF18					x			*P. × canadensis ᵃ*
Baldo			x		x		Unità di ricerca per le Produzioni Legnose fuori Foresta, Italy	*P. deltoides*
Oudenberg			x		x		Eigen Vermogen van het Instituut Voor Natuur en Bosonderzoek, Belgium	*P. × canadensis ᵃ*
Vesten			x		x			
Matrix11				x	x		Nordwestdeutsche Forstlichen Versuchsanstalt, Germany	*P. maximowiczii × P. trichocarpa*
Matrix24			x	x	x			
Matrix49			x		x			
Max1			x		x		Germany	*P. nigra × P. maximowiczii*
Max3			x		x			
Max4					x			
LV1			x	x	x		Swedish Forestry Agency, registration No KB-003, Sweden	*Tacamahara*
LV3			x	x	x			
LV4			x	x	x			
LV5				x	x			
LV7				x	x			
LV9				x	x			
LV10				x	x			
LV11				x	x			
LV12				x	x			
LV14				x	x			
LVX				x	x			
P0114	x	x		x	x		Progenies (cuttings) of poplars collected across Latvia, introduced (origin unknown) in 1960s (Saliņš, 1971)	*P. balsamifera × P. laurifolia*
Pop1				x	x			Unknown
Pop2				x	x			
Pop3				x				
Pop4				x	x			
Pop5				x	x			
Pop6				x	x			
Pop7				x				

Hybride275			x		x		North West Forest Research Station, Germany	*P. maximowiczii × P. trichocarpa*
OP42			x	x	x	x	The Netherland, initially bred by Oxford Paper Company (USA)	

2.1. Inter-annual dynamics of radial growth and its link to meteorological factors

2.1.1. Data collection

The link between inter-annual radial growth and meteorological factors was studied in two poplar hybrid *Populus balsamifera* L. × *P. laurifolia* Ledeb. stands on soils with normal moisture regime (site type *Oxalidosa*) near Auce (56° 31' N, 22° 56' E) and Šķēde (57° 14' N, 22° 37' E) (Fig. 2.1). According to stand inventory data, stand age was 62 and 64 years, respectively. The initial stand density in both stands was 5000 trees ha^{-1}, no thinning was done prior to the data collection.

We selected 12 and 10 visually healthy trees representing the diameter distribution of the stands in Auce and Šķēde, respectively. In the winter of 2013/2014, cross-section discs at a breast height of the trunk were collected from each tree. These disks were dried to an air-dry state in the laboratory and gradually ground with sandpaper with grain per inch from P80 to P400. The ring width measurements were done using the Lintab 5 (RinnTECH, Germany, Heidelberg) system with an accuracy of 0.01 mm. Measurements were made in two opposite directions of the discs.

Meteorological data were obtained from the UEA Climatic Research Unit (Harris et al., 2014) network, located as close as possible (< 30 km) to the studied stands. The studied meteorological factors were:

1. Minimum, maximum, and average monthly air temperature, monthly temperature amplitude, monthly precipitation, and potential evapotranspiration (PET) for the period from January year preceding the ring width formation to September in the year of the tree-ring formation;
2. Average monthly air temperature and amount of precipitation, and standardized precipitation evapotranspiration indices (SPEI) (Vicente-Serrano et al., 2010) for the period from July year preceding the ring width formation to September in the year of the tree-ring formation.

2.1.2. Statistical analysis

The validity and quality of the ring-width series within and between the stands were assessed visually and by statistical crossdating in the program COFECHA (Grissino-Mayer, 2001). Series that showed a low correlation (r < 0.40) with the total data set were discarded. A residual chronology of the tree ring series for each stand was calculated in the program ARSTAN (Cook & Holmes, 1986).

Double detrending for removal of age- and competition-related data variation was applied. The effect of age was removed by a negative exponential function and the effect of competition was removed and by a cubic spline with a wavelength of 40 years or 48 years, retaining 50% of the original data variation. Mean sensitivity (SENS), mean inter-series correlations (r-bar), synchronicity (Gleichläufigkeit (GLK)), expressed population signal (EPS), first-grade autocorrelation (AC), and signal to noise ratio (SNR) indices (Wigley et al., 1984) were used to characterize the residual chronologies.

The period between 1965 and 2009 was analyzed. The effect of meteorological factors on radial growth was assessed for poplar hybrid, silver birch (*Betula pendula* Roth), Norway spruce (*Picea abies* H. Karst.), Scots pine (*Pinus sylvestris* L.), black alder (*Alnus glutinosa* Gaertn.), European larch (*Larix decidua* Mill.), European beech (*Fagus sylvatica* L.), red oak (*Quercus rubra* L.), and hybrid aspen (*Populus tremuloides* Michx. × *P. tremula* L.). All species and hybrids were growing in stands on species-optimal sites.

The annual variability of the radial growth between species and stands was analyzed by principal component analysis (PCA) (Jolliffe, 1986), with residues chronologies used as samples and years as variables. The significance of the main principal components (PCs) was determined by a randomization test ('broken stick') with 10^3 iterations. The climatic signals captured by the PCs were determined by a bootstrapped (Johnson, 2001) Pearson correlation analysis between variable scores and climatic factors averaged for western, central, and eastern regions of Latvia. The significant meteorological factors were determined by bootstrapped Pearson correlation analysis. The statistical analysis was done in R 3.3.1 (R Core Team, 2020) using the package 'dplR' (Bunn, 2008).

2.2. The intra-annual height growth dynamics and its relation to meteorological factors within the vegetation season

2.2.1. Data collection

The growth dynamics of poplar clones and their relation to meteorological factors during the vegetation season were studied in the plantation in Vecumnieki (56° 34′ N, 24° 31′ E; Fig. 2.1). The plantation was established in the spring of 2016 in a fertile, drained peat soil with a pH level of 6. Unrooted cuttings with the length of 30 and 50 cm (hereinafter 'short' and 'long', respectively) were planted, leaving 3–5 cm above the ground. In total, 12 clones were represented (Table 2.2) in monoclonal rows in three replications with a distance between rows of 4 m and between trees in a row of 2 m.

Height was measured for 20 randomly selected ramets of each clone and cutting length group, with an average of 6 ramets per replication. Nine height measurements were performed with an average interval of 11 days between them (from 5 to 18 days). Height was measured from the ground level. About half of the

ramets were damaged by deer and snails; only intact tree data were used for data analysis.

The studied poplar clones

Clone	Number of ramets	Cutting length, cm
OP42	3	30
Max1	6	
Max3	7	
Matrix24	6	
Matrix49	7	
Hybride275	9	
LV1	3	
LV3	6	
LV4	6	
Baldo	7	30
	9	50
Oudenberg	8	30
	10	50
Vesten	7	50

For each tree, the average growth intensity (mm per day) for the period between measurements was calculated. For each clone and its cuttings length group, mean height and mean growth intensity was calculated. At the end of the observation period, 'short' clones were divided into three groups according to their height increase: (1) 'short-max'—Hybrid275, Oudenberg, (2) 'short-average'—Baldo, Max1, Max3, Matrix24, Matrix49, (3) 'short-min'—OP42, LV1, LV3, LV4. Only clones from Oudenberg and Vesten were included in the group of 'long' as clone Baldo was significantly ($p < 0.05$) shorter than them.

The mean hourly values of air temperature and precipitation sum were obtained from the nearest station of the Latvian Environment, Geology and Meteorology Center near Bauska (56° 22′ N, 24° 13′ E).

2.2.2. Statistical analysis

The differences in height growth and its dynamics between groups of cutting length groups and clones were assessed using one-way analysis of variance (ANOVA) and Tukey honest significance test. For each tree, height measurements were approximated by the Gompertz equation:

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

where:
α – asymptote parameter;
β – displacement parameter;
k – maximum relative intensity;
A – day of measurements.

Differences among the Gompertz model parameters (α, β, k) were assessed by ANOVA. The link between maximum relative intensity and meteorological factors from June till September was assessed using Pearson's correlation analysis. Differences in maximum relative intensity and air temperature among the measurement periods were assessed by ANOVA. All tests were done at α = 0.05. Mean values and their confidence intervals are shown. All calculations were done in R 3.3.1 (R Core Team, 2020).

2.3. Inter-annual height growth dynamics

2.3.1. Data collection

The inter-annual height growth dynamics were studied in plantations in Skrīveri (56° 39' N, 25° 7' E) and Kalsnava (56° 41' N, 25° 58' E) (Fig. 2.1). In Skrīveri, the plantation was established in 2011, using 23 poplar clones (Table 2.1). For each clone, at least 30 cuttings were planted in monoclonal rows with the distance between the rows 2.2 m and between trees 0.7 m.

The clone series AF was planted in three replications, all other clones in one or two replications that were evenly and randomly distributed in the field. After the first growing season all clones, except clones from the AF series, were browsed to the ground level. Height measurements were done after the second, third, and fifth growing season. For clone series AF, additional height measurements were done after the first and fourth growing season.

In Kalsnava, the plantation was established in spring 2016. In total, 34 poplar clones were represented. For each clone, 97 to 102 cuttings were planted in monoclonal rows with a distance between the rows of 3.5 m and between trees 0.5 m. The height of all living trees was measured after the first and third growing season, and the height of every second tree was measured after the fourth growing season.

2.3.2. Statistical analysis

The data normality was assessed using the Shapiro-Wilk test. The differences in height among the clones were assessed by ANOVA or Kruskal-Wallis test that was followed by Dunn multiple comparison post-hoc test. All tests were done at α = 0.05. Mean values and their confidence intervals are shown. All calculations were done in R 4.0.2 (R Core Team, 2020).

2.4. Autumn and winter frost damage and their link to tree height growth

2.4.1. Data collection

Autumn frost damage was studied in both plantations in Kalsnava, and winter frost damage was studied in one of the plantations in Kalsnava (Fig. 2.1). One of

(a)

1_L	2_L	3_L	4_L	5_L
intact leaves	several damaged leaves	damaged most leaves of the current-year leading shoot	damaged most leaves of the whole tree	already fallen leaves

(b)

1_{ST}	2_{ST}	3_T	4_{ST}	5_{ST}
intact stem	several stem injuries	the damaged current-year leading shoot	damage of more than $\frac{1}{3}$ of height	damage of the whole stem
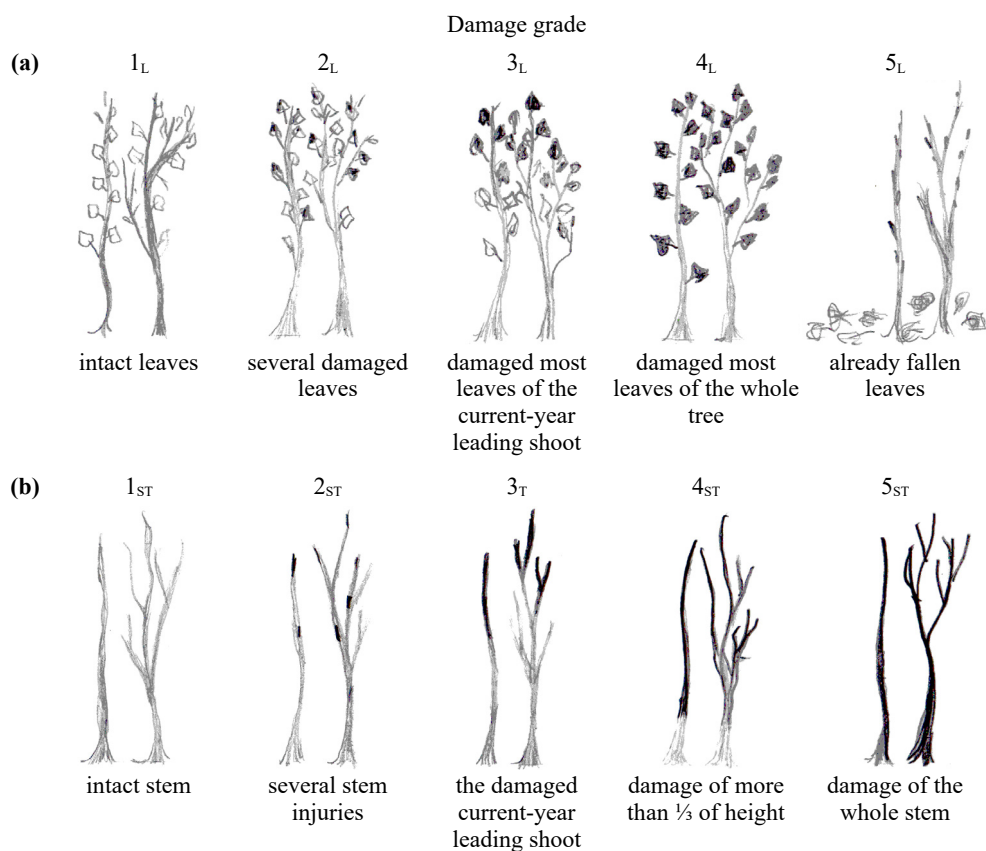
Fig. 2.2. **The schematic visualization of (a) leaf and (b) stem damage grades**
(drawn by D. Lazdiņa)

the plantations was established in 2014 and 2015, using cuttings from the Skrīveri plantation. It was established in a flat open field with monoclonal rows with no replications. Early autumn frost was observed in 2015 (detailed meteorological information, see in Chapter 2.5.1). Frost damage was assessed for 19 one- and two-year-old clones (Table 2.1). The relation between tree height and frost damage was assessed for 16 clones that overlapped in Kalsnava and Skrīveri plantations. In the other Kalsnava plantation autumn frost damage was observed after the first growing season in spring 2017.

Leaf and stem damage was visually assessed at the five-grade scale (Fig. 2.2) on the October 15. The status of active growth or dormancy was determined by bud phenology. In the other Kalsnava plantation, the number of autumn frost-damaged trees per clone was counted.

Winter frost damage was observed in one of the plantations in Kalsnava after the second growing season in spring 2018. Clones were visually evaluated on a five-scale grade: 0—dead, 1—severe damage, 2—mild damage, tree recovers, 3—minor damage, and 4—no visible winter frost damage.

2.4.2. Statistical analysis

The effect of tree age on its phenotypical state and autumn frost damage, as well as the effect of leaf and stem damage grade on tree height, were assessed using a generalized linear model. The effect of tree age on autumn frost damage was assessed for 10 clones at individual tree levels. The differences in the number of trees among the autumn frost leaf damage for one- and two-year-old ramets of clones LV4, LV11, and LV12 were assessed by Chi-squared test.

The differences in height of the damaged and undamaged trees at the clone level were done by the Mann-Whitney U test. The link between tree and clone growth parameters and autumn and winter frost damage was assessed by Spearmen's correlation analysis. All tests were done at $\alpha = 0.05$. Mean values and their confidence intervals are shown. All calculations were done in R 4.0.2 (R Core Team, 2020).

2.5. Sprouting after autumn frost damage

2.5.1. Data collection

Sprouting after autumn frost damage was observed in the plantation in Vecumnieki (Fig. 2.1). The plantation was established on drained peat soil (pH 6) in spring 2015 using 30 cm long cuttings from clone OP42 that were collected from mother-tree growing in the western part of Latvia. Trees were planted with a distance between rows 4 m and between trees 2 m. Weed control was done by plowing and applying herbicide in the autumn before planting and by manual weed control in a 25 cm radius around the trees during the vegetation season.

The autumn frost was observed in autumn 2015. Meteorological data were measured in the field once per hour: (1) air temperature 20 cm above the ground, (2) soil temperature at the ground level, and (3) in the depth of 20 cm (Fig. 2.3). The negative air temperature was first registered on September 11, and periodically (nine out of 22 days) recurred until October 6. During this period, the longest periods of negative temperature were observed on September 27 (nine hours, minimal temperature −2 °C) and September 30 (seven hours, minimal temperature −3 °C). Frost enhances on October 7th: negative air temperature persisted for 14 hours and reached −12.5 °C. Minimal air temperature form −9.5 to −13.5 °C with the duration from 11 to 16 hours continued for 10 days. Similar conditions occurred in the period from 28th to 31st of October. In both periods, the negative temperature was recorded also at the ground level. The negative temperature at the ground level was first recorded on October 8, and it persisted for two hours. On October 13, negative temperature persisted for seven hours but on October 30 and 31–15 hours (minimal temperature −2 °C). In the depth of 20 cm, negative soil temperature was not observed.

The long-term meteorological records for the studied period were obtained from the nearest Latvian Environment, Geology, and Meteorology Centre station
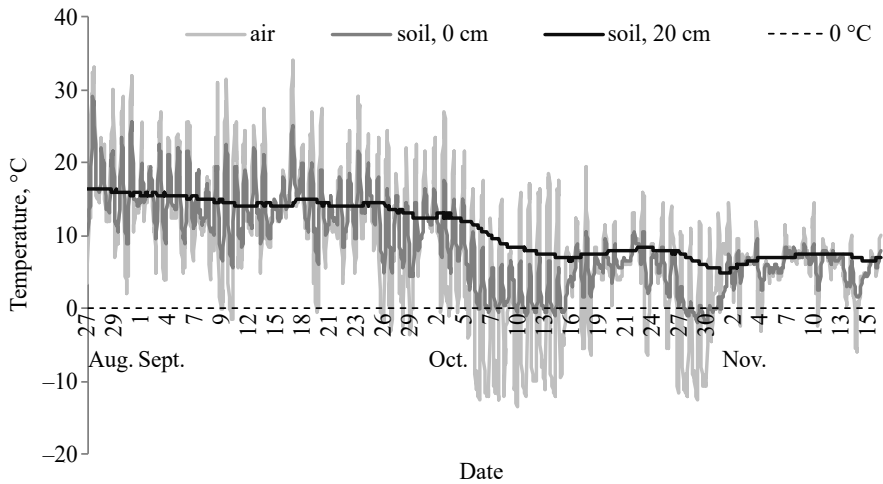
Fig. 2.3. **Soil temperature 20 cm above the ground and soil temperature at the ground level (0 cm) and in the depth of 20 cm during the period of 27.08.2015– 18.11.2015**
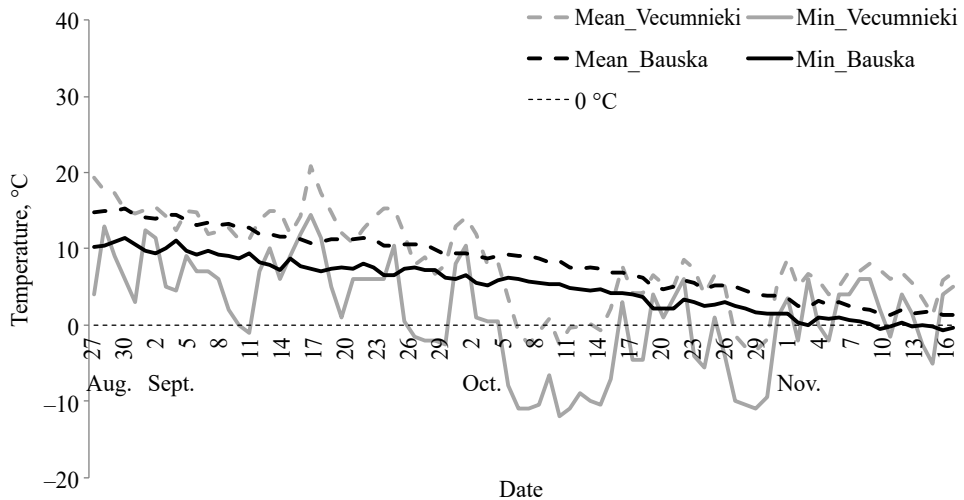
Fig. 2.4. **Air temperature in Vecumnieki plantation and the long-term records from the nearest Latvian Environment, Geology and Meteorology Centre station (Bauska) during the period of 27.08.2015–18.11.2015**
Mean_Vecumnieki—mean diurnal temperature, calculated from hourly measurements;
Min_Vecumnieki—mean minimal diurnal temperature;
Mean_Bauska—mean diurnal temperature for a 30-year period;
Min_Bauska—mean minimal diurnal temperature for a 30-year period.

near Bauska (56° 22' N, 24° 13' E). In the long-term data, the negative mean minimum air temperature was first observed on November 11 (Fig. 2.4).

In June of the next growing season, all trees had completely withered above-ground parts (stems), and part of the trees was sprouting from the ground level. For each tree, height, diameter at the root collar, and length of the longest branch were measured for the longest stem, and the number of stems and branches (longer than 5 cm) was counted. For each tree presence (0/1) of the browsing damage and sprouts was noted. In total, 3025 trees were measured. The repeated assessment was done in July for 1018 trees.

2.5.2. Statistical analysis

The data normality was assessed using the Shapiro-Wilk test. The differences in height, diameter, and length of branches for trees with one, two, three, and more than three stems were assessed using ANOVA. Chi-squared test was used to assess (1) differences in the number of branches and proportion of sprouting and browsed trees among trees with the different number of stems, (2) differences in the proportion of sprouting trees between browsed and undamaged trees, and (3) differences in the proportion of sprouting trees among the rows. Pearson's correlation analysis was used to assess the relationship between the proportion of sprouting trees and mean tree height in the row. Spearmen's correlation analysis was used to assess the relation between (1) number of branches and stems, (2) length and the number of branches, (3) and length of branches and number of stems. The spatial autocorrelation was assessed using Moran's I test. All tests were done at α = 0.05. Mean values and their confidence intervals are shown.

3. RESULTS AND DISCUSSION

3.1. Inter-annual radial growth and its relation to meteorological factors

The obtained ring-width time-series showed good agreement with mean inter-series correlation 0.42–0.51 and GLK 0.68–0.69, indicating a strongly uniform effect of the environmental factors on poplar radial growth. This was supported by tight (r > 0.75) relation between chronologies of stands. In both stands, growth dynamics were similar—mean relative radial increment peaks at the age of 10 to 15 years and flattens out after the age of 25 to 30 years (Fig. 3.1).

The high signal intensity indicator SNR (6.17–10.77) suggests homogenous conditions within the stand and uniform genetic material (single clone represented).
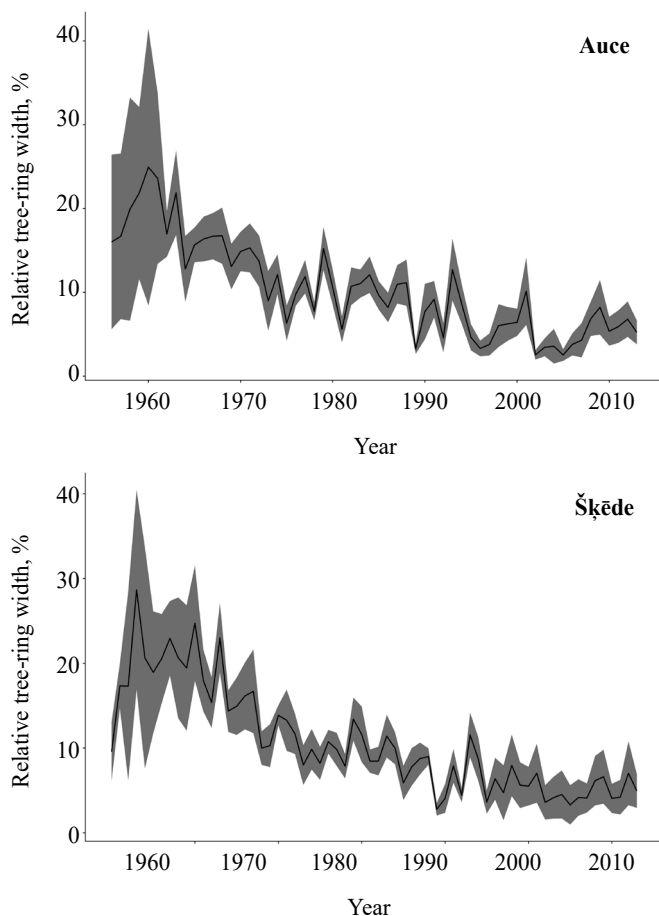

Fig. 3.1. **Mean relative tree-ring width of the poplar hybrid in Auce and Šķēde**

The relatively large differences in SNR indicate climatic differences between the stands that presumably are related to more continental conditions in Auce. The population signal (EPS) values were sufficiently high (0.86–0.92) to characterize factors that affect tree-ring width in both analyzed stands (Wigley et al., 1984). The effect of external factors was expressed by notable differences in tree-ring width among the years, sensitivity coefficient reaching values of 0.40–0.42. Moderate to high autocorrelation (0.56–0.74) indicates the effect of the previous growth on the formation of the current-year tree-ring width. The time series had several sudden changes (decrease in tree-ring width) in 1975, 1989, and 2002, that was caused by low temperature on autumn in a year before the formation of the tree-ring width that was followed by high mean temperature in a period between December before the tree-ring formation to August on the year of the tree-ring formation.

The residual chronologies had a significant correlation with 12 out of 132 assessed factors, and eight of them were significant in both stands. Each factor explained a relatively small part of the variation with correlation values not exceeding 0.35 as the ring-with is affected by a large number of factors that mutually interact. The low correlation values presumably are also affected by temporal changes in the significance of the factors (Cook et al., 1992; Büntgen et al., 2006).

Poplar hybrid showed sensitivity to a temperature at the end of the growing season (July to September) both on the year of tree-ring formation and a year prior to it. In Šķēde, tree-ring width was also affected by temperature in February, March, and June, whereas in Auce—a temperature range in September. The effect of meteorological factors in a year prior to tree-ring formation is linked to the accumulation of nutrients (Barbaroux & Bréda, 2002; Pallardy, 2008) that occurs at the end of the growing season, and is depleted in the following spring (Landhäusser & Lieffers, 2003; Jones et al., 2004; Regier et al., 2010). The increased temperature increases evapotranspiration (Trajkovic, 2005) that can cause short-term water deficiency and drought stress (Pallardy, 2008). In such conditions, the accumulation of nutrients is hampered (Regier et al., 2009), presumably, explaining the observed relation between tree-ring width and PET in August (Fig. 3.2). Moreover, hot summers typically have decreased amount of precipitation. Poplars, similarly to other fast-growing tree species, are characterized by intense evapotranspiration (Perry et al., 2001) that increases water deficit in soil, hence, reinforcing the effect of drought stress.

The effect of the current year meteorological factors is linked to nutrient use during the growing season (Deslauriers et al., 2009) that affects the wood formation (Lebourgeois et al., 2005). The increased temperature might hamper photosynthesis (Haldimann & Feller, 2004) and cambium activity during xylogenesis (Oberhuber & Gruber, 2010), whereas the negative effect of temperature range during the growing season is linked to the adaption of biochemical and physiological processes to these sudden changes (Pallardy, 2008).

The negative relation between radial growth and temperature in September is linked to the transition from active growth to dormancy when poplars are sensitive
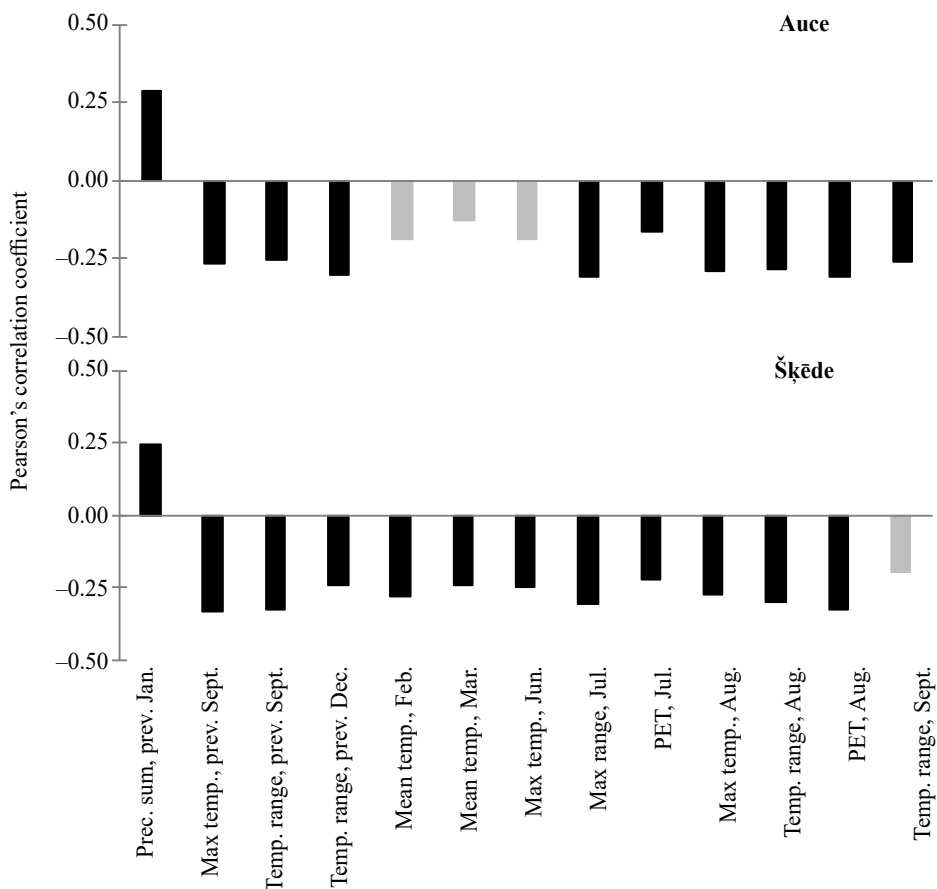
Fig. 3.2. **Significant Pearson correlation coefficients between climatic factors and residual chronologies of the TRW of hybrid poplar in Auce and Šķēde**
Factors that were not significant in either of the stands are colored grey.
Collinear factors have been omitted. Prec.—precipitation, prev.—previous year,
temp.—temperature, PET—potential evapotranspiration.

to frost. The negative effect of temperature on December, when trees are dormant, is linked to frost dehardening as a response to thaw events (Cox & Stushnoff, 2001) that poses trees to the more intense effect of frost when the temperature drops again (Hänninen, 2006). Hampered dormancy might increase depletion of nutrient reserves due to increased respiration (Ögren et al., 1997). Precipitation (typically snow) sum on January in a year prior to tree-ring formation was the only factor that had a positive effect on radial growth. A thick layer of snow ensures better thermoisolation, reducing the depth of the frozen soil and temperature changes in soil (Hardy et al., 2001), hence reducing root mortality (Tierney et al., 2001) and positively affecting water uptake.

The first three principal components were significant ($p < 0.01$) and together explained 32.1% of the total data variation (Fig. 3.3). The first principal component

Fig. 3.3. **The distribution of the residual chronologies according to the first three principal components (PC1, PC2, and PC3) was calculated for the tree-ring chronologies for the period 1965–2009**
On the axes, the numbers in parentheses show the percentage of explained variance (%).
B—*Betula pendula* Roth, E—*Picea abies* H. Karst., M—*Alnus glutinosa* Gaertn.,
P—*Pinus sylvestris* L., Le—*Larix decidua* Mill., Dsk—*Fagus sylvatica* L.,
Ozs—*Quercus rubra* L., H-poplar—*Populus balsamifera* L. × *P. laurifolia* Ledeb.,
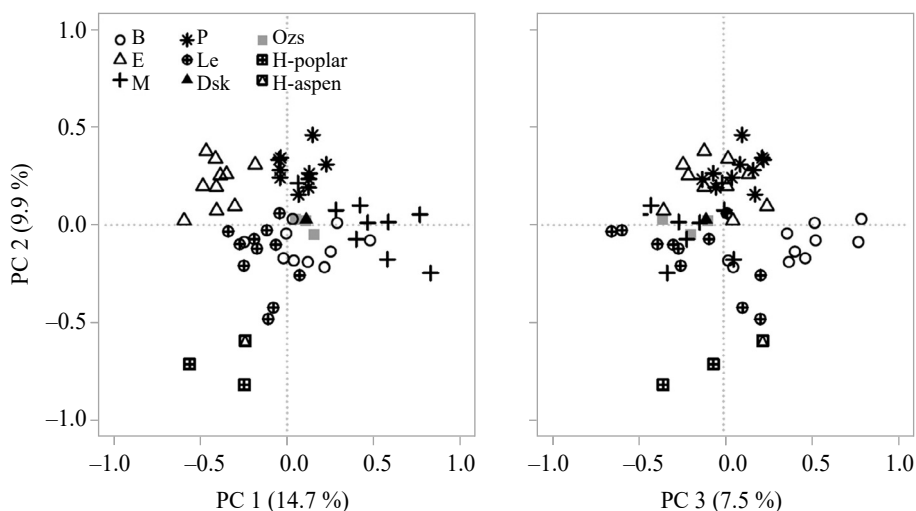H-aspen—*Populus tremuloides* Michx. × *P. tremula* L.

(PC1) was related to the length of the vegetation period and water availability during the active growth and was expressed as significant correlations with temperature on September in a year prior to tree-ring formation (r = 0.36) and precipitation sum on June (r = −0.33). The second principal component indicated the effect of temperature and correlated with temperature on the current year February and March (r = 0.38 and r = 0.55, respectively) and on the previous year July (r = 0.33). The third principal component (PC3) was related to tree reaction on water deficit in the middle of summer and correlated with temperature, precipitation sum, and SPEI in July in a year prior to tree-ring formation (r = 0.32, r = −0.39, and r = −0.30 respectively).

The distribution according to the first and second, as well as the second and third principal components showed grouping by species (Fig. 3.3), indicating different sensitivity to meteorological factors of the studied tree species. In both cases, the poplar chronologies were located separately, suggesting different features of tree-ring width variation. Presumably, this is related to the effect of heterosis, i.e. pronounced characteristics of the parental species and their combination, causing the specific reaction to the environment (Li et al., 1998).

3.2. Intra-annual height dynamics and its relation to meteorological factors

Tree height at the time of the first measurement was reached 4.0 ± 1.6 cm. Clones OP42 and 'short' Baldo were significantly (p < 0.05 shorter (1.6 and 1.8 cm, respectively), whereas clones 'short' Oudenberg and 'long' Vesten and Oudenberg— significantly longer (11.8, 12.1, and 14.2 cm) than plantation mean height.

Mean tree height at the end of the growing season was 81.0 ± 6.8 cm. Mean height significantly (p < 0.001) differed among the clones and was from 32 to 132 cm (Fig. 3.4). The mean height of the 'short' clones was 69.2 ± 6.9 cm. Clones Hybride275, Oudenberg, and Matrix49 were significantly (p < 0.05) higher but clones OP42 and LV1 were significantly shorter than the plantation mean. The mean height for clones with 'long' cuttings was 107.9 ± 13.4 cm. Clones Oudenberg and Venten were significantly (p < 0.05) longer than clone Baldo: height at the end of the first growing season was 131.8, 118.3, 73.3 cm, respectively.

For clones Oudenberg and Baldo, height was significantly (p < 0.001) affected by clone and length of the cuttings but not the interaction between these factors (p = 0.74; R² = 0.75). For clone Oudenberg, the height of the ramets with 'long' cuttings was 31% larger than for ramets with 'short' cuttings: 132 ± 12.0 cm and 101 ± 17.1 cm, respectively. For clone Baldo, the height of the ramets with 'long' cuttings was 55% larger than fir ramets with 'short' cuttings: 73 ± 20.0 cm and 47 ± 7.0 cm, respectively. The results indicate the superiority of longer cuttings for height growth that is in accordance with other studies (Burgess et al., 1990; Rossi, 1999; Camp et al., 2012) and, presumably, is related to larger nutrient reserves
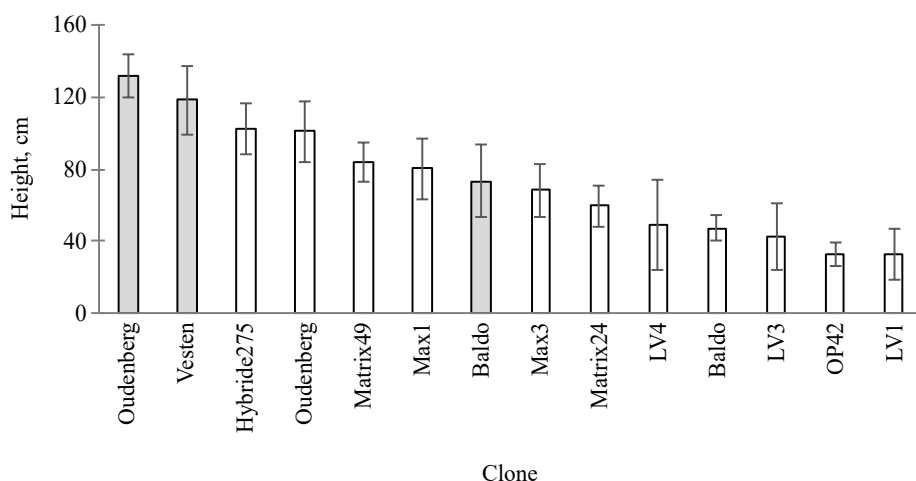

Fig. 3.4. **Mean height of the poplar clones at the end of the first growing season (± confidence interval)**
White bars indicate clones with 'short' (30 cm) cuttings,
grey bars indicate clones with 'long' (50 cm) cuttings.

(Buhler et al., 1998; Marino & Gross, 1998), ensuring advantage for their growth. For instance, in a study of 20 and 40 cm long cuttings of Max4, stem and leaf biomass after the first growing season was 46.6 ± 3.2 and 47.7 ± 3.3 g dry matter, respectively, for ramets of the long cuttings and 39.5 ± 2.8 and 33.1 ± 1.6 g dry matter, respectively, for ramets of the short cuttings (Vigl & Rewald, 2014). The total biomass after the first growing season is significantly positively correlated with initial weight of the cutting (Vigl & Rewald, 2014).

The mean growth intensity in all measurement periods was from 10 to 15 mm per day. For some clones (e.g. OP42, LV1, and LV3) growth intensity did not reach 10 mm per day whereas clones 'long' Vesten and 'short' Oudenberg and Hybride275 exceeded height growth of 15 mm per day, suggesting different height growth strategies (Devine et al., 2010).

The Gompertz model asymptote parameter (maximal value) was differed significantly ($p < 0.05$) among the groups of 'short' clones, although the timing of the growth onset was similar (Fig. 3.5). This led to significant ($p < 0.05$) differences in growth intensity parameter k between clone groups 'short-min' and 'short-max'. These differences indicate that clones with the largest height at the end of the growing season had more rapid growth at the beginning of July, and could be linked to genetically determined differences in leaf flush (Jansons et al., 2014). No significant differences were found between groups 'long' and 'short-max' for all model parameters (α, β, k).

Height growth intensity had moderately tight ($p > 0.05$, $r = 0.60$) positive correlation with precipitation sum but weak ($p > 0.05$, $r = 0.17$) correlation with temperature (Fig. 3.6). Similarly, Chhin (2010) has observed more pronounced effect of precipitation of poplar growth compared to temperature parameters. During the
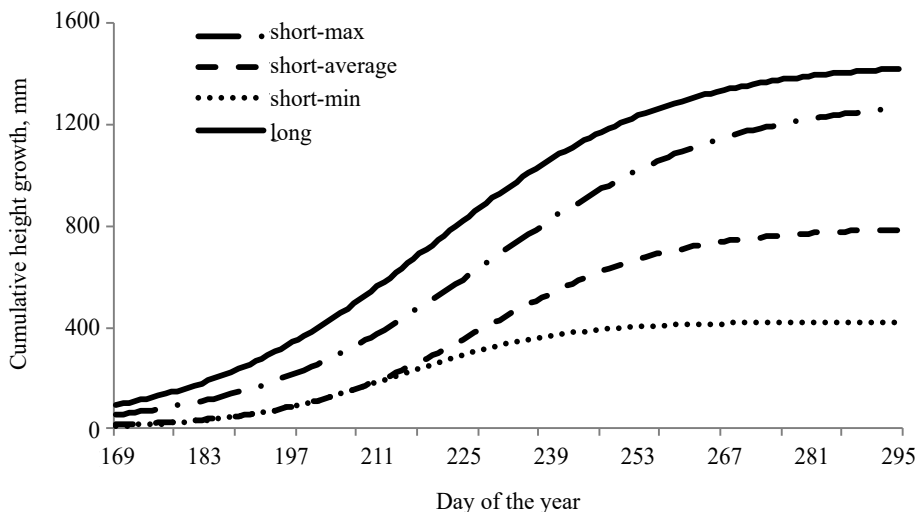
Fig. 3.5. **Gompertz model for groups of poplar clones 'short-max', 'short-average', 'short-min' (cutting length 30 cm), and 'long' (cutting length 50 cm)**
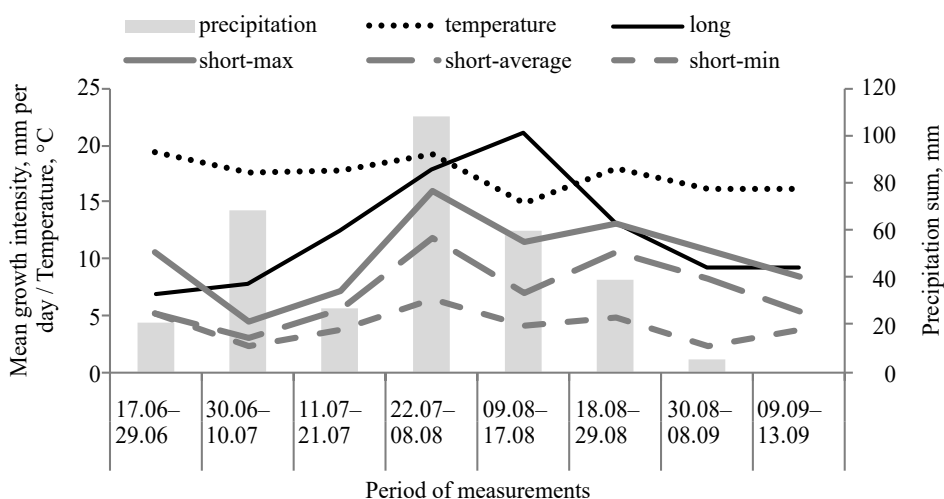
Fig. 3.6. **Mean growth intensity for clone groups 'short-max', 'short-average', 'short-min' (cutting length 30 cm), and 'long' (cutting length 50 cm) in relation to mean temperature and precipitation sum**

second measurement period (30.06–10.07) mean temperature decreased from 19.3 to 17.6 °C, causing a decrease of growth intensity by 2.2 mm per day. Maximal height increment intensity was 12.7 mm per day, and it occurred at the end of July (22.07–08.08) in a period with the maximum precipitation sum (108 mm). The growth intensity during the fourth measurement period showed notable differences among the clones and was from 4.6 mm per day for clone LV1 to 18.5 mm per day for clone 'long' Oudenberg.

Atypical changes in temperature and precipitation sum were observed in the middle of August (09.08–17.08) when these values were reduced to 14.9 °C and 60 mm, respectively, and caused growth reduction by 10.2 mm per day on average. Clones that were the highest at the end of the growing season ('long' Vesten and Oudenberg) continued their growth during this period, whereas other clones reduced growth (Fig. 3.5). in the next measurement period (18.08–29.08) temperature again increased but the growth intensity remained at the same level (10.3 mm per day). During the following measurement periods, temperature, precipitation sum, and growth intensity decreased.

Although the correlations between growth intensity and studied meteorological factors were not significant, the effect of temperature was expressed as notable changes in growth intensity between periods with sudden changes of temperature (Fig. 3.6), i.e. between the third and fourth, the fourth and fifth, and sixth and seventh measurement periods.

3.3. Inter-annual height growth dynamics

In Skrīveri the highest clones at the age of two years were AF6, LV3, and LV12: 159.5 ± 10.5, 154.3 ± 14.2, and 143.9 ± 8.5 cm, respectively (Fig. 3.7). The significant differences among the clonal height were mainly caused by clone AF6 that was higher and clones POP1, POP2, and POP6 that were shorter than the rest of the clones. Regardless of the browsing damage after the first growing season, most clones had a similar height to clones AF2, AF8, and AF7 that were not browsed. The rapid growth of the browsed clones, presumably, is related to already established root system (Christersson, 1986), that promotes larger yield of the second rotation compared to the first rotation after plantation establishment (Dillen et al., 2013).

In Kalsnava, mean height at the age of one year was from 51 ± 8 to 124 ± 5 cm for all alive trees (Fig. 3.8) and from 37 ± 9 to 159 ± 25 cm for undamaged trees. There was a tight, significant correlation between the height of alive and undamaged trees (rho = 0.82, p < 0.001). However, for some clones browsing had a considerable effect on mean height: for clone AF16, undamaged trees were 28% shorter than alive trees, while for clone LV3, undamaged trees were 39% higher than alive trees.

In both plantations, differences in tree height among the clones were significant at all studied ages (all p < 0.001; Figs. 3.7 and 3.8) and they increased by age. In Skrīveri, a number of pairs with significant differences were 80 at the age of two years, 124 at the age of three years, and 169 at the age of four years, while in Kalsnava difference between the highest and lowest clone increased from 2.4 times at the age of one year to 2.9 times at the age of three years. Between these years of assessment, clones were notably changed their ranking (Fig. 3.9a): correlation
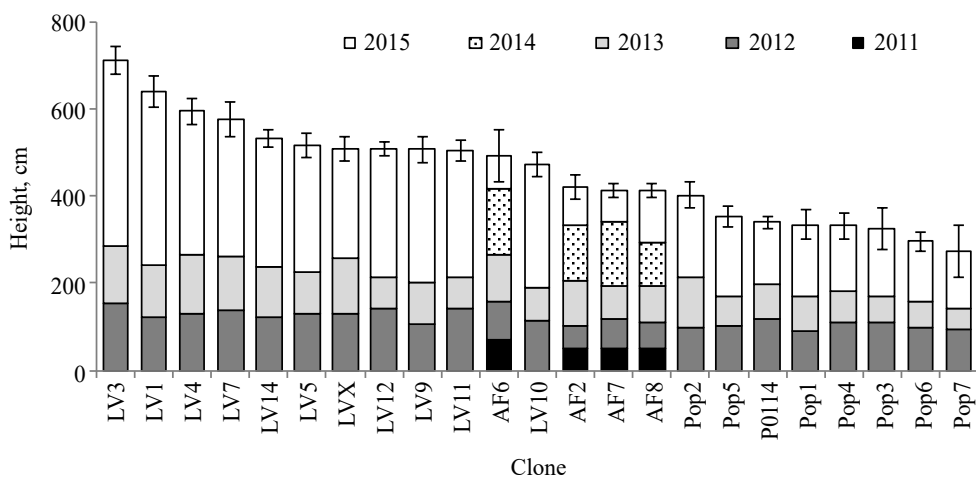
Fig. 3.7. **Height of the clones at the age of one (2011), two (2012), three (2013), four (2014), and five (2015; ± confidence interval) years**
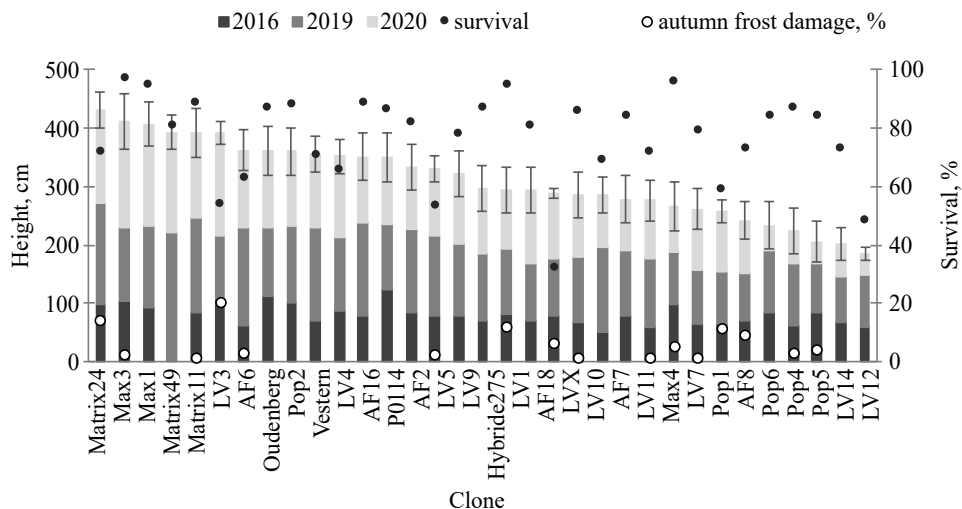
Fig. 3.8. **Height of the clones at the age of one (2016), three (2019), and four (2020; ± confidence interval) years and survival at the age of three years**
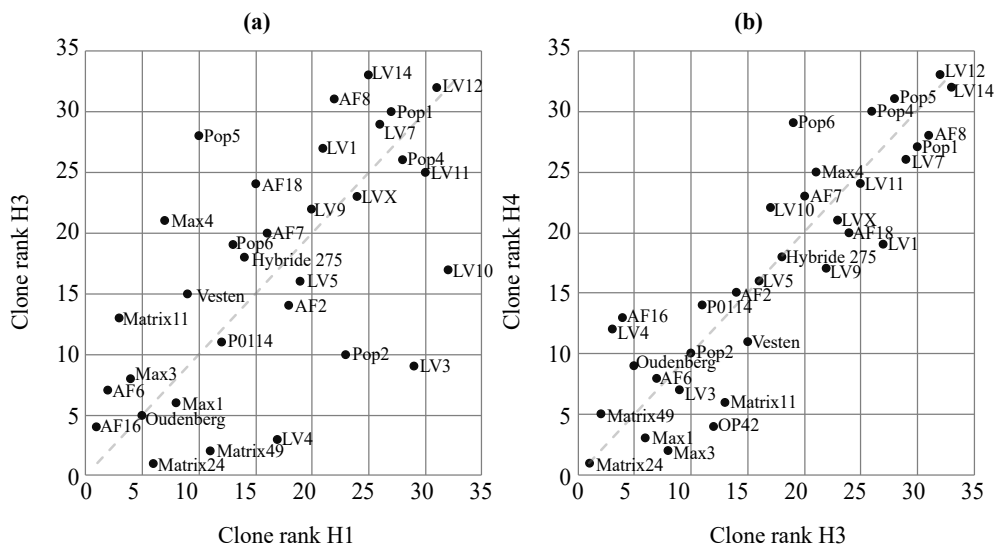
Fig. 3.9. **The changes in clone ranking for height (a) between the age of one (H1) and three years (H3) and (b) between the age of three (H3) and four (H4) years**
The dashed lines represent the unchanged position of a rank between the different ages. Clones above the line have decreased rank and clones below the line have increased the rank.

between the height measurements was rho = 0.61, p < 0.001. The change of ranking is linked to differences in growth dynamics that affect clone allometry (Karačić et al., 2021) and rooting ability (Zalesny et al., 2005; Zhao et al., 2014). At the age of four years, the difference between the height of the highest and lowest clone was slightly smaller, and the ranking between the ages of three and four years was changed less (rho = 0.90, p < 0.001; maximal difference: 10 positions for clone Pop6; Fig. 3.9b) than between the ages of one and three years (maximal difference: 20 positions for clone LV3; Fig. 3.9a).

3.4. Assessment of autumn and winter frost damage and its link to tree height

In one of the plantations in Kalsnava after the autumn frost in 2015, 65.4% of autumn frost-damaged trees were actively growing. For three clones, all ramets were dormant, for 10 clones, all ramets were actively growing, and for six clones, part of the ramets were both dormant and actively growing (Fig. 3.10a). Significant (p < 0.01) differences in the phenological state among the clones are linked to medium to the strong effect of genetics (Howe et al., 2000; Christersson, 2006; Hall et al., 2007; Friedman et al., 2008; Rohde et al., 2011).

Among the clones that were actively growing, leaf damage was observed for 81% of trees (Fig. 3.10b). Four clones had more than 80% of ramets with damaged most of the leaves (Grade 4_L). Clone LV4 had the highest frost tolerance with 76% of the ramets with intact leaves (Grade 1_L).

Damage to the stem was observed rarely (Fig. 3.10c). Among the dormant clones, clone LV3 had one ramet with several stem injuries (Grade 2_{ST}), while among the actively growing clones, clones Matrix24 and LV14 had 87% and 100% of ramets with several stem injuries (Grade 2_{ST}), respectively. Only clone LV3 had damaged more than ⅓ of the stem (Grade 4_{ST}). The results support the findings of other studies that trees that set buds later in autumn are more susceptible to frost damage (Junttila & Kaurin, 1990; Howe et al., 2000).

In the other plantation in Kalsnava after the autumn frost in 2016, autumn frost damage was observed for 16 out of 33 clones (Fig. 3.11). For the majority of clones, only a small part of ramets was damaged: the median of the proportion of damaged trees was 4%. Clones of the crossing *P. maximowiczii × P. trichocarpa* were more sensitive to frost than others: clones Hybride275, Matrix24, and Matrix11 had damaged 21%, 14%, and 11% of ramets.

At the individual tree level, tree age significantly affected autumn frost damage to leaves (p < 0.01) but not to stems (p > 0.05). Significant (p < 0.01) differences were observed also for clones at the same age. For clones LV4 and LV11 all ramets were actively growing regardless of age. Also, for clone LV12 all two-year-old and most (87%) of the one-year-old ramets were actively growing. For these three clones, ramets of different ages had significant (p < 0.01) differences in leaf damage. For clones LV4 and LV11, all two-year-old ramets were intact (Grade 1_L), while for one-year-old ramets had damaged several or most of the leaves (Grades 2_L and 3_L). For clone LV12, most of the two-year-old trees gad damaged most of the
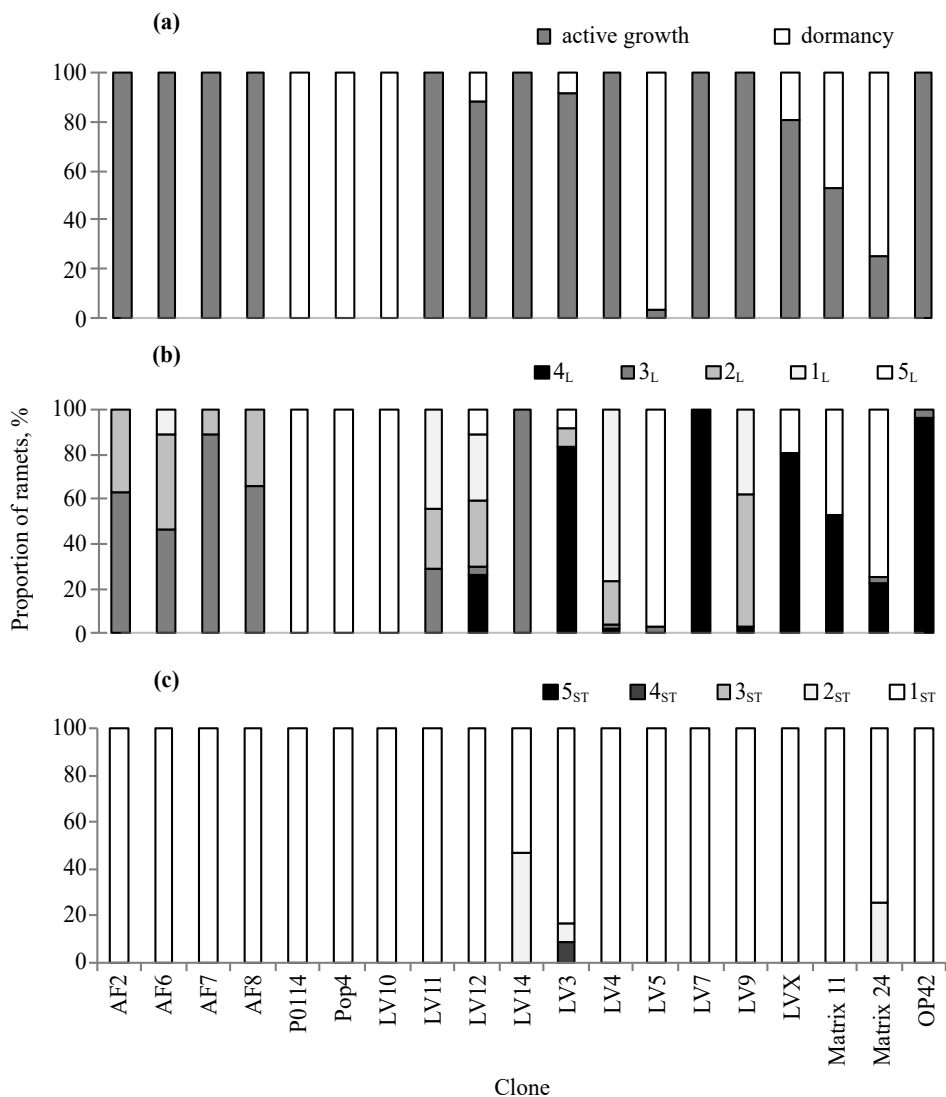
Fig. 3.10. **The proportion of ramets according to (a) phenological state, (b) leaf, and (c) stem damage grades**

Leaf frost damage grades: 1_L—intact leaves, 2_L—several damaged leaves, 3_L—damaged most leaves of the current-year leading shoot, 4_L—damaged most leaves of the whole tree, 5_L—already fallen leaves. Stem frost damage grades: 1_{ST}—intact stem, 2_{ST}—several stem injuries, 3_{ST}—damaged current-year leading shoot, 4_{ST}—damage of more than ⅓ of height, 5_{ST}—damage of the whole stem.
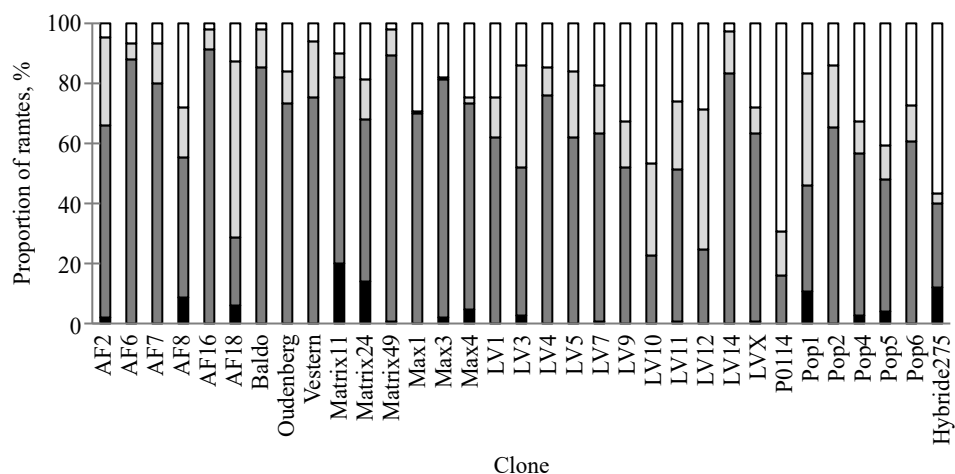
Fig. 3.11. **The proportion of damaged ramets after the first growing season**
Color of the stacked bard: black—autumn frost- damage, dark grey—browsing damage,
light grey—dead, white—undamaged.

leaves (Grade 4_L) while for one-year-old ramets less severe damage was observed (Grades 3_L and 4_L).

Autumn frost damage did not have negative effect on survival (rho = 0.53, p < 0.001). Tree height was not related to leaf damage (p > 0.05) but in both plantations, tree height was linked to stem damage. In one of the plantations, this relation was caused by clones LV14 and LV3—relatively high trees that had damaged 46.5% and 16.6% of ramets, respectively. In the other plantation, no link between clone height and proportion of autumn-damaged trees was found (rho = 0.42, p > 0.05) but frost-damaged trees were significantly higher (p < 0.001) than the undamaged trees: 105.3 ± 7.9 un 72.0 ± 2.5 cm, respectively. These differences concur that fast-growing trees are sensitive to frost at the end of the growing season (Pliura et al., 2014).

The proportion of autumn-damaged trees was not related to the winter damage grade of the same clone (Fig. 3.12). Unlike for autumn frost damage, clones with winter frost damage were shorter (Fig. 3.13) and with lower survival (rho = 0.47, p < 0.01) than undamaged trees. Clones with severe winter frost damage (Grade 1) had survival of 32%, moderately damaged clones (Grade 2) of 72%, clones with mild damage (Grade 3) of 78%, and intact clones (Grade 4) of 85%. This is related to structural traits of wood, namely, xylem vessel size that also affects tree cold tolerance (Schreiber et al., 2013).

The results suggest that fast-growing clones with sufficient frost tolerance could be selected (e.g. clones Max1 and Matrix49, Fig. 3.8). Other clones (e.g. clones Matrix24 and Matrix11), however, were among the highest despite the autumn frost damage, i.e. their damage was compensated by the fast growth. Progenies of the same parental species as clone series Matrix (*P. maximowiczii × P. trichocarpa*) have
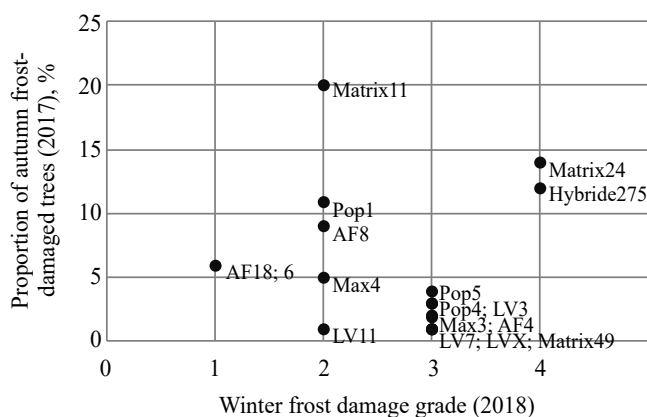
Fig. 3.12. **The proportion of autumn frost-damaged trees (assessed in spring 2017) and winter frost damage grade (assessed in spring 2018)**
Winter frost damage grades: 0—dead, 1—severe damage, 2—mild damage, tree recovers, 3—minor damage, 4—no visible winter frost damage.
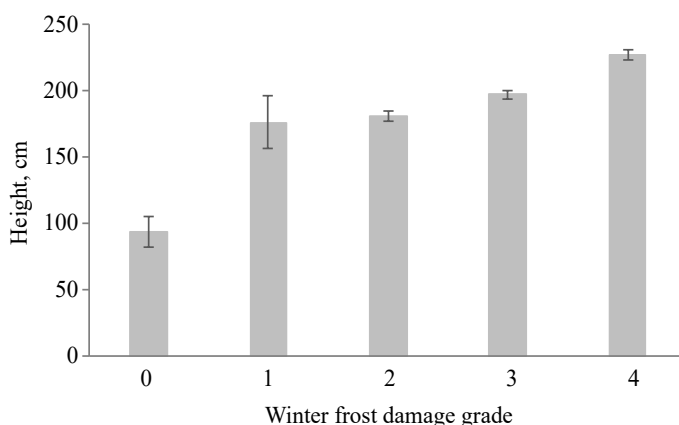
Fig. 3.13. **Height at the age of three years according to winter frost damage grade**
Winter frost damage grades: 0—dead, 1—severe damage, 2—mild damage, tree recovers, 3—minor damage, and 4—no visible winter frost damage.

shown similar results by remaining position among the tallest clones regardless of significant height loss due to stem withering (Gudynaitė-Franckevičienė et al., 2020). Overall, suitable tolerance to cold injuries of locally collected clones has not sufficient advantage to gain a higher yield, as compared to highly productive, although more sensitive, introduced clones.

3.5. Sprouting after the autumn frost damage

Before the autumn frost damage in Vecumnieki at the end of the first growing season (Fig. 2.1), 49% of trees had formed one, 31% had formed two, 10% had formed three, and 10% had formed four or more stems. Tree height

was from 10 to 215 cm (mean 118 ± 1.18 cm). Trees that had formed one stem were significantly (p < 0.001) higher than trees that had formed more stems: 121 ± 2.5 and 114 ± 2.6 cm, respectively. The mean diameter at the root collar was 6.6 ± 0.32 mm, and trees with a larger number of stems were thinner (Fig. 3.14). The mean diameter for trees with one and two stems was similar (p > 0.05; 7.1 ± 0.48 and 7.0 ± 0.49 mm, respectively) and they were significantly (p < 0.05) thicker than trees with more than three stems (4.9 ± 1.0 and 4.0 ± 0.73 cm, respectively).

After the autumn frost, all trees had completely withered the above-ground part. At the first assessment in June, new shoots were noted for 19.6% of trees. A number of studies have showed that poplars have good sprouting ability, and biomass from the second rotation typically exceeds that after the first (establishment) rotation, and harvesting of the aboveground part has no negative effect on stool survival (Laureysens et al., 2003, 2005; Dillen et al., 2013; Verlinden et al., 2015). However, it should be stressed that in the studied plantation the aboveground biomass was not harvested, instead, it was withered in a result of a frost damage, hence, trees, possibly, had negatively affected vitality of the root system.

Regardless of the number of stems, trees that were sprouting were slightly but significantly lower than trees that did not sprout, 110 ± 3.9 and 119 ± 2.0 cm, respectively (Fig. 3.15). Studied have showed that this link might be related to structural properties of wood—tree height is positively correlated to vessel diameter (Martínez-Cabrera et al., 2011) that is the main parameter that determined tree sensitivity to embolism (Sperry & Sullivan, 1992). Plants most effectively ensure conductivity by forming few wide and long vessels (Sperry et al., 2008), while trees with many narrow vessels are more resistant to embolism (Davis et al., 1999).
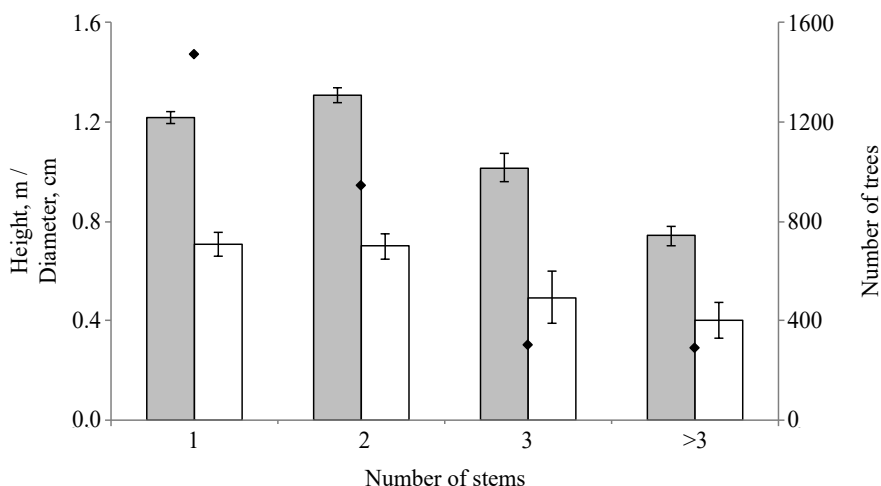
Fig. 3.14. **Mean height (grey bars), diameter (white bars) at root collar (± confidence interval), and number of trees (bullets) at the first assessment according to number of stems**
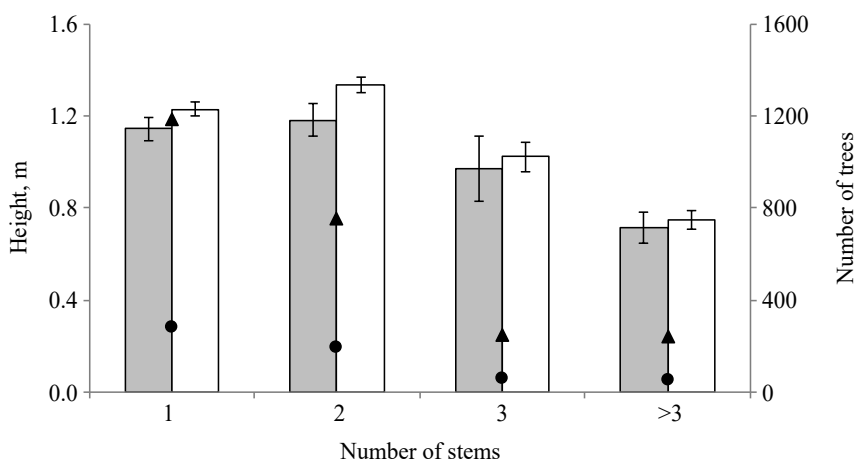
Fig. 3.15. **Mean height (bars; ± confidence interval) and number of trees (symbols) for trees with (grey bars and bullets) and without (white bars and triangles) at the first assessment according to number of stems**

The proportion of sprouting trees was not related (p = 0.89) to the number of stems: trees with one, two, three, or more stems had 19.4%, 20.1%, 20.0% un 18.2% of sprouting trees, respectively. Significant (p = 0.006) differences in the proportion of sprouting trees were noted for browsed (12.6%) and undamaged (20.1%) trees. The proportion of sprouting trees differed significantly (p < 0.001), but no link (p > 0.90) was found between mean height in a row and the proportion of sprouting trees. The spatial distribution of sprouting trees was random (p > 0.05).

At the repeated assessment in July, the proportion of sprouting trees was increased to 44.0%. The observed relation between the height of the previous year's shoots and the number of stems remained: the sprouting trees were significantly lower than trees that did not sprout, 111 ± 4.6 and 123 ± 4.5 cm, respectively.

CONCLUSIONS

1. Poplar radial growth is negatively affected by drought stress in summer, indicated by increased temperature and reduced standardized precipitation evapotranspiration index. It is also negatively affected by increased temperature range in December, affecting/hampering tree physiological processes during dormancy. In the context of climate change, clone selection should include clones with lower sensitivity to these meteorological factors.

2. Height increment is significantly affected by clone and cutting length. Longer cuttings ensure faster initial growth: at the end of the first growing season, the height of the 50 cm long cuttings exceeded the height of the 30 cm long cuttings by 31–55%. Fast-growing clones have higher phenotypical plasticity, i.e., lower sensitivity to meteorological changes during the growing season.

3. Autumn frost damage to the top of the leading shoot is typical for fast-growing trees (trees with frost damage were significantly higher than the undamaged trees). Winter frost damage is typical for trees with inferior growth, and survival at the age of three years was from 32% for clones with severe winter frost damage to 85% for visually intact trees.

4. The use of clones that are suitable to the Latvia climate is crucial. Trees that, as a result of frost, had completely withered aboveground parts are sprouting but their growth is delayed: at the beginning of June, sprouts were noted for 19.6% of trees and in the middle of June for 44.0% of trees.

5. Fast-growing clones with sufficient autumn and winter frost tolerance and survival could be selected. This is indicated by from a breeding perspective positive or not significant clone mean (genetic) correlations between the growth and other parameters.

RECOMMENDATIONS

Clones Matrix49, Max1, and Max3 with decent growth and survival and low risk of frost damage are recommended for plantations. Poplar plantations should be established on sites with a low risk of frost occurrence. Mean radial increment of the clone *Populus balsamifera × P. laurifolia* peaks at the age of 10 to 15 years and levels out after the age of 25 to 30 years. More research is needed for the optimal length of the rotation period. Sensitivity to drought stress during the growing season and autumn frost should be tested in a controlled environment during the initial clonal testing.

ACKNOWLEDGEMENTS

LITERATŪRAS SARAKSTS / REFERENCES

Barbaroux C., Bréda 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. 10.1093/treephys/22.17.1201

Buhler D.D., Netzer D.A., Riemenschneider D.E., Hartzler R.G. (1998) Weed management in short rotation poplar and herbaceous perennial crops grown for biofuel production. Biomass and Bioenergy, 14, 385–394. 10.1016/S0961-9534(97)10075-7

Bunn A.G. (2008) A dendrochronology program library in R (dplR). Dendrochronologia, 26, 115–124. 10.1016/j.dendro.2008.01.002

Büntgen U., Frank D.C., Schmidhalter M., Neuwirth B., Seifert M., Esper J. (2006) Growth/climate response shift in a long subalpine spruce chronology. Trees, 20, 99–110. 10.1007/s00468-005-0017-3

Burgess D., Hendrickson O.Q., Roy L. (1990) The importance of initial cutting size for improving the growth performance of *Salix alba* L. Scand. J. For. Res., 5, 215–224. 10.1080/02827589009382607

Camp J.C., Rousseau R.J., Gardiner E.S. (2012) Longer black willow cuttings result in better initial height and diameter growth in biomass plantations. In: Butnor J.R. (Ed.) Proceedings of the 16th Biennial Southern Silvicultural Research Conference. U.S. Department of Agriculture Forest Service, Southern Research Station, Asheville, NC, p. 43–46.

Charrier G., Ngao J., Saudreau M., Améglio T. (2015) Effects of environmental factors and management practices on microclimate, winter physiology, and frost resistance in trees. Front. Plant Sci., 6. 10.3389/fpls.2015.00259

Chhin S. (2010) Influence of climate on the growth of hybrid poplar in Michigan. Forests, 1, 209–229. 10.3390/f1040209

Christersson L. (2006) Biomass production of intensively grown poplars in the southernmost part of Sweden: Observations of characters, traits and growth potential. Biomass and Bioenergy, 30, 497–508. 10.1016/j.biombioe.2005.10.003

Christersson L. (1996) Future research on hybrid aspen and hybrid poplar cultivation in Sweden. In: Biomass and Bioenergy. Pergamon Press Inc, p. 109–113. 10.1016/0961-9534(96)00014-1

Christersson L. (1986) High technology biomass production by *Salix* clones on a sandy soil in southern Sweden. Tree Physiol., 2, 261–272. 10.1093/TREEPHYS/2.1-2-3.261

Cook E.R., Briffa K., Shiyatov S., Mazepa V. (1992) Tree-ring standardization and growth trend estimation. In: Cook E.R., Kairiukstis L.A. (Eds.) Methods of Dendrochronology. Kluwer Academic Publishers, Dordrecht, p. 104–123.

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 Press, Tucson, p. 50–65.

Cox S.E., Stushnoff C. (2001) Temperature-related shifts in soluble carbohydrate content during dormancy and cold acclimation in *Populus tremuloides*. Can. J. For. Res., 31, 730–737. 10.1139/x00-206

Cunti X., Haifeng S., Guisheng L., Xingyin W., Zhuo L., Wenqiang D., Jinghua Z., Xipin Z. (1991) Bacterial swollen stem canker on poplar: The disease and its causes. J. Northeast For. Univ., 2, 48–55. 10.1007/bf02874791

Davis S.D., Sperry J.S., Hacke U.G. (1999) The relationship between xylem conduit diameter and cavitation caused by freezing. Am. J. Bot., 86, 1367–1372. 10.2307/2656919

Deslauriers A., Giovannelli A., Rossi S., Castro G., Fragnelli G., Traversi L. (2009) Intra-annual cambial activity and carbon availability in stem of poplar. Tree Physiol., 29, 1223–1235. 10.1093/treephys/tpp061

Devine W.D., Harrington C.A., Debell D.S. (2010) Intra-annual growth and mortality of four *Populus* clones in pure and mixed plantings. New For., 39, 287–299. 10.1007/s11056-009-9171-6

Diamandis S., Koukos P. (1992) Effect of bacteria on the mechanical and chemical properties of wood in poplars damaged by frost cracks. Eur. J. For. Pathol., 22, 362–370. 10.1111/j.1439-0329.1992.tb00308.x

Dillen S.Y., Djomo S.N., Al Afas N., Vanbeveren S., Ceulemans R. (2013) Biomass yield and energy balance of a short-rotation poplar coppice with multiple clones on degraded land during 16 years. Biomass and Bioenergy, 56, 157–165. 10.1016/j.biombioe.2013.04.019

FAO (2016) Poplars and other fast-growing trees—renewable resources for future green economies. Synth. Ctry. Prog. Reports. 25th Sess. Int. Poplar Comm. Berlin, Fed. Repub. Ger. 120.

Ferm A., Hytönen J., Vuori J. (1989) Effect of spacing and nitrogen fertilization on the establishment and biomass production of short rotation poplar in Finland. Biomass, 18, 95–108. 10.1016/0144-4565(89)90087-5

Friedman J.M., Roelle J.E., Gaskin J.F., Pepper A.E., Manhart J.R. (2008) Latitudinal variation in cold hardiness in introduced *Tamarix* and native *Populus*. Evol. Appl., 1, 598–607. 10.1111/j.1752-4571.2008.00044.x

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

Gudynaitė-Franckevičienė V., Pliūra A., Suchockas V. (2020) Ecogenetic plasticity and genetic variation in *Populus* hybrids under the impact of simulated climate change related stressors. Balt. For., 26, 157–169. 10.46490/BF462

Haldimann P., Feller U. (2004) Inhibition of photosynthesis by high temperature in oak (*Quercus pubescens* L.) leaves grown under natural conditions closely correlates with a reversible heat-dependent reduction of the activation state of the ribulose-1,5-bisphosphate carboxylase/oxygenase. Plant, Cell Environ., 27, 1169–1183. 10.1111/j.1365-3040.2004.01222.x

Hall D., Luquez V., Garcia V.M., St Onge K.R., Jansson S., Ingvarsson P.K. (2007) Adaptive population differentiation in phenology across a latitudinal gradient in European aspen (*Populus tremula* L.): A comparison of neutral markers, candidate genes and phenotypic traits. Evolution, 61, 2849–2860. 10.1111/j.1558-5646.2007.00230.x

Hänninen H. (2006) Climate warming and the risk of frost damage to boreal forest trees: Identification of critical ecophysiological traits. Tree Physiol., 26, 889–898. 10.1093/treephys/26.7.889

Hardy J.P., Groffman P.M., Fitzhugh R.D., Henry K.S., Welman A.T., Demers J.D., Fahey T.J., Driscoll C.T., Tierney G.L., Nolan S. (2001) Snow depth manipulation and its

influence on soil frost and water dynamics in a northern hardwood forest. Biogeochemistry, 56, 151–174. 10.1023/A:1013036803050

Harris I., 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. 10.1002/joc.3711

Howe G.T., Saruul P., Davis J., Chen T.H.H. (2000) Quantitative genetics of bud phenology, frost damage, and winter survival in an F2 family of hybrid poplars. Theor. Appl. Genet., 101, 632–642. 10.1007/s001220051525

Ilstedt B. (1996) Genetics and performance of Belgian poplar clones tested in Sweden. For. Genet., 3, 183–195.

Ingvarsson P.K., García M.V., Hall D., Luquez V., Jansson S. (2006) Clinal variation in phyB2, a candidate gene for day-length-induced growth cessation and bud set, across a latitudinal gradient in European aspen (*Populus tremula*). Genetics, 172, 1845–1853. 10.1534/genetics.105.047522

Jansons Ā., Zeps M., Rieksts-Riekstiņš J., Matisons R., Krišāns O. (2014) Height increment of hybrid aspen *Populus tremuloides × P. tremula* as a function of weather conditions in south-western part of Latvia. Silva Fenn., 48(5). 10.14214/sf.1124

Johnson R.W. (2001) An introduction to the bootstrap. Teach. Stat., 23, 49–54.

Jolliffe I.T. (1986) Principal Component Analysis. Springer-Verlag, Berlin.

Jones B., Tardif J., Westwood R. (2004) Weekly xylem production in trembling aspen (*Populus tremuloides*) in response to artificial defoliation. Can. J. Bot., 82, 590–597. 10.1139/b04-032

Junttila O., Kaurin Å. (1990) Environmental control of cold acclimation in *Salix pentandra*. Scand. J. For. Res., 5, 195–204. 10.1080/02827589009382605

Kalcsits L.A., Silim S., Tanino K. (2009) Warm temperature accelerates short photoperiod-induced growth cessation and dormancy induction in hybrid poplar (*Populus × spp.*). Trees, 23, 971–979. 10.1007/s00468-009-0339-7

Karačić A., Adler A., Weih M., Christersson L. (2021) An analysis of poplar growth and quality traits to facilitate identification of climate-adapted plant material for Sweden. Bioenergy Res., 14, 409–425. 10.1007/s12155-020-10210-y

Karačić A., Verwijst T., Weih M. (2003) Above-ground woody biomass production of short-rotation *Populus* plantations on agricultural land in Sweden. Scand. J. For. Res., 18, 427–437. 10.1080/02827580310009113

Karačić A., Weih M. (2006) Variation in growth and resource utilisation among eight poplar clones grown under different irrigation and fertilisation regimes in Sweden. Biomass and Bioenergy, 30, 115–124. 10.1016/j.biombioe.2005.11.007

Landhäusser S.M., Lieffers V.J. (2003) Seasonal changes in carbohydrate reserves in mature northern *Populus tremuloides* clones. Trees, 17, 471–476. 10.1007/s00468-003-0263-1

Laureysens I., Deraedt W., Indeherberge T., Ceulemans R. (2003) Population dynamics in a 6-year old coppice culture of poplar. I. Clonal differences in stool mortality, shoot dynamics and shoot diameter distribution in relation to biomass production. Biomass and Bioenergy, 24, 81–95. 10.1016/S0961-9534(02)00105-8

Laureysens I., Pellis A., Willems J., Ceulemans R. (2005) Growth and production of a short rotation coppice culture of poplar. III Second rotation results. Biomass and Bioenergy, 29, 10–21. 10.1016/j.biombioe.2005.02.005

Lebourgeois F., Bréda N., Ulrich E., Granier A. (2005) Climate-tree-growth relationships of European beech (*Fagus sylvatica* L.) in the French Permanent Plot Network (RENECO-FOR). Trees, 19, 385–401. 10.1007/s00468-004-0397-9

Li B., Howe G.T., Wu R. (1998) Developmental factors responsible for heterosis in aspen hybrids (*Populus tremuloides* × *P. tremula*). Tree Physiol., 18, 29–36. 10.1093/treephys/18.1.29

Li C., Puhakainen T., Welling A., Viherä-Aarnio A., Ernstsen A., Junttila O., Heino P., Palva E.T. (2002) Cold acclimation in Silver birch (*Betula pendula*). Development of freezing tolerance in different tissues and climatic ecotypes. Physiol. Plant., 116, 478–488. 10.1034/j.1399-3054.2002.1160406.x

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. 10.1016/j.foreco.2009.09.023

Marino P.C., Gross K.L. (1998) Competitive effects of conspecific and herbaceous (weeds) plants on growth and branch architecture of *Populus × euramericana* cv. Eugenei. Can. J. For. Res., 28, 359–367. 10.1139/x97-223

Martínez-Cabrera H.I., Schenk H.J., Cevallos-Ferriz S.R.S., Jones C.S. (2011) Integration of vessel traits, wood density, and height in angiosperm shrubs and trees on JSTOR. Am. J. Bot., 98, 915–922.

Mola-Yudego B., Arevalo J., Díaz-Yáñez O., Dimitriou I., Freshwater E., Haapala A., Khanam T., Selkimäki M. (2017) Reviewing wood biomass potentials for energy in Europe: the role of forests and fast growing plantations. Biofuels, 8(4), 401–410. 10.1080/17597269.2016.1271627

Niemczyk M., Kaliszewski A., Jewiarz M., Wróbel M., Mudryk K. (2018) Productivity and biomass characteristics of selected poplar (*Populus* spp.) cultivars under the climatic conditions of northern Poland. Biomass and Bioenergy, 111, 46–51. 10.1016/j.biombioe.2018.02.002

Oberhuber W., Gruber A. (2010) Climatic influences on intra-annual stem radial increment of *Pinus sylvestris* (L.) exposed to drought. Trees, 24, 887–898. 10.1007/s00468-010-0458-1

Ögren E., Nilsson T., Sundblad L.G. (1997) Relationship between respiratory depletion of sugars and loss of cold hardiness in coniferous seedlings over-wintering at raised temperature: Indications of different sensitivities of spruce and pine. Plant, Cell Environ., 20, 247–253. 10.1046/j.1365-3040.1997.d01-56.x

Pallardy S.G. (2008) Physiology of woody plants. Elsevier, London, UK.

Pawson S.M., Brin A., Brockerhoff E.G., Lamb D., Payn T.W., Paquette A., Parrotta J.A. (2013) Plantation forests, climate change and biodiversity. Biodivers. Conserv., 22, 1203–1227. 10.1007/s10531-013-0458-8

Perry C.H., Miller R.C., Brooks K.N. (2001) Impacts of short-rotation hybrid poplar plantations on regional water yield. For. Ecol. Manag., 143, 143–151. 10.1016/S0378-1127(00)00513-2

Pliura A., Suchockas V., Sarsekova D., Gudynaite V. (2014) Genotypic variation and heritability of growth and adaptive traits, and adaptation of young poplar hybrids at northern margins of natural distribution of *Populus nigra* in Europe. Biomass and Bioenergy, 70, 513–529. 10.1016/j.biombioe.2014.09.011

R Core Team (2020) R: The R project for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Regier N., Streb S., Cocozza C., Schaub M., Cherubini P., Zeeman S.C., Frey B. (2009) Drought tolerance of two black poplar (*Populus nigra* L.) clones: Contribution of carbohydrates and oxidative stress defense. Plant, Cell Environ., 32, 1724–1736. 10.1111/j.1365-3040.2009.02030.x

Regier N., Streb S., Zeeman S.C., Frey B. (2010) Seasonal changes in starch and sugar content of poplar (*Populus deltoids × nigra* cv. Dorskamp) and the impact of stem girdling on carbohydrate allocation to roots. Tree Physiol., 30, 979–987. 10.1093/treephys/tpq047

Rohde A., Bastien C., Boerjan W. (2011) Temperature signals contribute to the timing of photoperiodic growth cessation and bud set in poplar. Tree Physiol., 31, 472–482. 10.1093/treephys/tpr038

Rossi P. (1999) Length of cuttings in establishment and production of short-rotation plantations of *Salix* 'Aquatica'. New For., 18, 161–177. 10.1023/A:1006525716499

Saliņš S. (1971) Speciālo kultūru veidi. Grām.: Meža Kultūras. Zvaigzne, Rīga, 379.–409. lpp.

Schreiber S.G., Ding C., Hamann A., Hacke U.G., Thomas B.R., Brouard J.S. (2013) Frost hardiness vs. growth performance in trembling aspen: An experimental test of assisted migration. J. Appl. Ecol., 50, 939–949. 10.1111/1365-2664.12102

Sperry J., Meinzer F., McCulloh K. (2008) Safety and efficiency conflicts in hydraulic architecture: scaling from tissues to trees. Plant, Cell Environ., 31, 632–645. 10.1111/J.1365-3040.2007.01765.X

Sperry J.S., Sullivan J.E.M. (1992) Xylem Embolism in Response to Freeze-Thaw Cycles and Water Stress in Ring-Porous, Diffuse-Porous, and Conifer Species. Plant Physiol., 100, 605. 10.1104/PP.100.2.605

Stener L.-G., Westin J. (2017) Early growth and phenology of hybrid aspen and poplar in clonal field tests in Scandinavia. Silva Fenn., 51, 5656. 10.14214/sf.5656

Sulaiman C., Abdul-Rahim A.S., Ofozor C.A. (2020) Does wood biomass energy use reduce CO_2 emissions in European Union member countries? Evidence from 27 members. J. Clean. Prod., 253, 119996. 10.1016/j.jclepro.2020.119996

Sykes M.T., Prentice I.C. (1996) Climate change, tree species distributions and forest dynamics: A case study in the mixed conifer/northern hardwoods zone of northern Europe. Clim. Change, 34, 161–177. 10.1007/BF00224628

Telenius B.F. (1999) Stand growth of deciduous pioneer tree species on fertile agricultural land in southern Sweden. Biomass and Bioenergy, 16, 13–23. 10.1016/S0961-9534(98)00073-7

Tierney G.L., Fahey T.J., Groffman P.M., Hardy J.P., Fitzhugh R.D., Driscoll C.T. (2001) Soil freezing alters fine root dynamics in a northern hardwood forest. Biogeochemistry, 56, 175–190. 10.1023/A:1013072519889

Trajkovic S. (2005) Temperature-based approaches for estimating reference evapotranspiration. J. Irrig. Drain. Eng., 131, 316–323. 10.1061/(asce)0733-9437(2005)131:4(316)

Tullus A., Rytter L., Tullus T., Weih M., Tullus H. (2012) Short-rotation forestry with hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.) in Northern Europe. Scand. J. For. Res., 27(1), 10–29. 10.1080/02827581.2011.628949

Tullus H., Tullus A., Rytter L. (2013) Short-rotation forestry for supplying biomass for energy production. In: Forest BioEnergy Production: Management, Carbon Sequestration and Adaptation. Springer New York, p. 39–56. 10.1007/978-1-4614-8391-5_3

Verlinden M.S., Broeckx L.S., Ceulemans R. (2015) First vs. second rotation of a poplar short rotation coppice: Above-ground biomass productivity and shoot dynamics. Biomass and Bioenergy, 73, 174–185. 10.1016/j.biombioe.2014.12.012

Verwijst T., Elowson S., Li X., Leng G. (1996) Production losses due to a summer frost in a *Salix viminalis* short-rotation forest in southern Sweden. Scand. J. For. Res., 11, 104–110. 10.1080/02827589609382917

Vicente-Serrano S.M., Beguería S., López-Moreno J.I. (2010) A multiscalar drought index sensitive to global warming: The standardized precipitation evapotranspiration index. J. Clim., 23, 1696–1718. 10.1175/2009JCLI2909.1

Vigl F., Rewald B. (2014) Size matters?—The diverging influence of cutting length on growth and allometry of two Salicaceae clones. Biomass and Bioenergy, 60, 130–136. 10.1016/j.biombioe.2013.11.020

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. 10.1175/1520-0450(1984)023<0201:OTAVOC>2.0.CO;2

Yu Q., Tigerstedt P.M.A., Haapanen M. (2001) Growth and phenology hybrid aspen clones (*Populus tremula* L. × *Populus tremuloides* Michx.). Silva Fenn., 35, 15–25. 10.14214/sf.600

Zalesny R.S., Riemenschneider D.E., Hall R.B. (2005) Early rooting of dormant hardwood cuttings of *Populus*: Analysis of quantitative genetics and genotype x environment interactions. Can. J. For. Res., 35, 918–929. 10.1139/x05-018

Zhao X., Zheng H., Li S., Yang C., Jiang J., Liu G. (2014) The rooting of poplar cuttings: A review. New For., 45, 21–34. 10.1007/s11056-013-9389-1

Silva Šēnhofa, Mārtiņš Zeps, Roberts Matisons, Jānis Smilga, Dagnija Lazdiņa, Āris Jansons

Effect of climatic factors on tree-ring width of *Populus* hybrids in Latvia

Highlights

- Hybrid poplar and hybrid aspen were sensitive to temperature in summer and dormant periods, but none of the tested factors were strictly limiting.
- Hybrid poplar was sensitive to a higher number of climatic factors than hybrid aspen.
- Temperature showed a negative correlation with tree-ring width.

Abstract

Fast-growing hybrids of *Populus* L. have an increasing importance as a source of renewable energy and as industrial wood. Nevertheless, the long-term sensitivity of *Populus* hybrids to weather conditions and hence to possible climatic hazards in Northern Europe have been insufficiently studied, likely due to the limited age of the trees (short rotation). In this study, the climatic sensitivity of ca. 65-year-old hybrid poplars (*Populus balsamifera* L. × *P. laurifolia* Ledeb.), growing at two sites in the western part of Latvia, and ca. 55-year-old hybrid aspens (*Populus tremuloides* Michx. × *P. tremula* L.), growing in the eastern part of Latvia, have been studied using classical dendrochronological techniques. The high-frequency variation of tree-ring width (TRW) of hybrid poplar from both sites was similar, but it differed from hybrid aspen due to the diverse parental species and geographic location of the stands. Nevertheless, some common tendencies in TRW were observed for both hybrids. Climatic factors influencing TRW were generally similar for both hybrids, but their composition differed. The strength of climate-TRW relationships was similar, but the hybrid poplar was affected by a higher number of climatic factors. Hybrid poplar was sensitive to factors related to water deficit in late summer in the previous and current years. Hybrid aspen was sensitive to conditions in the year of formation of tree-ring. Both hybrids also displayed a reaction to temperature during the dormant period. The observed climate-growth relationships suggest that increasing temperatures might burden the radial growth of the studied hybrids of *Populus*.

1 Introduction

Growing demand for timber and renewable energy from biomass (Schueler et al. 2013) is increasing the importance of *Populus* L. hybrids, which are known for high productivity (Yu et al. 2001; Tullus et al. 2013). In the Baltic Sea region, *Populus* hybrids appear especially promising for use on abandoned agricultural lands (Christersson 2007; Tullus et al. 2011, 2013). Still, before wider application of any planting materials, possible interactions with the environment should be comprehensively evaluated. Considering that climate is one of the main factors affecting tree growth and productivity of forest ecosystems (Kirschbaum 2000; Lindner et al. 2010), increments of *Populus* hybrids might be altered due to changes of climate in the future. This has been suggested by the significant short-term (intra-annual) relationships observed between meteorological factors and increment of young *Populus* hybrids (Yu et al. 2001; Tullus et al. 2011; Jansons et al. 2014). Nevertheless, the long-term (inter-annually) variation of increment might be affected by distinct climatic factors compared to that observed for intra-annual variation (Hughes and Funkhouser 2003; Čufar et al. 2008; Seo et al. 2011), and such knowledge might be crucial for sufficient and sustainable management (Burton 2012).

Detailed information about the effects of climatic factors on tree growth in a long-term can be obtained via retrospective analysis of tree-ring parameters by applying dendrochronological techniques (Fritts 2001). The most common parameter for such studies is tree-ring width (TRW) (Speer 2010), although radial increment is formed during a certain part of the growing period (Yu et al. 2001; Deslauriers et al. 2009) and it might be affected by several factors (Cook 1992). Still, there is poor knowledge regarding long-term climate-growth relationships for *Populus* hybrids, likely due to the short rotation (20–30 years) period (Tullus et al. 2013) and hence the young age of trees, which is not sufficient for a dendrochronological analysis (Cook 1992; Fritts 2001). In Latvia, many experimental plantations of hybrid poplar and aspen were established around the 1960s (Mangalis 2004), and some of them have remained as long-term experiments until today. These plantations have provided a unique opportunity to study long-term variation in the radial growth of *Populus* hybrids. Therefore, the aim of this study was to assess the relationships between climatic factors and TRW of hybrid poplar (*Populus balsamifera* L. × *P. laurifolia* Ledeb.) and hybrid aspen (*Populus tremuloides* Michx. × *P. tremula* L.), which were older than 50 and 60 years, respectively. Considering the rapid growth and high transpiration rates of these hybrids, we assumed that factors related to the availability of water during the growing period have mainly affected their growth.

2 Materials and methods

2.1 Study areas, sampling, and measurements

Hybrid poplars (no additional information about the origin was available) were sampled in two experimental plantations in the western part of Latvia near Auce (AUC) (56°31´N, 22°56´E) and Šķēde (SKD) (57°14´N, 22°37´E). Hybrid aspens, the progenies of *P. tremuloides* growing in a botanical garden in the central part of Latvia (no information on the origin was available) and 10 local *Populus tremula* plus trees from the eastern part of Latvia, were sampled in one plantation in the eastern part of Latvia near Jaunkalsnava (KLN) (56°41´N, 25°54´E). The ages of the AUC, SKD and KLN plantations were 63, 68 and 56, respectively. The initial spacing of the trees at all sites was 3 × 3 m. The elevations of the studied stands were low, about 70, 110, and 100 m a.s.l. at the AUC, SKD, and KLN sites, respectively. The topography of all stands was flat. The studied stands were growing on fertile loamy soil under normal moisture conditions (corresponding to the

Oxalidosa forest type). The climate in the studied sites was mild due to dominant winds, which bring cool and moist air masses from the Baltic Sea and the Atlantic; hence, the continentality of the climate was stronger in the eastern site. The mean monthly temperature ranged from ca. –3.5 and –6.0 to ca. +15.4 and +16.8 °C in January and July (the mean annual temperature was ca. +6 and +5 °C) in the sites in the western and eastern part of Latvia, respectively. The growing period usually extends from mid-April to mid-October. The mean annual precipitation in all sites was ca. 620 mm. The highest monthly precipitation occurs in the summer months (May–September), which usually results in a positive water balance throughout the year (Klavins and Rodinov 2010). A stable snow cover usually forms beginning with the last week of December, and it lasts until the first week of April. Climatic changes are mainly expressed as an increase of temperature in the autumn to spring period and as an extension of the growing period (Lizuma et al. 2007), while the precipitation regime in the summer is becoming more variable (Avotniece et al. 2010).

Visually healthy trees representing the diameter distribution of the plantations were selected according to trial inventories and felled in November and December of 2013. In total, 26 hybrid poplars (13 trees from each site) and 22 hybrid aspens were sampled. From each log, a stem disk at 1.3 m above the root collar was taken. In the laboratory, the surface of air-dried stem disks was gradually grinded with sandpaper (80, 120, 240 and 400 grains per inch). Tree-ring width was measured using the Lintab 5 (RinnTECH, Germany, Heidelberg) measurement system with the precision of 0.01 mm along two opposite radii of the stem, avoiding the reaction wood.

2.2 Data analysis

The time series of TRW were crossdated, and the quality was checked by a graphical inspection and statistically using the program COFECHA (Grissino-Mayer 2001). The time series, which showed low agreement with the rest of the dataset (r<0.40), were rejected from further analysis rather than corrected. The statistics of the crossdated datasets, expressed population signal (EPS) (Wigley et al. 1984), Gleichläufigkeit (GLK), mean interseries correlation, signal to noise ratio (SNR) and first order autocorrelation, for the detrended time series were calculated in program R using the library "dplR" (Bunn 2008). Residual chronologies of TRW were established using the program ARSTAN (Cook and Holmes 1986). Double detrending by a negative exponential curve and cubic spline with rigidity of 40 years was applied and autocorrelation was removed. The effect of climatic factors on the annual variation of the TRW was assessed by a bootstrapped Pearson correlation analysis (Johnson 2001). The tested climatic factors were minimum, maximum, and mean monthly temperature, monthly range of temperature, monthly precipitation, and potential evapotranspiration (PET). Considering the number of tested factors and the length of chronology, a response function analysis was not performed. Local climatic data were obtained from the high-resolution database of the Climatic Research Unit of UEA (Harris et al. 2014) for grid centres located less than 20 km from the studied plantations. Climatic factors were arranged according to the time window from January of the year preceding the formation of tree-ring to September of the year of tree-ring formation. Multicolinearity was assessed for significant factors.

3   Results

Most of the measured time-series of the TRW of hybrid poplar and hybrid aspen were used for the construction of local chronologies (one series for the AUC and KLN and three series for the SKD datasets were rejected). Crossdated time series of TRW showed good agreement (Fig. 1 A, B, C), as the values of EPS exceeded 0.85 and the mean interseries correlation of the datasets was
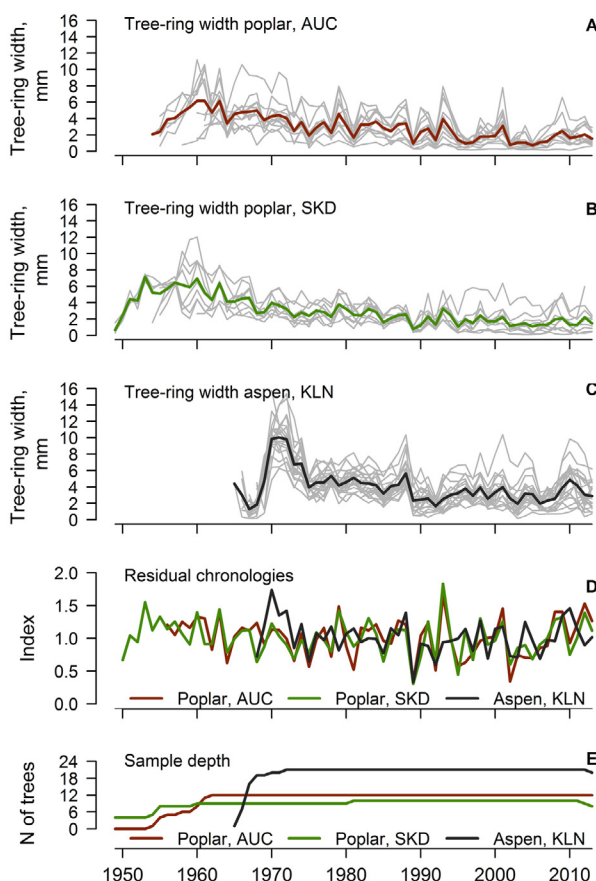
Fig. 1. Crossdated time series of tree-ring width of hybrid poplar in Auce (AUC) (A) and Šķēde (SKD) (B) sites in the western part of Latvia (thick lines represent mean values), crossdated time series of hybrid aspen (C) from Kalsnava (KLN) site in the eastern part of Latvia, residual chronologies of tree-ring width (D) and sample depth of the datasets (E).

above 0.40 (Table 1). Hybrid poplar displayed a pronounced annual variation of TRW as shown by the mean sensitivity exceeding 0.40. The agreement of TRW of hybrid poplar was better in the AUC than the SKD site, where the environmental signal in the TRW was stronger, as shown by the higher SNR of the time series (10.77 and 6.17, respectively). The agreement and signal strength of the TRW series was even better for the hybrid aspen, as shown by the higher values of interseries correlation, EPS and SNR, although the mean sensitivity was slightly lower (Table 1). The range and mean value of the TRW was higher for hybrid aspens than for poplars, which were older (Table 1); however, at a similar cambial age, the TRW appeared the same (not shown). A decrease in the sample depth was observed after 2010 due to the occurrence of missing rings in a few trees.

Table 1. Statistics of crossdated datasets of tree-ring width (TRW) of hybrid poplar and hybrid aspen in stands near Auce (AUC), Šķēde (SKD) and Kalsnava (KLN).

	Hybrid poplar		Hybrid aspen
	AUC	SKD	KLN
Covered period	1954–2013	1949–2013	1965–2013
Number of crossdated trees	12	10	21
Min. TRW, mm	0.12	0.09	0.14
Max. TRW, mm	11.19	12.01	15.74
Mean TRW, mm	2.88	2.86	4.01
Standard deviation, mm	1.86	0.92	2.28
Mean sensitivity	0.42	0.40	0.35
Mean interseries correlation	0.51	0.42	0.51
Autocorrelation	0.56	0.74	0.69
Expressed population signal	0.92	0.86	0.95
Gleichläufigkeit	0.69	0.68	0.70
Signal to noise ratio	10.77	6.17	19.74

Residual chronologies of TRW were established for each stand (Fig. 1 D). The ranges of chronology indices of hybrid poplar and aspen were similar, but the hybrid aspen had a slightly lower annual variation of TRW indices. Residual chronologies of hybrid poplar were rather synchronous (Fig. 1 D), as the GLK and correlation coefficients calculated between them were 0.77 and 0.78, respectively. In contrast, the high-frequency variation of the TRW of hybrid aspen differed from poplar as suggested by weak correlations between the chronologies (mean r = 0.24). Nonetheless, the mean GLK index calculated between the chronologies of aspen and poplar was 0.51, suggesting similar tendencies in the growth of both hybrids. A few common abrupt changes (decrease) in the TRW occurred in 1975, 1989 and 2002 for both aspen and poplar (Fig. 1 D). These decreases of TRW coincided with extremely high mean monthly temperatures in the December–August period from 1974–1975, 1988–1989 and 2001–2002, accompanied by a rapid drop of temperature in the autumn or winter preceding the formation of the tree-ring.

Residual chronologies of TRW of hybrid poplar and hybrid aspen significantly correlated with 12 and four of the 132 tested factors, respectively, but the values of correlation coefficients did not exceed 0.35. In the case of the hybrid poplar, the sets of the significant correlations were similar at both sites, although some local specifics were apparent (Fig. 2 A, B). Generally, the TRW of hybrid poplar was sensitive to the temperature regime in late summer in the year of tree-ring formation and in the preceding year. A significant effect of PET in August was observed. Precipitation in January of the previous year was the only factor that correlated positively with the TRW of hybrid poplar at both sites. Nevertheless, in the SKD site, the TRW of the hybrid poplar was additionally sensitive to temperature in February, March and June, while the monthly range of temperature in September of the current year was significant at the AUC site. Although the number of significant relationships was lower, the TRW of hybrid aspen generally correlated with the same climatic factors as the hybrid poplar (Fig. 2 C). The mean temperature in March and the temperature range in July and September of the current year had a negative effect on the TRW. Additionally, hybrid aspen showed sensitivity to precipitation in July of the current year, but the value of the correlation coefficient was lower than that observed for other factors.
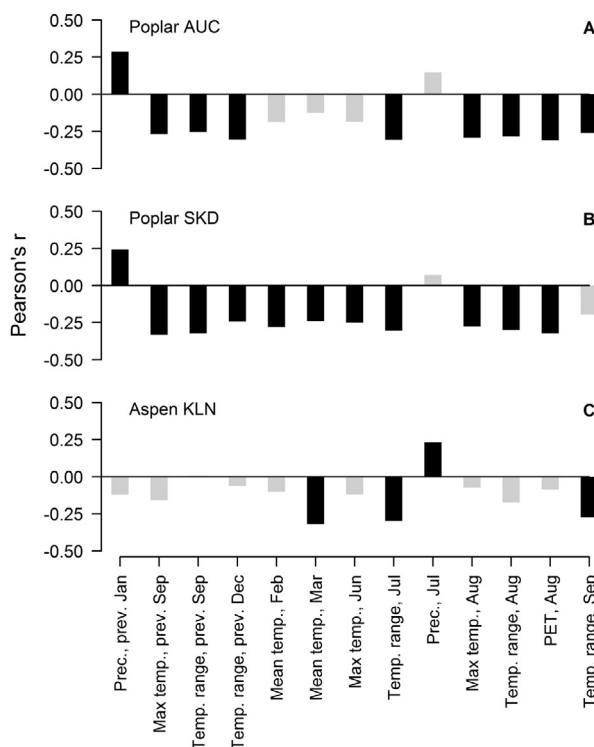
Fig. 2. Significant Pearson correlation coefficients (black bars) between climatic factors and residual chronologies of the TRW of hybrid poplar in Auce (AUC) (A) and Šķēde (SKD) (B) sites in the western part of Latvia and the residual chronology of hybrid aspen at the Kalsnava (KLN) site in the eastern part of Latvia (C). Collinear factors have been omitted. PET-potential evapotranspiration.

4   Discussion

Good agreement and similarity of the high-frequency variation of the time series of the TRW among trees within each stand (Fig. 1 A, B, C) suggested a pronounced effect of common environmental factors on the radial growth of hybrid aspen and hybrid poplar. The EPS values, which exceeded 0.85 (Table 1), showed that the obtained datasets of the TRW were sufficient for the assessment of the local variability of growth (Wigley et al. 1984). The mean sensitivity of the trees was rather high (> 0.35), and the autocorrelation was intermediate (ca. 0.66), suggesting that trees have been promptly reacting to environmental changes (Speer 2010). The SNR of TRW datasets was high (> 6, Table 1), which might be explained by the similar growing conditions (plantation) and by the genetic similarity of the planted material within each of the plantations. The contrast in SNR between the poplar stands (Table 1) likely rose from the difference in climate due to the distance from the sea, which was higher at the AUC site than at the SKD site, resulting in slightly stronger continentality. This is also supported by an even higher SNR (> 19) observed for hybrid aspen (Table 1) in the eastern part of Latvia, where the climate is harsher.

The established local chronologies of hybrid poplar (Fig. 1 D) were similar ($r > 0.75$), as the same hybrids had been planted, although the sites were located at a ca. 90 km distance away. This suggested that the growth has been affected by common regional-scale factors. The distinction of the high-frequency variation of the TRW of hybrid aspen from hybrid poplar (Fig. 1 D) likely occurred due to the different parental species and their origins. The studied aspens were a hybrid of a northern species, while the parents of the poplars were southern species (Tullus et al. 2013), which are adapted to different conditions (Stettler 1996) and therefore differ in their sensitivity to weather conditions. The differences in the high-frequency variation between aspen and poplar (Fig. 1 D) also might be related to the geographic distance between the sites (ca. 200 km) and to the differences in climate (Fritts 2001) or site conditions. Nevertheless, the occurrence of common decreases in the TRW in 1975, 1989 and 2002 (Fig. 1 D) suggested that both hybrids exhibited similar reaction to weather anomalies. The sensitivity to some common factors has been also supported by the intermediate synchrony between the chronologies of the studied hybrids.

Radial growth of the studied hybrids was sensitive to weather conditions as shown by the significant correlations, but the effect of the tested climatic factors was not strictly limiting for the TRW, as the coefficient values were low (Fig. 2). Considering the higher number of significant factors (Fig. 2), hybrid poplar appeared more sensitive to climate than hybrid aspen although the SNR in the TRW of poplar was lower (Table 1). The weaker signal has apparently been caused by interference among more numerous influencing factors and/or by a shift of their effects over time (Cook 1992; Büntgen et al. 2006). This might be also related to the differences in the high-frequency variation of the TRW between poplar and aspen (Fig. 1 D), although the significant factors for TRW have generally been similar (Fig. 2).

The TRW of hybrid poplar correlated with climatic factors in the current and previous years (Fig. 2 A, B), suggesting a dual effect of weather conditions on the radial increment. The relationships between the TRW and weather conditions in the year preceding the formation of the tree-ring might be explained by the amount of nutrient reserves (Barbaroux and Breda 2002; Pallardy 2008) that accumulate at the end of the growing period and are deployed for early growth in the next spring (Landhäusser and Lieffers 2003; Jones et al. 2004; Regier et al. 2010). The effect of weather conditions of the current year on the TRW might be related to the altered assimilation of nutrients (Berry and Downton 1982), influencing xylogenesis later in the growing period (Miina 2000; Lebourgeois et al. 2005).

Late summer is the period when nutrient reserves are produced (Barbaroux and Breda 2002; Landhäusser and Lieffers 2003; Regier et al. 2010). Increased temperature intensifies evapotranspiration (Traykovic 2005), which might cause a temporary water deficit, resulting in drought stress (Pallardy 2008) and hindering the assimilation (Regier et al. 2009), which would explain the observed negative correlations of the TRW with temperature and PET (Fig. 2 A, B). The hot summers are also usually dry, thus supporting the observed relationships. Additionally, stands of fast growing broadleaved trees are known for intense evapotranspiration, performing as natural pumps (Perry et al. 2001), thus magnifying the effect of a water deficit. Increased summer temperature can also directly hinder cambial activity (xylogenesis) (Deslauriers et al. 2007; Oberhuber and Gruber 2010) and/or photosynthesis (Haldimann and Feller 2004). Formation of latewood, which occurs around August (Deslauriers et al. 2009), is influenced by the current assimilation (Jones et al. 2004), explaining the negative effect of temperature factors of the current summer (Fig. 2). *Populus* hybrids have a longer growing period compared to their parental species (Yu et al. 2001; Tullus et al. 2011); therefore, the TRW has been sensitive to conditions (temperature) in September (Fig. 2 B). The negative effect of the monthly temperature range during the growing period (Fig. 2) might be related to the stress caused by the shifting environment, as biochemical and physiological processes in trees need to be adjusted to certain conditions (Berry and Downton

1982; Pallardy 2008). September is the time when the first frosts usually occur, particularly when high-pressure systems determine weather; therefore, correlation of the TRW with the temperature range in September (Fig. 2) might be related to a frost damage. The negative effect of temperature and its shifts in the dormant period (Fig. 2) might be explained by cold dehardening in response to thaws (Alden and Herman 1971; Cox and Stushnoff 2001), thus subjecting trees to stronger cold damage in a following drop of temperature (Hänninen 2006). Increased winter temperature can also burden dormancy and cause a depletion of nutrient reserves due to respiration (Foote and Scheadle 1976; Ögren et al. 1997). Precipitation in January is usually in the form of snow. A thicker snow layer has better insulating properties that decrease the depth of soil freeze and minimise fluctuation of soil temperature (Hardy et al. 2001), decreasing root mortality (Tierney et al. 2001) and facilitate water uptake, thus promoting growth (Fig 2, A, B). The one-year lag in reaction of the TRW to winter precipitation (Fig. 2 A, B) might be explained by the allocation of the spared resources to stem growth in the following year (Nguyen et al. 1990; Jones et al. 2004).

The radial increment of hybrid aspen was more affected by the current assimilation than that of poplar as the TRW showed significant correlations with climatic factors in the year of the tree-ring formation (Fig. 2 C). Nevertheless, temperature in March had the strongest effect on the TRW, likely increasing the respiratory loss of nutrient reserves before bud swelling due to burdened dormancy (Foote and Scheadle 1976; Ögren et al. 1997) or increasing the susceptibility to frost damage (Alder and Herman 1971). The negative correlation with July temperature (Fig. 2 C) implied the effect of a water deficit, as observed for the hybrid poplar. However, the hybrid aspen showed a positive reaction to precipitation in the summer (Fig. 2 C), suggesting that it has been able to recover from drought stress more quickly than the poplar and utilise available precipitation for growth as observed for other hybrids (Mazzoleni and Dickmann 1988).

In general, the strength of the observed climate-TRW correlations and number of significant factors for the studied *Populus* hybrids (Fig. 2), the native pedunculate oak (*Quercus robur* L.) (Matisons and Brūmelis 2012) and Scots pine (*Pinus sylvestris* L.) (Elferts 2008) were comparable. *Populus* hybrids and oak were both sensitive to factors related to water stress in the summer. In contrast, oak and pine showed positive correlations with temperature in the winter months, suggesting that the warming of the climate might be less favourable for the studied hybrids, which have been selected to fit past climates.

5 Conclusions

The growth of the studied *Populus* hybrids has been significantly affected by weather conditions; however, the observed correlations suggest that none of the tested factors have been strictly limiting. Climatic factors, which are related to water deficit and to drought stress in the summer, have been the main climatic determinants of the TRW, likely via influence on nutrient reserves, current assimilation and hence xylogenesis. Nevertheless, hybrid poplar appeared more affected by the stored nutrient reserves than hybrid aspen. Both of the studied hybrids showed sensitivity to temperature in the winter; however, the correlations were negative, implying that increased temperature burdened the formation of the tree-ring, likely facilitating respiratory loss of nutrient reserves and/ or decreasing cold hardiness and subjecting the trees to damage from low temperature. Although the strength of relationships between the TRW and climatic factors was similar, hybrid poplar appeared more sensitive to climatic factors than hybrid aspen, as suggested by the higher number of significant climatic factors. Nevertheless, the observed relationships show that in a warming climate, the radial growth of both poplar hybrids might be burdened due to the increasing water deficit and damage by shifting weather in the winter.

Acknowledgements

References

Alden J., Herman R.K. (1971). Aspects of the cold-hardiness mechanism in plants. The Botanical Review 37: 37–142. http://dx.doi.org/10.1007/BF02860300.

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.

Berry J.A., Downton W.J.S. (1982). Environmental regulation of photosynthesis. In: Govindjee (ed.). Photosynthesis: development, carbon metabolism and plant productivity, Vol. 2. Academic Press, New York. p. 265–345.

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.

Büntgen U., Frank D.C., Schmidhalter M., Neuwirth B., Seifert M., Esper J. (2006). Growth/climate response shift in a long subalpine spruce chronology. Trees 20: 99–110. http://dx.doi.org/10.1007/s00468-005-0017-3.

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

Christersson L. (2007). Poplar plantations for paper and energy in the south of Sweden. Biomass and Bioenergy 32: 997–1000. http://dx.doi.org/10.1016/j.biombioe.2007.12.018.

Cook E.R. (1992). A conceptual linear aggregate model for tree rings. In: Cook E.R., Kairiukstis L.A. (eds.). Methods of dendrochronology: application in the environmental sciences. Kluwer Academic Publishers, Dordrecht. p. 98–104.

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 Press, Tucson, Arizona. p. 50–65.

Cox S.E., Stushnoff C. (2001). Temperature-related shifts in soluble carbohydrate content during dormancy and cold acclimation in *Populus tremuloides*. Canadian Journal of Forest Research 34: 730–737. http://dx.doi.org/10.1139/x00-206.

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: 749–758. http://dx.doi.org/10.1007/s00468-008-0235-6.

Deslauriers A., Anfodillo T., Rossi S., Carraro V. (2007). Using simple causal modeling to understand how water and temperature affect daily stem radial variation in trees. Tree Physiology 27: 1125–1136. http://dx.doi.org/10.1093/treephys/27.8.1125.

Deslauriers A., Giovannelli A., Rossi S., Castro G., Frangelli G., Traversi L. (2009). Intra-annual cambial activity and carbon availability in stem of poplar. Tree Physiology 29: 1223–1235. http://dx.doi.org/10.1093/treephys/tpp061.

Elferts D. (2008). Influence of climatic factors on the radial growths of Scots pine *Pinus sylvestris* L. in Western Latvia on dry soils. University of Latvia, doctoral thesis. 84 p.

Foote K.C., Scheadle M. (1976). Diurnal and seasonal patterns of photosynthesis and respiration by stems of *Populus tremuloides* Michx. Plant Physiology 58: 651–655. http://dx.doi.org/10.1104/pp.58.5.651.

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.

Haldimann P., Feller U. (2004). Inhibition of photosynthesis by high temperature in oak (*Quercus pubescens* L.) leaves grown under natural conditions closely correlates with a reversible heat dependent reduction of the activation state of ribulose-1,5-bisphosphate carboxylase/oxygenase. Plant Cell and Environment 27: 1169–1183. http://dx.doi.org/10.1111/j.1365-3040.2004.01222.x.

Hänninen H., 2006. Climate warming and the risk of frost damage to boreal forest trees: identification of critical ecophysiological traits. Tree Physiology 26: 889 –898. http://dx.doi.org/10.1093/treephys/26.7.889.

Hardy J.P., Groffman P.M., Fitzhugh R.D., Henry K.S., Welman A.T., Demers J.D., Fahey T.J., Driscoll C.T., Tierney G.L., Nolan S. (2001). Snow depth manipulation and its influence on soil frost and water dynamics in a northern hardwood forest. Biogeochemistry 56: 151–174. http://dx.doi.org/10.1023/A:1013036803050.

Harris I., 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. http://dx.doi.org/10.1002/joc.3711.

Hughes M.K., Funkhouser G. (2003). Frequency-dependent climate signal in upper and lower forest border tree rings in the mountains of the Great Basin. In: Diaz H.F. (ed.). Climate variability and change in high elevation regions: past, present and future. Springer, New York. p. 233–244. http://dx.doi.org/10.1007/978-94-015-1252-7_11.

Jansons Ā., Zeps M., Rieksts-Riekstiņš J., Matisons R., Krišāns O. (2014). Height increment of hybrid aspen *Populus tremuloides × P. tremula* as a function of weather conditions in southwestern part of Latvia. Silva Fennica vol. 48 no. 5 article 1124. 13 p. http://dx.doi.org/10.14214/sf.1124.

Johnson R.W. (2001). An introduction to bootstrap. Teaching Statistics 23: 49–54. http://dx.doi.org/10.1111/1467-9639.00050.

Jones B., Tardif J., Westwood R. (2004). Weekly xylem production in trembling aspen (*Populus tremuloides*) in response to artificial defoliation. Canadian Journal of Botany 82: 590 –597. http://dx.doi.org/10.1139/b04-032.

Kirschbaum M.U.F. (2000). Forest growth and species distribution in a changing climate. Tree Physiology 20: 309–322. http://dx.doi.org/10.1093/treephys/20.5-6.309.

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

Landhäusser S.M., Lieffers V.J. (2003). Seasonal changes in carbohydrate reserves in mature northern *Populus tremuloides* clones. Trees 17: 471–476. http://dx.doi.org/10.1007/s00468-003-0263-1.

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 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. Forest Ecology and Management 259: 698–709. http://dx.doi.org10.1016/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, Latvia. p. 11–20.

Mangalis I. (2004). Regeneration and establishment of forest. [Meža atjaunošana un ieaudzēšana]. Et Cetera, Riga. 455 p [In Latvian].

Matisons R., Brūmelis G (2012). Influence of climate on tree-ring and earlywood vessel formation in *Quercus robur* in Latvia. Trees-Structure and Function 26: 1251–1266. http://dx.doi.org/10.1007/s00468-012-0701-z.

Mazzoleni S., Dickmann D.I. (1988). Differential physiological and morphological responses of two hybrid *Populus* clones to water stress. Tree Physiology 4: 61 –70. http://dx.doi.org/10.1093/treephys/4.1.61.

Miina J. (2000). Dependence of tree-ring, earlywood and latewood indices of Scots pine and Norway spruce on climatic factors in eastern Finland. Ecological Modelling 132: 259–273. http://dx.doi.org/10.1016/S0304-3800(00)00296-9.

Nguyen P.V., Dickmann D.I., Pregitzer K.S., Hendrick R. (1990). Late-season changes in allocation of starch and sugar to shoots, coarse roots, and fine roots in two hybrid poplar clones. Tree Physiology 7: 95–105. http://dx.doi.org/10.1093/treephys/7.1-2-3-4.95.

Oberhuber W., Gruber A. (2010). Climatic influences on intra-annual stem radial increment of *Pinus sylvestris* (L.) exposed to drought. Trees 24: 887–898. http://dx.doi.org/10.1007/s00468-010-0458-1.

Ögren E., Nilsson T., Sundblad L.G. (1997). Relationship between respiratory depletion of sugars and loss of cold hardiness in coniferous seedlings over-wintering at raised temperatures: indications of different sensitivities of spruce and pine. Plant, Cell and Environment 20: 47–253. http://dx.doi.org/10.1046/j.1365-3040.1997.d01-56.x.

Pallardy S.G. (2008). Physiology of woody plants, third ed. Elsevier, London, UK. 464 p.

Perry C.H., Miller R.C., Brooks K.N. (2001). Impacts of short-rotation hybrid poplar plantations on regional water yield. Forest Ecology and Management 143: 143 –151. http://dx.doi.org/10.1016/S0378-1127(00)00513-2.

Regier N., Streb S., Cocozza C., Schaub M., Cherubini P., Zeeman S.C., Frey B. (2009). Drought tolerance of two black poplar (*Populus nigra* L.) clones: contribution of carbohydrates and oxidative stress defence. Plant, Cell and Environment 32: 1724 –1736. http://dx.doi.org/10.1111/j.1365-3040.2009.02030.x.

Regier N., Streb S., Zeeman S.C., Frey B. (2010). Seasonal changes in starch and sugar content of poplar (*Populus deltoides* × *nigra* cv. Dorskamp) and the impact of stem girdling on carbohydrate allocation to roots. Tree Physiology 30: 979–987. http://dx.doi.org/10.1093/treephys/tpq047.

Schueler V., Weddige U., Beringer T., Gamba L., Lamers P. (2013). Global biomass potentials under sustainability restrictions defined by the European Renewable Energy Directive 2009/28/ EC. GCB Bioenergy 5: 652–663. http://dx.doi.org/10.1111/gcbb.12036.

Seo J.W., Eckstein D., Jalkanen R., Schmitt U. (2011). Climatic control of intra- and inter-annual wood-formation dynamics of Scots pine in northern Finland. Environmental and Experimental Botany 72: 422–431. http://dx.doi.org/10.1016/j.envexpbot.2011.01.003.

Speer J.H. (2010). Fundamentals of tree-ring research. The University of Arizona Press, Tucson, Arizona. 333 p.

Stettler R.F. (1996). Biology of *Populus* and its implications for management and conservation. NRC Research Press, Ottawa. 539 p. http://dx.doi.org/10.1139/cjm-2014-0362.

Tierney G.L., Fahey T.J., Groffman P.M., Hardy J.P., Fitzhugh R.D., Driscoll C.T. (2001). Soil freezing alters fine root dynamics in a northern hardwood forest. Biogeochemistry 56: 175–190. http://dx.doi.org/10.1023/A:1013072519889.

Traykovic S. (2005). Temperature-based approaches for estimating reference evapotranspiration. Journal of Irrigation and Drainage Engineering-ASCE 131: 316–323. http://dx.doi.org/10.1061/(ASCE)0733-9437(2005)131:4(316).

Tullus A., Rytter L., Tullus T., Weih M., Tullus H. (2011). Short-rotation forestry with hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.) in Northern Europe. Scandinavian Journal of Forest Research 27: 10–29. http://dx.doi.org/10.1080/02827581.2011.628949.

Tullus H., Tullus A., Rytter L. (2013). Short-rotation forestry for supplying biomass for energy production. In: Kellomäki S., Kilpeläinen A., Alam A. (eds.). Forest bioenergy production. Springer, New York. p. 39–56. http://dx.doi.org/10.1007/978-1-4614-8391-5_3.

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.

Yu Q., Tigerstedt P.M.A., Haapanen M. (2001). Growth and phenology of hybrid aspen clones (*Populus tremula* L. × *Populus tremuloides* Michx.). Silva Fennica 35: 15–25. http://dx.doi.org/10.14214/sf.600.

Total of 53 references.

ORIGINAL ARTICLE

High-frequency variation of tree-ring width of some native and alien tree species in Latvia during the period 1965–2009

Āris Jansons, Roberts Matisons *, Silva Šēnhofa, Juris Katrevičs, Jānis Jansons

Latvian State Forest Research Institute "Silava", Rigas str. 111, Salaspils, LV2169, Latvia

ABSTRACT

The plasticity of climate-growth relationships of trees is one of the main factors determining the climate-induced changes in forest productivity and composition. In this study, high-frequency variation of tree-ring width (TRW) of four native and three alien tree species and two hybrids of *Populus* L. growing in Latvia (hemiboreal zone) was compared using a principal component analysis based on TRW indices for the period 1965–2009. The effect of climatic factors was assessed using a bootstrapped correlation analysis. Influence of common climatic factors related to the length of the vegetation season, winter temperature, and water regime in summer was traced in the TRW of the studied species and hybrids. The combination and effect of the identified factors differed by species (and hybrids), to a certain extent explaining the diversity of TRW patterns. Nevertheless, some similarities among the species were also observed, suggesting the plasticity of growth response. Scots pine was generally sensitive to winter temperatures, but Norway spruce was mainly sensitive to summer water regime, while black alder was sensitive to winter temperatures and precipitation in spring. In contrast, silver birch showed the lowest sensitivity to the tested climatic factors (demonstrating sensitivity to winter precipitation in a few sites), suggesting tolerance to weather fluctuations. The TRW of the alien species was primarily sensitive to climatic factors related to water regime in the summer of the year preceding the formation of tree-ring, implying differences in mechanisms regulating wood increment. Nevertheless, temperature in the dormant period was significant for European larch in a few sites, suggesting sensitivity to cold damage. The variation of TRW of *Populus* hybrids diverged from others, as their growth was negatively correlated with the temperature in autumn, spring, and summer and positively correlated with water balance. Although the annual water balance in Latvia is positive, the effect of water deficit on tree growth was apparent.

© 2016 Published by Elsevier GmbH.

1. Introduction

Considerable shifts in vegetation zones are predicted in response to climatic changes (Hickler et al., 2012) altering forest productivity (Lindner et al., 2010) and leading to economic consequences (Hanewinkel et al., 2012). Such changes already have been explicit in southern margins of the boreal zone, where thermophilic species have gained advantage over species favouring cooler climates, thus shifting stand composition (Goldblum and Rigg, 2005; Kullman, 2008). Hence, adjustments in forest management might be necessary to cope with the shifting conditions and to take advantage of them (Spittlehouse and Stewart, 2004; Kirilenko and Sedjo, 2007). Considering the predicted changes in vegetation zones in Eastern and Northern Europe (Reich and Oleksyn, 2008; Hickler

et al., 2012), use of species or provenances suitable for a future climate (i.e., with high ecological plasticity or native to the regions with warmer climates) has been advised as one of the means for maintaining or even increasing forest productivity (Lindner, 2000; Bolte et al., 2009). Still, before applying any changes in policies, the advantages of novel and conventional species should be comprehensively evaluated. For this reason, information about tree growth patterns and sensitivity to climatic factors can be expedient.

Detailed information about tree growth and its reaction to climatic factors can be obtained through a retrospective analysis of increment, which is archived in the wood, e.g., in tree-ring width (TRW) (Speer, 2010). In this respect, trees that are growing near or even outside of their natural (climate-determined) distribution area are considered good indicators of environmental changes due to the expressed effect of limiting factors (Grace et al., 2002; Chmura, 2004; Kullman, 2008). Nevertheless, trees that are growing in the non-marginal parts of the distribution areas are also sensitive to climatic factors, but the influence is more complex

---

* Corresponding author.
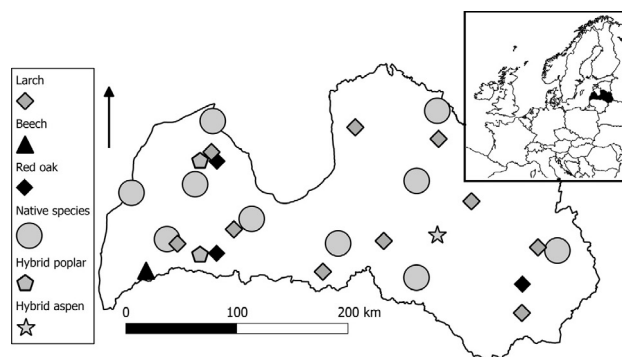 *E-mail address:* robism@inbox.lv (R. Matisons).

Fig. 1. The location of the studied stands of Scots pine, Norway spruce, silver birch, black alder, European larch, red oak, European beech, hybrid poplar, and hybrid aspen. The circles represent the locality of the sampled stands of native species (Scots pine, Norway spruce, silver birch, and black alder).

(Wilson and Elling, 2004; Friedrichs et al., 2009). Hence, the analysis of increment and its relationships with climate might be used to assess the growth potential of different species (Stott and Loehle, 1998; Scheller and Mladenoff, 2005). The effect of climate and its changes on tree growth may vary regionally or even locally (Wilmking et al., 2004; Lindner et al., 2010); therefore, wide spatial extrapolation of such knowledge might be misleading, and local information is needed.

Latvia is located in the hemiboreal zone (Sjors, 1963), and more than half of its territory is covered by forests, which are often mixed. According to the data from the National Forest Inventory, at present, Scots pine (*Pinus sylvestris* L.), silver birch (*Betula pendula* Roth), Norway spruce (*Picea abies* H. Karst.), Eurasian aspen (*Populus tremula* L.), and black alder (*Alnus glutinosa* Gaertn.) are the most common and economically important tree species that occur in the mid-part of their distribution areas (EUFORGEN, 2009). Still, considerable changes in forest growth and species composition (i.e., expansion of the deciduous trees) is expected during the 21st century (Reich and Oleksyn, 2008; Hickler et al., 2012). Hence, the native deciduous and introduced southern species might already have some advantages over the native conifers.

Several introduction experiments have been established since the 19th century in Latvia (Laiviņš et al., 2009). European larch (*Larix decidua* Mill.) is the most commonly introduced tree species (ca. 1100 ha), which occurs north of its natural range (EUFORGEN, 2009). Red oak (*Quercus rubra* L.), which is native to central regions of North America, where the climatic conditions are comparable with Latvia (Sander, 1990), has been planted on ca. 50 ha, particularly since the 1960s. European beech (*Fagus sylvatica* L.) has been planted since the 1870s, and at present, occupies ca. 40 ha, particularly in the western part of Latvia, which, at present, comprises the north-easternmost beech stands in Europe (Bolte et al., 2007). The growth of these species has not been suppressed and successful self-regeneration has been observed (Laiviņš et al., 2009). Several plantations of hybrid aspen (*Populus tremuloides* Michx. × *P. tremula* L.) and hybrid poplar (*Populus balsamifera* L. × *P. laurifolia* Ledeb.) have remained as the long-term experiments since the 1960s (Mangalis, 2004).

The aim of the study was to assess the similarity of the high-frequency (i.e., annual) variation of TRW of the most common native and introduced tree species and hybrids, and to characterise their sensitivity to climatic factors during recent decades, when climate change has been accelerating. We hypothesised that

species and hybrids express specific variation of TRW due to distinct ecological demands, and hence sensitivity to diverse climatic factors; yet, some common variation in TRW might be imposed by the changing climate.

2. Material and methods

2.1. Datasets

The studied datasets consisted of the time series of TRW (measured with the accuracy of 0.01 mm along two opposite radii) representing stem increment at 1.3 m height of the four most common native tree species (Scots pine, Norway spruce, silver birch, and black alder), three alien tree species (European beech, European larch, and red oak), and two hybrids of *Populus* L. (hybrid poplar and hybrid aspen). The native species were sampled in stands in 10 localities, and European larch was sampled in 11 stands that were regularly distributed across the country (Fig. 1). The number of the sampled stands of other alien species and hybrids was lower (Table 1), and they were distributed irregularly (Fig. 1). In each stand, 10 to 25 dominant trees were sampled. Stands of pine, spruce, birch, and larch were growing in dry mesotrophic sites on sandy or silty soils. Beech, red oak, and *Populus* hybrids were growing in dry fertile sites on silty soils, but alder was growing in periodically (in spring) waterlogged sites (particularly in depressions). The topography of all sites was flat. The elevation of the studied stands was low, ranging from 10 to 190 m a.s.l. The age of the studied trees, as determined from the collected wood samples, predominantly ranged from 70 to 110 years, except for beech and *Populus* hybrids, which were younger (45–70 years), and larch, which was older in a few stands (Table 1). The climate was temperate continental (Lindner et al., 2010); yet, the continentality increases in the eastern direction with the growing distance from the Baltic Sea. The mean annual temperature during the recent four decades was 6.7, 6.6, and 5.7 °C and the mean annual precipitation was 720, 640, and 610 mm in the western, central, and eastern part of Latvia, respectively. January and July were the coldest and the warmest months, respectively. The highest monthly precipitation occurred in summer months (Fig. 2). The vegetation period, when the mean diurnal temperature exceeds +5 °C, extended from mid-April to October; however, it was usually 10–15 days longer in the central part of Latvia. The climatic changes were mainly expressed as the increase of mean annual temperature (Lizuma et al., 2007),

Table 1

Statistics of the studied datasets. The range of each parameter is shown. The mean r-bar among stands is calculated based on the residual chronologies. NA – not available.

	Scots pine	Norway spruce	Silver birch	Black alder	European larch	Red oak	Hybrid poplar	Hybrid aspen	European beech
Number of sample stands	10	10	10	10	11	3	2	1	1
Number of crossdated trees per site	17–25	16–24	14–21	15–23	9–15	7–16	10–12	21	9
Age of trees	71–110	79–110	73–100	65–110	72–144	106–109	59–64	48	65
Tree-ring width (mean ± conf. int.)	0.80 ± 0.04–1.69 ± 0.04	0.94 ± 0.06–2.05 ± 0.08	0.99 ± 0.04–1.745 ± 0.06	0.81 ± 0.04–2.16 ± 0.10	0.67 ± 0.03–1.79 ± 0.07	1.79 ± 0.08–2.92 ± 0.09	2.62 ± 0.09–2.73 ± 0.10	4.00 ± 0.13	2.41 ± 0.09
Mean sensitivity	0.17–0.27	0.22–0.32	0.24–0.38	0.25–0.38	0.25–0.36	0.17–0.21	0.39–0.40	0.35	0.21
First order autocorrelation	0.57–0.78	0.46–0.67	0.44–0.71	0.40–0.67	0.37–0.72	0.52–0.68	0.51–0.57	0.69	0.58
r-bar	0.30–0.49	0.36–0.57	0.21–0.57	0.33–0.59	0.31–0.55	0.46–0.50	0.44–0.56	0.51	0.46
Expressed population signal	0.87–0.96	0.89–0.96	0.79–0.96	0.89–0.97	0.87–0.95	0.87–0.93	0.88–0.92	0.95	0.87
Gleichläufigkeit	0.60–0.66	0.60–0.73	0.57–0.70	0.59–0.74	0.60–0.73	0.64–0.68	0.68–0.69	0.71	0.70
Signal to noise ratio	7.30–22.64	8.19–27.00	3.68–17.94	7.99–18.49	6.63–18.10	6.86–13.53	6.16–10.85	19.74	12.67
Gleichläufigkeit, chronologies	0.68	0.71	0.57	0.7	0.62	0.65	0.63	NA	NA
r-bar, chronologies	0.46	0.58	0.27	0.55	0.30	0.54	0.78	NA	NA
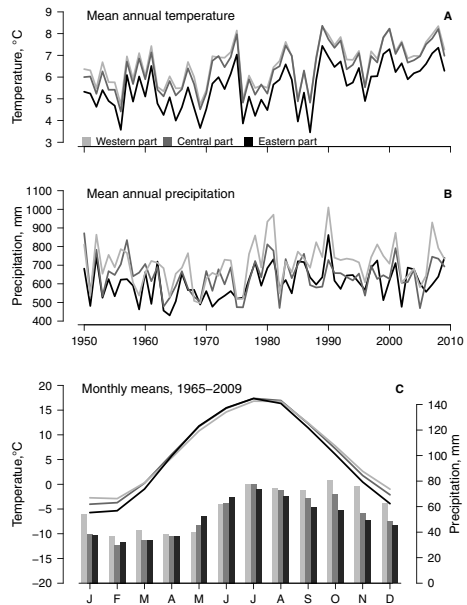
Fig. 2. Mean annual temperature (A) and precipitation sums (B) for the period 1951–2009 and the mean monthly temperature (line) and precipitation sums (bars) calculated for the period 1965–2009 (C) for the western, central, and eastern regions of Latvia.

particularly since the 1970s (Fig. 2), and hence as an extension of the vegetation period. The amount of annual precipitation during recent decades was rather stable (Fig. 2); yet, the summer precipitation regime has been becoming more heterogeneous (Avotniece et al., 2010).

The local climatic data for the grid points, located as close as possible to the studied stands (<30 km), were obtained from the high-resolution data repository of the Climatic Research Unit of the University of East Anglia (Harris et al., 2014). Mean monthly temperature, precipitation, and standardised precipitation evapotranspiration indices (SPEI) (Vicente-Serrano et al., 2010) for the time windows from July of the year preceding the tree-ring formation (previous July) to September in the year of the tree-ring formation (current September) were used.

2.2. Data analysis

The validity and quality of the TRW time series were verified by graphical inspection and by statistical crossdating within and among the stands using the program COFECHA (Grissino-Mayer, 2001). For each stand, a residual chronology of the TRW was calculated using the program ARSTAN (Cook and Holmes, 1986). Double detrending, by a negative exponential function and by a cubic spline with the wavelength of 48 years (considering different species and series length), preserving 50% of the variation, was applied. Auto-correlation was removed. The variation of the TRW was described by mean sensitivity (SENS), first order autocorrelation (AC), r-bar, Gleichläufigkeit (GLK), expressed population signal (EPS), and sig-

nal to noise ratio (SNR) (Wigley et al., 1984), calculated for the detrended time series.

The similarity of the high-frequency variation of TRW among species and stands was assessed by principal component analysis (PCA) (Jolliffe, 1986). The residual chronologies (for stands) were used as samples, and years (TRW indices) were used as variables. The cross-product matrix was calculated based on correlation, and scores of the variables were calculated as the distance-based biplots. The significance of the principal components (PCs) was determined by a randomisation test ('broken stick'), performing 10^4 iterations. To assess the climatic signals captured by the PCs, a bootstrapped (Johnson, 2001) Pearson correlation analysis (10^4 iterations) between variable scores and climatic factors averaged for western, central, and eastern regions of Latvia was conducted. A bootstrapped correlation analysis was also used to assess the set of significant climatic factors for each stand (residual chronology). All analyses were based on the data for the common period 1965–2009. Data analysis was conducted in the program R v. 3.3.1 (R Core Team, 2016) using package 'dplR' (Bunn, 2008).

3. Results

Time series of 7–24 trees were crossdated per stand (Table 1). The mean r-bar for stands ranged 0.30–0.60. The highest mean r-bar was observed for hybrid aspen and alder (0.51), but the lowest – for pine and birch (0.41 and 0.38, respectively). The SENS was intermediate (0.17–0.40) with the highest mean values for *Populus* hybrids (0.40) and the lowest mean values for pine and red oak (~0.20). Mainly, GLK ranged from 0.60 to 0.70, and the EPS exceeded 0.85. The SNR ranged from 3.68 to 27.00. The mean SNR was the highest for hybrid aspen (~ 19.74), but the lowest for red oak and hybrid poplar (~10.10 and 8.80, respectively). Pine and hybrid aspen had the highest (~ 0.70), but larch and hybrid poplar had the lowest (~ 0.50) AC in TRW. The produced stand residual chronologies (Fig. 3) of each species were comparable, as the mean GLK ≥ 0.57 (Table 1); still, the r-bar values differed between species and hybrids. Birch and larch showed the highest diversity of the chronologies (r-bar was 0.26 and 0.30, respectively), while the chronologies of other species were more similar (r-bar ranged from 0.45 to 0.78 for Scots pine and hybrid poplar, respectively). The range of chronology indices was similar for most of the species; yet, the *Populus* hybrids had a wider range (Fig. 3). The mean GLK and r-bar among all chronologies were 0.56 and 0.17, respectively.

The PCA of the residual chronologies showed that the first three PCs of high-frequency variation of the TRW were significant (*p*-values < 0.01) and together corresponded to 32.1% of the total variance in data (Fig. 4). The first PC significantly (at α = 0.05) correlated with June precipitation (r ~-0.33) and previous September temperature (r ~0.36). The second PC could be associated with the temperature in February, March, and in previous July (r ~0.38, 0.55, and 0.33, respectively). The third PC correlated with temperature, precipitation, and SPEI in previous July (r ~0.32, −0.39, and −0.30, respectively). These correlations were similar among the regions. The ordination of chronologies (Fig. 4) according to the first and second PC showed distinct grouping by species irrespectively of their origin (native or introduced). Chronologies of spruce and alder as well as pine and larch were located on the opposite quadrants of the ordination space (Fig. 4), suggesting contrasts in the annual variation of TRW. The chronologies of larch were mainly similar to spruce and birch, as demonstrated by their location in the ordination space between these species. Still, some overlaps between species were observed, implying similarities in growth patterns. The hybrids of *Populus* formed a clearly distinctive group, suggesting diverse patterns of TRW variation. The introduced broadleaves (red oak and beech) had low values of the first and second PCs;
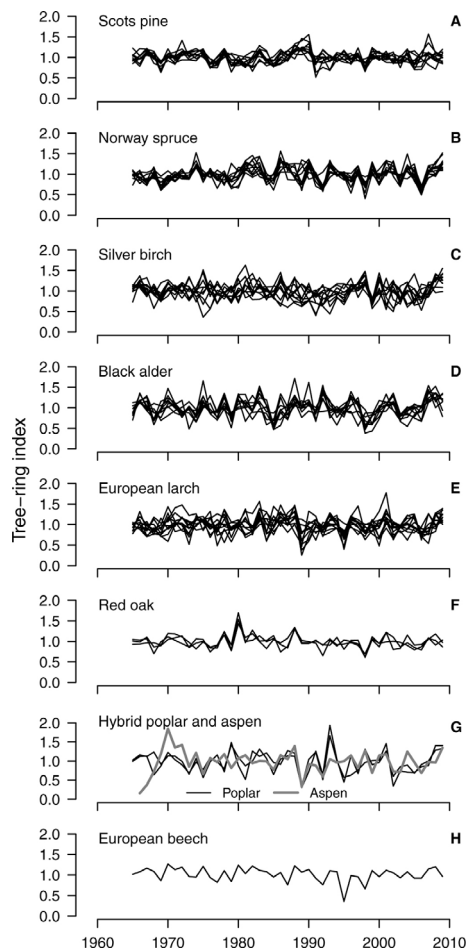
Fig. 3. Residual chronologies of tree-ring width of the native Scots pine (A), Norway spruce (B), silver birch (C), and black alder (D) and the introduced European larch (E), red oak (F), and European beech (H) as well as the *Populus* hybrids (G) for the period 1965–2009.

yet, the scores of the third PC of the red oak were higher. The ordination of chronologies according to the third PC distinguished most of the birch chronologies from the other species, which clearly overlapped.

The differences in variation of TRW (Fig. 4) were apparently caused by the sensitivity to diverse climatic factors, as shown by the correlation analysis (Fig. 5). During the period 1956–2009, pine was mainly sensitive to temperature in February and March, although some local correlations (e.g., with temperature in previous August or current September and precipitation in summer months) were observed. In contrast, birch predominantly showed
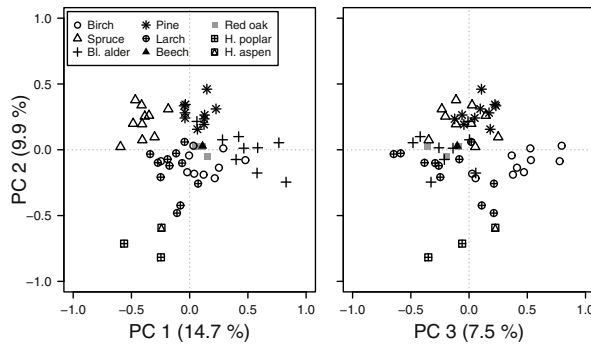
Fig. 4. The distribution of the residual chronologies according to the first three principal components (PC) calculated for the tree-ring indices (chronologies) for the common period 1965–2009. On the axes, the numbers in parentheses show the percentage of explained variance.

site-specific correlations, as none of the tested climatic factors was significant for TRW in more than three stands (Fig. 5). Mainly, TRW of birch correlated with precipitation and SPEI, but the relationships were weaker compared to pine (not shown). Spruce was sensitive to moisture regime, as shown by the prevailing correlations with precipitation and SPEI in April, June, and in previous July and August (Fig. 5). In some stands, correlation with winter temperature was also observed. In half of the stands, the TRW of alder was correlated with precipitation in March and temperature in previous December, while, in some individual stands, it was also correlated with temperature during the dormant period and precipitation in summer (Fig. 5). Larch was mainly sensitive to temperature in the preceding summer, as shown by the significant correlations in six stands; nevertheless, several climatic factors (e.g., winter-spring temperatures, summer precipitation and SPEI), were significant for TRW in a few stands (Fig. 5). The introduced broadleaves were particularly sensitive to temperature in the preceding summer (Fig. 5). The *Populus* hybrids were sensitive to temperature in March, August, and previous September, to precipitation in July (hybrid aspen), and to SPEI in late summer.

4. Discussion

The datasets were sufficient for representation of the weather-related variability of TRW, as the EPS (Table 1) mostly exceeded 0.85 (Wigley et al., 1984), and the SENS was intermediate (Speer, 2010). The AC in TRW was high (~0.59, Table 1), particularly for pine and hybrid aspen, indicating the influence of previous growth on TRW (Ericsson, 1979; Barbaroux and Breda, 2002). Larch had lower AC (~0.48) and was apparently more affected by the current assimilation. Lower AC also implies clearer reflection of the environmental factors in variation of TRW (Cook et al., 1992). The r-bar and SNR at the stand level (Table 1) suggested different forcing of growth (Speer, 2010). The stress-tolerant pine and pioneer-species birch had the most individual patterns of TRW within stands (Table 1), likely due to the location in the non-marginal part of the distribution area, where the growth controls are complex (Friedrichs et al., 2009); yet, other species had more similar variation. The r-bar among the chronologies (Table 1) exceeded 0.45 for most of the species, indicating common regional-scale factors. The chronologies of birch and larch had lower r-bar (≤ 0.30), suggesting higher variability among stands that, for larch, might be related to the occurrence outside its natural range (Speer, 2010). Never-

theless, the presence of common tendencies was evidenced by the intermediate GLK calculated among all chronologies.

The common variation of TRW extracted by the first three PCs was significant; yet, the amount of explained variance was limited (Fig. 4), as diverse species were compared (García-Suárez et al., 2009), and tree growth in Latvia varies regionally (Jansons and Baumanis, 2005). Nevertheless, correlation analysis showed that the first PC captured the common growth signal related to the length of the vegetation season (September temperature) and the availability of water in summer (June precipitation). Moreover, the second PC was related to the annual temperature regime, as it correlated with temperature in both winter and summer. The third PC apparently represented a mid-summer water deficit that often affects tree growth in Central Europe (Lebourgeois et al., 2004; Neuwirth et al., 2007). These factors largely reflect climatic changes in Latvia (Lizuma et al., 2007; Avotniece et al., 2010).

The values of the first two PCs clearly grouped chronologies by species (Fig. 4); yet, the signals captured in PCs were reflected in the individual chronologies to different extents (Fig. 5), implying complex growth controls (Wilson and Elling, 2004; Friedrichs et al., 2009; Speer, 2010). The common sensitivity of pine to temperature in February and March (Fig. 5), as highlighted by positive scores of the second PC, might be explained by alterations in root dynamics and water uptake (Jalkanen, 1993) or, alternatively, by cold damage (Pearce, 2001), which is promoted by the loss of cold-hardiness under a warming climate (Ögren et al., 1997). Additionally, the correlations with precipitation and temperature in previous August (Fig. 5) imply the local effect of the water deficit (Lebourgeois et al., 2004). Nevertheless, warmer summers (likely in moist years) might also favour growth, as positive correlations with temperature were also observed (Fig. 5). The correlations with September temperature might be related to the extension of the growing period and additional assimilation (Menzel and Fabian, 1999).

The sensitivity of spruce TRW to water balance (Mäkinen et al., 2002) was demonstrated by the prevailing correlations with precipitation and SPEI (Fig. 5) in summer months and also by negative scores of the first PC (Fig. 4). Half of the chronologies correlated with April precipitation and May SPEI, which might be explained by the negative effect of excessive soil moisture (Simard et al., 2007). Although scores of the second PC of spruce chronologies were comparable to pine (Fig. 4), winter temperature was significant only in a few sites (Fig. 5). However, clear and abrupt decreases in TRW were observed after cold winters (Figs. 2 and 3; e.g., in 1967, 1969, and 1996), indicating sensitivity to extreme cold events.
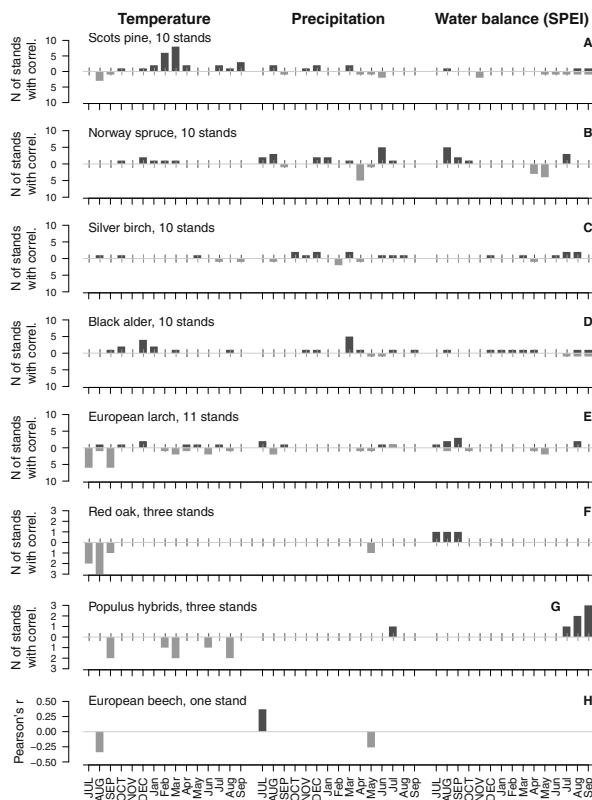
Fig. 5. The number of stands with significant correlations (positive in black and negative in grey) between climatic factors (mean monthly temperature, precipitation, and standardised precipitation evapotranspiration indices (SPEI)) and residual chronologies of tree-ring width of Scots pines (A), Norway spruce (B), silver birch (C), black alder (D), European larch (E), red oak (F), and *Populus* hybrids (G) and the significant Pearson correlation coefficients for European beech (H) (from one stand). Correlations were calculated for the period 1965–2009. Months in uppercase correspond to previous calendar year.

The prevailing sensitivity of alder to precipitation in March (Fig. 5) might be explained by alterations in the water table that affect the growth of the species (McVean, 1953). In several sites, correlation with winter temperature (Fig. 5) suggested sensitivity to cold damage, likely via root damage (Pearce, 2001; Weih and Karlsson, 2002). The climatic factors identified by the PCs (June precipitation), however, were significant only in single sites (Fig. 5), implying that their effect might be indirect, probably via alterations in the water table.

The TRW of the alien species (larch, red oak, and beech), irrespectively of the systematic affiliation and origin, were mainly correlated to temperature in previous July–September (Fig. 5), suggesting influence of the water deficit, likely via formation of nutrient reserves, as previously explained for red oak (Matisons et al., 2015). The effect of the water deficit was also approved by the positive correlations with precipitation and SPEI (Fig. 5). Similar climate-growth relationships have been observed for tree growth in the Central Europe (Mäkinen et al., 2002; Lebourgeois et al., 2004; Wilson and Elling, 2004; Neuwirth et al., 2007). Winter temperature

did not appear to be clearly limiting for TRW (except in a few larch stands) (Fig. 5), although the species occurred in northern locations. Alternatively, this might be related to genetically determined sensitivity to environmental fluctuations (Savva and Vaganov, 2006; Helama et al., 2008). Although the TRW of alien species was correlated to similar factors (Fig. 5), larch was clearly distinguished by the first two PCs (Fig. 4), and hence by the sensitivity to temperature in the previous July, September, and winter. In contrast, red oak and beech had low values of the first three PC scores, likely due to different limiting factors (temperature in previous August) (Fig. 5). The TRW of larch, pine, and spruce was affected by similar climatic factors (Fig. 5), as in neighbouring Estonia and Lithuania (Vitas, 2004, 2006, 2015; Hordo et al., 2009; Läänelaid and Eckstein, 2012), implying a regional scale of the observed climatic signals. Nevertheless, the TRW of beech was not sensitive to winter-spring temperature (Fig. 5), as observed by Augustaitis et al. (2015), likely due to the occurrence in coastal area (Fig. 1) where the climate is milder (Fig. 2).

Distinct growth patterns for *Populus* hybrids, as suggested by low scores of the first two PCs (Fig. 4), might be explained by heterosis (i.e., combination and enhancement of parental traits) causing specific reaction to environmental fluctuation (Li et al., 1998). Unlike others, *Populus* hybrids showed clear negative correlations with temperature in spring and autumn (Fig. 5) that can be explained by frost/cold damage in response to delayed cold hardening and/or interrupted dormancy (Welling et al., 2002). Hence, the extension of vegetation period (Menzel and Fabian, 1999) have had a negative effect on the TRW of the studied hybrids, contrasting e.g. with pine. Additionally, the correlation with precipitation in July, temperature in August, and, particularly, SPEI in September (Fig. 5) suggested sensitivity to the availability of water, as observed for the fast growing hybrids of *Populus* (Perry et al., 2001).

Birch appeared to be the most robust against weather fluctuation (Fig. 5), as observed by Briceno-Elizondo et al. (2006), explaining the variability of TRW patterns among trees and stands (Fig. 3, Table 1). Still, the most frequent correlations to precipitation in the dormant period (Fig. 5) might be explained by the effect of soil temperature on root functionality (Weih and Karlsson, 2002). The distinct grouping of birch chronologies according to the increased scores of the third PC (Fig. 4) was apparently caused by weaker water deficit signal in TRW (Fig. 5) or by an uncontrolled factor.

5. Conclusions

Although diverse species and hybrids were compared, the influence of common climatic factors was traced in TRW for recent decades; however, the combination and effect of these factors differed, causing specifics in the variation of increment. The identified common factors were related to the length of the vegetation season, winter temperature, and water regime in summer, which mainly reflect the climatic changes in Northern and Eastern Europe. Hence, considering the projected climate changes, Scots pine and black alder might lose variation of TRW related to low temperature in winter; yet, the effect of water availability in summer might strengthen, as sensitivity to drought-related factors was already observed in some stands. Under such a scenario, the effect of the water deficit on the TRW of Norway spruce would intensify. The TRW of European beech, red oak, and European larch was prevailingly sensitive to factors related to water deficit, stressing the importance of the water regime for their growth, which might intensify in the future, as already observed under warmer climates (e.g., in Central Europe). Still, the effect of winter temperature was observed in some European larch stands, indicating some influence of cold damage. The negative correlations with temperature in combination with positive correlation with SPEI, which distinguished *Populus* hybrids from others, implied that warming might have a negative effect on the increment of the studied clones, and hence improvement of the planting material might be necessary. Silver birch appeared less sensitive to the tested climatic factors, implying tolerance to weather fluctuations and likely to climatic changes.

References

Ögren, E., Nilsson, T., Sundblad, L.G., 1997. Relationship between respiratory depletion of sugars and loss of cold hardiness in coniferous seedlings overwintering at raised temperatures: indications of different sensitivities of spruce and pine. Plant Cell Environ. 20, 247–253, http://dx.doi.org/10.1046/j.136-3040.1997.d01-56.x.

Augustaitis, A., Kliučius, A., Marozas, V., Pilkauskas, M., Augustaitiene, I., Vitas, A., Staszewski, T., Jansons, Ā., Dreimanis, A., 2015. Sensitivity of European beech trees to unfavourable 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.

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.

Bolte, A., Ammer, C., Löf, M., Madsen, P., Nabuurs, G.J., Schall, P., Rock, J., 2009. Adaptive forest management in central Europe: climate change impacts, strategies and integrative concept. Scand. J. Forest Res. 24, 473–482, http://dx.doi.org/10.1080/02827580903418224.

Briceno-Elizondo, E., Garcia-Gonzalo, J., Peltola, H., Matala, J., Kellomäki, S., 2006. Sensitivity of growth of Scots pine, Norway spruce and silver birch to climate change and forest management in boreal conditions. For. Ecol. Manage. 232, 152–167, http://dx.doi.org/10.1016/j.foreco.2006.05.062.

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.

Chmura, D., 2004. Penetration and naturalization of invasive plant species (neophytes) in woodlands of the Silesian upland (Southern Poland). Nat. Conserv. 60, 3–11.

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 Press, Tucson, pp. 50–65.

Cook, E.R., Briffa, K., Shiyatov, S., Mazepa, V., 1992. Tree-ring standardization and growth trend estimation. In: Cook, E.R., Kairiukstis, L.A. (Eds.), Methods of Dendrochronology. Kluwer Academic Publ, Dordrecht, pp. 104–123.

EUFORGEN, 2009. Distribution maps. URL: http://www.euforgen.org/distribution-maps/. (accessed 12.12.15.).

Ericsson, A., 1979. Effects of fertilization and irrigation on the seasonal changes of carbohydrate reserves in different age-classes of needle on 20-year-old Scots pine trees (*Pinus sylvestris*). Physiol. Plantarum 45, 270–280, http://dx.doi.org/10.1111/j.1399-3054.1979.tb01700.x.

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.

García-Suárez, A.M., Butler, C.J., Baillie, M.G.L., 2009. Climate signal in tree-ring chronologies in a temperate climate: a multi-species approach. Dendrochronologia 27, 183–198, http://dx.doi.org/10.1016/j.dendro.2009.05.003.

Goldblum, D., Rigg, L.S., 2005. Tree growth response to climate change at the deciduous-boreal forest ecotone, Ontario, Canada. Can. J. Forest Res. 35, 2709–2718, http://dx.doi.org/10.1139/x05-185.

Grace, J., Berninger, F., Nagy, L., 2002. Impacts of climate change on the tree line. Ann. Bot.-London 90, 537–544, http://dx.doi.org/10.1093/aob/mcf222.

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

Hanewinkel, M., Cullmann, D.A., Schelhaas, M.J., Nabuurs, G.J., 2012. Climate change may cause severe loss in the economic value of European forest land. Nat. Clim. Change 3, 203–207, http://dx.doi.org/10.1038/nclimate1687.

Harris, I., 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.

Helama, S., Salminen, H., Timonen, M., Varmola, M., 2008. Dendroclimatological analysis of seeded and thinned Scots pine (*Pinus sylvestris* L.) stands at the coniferous timberline. New For. 35, 267–284, http://dx.doi.org/10.1007/s11056-007-9076-1.

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. Global Ecol. Biogeogr. 21, 50–63, http://dx.doi.org/10.1111/j.1466-8238.2010.00613.x.

Hordo, M., Metslaid, S., Kiviste, A., 2009. Response of Scots pine (*Pinus sylvestris* L.) radial growth to climate factors in Estonia. Balt. For. 15, 196–205.

Jalkanen, R., 1993. Defoliation of pines caused by injury to roots resulting from low temperatures. Finn. For. Res. Inst. Res. Pap. 451, 77–88.

Jansons, Ā., Baumanis, I., 2005. Growth dynamics of Scots pine geographical provenances in Latvia. Bal. For. 11, 29–37.

Johnson, R.W., 2001. An introduction to the bootstrap. Teach. Stat. 23, 49–54, http://dx.doi.org/10.1111/1467-9639.00050.

Jolliffe, I.T., 1986. Principal Component Analysis. Springer-Verlag, Berlin, http://dx.doi.org/10.1007/b98835 (487p.).

Kirilenko, A.P., Sedjo, R.A., 2007. Climate change impacts on forestry. PNAS 104, 19697–196702, http://dx.doi.org/10.1073/pnas.0701424104.
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.
Läänelaid, A., Eckstein, D., 2012. Norway spruce in Estonia reflects the early summer weather in its tree-ring widths. Balt. For. 18, 194–204.
Laiviņš, M., Bice, M., Krampis, I., Knape, D., Šmite, D., Šulcs, V., 2009. Atlas of Latvian Woody Plants. Apgāds Mantojums, Rīga, 606 p. (in Latvia).
Lebourgeois, F., Cousseau, G., Ducos, Y., 2004. Climate-tree-growth relationships of Quercus petraea Mill. stand in the Forest of Bercé (Futaie des Clos, Sarthe, France). Ann. For. Sci. 61, 361–372, http://dx.doi.org/10.1051/forest:2004029.
Li, B., Howe, G.T., Wu, R., 1998. Developmental factors responsible for heterosis in aspen hybrids (Populus tremuloides × P. tremula). Tree Physiol. 18, 29–36, http://dx.doi.org/10.1093/treephys/18.1.29.
Lindner, M., Maroschek, M., et al., 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. For. Ecol. Manage. 259, 698–709, http://dx.doi.org/10.1016/j.foreco.2009.09.023.
Lindner, M., 2000. Developing adaptive forest management strategies to cope with climate change. Tree Physiol. 20, 299–307, http://dx.doi.org/10.1093/treephys/20.5-6.299.
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.
Mäkinen, H., Nöjd, P., Kahle, P.H., Neumann, U., Tveite, B., Mielikäinen, K., Röhle, H., Spiecker, H., 2002. Radial growth variation of Norway spruce (Picea abies (L.) Karst.) across latitudinal and altitudinal gradients in central and northern Europe. For. Ecol. Manag. 171, 243–259, http://dx.doi.org/10.1016/S0378-1127(01)00786-1.
Mangalis, I., 2004. Regeneration and Establishment of Forest. Et Cetera, Riga, 455 p. (in Latvian).
Matisons, R., Jansons, J., Katrevičs, J., Jansons, Ā., 2015. Relation of tree-ring width and earlywood vessel size of alien Quercus rubra L. with climatic factors in Latvia. Silva Fenn 49, N 4, http://dx.doi.org/10.14214/sf.1391.
McVean, D.N., 1953. Alnus glutinosa (L.) Gaertn. J. Ecol. 41, 447–466 (http://www.jstor.org/stable/2257070).
Menzel, A., Fabian, P., 1999. Growing season extended in Europe. Nature 397, N 659, http://dx.doi.org/10.1038/17709.
Neuwirth, B., Schweingruber, F.H., Winiger, M., 2007. Spatial patterns of central Europe pointer years from 1901 to 1971. Dendrochronologia 24, 79–89, http://dx.doi.org/10.1016/j.dendro.2006.05.004.
Pearce, R.S., 2001. Plant freezing and damage. Ann. Bot.-London 87, 417–424, http://dx.doi.org/10.1006/anbo.2000.1352.
Perry, C.H., Miller, R.C., Brooks, K.N., 2001. Impacts of short-rotation hybrid poplar plantations on regional water yield. For. Ecol. Manage. 143, 143–151, http://dx.doi.org/10.1016/S0378-1127(00)00513-2.
Core Team, R., 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria (URL: https://www.R-project.org/).
Reich, P.B., Oleksyn, J., 2008. Climate warming will reduce growth and survival of Scots pine except in the far north. Ecol. Lett. 11, 588–597, http://dx.doi.org/10.1111/j.1461-0248.2008.01172.x.

Sander, I.L., 1990. Quercus rubra L. northern red oak. In: Burns, R.M., Honkala, B.H. (Eds.), Silvics of North America, Vol. 2. Hardwoods. Forest Service United States Department of Agriculture, Washington DC, pp. 727–733.
Savva, J.V., Vaganov, E.A., 2006. Genetic and environmental effects assessment in Scots pine provenances planted in central Siberia. Mitig. Adapt. Strategy Glob. Change 11, 269–290, http://dx.doi.org/10.1007/s11027-006-1026-2.
Scheller, R.M., Mladenoff, D.J., 2005. A spatially interactive simulation of climate change, harvesting, wind, and tree species migration and projected changes to forest composition and biomass in northern Wisconsin, USA. Glob. Change Biol. 11, 307–321, http://dx.doi.org/10.1111/j.1365-2486.2005.00906.x.
Simard, M., Lecomte, N., Bergeron, Y., Bernier, P., Pare, D., 2007. Forest productivity decline caused by successional paludification of boreal soils. Ecol. Appl. 17, 1619–1637, http://dx.doi.org/10.1890/06-1795.1.
Sjors, H., 1963. Amphi-Atlantic zonation, nemoral to arctic. In: Love, A., Love, D. (Eds.), North Atlantic Biota and Their History. Pergamon press, Oxford, pp. 109–126.
Speer, J.H., 2010. Fundamentals of Tree-ring Research. The University of Arizona Press Tucson (333 pp).
Spittlehouse, D.L., Stewart, R.B., 2004. Adaptation to climate change in forest management. J. Ecosyst. Manage. 4, N1 (http://www.forrex.org/jem/2003/vol4/no1/art1.pdf).
Stott, P., Loehle, C., 1998. Height growth rate tradeoffs determine northern and southern range limits for trees. J. Biogeogr. 25, 735–742, http://dx.doi.org/10.1046/j.1365-2699.1998.2540735.x.
Vicente-Serrano, S.M., Begueria, S., Lopez-Moreno, J.I., 2010. Multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. J. Clim. 23, 1696–1718, http://dx.doi.org/10.1175/2009JCLI2909.1.
Vitas, A., 2004. Tree rings of Norway spruce (Picea abies (L.) Karst.) in Lithuania as drought indicators: dendroecological approach. Pol. J. Ecol. 52, 201–210.
Vitas, A., 2006. Sensitivity of Scots pine trees to winter colds and summer droughts: dendroclimatological investigation. Balt. For. 12, 220–226.
Vitas, A., 2015. A dendroclimatical analysis of European larch (Larix decidua Mill.) from Lithuania. Balt. For. 20, 67–72.
Weih, M., Karlsson, P.S., 2002. Low winter soil temperature affects summertime nutrient uptake capacity and growth rate of mountain birch seedlings in the subarctic, Swedish Lapland. Arct. Antarct. Alp. Res. 34, 434–439 (http://www.jstor.org/stable/1552201).
Welling, A., Moritz, T., Palva, E.T., Junttila, O., 2002. Independent activation of cold acclimation by low temperature and short photoperiod in hybrid aspen. Plant Physiol. 129, 1633–1641, http://dx.doi.org/10.1104/pp.003814.
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.
Wilson, R., Elling, W., 2004. Temporal instability in tree-growth/climate response in the Lower Bavarian Forest region: implications for dendroclimatic reconstruction. Trees-Struct. Funct. 18, 19–28, http://dx.doi.org/10.1007/s00468-003-0273-z.

Intra–annual height growth of hybrid poplars in Latvia. Results from the year of establishment

S. Šēnhofa, M. Zeps, L. Ķēniņa[*], U. Neimane, R. Kāpostiņš, A. Kārkliņa and Ā. Jansons

Latvia State Forest Research Institute Silava, Rigas street 111, LV–2169 Salaspils, Latvia
[*]Correspondence: laura.kenina@silava.lv

Abstract. Fast growing hybrid poplars (*Populus* spp.) could be successfully used for bioenergy as well as wood production. Productivity of clones had been studied in Baltic States recently, however, little is known about the impact of weather conditions on poplar height growth, thus the potential effect of climate change. Therefore, the aim of this study was to characterize the intra–annual height growth of hybrid poplar clones in Latvia. Height increment of 12 hybrid poplar clones was measured on average with an 11–day interval in the first vegetation season in 2016. Annual shoot height was on average 81.0 ± 6.8 cm, significantly ($p < 0.001$) depending on the poplar clone. Use of long (0.5 m) instead of short (0.3 m) cuttings leaded to larger annual height increment during the year of establishment of the plantation. From June to September the mean growth intensity was 10 to 15 mm day^{-1}. The trend of height growth intensity, described by Gompertz model, indicated that the poplar clones with largest height had relatively fast increase of the growth intensity from June to July. Changes of growth intensity was linked both with the temperature and sum of precipitation. This tendency was not so pronounced for clones with largest height increment, emphasizing the importance of the phenotypic plasticity in selection of clones for plantations.

Key words: *Populus* spp., short–rotation forestry, cutting length, growth intensity.

INTRODUCTION

The importance of short–rotation forestry has been recognized lately in context of carbon sequestration both as a source for the fibre and solid–wood production as well as the fuelwood (Uri et al., 2011; Bronisz et al., 2016; Wang et al., 2016). Poplars (*Populus* spp.), mostly their hybrid clones, are promising tree species for intensive cultivation in boreal climate, considering their productivity, multiple use of the wood and relatively high resistance against biotic and abiotic stresses (Weih, 2004; Ball et al., 2005; Christersson, 2010; Tullus et al., 2013; Kutsokon et al., 2015).

The growth of poplars is determined by genetic properties of clones (Zhang et al., 2003; Mead, 2005), applied management strategies (DeBell et al., 1996; Mead, 2005; Bilodeau–Gauthiera et al., 2011; Wang et al., 2016), and climate (Olivar et al., 2009; Wang et al., 2016; Štícha et al., 2016). Genetics (species, as well as clones) has strong impact on growth traits and wood properties (Zhang et al., 2003), as well tolerance of trees against different stresses: drought, frost etc. (Mazzoleni & Dickmann, 1988; Ilstedt,

1996; Giovannelli et al., 2007; Chhin, 2010; Pollastrini et al., 2013; Lazdiņa et al., 2016), water–use strategy and efficiency (Schreiber et al., 2011). Therefore, effective selection of best genotypes for specific set of conditions (regions) can be carried out and its results applied in praxis promptly due to simple and cheap vegetative propagation (Mead, 2005; Tullus et al., 2013).

The impact of climatic factors such as temperature (Šēnhofa et al., 2016), length of vegetation period (Wang et al., 2016), frequency and severity of drought (Giovannelli et al., 2007; Olivar et al., 2009; Pollastrini et al., 2013) to growth rate of poplars have been studied extensively. However, under changing climate (Kirschbaum, 2000), the knowledge about the environmental stresses affecting poplar growth, is necessary for development of the sustainable short–rotation forestry (Kozlowski & Pallardy, 2002). Since that, the influence of temperature and precipitation might be modified to some extent by management decisions (Kutsokon et al., 2015) and selection of clones with proper adaptation to certain climate (DeBell et al., 1996; Chhin, 2010).

In different ecotypes the poplar growth has been determined by the photoperiod (Howe et al., 1995), although, temperature has been recognised as strong additional environmental factor, which modifies the sensitivity of the day–length signals at growth cessation and influence the duration of growth and bud formation (Rohde et al., 2011). Differences between the frost tolerance of poplar clones (Lazdiņa et al., 2016), as well as regeneration of trees after serious frost damages (Šēnhofa et al., 2017) have been studied also in Latvia. However, little is known about the intra–annual growth patterns and response to weather conditions. Numerous studies regarding effect of water availability on poplar productivity found that the precipitation has large effect of tree growth during the vegetation period (Leonelli et al., 2008; Jules et al., 2010), however, in Nordic countries it has not been recognised as a limiting factor (Messaoud & Chen, 2011). Temperature has been found as primary controlling factor of height growth intensity of a most widely used hybrid aspen (*Populus tremula* L. × *P. tremuloides* Michx.) in our region (Jansons et al., 2014). The impact of diurnal temperature and precipitation to variation of height growth intensity and, cumulatively, to annual height increment has not been widely discussed, however, it can be crucial for achieving growth superiority of poplars in expected changing climate in northern Europe. Therefore, the aim of this study was to characterize the intra–annual height growth of hybrid poplar clones in Latvia.

MATERIALS AND METHODS

Study area is located in central part of Latvia, near Vecumnieki (56º34´ N, 24º31´ E), on former agricultural land. In the spring of 2016 the plantation of poplars was established on flat area with deep drained fertile peat soil of pH 6.

Monoclonal row–plots in three replications were used; the distance between rows was 4 m, between the trees within a row 2 m. Unrooted 0.3 m and 0.5 m long (further 'short' and 'long', respectively) poplar cuttings of 12 clones were planted leaving 3–5 cm above ground (Table 1).

During the study, 20 ramets per clone and type of cutting were randomly selected (on average 6 per replication) for shoot height measurements. Nine measurements of shoot height with the interval of approximately 11 days (ranging from 5 to 18 days) were taken from the ground level in year of establishment. Eight periods of measurements

were defined: 17.06.–29.06., 30.06.–10.07., 11.07.–21.07., 22.07.–08.08., 09.08.–17.08., 18.08.–29.08., 30.08.–08.09., 09.09.–13.09.. About 50% of poplar shoots during the study period were browsed by cervids and damaged by snails; only undamaged trees were included in data analysis (Table 1).

Table 1. Description of the tested poplar clones

Clone	Number of ramets*	Length of cuttings, m	Species	Origin of cuttings**
OP 42	3	0.3	*P.maximowiczii × P.trichocarpa*	Germany
Max 1	6	0.3	*P.maximowiczii × P.nigra*	Germany
Max 3	7	0.3		
Matrix 24	6	0.3	*P.maximowiczii × P.trichocarpa*	Germany
Matrix 49	7	0.3		
Hybride 275	9	0.3	*P.maximowiczii × P.trichocarpa*	Germany
LV 1	3	0.3	Clones from section *Tacahamaca*	Sweden
LV 3	6	0.3		
LV 4	6	0.3		
Baldo	7	0.3	*P.deltoides* clones	Italy
	9	0.5		
Oudenberg	8	0.3	*P.deltoides × P.nigra*	Italy
	10	0.5		
Vesten	7	0.5	*P.deltoides × P.nigra*	Italy

* undamaged by cervids and snails; ** country from which the cuttings were obtained.

Mean growth intensity (mm day^{-1}) during measurement periods were calculated for individual trees. The mean annual height increment ± 95% confidence interval (CI) and mean growth intensity ± CI for each variant of planting material of poplar cuttings were calculated. At the end of the period of measurements all 'short' poplar clones were grouped depending on the length of annual height increment assessment: 1 – 'short–max' – Hybrid 275, Oudenberg 0.3 m; 2 – 'short–average' – Baldo 0.3 m, Max 1, Max 3, Matrix 24, Matrix 49; 3 – 'short–min' – OP 42, LV 1, LV 3, LV 4. Hourly data of weather parameters (i.e., temperature, precipitation) were obtained from the nearest weather station of Latvian Environmental, Geology and Meteorology Centre from the study site.

Analysis of variance (ANOVA) and the Tukey Honest Significant difference (HSD) test were used to assess the differences of height increment and growth intensity between cuttings of different length, as well as the differences between clones. The non–linear Gompertz model (Eq. 1) was fitted for individual trees to assess the intra–annual growth trend in growing season (Fekedulegn et al., 1999)

$$f(A) = \alpha \exp(-\beta \exp(-kA)) \qquad (1)$$

where α – asymptote parameter; β – displacement parameter; k – growth intensity parameter; A – day since the start of the measurements.

The differences between obtained parameters (α, β, k) were compared using ANOVA to assess the clone effect. The Pearson correlation test was used to assess the relationship between height growth intensity from June till September and values of meteorological factors (i.e., including mean temperature and precipitation sum in the period). The differences in growth intensity and temperature between the measurement

periods were estimated using ANOVA; mean temperature ± CI was calculated from temperatures of each day of a particular period. All statistical analyses were performed using R v.3.3.1 (R Core Team, 2016).

RESULTS AND DISCUSSION

Measurements had been started, when the length of annual shoot ± CI had reached 4.0 ± 1.6 cm; it was significantly ($p < 0.05$) smaller for 'short' Baldo (1.6 cm) and OP 42 (1.8 cm). Contrary, 'short' Oudenberg as well as 'long' Vesten and Oudenberg had significantly ($p < 0.05$) larger shoot height before the measurements, 11.8, 12.1 and 14.2 cm, respectively. The mean height ± CI of poplars at the end of the first growing season (June – September) was 81.0 ± 6.8 cm; it significantly differed ($p < 0.001$) between the poplar clones, ranging from 32 to 102 cm for 'short' cuttings and 73 to 132 cm for 'long' cuttings, respectively (Fig. 1).
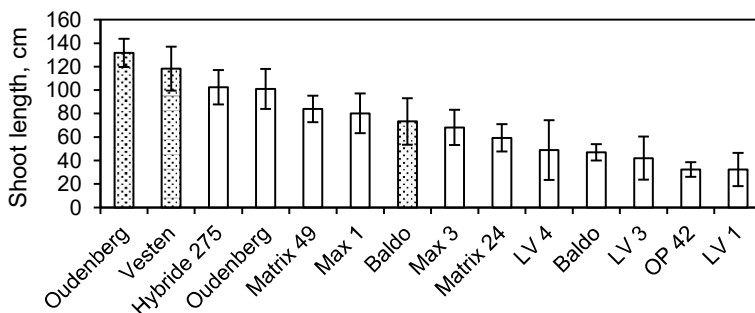
Figure 1. Height increment of poplar clones at the end of the first growing season ± CI. Different fill patterns separate groups of different cuttings length: 'short', (0.3 m) – white columns; 'long', (0.5 m) – dotted columns.

At the end of September, mean height ± CI of 'short' clones was 69.2 ± 6.9 cm. Shoot height of 'short' Hybride 275, Oudenberg and Matrix 49 were significantly higher than 'short' Baldo, LV 3, OP 42 and LV 1 clones. The significantly ($p < 0.05$) smaller height at the end of period of measurements was reached by clones LV 1 and OP 42 with 32 ± 14.1 cm and 32 ± 6.3 cm, respectively. Although clone OP 42 had poor growth, likely due to specific site conditions, it has been widely and successfully used in the south of Sweden, reaching the biomass of approximately 8 t dry mass ha^{-1} yr^{-1} (Christersson, 2008), suggesting that the limited number of replications requires additional studies.

The mean shoot height ± CI of 'long' clones was 107.9 ± 13.4 cm. The 'long' Oudenberg and Vesten clones had significantly ($p < 0.05$) higher shoot height (131.8 cm and 118.3 cm, respectively) compared to 'long' Baldo (73.3 cm) at the end of September, likely due to the differences in the late–summer growth strategy (Devine et al., 2010).

For the clones with two different cutting lengths, Oudenberg and Baldo, shoot height was significantly ($p < 0.001$) influenced both by clone and length of the cuttings, while the effect of the interaction between these two factors was non–significant ($p = 0.74$; $R^2 = 0.75$). The 'long' cuttings of Oudenberg clone exceeded the shoot height

257

by 30% compared to 'short' cuttings, 132 ± 12.0 cm and 101 ± 17.1 cm, respectively. For Baldo, the 'long' cuttings exceeded the shoot height of 'short' cuttings by 50% (73 ± 20.0 cm and 47 ± 7.0 cm, respectively), suggesting that the 'long' cuttings resulted in largest height and biomass production (depending from the clone); it is in accordance to findings of other studies (Burgess et al., 1990; DeBell et al., 1996; Rossi, 1999; Camp et al., 2012). Such tendency can be explained by larger nutrient reserves for shoots of longer cuttings (Buhler et al., 1997; Marino & Gross, 1998). Moreover, the higher shoot height of 'long' cuttings may have occurred due to higher ability to reach the capillary flow of ground water compared to 'short' cuttings, considering the planting depth (Bloomberg, 1963; Vigl & Rewald, 2014). The mean growth intensity in all periods was 10 to 15 mm day^{-1}. Some of the clones (e.g., OP 42, LV 1, LV 3) did not show the height increment greater than 10 mm day^{-1} in any period of measurements – contrary the 'long' Vesten, 'long' and 'short' Oudenberg, as well as 'short' Hybride 275 exceeded 15 mm day^{-1} at least in two measuring periods. It suggests, that clones have different intra–annual growth trends (Devine et al., 2010).
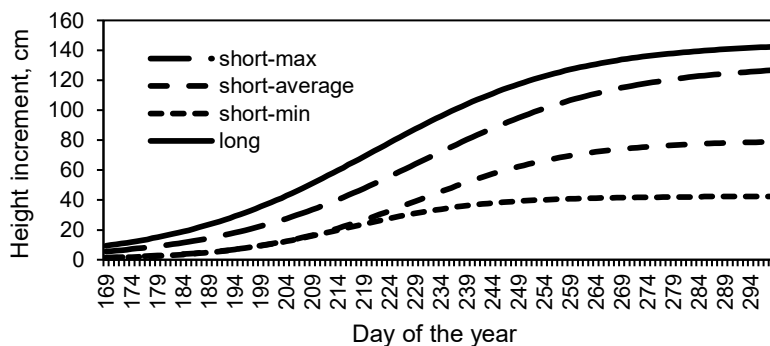
Figure 2. Gompertz model for groups of poplar clones. Clone groups of poplar: 'short–max' – Hybride 275, Oudenberg 0.3 m cuttings; 'short–average' – Baldo 0.3 m, Max 1, Max 3, Matrix 24, Matrix 49; 'short–min' – OP 42, LV 1, LV 3, LV 4; 'long' – Oudenberg 0.5 m, Vesten 0.5 m.

The non–linear Gompertz model was fitted to height growth intensity data for 4 clone groups of poplars after the mutual growth trend analysis: 'short–min', 'short–average', 'short–max', and 'long' (clone Baldo was excluded from this group due to significantly ($p < 0.05$) lower height compared to Oudenberg and Vesten) (Fig. 2). Model parameter α, showing the maximum value of the height increment, significantly ($p < 0.05$) differed between all 'short–' clone groups, although, parameter β, describing the initial phase of the growth, was similar. Significant ($p < 0.05$) differences between the slope (parameter k) of 'short–min' and 'short–max' groups indicated the sharper increase of height increment at the beginning of July for poplars with largest annual height increment at the end of the September. Obtained model parameters (α, β, k) revealed that the growth dynamics was similar between 'long' and 'short–max' poplar clones, showing that weather conditions (primarily temperature) play a significant role in their growth (Ilstedt, 1996; Šēnhofa et al., 2016). Generally, clones with largest height increment at the end of growing season showed the highest growth intensity in the beginning of growth and relatively fast increase during first part of the season; that partly

258

might be a result of genetically determined differences in leaf flushing (Jansons et al., 2014).

Link between growth intensity and meteorological parameters (i.e., temperature and precipitation) was observed (Fig. 3). In second period (30.06.–10.07.) the mean diurnal temperature decreased (from 19.3 °C to 17.6 °C) causing the growth intensity decrease by on average 2.2 mm day^{-1} for all trees, although, the precipitation sum was 69 mm (Fig. 3). The maximum growth intensity was recorded when the precipitation reached the maximum (108 mm; 19.2 °C) at the end of July (22.07.–08.08.), increasing to an on average 12.7 mm day^{-1}. The growth intensity in fourth period varied greatly between the poplar clones, ranging from 4.6 mm day^{-1} (LV 1) to 18.5 mm day^{-1} ('long' Oudenberg). In the mid–August (09.08.–17.08.) temperature and precipitation felled to 14.9 °C and 60 mm, respectively, caused the growth intensity decrease to on an average of 10.2 mm day^{-1}. Although, the temperature increased in the next period (18.08.–29.08), the growth intensity remained approximately the same as in the previous period (10.3 mm day^{-1}). This suggests different late–summer growth strategy (Devine et al., 2010) for analysed poplar genotypes, confirming that weather conditions have a strong influence on growth and inwintering of poplars during the last month of growing season (Ilstedt, 1996). Further, the growth intensity decreased gradually with the decrease of temperature and precipitation as sum until the end of measuring.
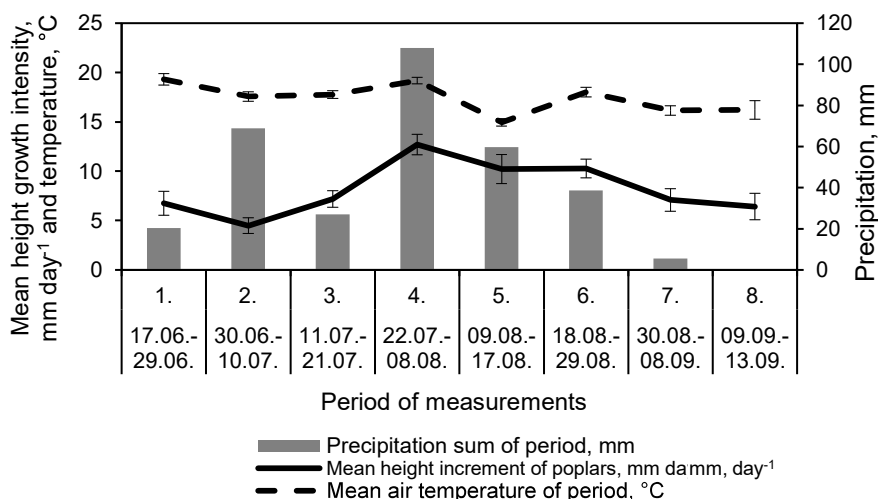
Figure 3. Mean height growth intensity (mm day^{-1}) of poplar ± CI in relation to meteorological parameters. The temperature for the period of measurements has been calculates as mean value of the recorded diurnal temperatures ± CI.

Growth intensity of the poplar clones had notable ($p > 0.05$) positive correlation with the precipitation sum, weaker – with the mean diurnal temperature, mean $r = 0.60$ and $r = 0.17$, respectively. Clones with longest annual height ('long' Vesten and 'long' Oudenberg) during the unusually cold period (09.08.–17.08.) continued their growth, when other poplar clones reduced it (Figs 1, 3). This suggested the robustness of fast–growing genotypes to weather conditions, as previously shown by Jansons et al. (2014).

Despite non–significant correlation, the temperature effect on poplar growth was evident by the notable differences of the height growth intensity between the periods with the prompt changes of mean diurnal temperature (Fig. 3), i.e.: between the first and second, the third and fourth, the fourth and fifth, as well as the sixth and seventh periods. It may indicate the short term acclimatization of poplars to environmental signals, showed by Rohde et al. (2011). However, at the first part of the growing season (i.e., between the second and third period) temperature was not deciding factor to ensure significant growth intensity increase (Fig. 3). It might be due to interaction with other environmental factors, like precipitation (Leonelli et al., 2008; Chhin, 2010). Also towards the end of the growing season (between the fifth and sixth period), sharp increase of temperature was not followed by notable rise of growth intensity, suggesting that other factors, e.g., photoperiod (Howe, 1995; Rohde et al., 2011; Soolanayakanahally et al., 2015) may have reduced the importance of temperature.

CONCLUSIONS

Mean annual shoot height of poplar clones was 81.0 ± 6.8 cm; it was significantly affected by genotype (clone). Slightly longer (0.5 vs. 0.3 m) cuttings (Baldo, Oudenberg) ensured notably (30–50%) larger annual shoot length. Intra–annual height curves, described by Gompertz model, indicated that the poplar clones with largest annual shoot height ('long' Vesten and 'long' Oudenberg) had relative sharp increase of the growth intensity from June to July. Link between growth intensity and temperature, precipitation was observed; it was weaker for the clones with largest annual height increment.

REFERENCES

Ball, J., Carle, J. & Lungo, A.D. 2005. Contribution of poplars and willows to sustainable forestry and rural development. *Unasylva* **221**(56), 3–9.

Bilodeau–Gauthiera, S., Pareb, D., Messiera, C. & Belangerc, N. 2011. Juvenile growth of hybrid poplars on acidic boreal soil determined by environmental effects of soil preparation, vegetation control, and fertilization. *For. Ecol. Manage* **261**, 620–629.

Bloomberg, W.J. 1963. The significance of initial adventitious roots in poplar cuttings and the effect of certain factors on their development. *For. Chron*. **39**(3), 279–289.

Bronisz, K., Strub, M., Cieszewski, C., Bijak, S., Bronisz, A., Tomusiak, R., Wojtan, R. & Zasada, M. 2016. Empirical equations for estimation aboveground biomass of *Betula pendula* growing on former farming in central Poland. *Silva Fenn.* **50**(4), id1559, doi:10.14214/sf.1559.

Buhler, D.D., Netzer, A.D., Riemenschneider, D.E. & Hartzler, R.G. 1997. Weed management in short rotation poplar and herbaceous perennial crops grown for biofuel productions. *Biomass Bioenergy* **14**, 385–394.

Burgess, D., Hendrickson, O.Q. & Roy, L. 1990. The importance of initial cutting size for improving the growth performance of Salix alba L. *Scand. J. For. Res.* **5**, 215–224.

Camp, J.C., Rousseau, R.J. & Gardiner, E.S. 2012. Longer black willow cuttings result in better initial height and diameter growth in biomass plantations. In Butnor, J.R. (ed): *Proceedings of the 16th Biennial Southern Silvicultural Research Conference*. Southern Research Station, Ashville, NC, USA. pp. 43–46.

Chhin, S. 2010. Influence of climate on the growth of hybrid poplar in Michigan. *Forests* **1**, 209–229.

Christersson, L. 2010. Wood production potential in poplar plantations in Sweden. *Biomass Bioenergy* **34**(9), 1289–1299.

Christersson, L. 2008. Poplar plantations for paper and energy in the south of Sweden. *Biomass Bioenergy* **32**(11), 997–1000.

DeBell, D.S., Clendenen, G.W., Harrington, C.A. & Zasada, J.C. 1996. Tree growth and stand development in short–rotation *Populus* plantings: 7–year results for two clones at three spacings. *Biomass Bioenergy* **11**, 253–269.

Devine, W.D., Harrington, C.A. & DeBell, V.B. 2010. Intra–annual growth and mortality of four *Populus* clones in pure and mixed plantings. *New For.* **39**, 287–299.

Fekedulegn, D., Mac Siurtain, M.P. & Colbert, J.J. 1999. Parameter estimation of nonlinear growth models in forestry. *Silva Fenn.* **33**, 327–336.

Giovannelli, A., Deslauriers, A., Fragnelli, G., Scaletti, L., Castro, G., Rossi, S. & Crivellaro, A. 2007. Evaluation of drought response of two poplar clones (*Populus×canadensis* Mönch 'I–214' and *P.deltoides* Marsh. 'Dvina') through high resolution analysis of stem growth. *J. Exp. Bot.* **58**, 2673–2683.

Howe, G.T., Hackett, W.P., Furnier, G.R. & Klevorn, R.E. 1995. Photoperiodic responses of a northern and southern ecotype of black cottonwood. *Physiol. Plant.* **93**, 695–708.

Ilstedt, B. 1996. Genetics and performance of Belgian poplar clones tested in Sweden. *For. Genet.* **3**(4), 183–195.

Jansons, Ā., Zeps, M., Rieksts–Riekstiņš, J., Matisons, R. & Krišāns, O. 2014. Height increment of hybrid aspen *Populus tremuloides* x *P. tremula* as a function of weather conditions in central part of Latvia. *Silva Fenn.* **48**(5), id1124, doi: 10.14214/sf.1124.

Jules, E.S., Carroll, A.L. & Kauffman, M.J. 2010. Relationship of climate and growth of quaking aspen (*Populus tremuloides*) in Yellowstone National Park. Final Report for RWO 81 Rocky Mountain Ungulates, Arcata, 26 pp. *http://digitalcommons.usu.edu/aspen_bib/7056/*. Accessed: 13.09.2017.

Kirschbaum, M.U.F. 2000. Forest growth and species distribution in a changing climate. *Tree Physiol.* **20**, 309–322.

Kozlowski, T.T. & Pallardy, S.G. 2002. Acclimation and adaptive responses of woody plants to environmental stresses. *Bot. Rev.* **68**(2), 270–334.

Kutsokon, N.K., Jose, S. & Holzmueller, E. 2015. A global analysis of temperature effects on *Populus* plantation production potential. *Am. J. Plant Sci.* **6**, 23–33.

Lazdiņa, D., Šēnhofa, S., Zeps, M., Makovskis, K., Bebre, I. & Jansons, A. 2016. The early growth and fall frost damage of poplar clones in Latvia. *Agronomy Research* **14**(1), 109–122.

Leonelli, G., Denneler, B., Bergeron, Y. 2008. Climate sensitivity of trembling aspen radial growth along a productivity gradient in northeastern British Columbia, Canada. *Can. J. For. Res.* **38**(5), 1211–1222.

Marino, P.C. & Gross, K.L. 1998. Competitive effects of conspecific and herbaceous (weeds) plants on growth and branch architecture of *Populus × euramericana* cv. Eugenei. *Can. J. For. Res.* **28**, 359–367.

Mazzoleni, S. & Dickmann, D.I. 1988. Differential physiological and morphological responses of two hybrid *Populus* clones to water stress. *Tree Physiol.* **4**(1), 61–70.

Mead, D.J. 2005. Opportunities for improving plantation productivity. How much? How quickly? How realistic? *Biomass Bioenergy* **28**, 249–266.

Messaoud, Y. & Chen, H.Y.H. 2011. The influence of recent climate change on tree height growth differs with species and special environment. *PLoS One* **6**(2), e14691, doi: 10.1371/journal.pone.0014691.

Olivar, J., Duncker, P. & Spiecker, H. 2009. Impact of climatic variation on growth and wood density of young short rotation poplar trees. In Kaczka, R., Malik, I., Owczarek, P., Gärtner, H., Helle, G., Heinrich, I. (eds.): *Proceedings of the Dendrosymposium 2008. TRACE – Tree Rings in Archaeology, Climatology and Ecology.* Zakopane, Finland, Vol **7**, pp. 64–70.

Pollastrini, M., Desotgiu, R., Camin, F., Ziller, L., Marzuoli, R., Gerosa, G. & Bussotti, F. 2013. Intra–annual pattern of photosynthesis, growth and stable isotope partitioning in a poplar clone subjected to ozone and water stress. *Water Air Soil Pollut.* **224**, 1761, doi:10.1007/s11270-013-1761-4.

R Core Team 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R–project.org/.

Rohde, A., Bastien, C., Boerjan, W. & Thomas, S. 2011. Temperature signals contribute to the timing of photoperiodic growth cessation and bud set in poplar. *Tree Physiol.* **31**(5), 472–482.

Rossi, P. 1999. Length of cuttings in establishment and production of short–rotation plantations of Salix 'Aquatica'. *New For.* **18**, 161–177.

Schreiber, S.G., Hacke, U.G., Hamann, A. & Thomas, B.R. 2011. Genetic variation of hydraulic and wood anatomical traits in hybrid poplar and trembling aspen. *New Phytol.* **190**, 150–160.

Soolanayakanahally, R.Y., Guy, R.D., Street, N.R., Robinson, K.M., Silim, S.N., Albrectsen, B.R. & Jansson, S. 2015. Comparative physiology of allopatric *Populus* species: geographic clines in photosynthesis, height growth, and carbon isotope discrimination in common gardens. *Front. Plant. Sci.* **5**, 528, doi: 10.3389/fpls.2015.00528.

Šēnhofa, S., Neimane, U., Grava, A., Sisenis, L., Lazdina, D. & Jansons, A. 2017. Juvenile growth and frost damages of poplar clone OP42 in Latvia. *Agronomy Research* **15**, doi: doi.org/10.15159/AR.17.061.

Šēnhofa, S., Zeps, M., Matisons, R., Smilga, J., Lazdiņa, D. & Jansons, Ā. 2016. Effect of climatic factors on tree–ring width of *Populus* hybrids in Latvia. *Silva Fenn.* **50**(1), id 1442, doi: doi.org/10.14214/sf.1442.

Štícha, V., Macků, J. & Nuhlíček, O. 2016. Effect of permanent waterlogging on the growth of poplar clones MAX 4, MAX 5 (J–104, J–105) (*Populus maximowiczii* A. Henry × *P. nigra* Linnaeus) and evaluation of wood moisture content in different stem parts. *J. For. Sci.* **62**, 186–190.

Tullus, H., Tullus, A. & Rytter, L. 2013. Short–rotation forestry for supplying biomass for energy production. In Kellomäki, S., Kilpeläinen, A., Alam, A. (eds.): *Forest bioenergy production*. Springer, New York. pp. 39–56.

Uri, V., Lõhmus, K., Mander, Ü., Ostonen, I., Aosaar, J., Maddison, M., Helmisaari, H.S. & Augustin, J. 2011. Long–term effects on the nitrogen budget of a short–rotation grey alder (*Alnus incana* (L.) Moench) forest on abandoned agricultural land. *Ecol. Eng.* **37**(6), 920–930.

Vigl, F. & Rewald, B. 2014. Size matters? The diverging influence of cutting length on growth and allometry of two Salicaceae clones. *Biomass Bioenergy* **60**, 130–136.

Wang, D., Fan, J., Jing, P., Cheng, Y. & Ruan, H. 2016. Analyzing the impact of climate and management factors on the productivity and soil carbon sequestration of poplar plantations. *Environ. Res.* **144**(B), 88–95.

Weih, M. (2004). Intensive short rotation forestry in boreal climates: present and future perspectives. *Can. J. For. Res.* **34**(7), 1369–1378.

Zhang, S.Y., Yu, Q., Chauret, G. & Koubaa, A. 2003. Selection for both growth and wood properties in hybrid poplar clones. *For. Sci.* **49**(6), 1–8.

The early growth and fall frost damage of poplar clones in Latvia

D. Lazdiņa[*], S. Šēnhofa, M. Zeps, K. Makovskis, I. Bebre and Ā. Jansons

Latvian State Forest Research Institute 'Silava', Rigas 111, LV 2169 Salaspils, Latvia
[*]Correspondence: dagnija.lazdina@silava.lv

Abstract. The early growth and frost damage of *Populus* spp. was studied in two sites. The height of 23 five-year-old poplar clones was measured in the central part of Latvia; and the early-fall frost damage of 19 one-year-old and two-year-old poplar clones were assessed in the eastern part of Latvia. The relation between the height growth and frost damage of 16 clones, which were common for both sites, was assessed. The phenologically dormant stage was denoted for three clones, among which two are collected across Latvia (the origin un-known; introduced in 1960s). All the other clones had trees with damaged leaves and two clones had stem damage. The height of the clones ranged from 273.3 ± 60.2 to 711.0 ± 32.0 cm. The 3 most productive clones (LV3, LV1 and LV4) significantly ($P < 0.01$) exceeded others, by 34 and 65% for height and biomass, respectively. The mean height of these clones was 649.0 ± 21.5 cm and stem biomass varied from 33.7 ± 4.2 to 55.0 ± 6.4 $t_{fresh} \cdot ha^{-1}$ (planting density 6,500 trees·ha^{-1}). The clone had significant ($P < 0.01$) effect on the phenological stage, leaf and stem frost damage, as well as on the height and stem biomass. No relation ($P > 0.05$) between the frost damage of leaves and both tree height and stem biomass was found. The results suggest that fast-growing frost-tolerant clones might be selected.

Key words: height growth, height increment, biomass, frost damage, frost tolerance, short rotation coppice.

INTRODUCTION

A high productivity of the intensively grown *Populus spp*. has been reported (Heilman & Xie, 1993; DeBell et al., 1996; Scarascia-Mugnozza et al., 1997; Rae et al., 2004). It is strongly determined by genetics, and the growth and yield of the *Populus* clones substantially differs. A high number of *Populus* clones is introduced in the northern Europe (Karačić et al., 2003; Christersson, 2006; Karačić & Weih, 2006), mainly for the establishment of the plantations with the optimum (intended) rotation period of 5–10 to 20–30 years for biomass and solid wood production, respectively (Hynynen et al., 2004; Rytter & Stener, 2005; Tullus et al., 2012). For the last 15 years, substantial amount of *Populus* plantations has been established on abandoned agricultural land (Lazdiņš et al., 2010; Jansons et al., 2014) as well as in forest (Rytter et al., 2015). Nevertheless, poplars are suitable for biomass production also as the agricultural crop (Daugaviete et al., 2015; Smilga et al., 2015; Zeps et al., 2015).

High productivity of *Populus* hybrids is related to the prolonged vegetation period, in comparison to the parental species (Yu et al., 2001). Many of these hybrids can be

grown beyond the natural range of their parents (Sykes et al., 1996). The growth cessation is affected by a complex of environmental factors, among which the increased photoperiod might delay the bud set if the clone is moved northward from the region of the genotype origin (Li et al., 2002; Ingvarsson et al., 2006; Kalcsits et al., 2009). Trees which are not acclimatised to the growing site could be damaged by cold injuries (Sykes et al., 1996). In the northern Europe, the severe frost damage of the introduced poplar clones has been reported (Ferm et al., 1989; Christersson, 1996; Ilstedt, 1996; Telenius, 1999; Karačić et al., 2003; Christersson, 2006; Pliura et al., 2014), linked with the decreased vitality and mortality of trees (Xiang et al., 1991; Diamandis & Koukos, 1992; Pliura et al., 2014). Frost damage has negative effect on the stem quality, e.g. formation of multiple leaders, deformed stem straightness, stem cracks (Verwijst et al., 1996; Christersson, 2006), which is important shortage for solid wood production. However, Schreiber (2012) have suggested that the potential benefits (biomass production) of northward transferred *P. tremuloides* outweigh the potential frost-related risks in western Canada. He has observed almost twice increased biomass for ten-year-old *P. tremuloides* clones which were transferred even 7° latitude to the north with no decrease of the survival rate (Schreiber et al., 2013). These clones showed delay of the leaf shedding and their frost hardiness was lower than that of the local origin clones; still it was sufficient to not experience the early-fall frost damage. Similarly, some, but not severe, adaptation problems for northward transferred poplar clones has been reported in Lithuania (Pliura et al., 2014).

The aim of the study was to assess the productivity and early-frost damage of the *Populus* clones in Latvia. We hypothesed that (1) the recently introduced clones are more productive, as a result of continuous breeding; but (2) the clones introduced in the 1960s (cuttings from mature trees collected across Latvia) are more tolerant to the frost damage due to the appropriate frost-tolerance of their parent trees.

MATERIALS AND METHODS

The study sites are located in the central and eastern part of Latvia, near Skrīveri (56°39′ N, 25°7′ E) and Kalsnava (56°41′ N, 25°58′ E), respectively. In Skrīveri, height of 23 *Populus* clones (Table 1; planting density c.a. 6,500 trees ha^{-1}) was measured after the second, third and fifth growing season. The clones (at least 30 cuttings from each) are planted in mono-clonal row-plots on flat area with similar growing conditions (former agricultural land) in spring 2001. The distance between the rows 2.2 m, between the trees within the row 0.7 m. Clones AF2, AF6, AF7 and AF8 are planted in 3 replications, all the other clones in 1–2 replications, distributed evenly and randomly over the site. After the first growing season, all clones with the exception of AF2, AF6, AF7 and AF8 were browsed by cervids to the ground level. These clones have additional measurements of height after the first and fourth growing season. Planting material (cuttings) from Skrīveri was used to establish clonal collection in Kalsnava in 2014 and 2015. In Kalsnava, the frost damage of 19 one-year-old and two-year-old *Populus* clones was assessed. The clones were planted in narrow spacing mono-clonal rows in nursery bed with no replications within small area. The terrain was flat, no frost-shelter were provided from any side of the site (open-field).

Table 1. The number of trees and origin of clones studied in Skrīveri (N_H and N_{ABG}) and Kalsnava (N_{FD-1} and N_{FD-2})

Clone	N_H	N_{FD-1}	N_{FD-2}	N_{ABG}	Origin of planting material
LV1	22	–	–	8	mix of 12 commercial poplar clones from Sweden
LV3	22	10	2	10	(registration number KB-003, Swedish Forestry
LV4	22	18	37	9	Agency); *Tacahamaca* section
LV5	17	29	2	6	
LV7	18	22	1	12	
LV9	17	27	2	9	
LV10	21	16	2	13	
LV11	18	21	27	11	
LV12	16	12	102	7	
LV14	21	–	43	13	
LVX	19	25	1	10	
AF2	72	27	–	–	Alasia New Clones, produced by ALASIA Franco
AF6	55	28	–	–	Company, Italy;
AF7	100	27	–	–	AF2 (*P. canadensis*), AF6 (*P. generosa* × *P. nigra*),
AF8	122	29	–	–	AF7 (*P. generosa* × *P. canadensis*) and AF8
					(*P. generosa* × *P. trichocarpa*)
Max11	–	126	–	–	clone series from Germany;
Max24	–	191	–	–	hybrids of *P. maximowiczii* and *P. trichocarpa*
OP42	–	27	–	–	*P. maximowiczii* × *P. trichocarpa*
P0114	40	26	1	26	*Populus* × *woobstii* (R.I. Schröd. ex Regel) Dode; progenies (cuttings) of poplar trees collected across Latvia (Jansons et al., 2014)
POP1	14	–	–	2	progenies (cuttings) of poplar trees collected across
POP2	20	–	–	10	Latvia; presumably *Tacahamaca* and *Aigeiros*
POP3	14	–	–	8	sections, introduced (origin unknown) in 1960s
POP4	15	14	–	14	(Saliņš, 1971)
POP5	15	–	–	5	
POP6	13	–	–	10	
POP7	6	–	–	–	

N_H – number of trees measured for height after the fifth growing season;
N_{FD-1} – number of one-year-old trees, which have assessment of frost damage;
N_{FD-2} – number of two-year-old trees, which have assessment of frost damage;
N_{ABG} – number of trees used to develop the above-ground biomass equation.

The relation between height and frost damage of the 16 clones (common for both study sites) was assessed. In both sites, clones might be divided into groups, according to the origin of the used planting material. The clones of Swedish, Italian, German origin, as well as the clone OP42 are introduced recently, during the last 10 years. Clones collected across Latvia are progenies (cuttings) of the poplars that survived after introduction, most likely, in 1960s. Among them, clone P0114 has been tested and is registered as the forest reproductive material (Community Plant Variety Office, 2014). All the available information of the origin of planting material (region, species) is given in Table 1.

The frost event occurred in the beginning of October, 2015 (Fig. 1). From September 7th to October 6th, the mean of diurnal minimum and maximum temperatures were +8.0 and +17.8 °C, respectively. The temperature first dropped below zero at night to October 7th. From October 7th to 15th, the mean diurnal temperature ranged from −3.3 to +10.2 °C. The minimum temperature was −5.2 °C, recorded in October 12th.
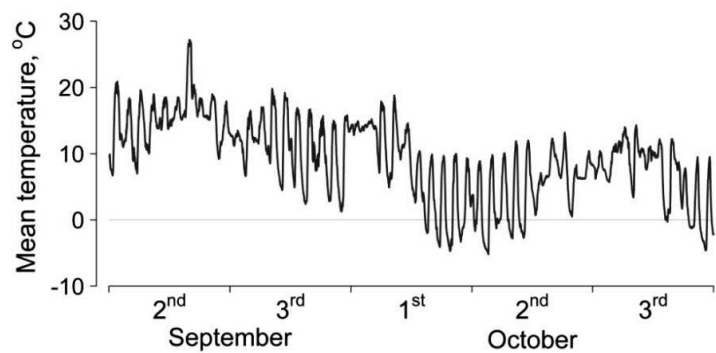
Figure 1. Temperature fluctuation (Δt = 15 min) for the period from the 2nd decade of September to the 3rd decade of October.

Damaged part	Grade 1	Grade 2	Grade 3	Grade 4	Grade 5
Canopy	intact leaves	several damaged leaves	damaged most leaves of current-year leading shoot	damaged most leaves of the whole tree	already fallen leaves
Stem and/or branches	intact stem	several stem injuries	damaged current-year leading shoot	damage of more than ⅓ of height	damage of whole stem

Figure 2. The schematic visualization of leaf and stem damage grades.

112

In October 15th, the visual frost damage was assessed (Fig. 2). The bud set was used to determine if trees were still in phenologically active stage or dormant. The damage of the leaves was evaluated at five grade scale. Grade 1_L ('intact leaves') corresponds to the visually intact leaves, Grade 2_L ('mild damage') to the several frost damaged leaves, Grade 3_L ('moderate damage') to the damage of most leaves in the current-year leading shoot and Grade 4_L ('severe damage') to the damage of most leaves of the whole tree. The Grade 5_L corresponds to the trees in the phenologically dormant stage, i.e. leaves were already fallen before the freezing-event and buds were set. Similarly, the damage of stem was evaluated according to five grades. The Grade 1_{ST} ('intact stem') corresponds to the visually intact stem, Grade 2_{ST} ('mild damage') to the several stem injuries, Grade 3_{ST} ('moderate damage') to the damaged current-year leading shoot, Grade 4_{ST} ('severe damage') to stem damage of more than ⅓ of height and Grade 5_{ST} to the damage of whole stem.

The effect of tree age on the frost damage was assessed at the individual tree level for 10 clones. Clone LV4, LV11 and LV12 had sufficient number of one-year-old and two-year-old trees, thus the distribution of number of trees among the grades of leaf and stem damage were assessed for only these clones.

The fresh above-ground biomass in the leafless stage was calculated by Equation 1. This equation is developed based on the biomass measurement of randomly selected ramets (number by clone is shown in Table 1) in Skrīveri after the fourth growing season (height range from 159 to 546 cm).

$$ABG_{fresh} = 10^{-6} \cdot H^{2.7759}, \qquad (1)$$

where: ABG_{fresh} – fresh above-ground biomass in leafless state, kg; H – tree height, cm.

To model potential productivity of different clones at the stand level (6,500 trees ha^{-1}), three assumptions of the tree recovery were made: (1) the undamaged trees (Grade 1_L and 1_{ST}) and trees with the several frost damaged leaves (Grade 2_L) have no biomass reduction; (2) trees with the damage of most leaves in the last-year leading shoot (Grade 3_L) or with the several stem injuries (Grade 2_{ST}) have biomass reduction by 20%; (3) trees with the more severe damage (Grade 4_L and 5_L of leaf damage and/or Grade 3_{ST}–5_{ST} of stem damage) experience mortality. These assumptions are not tested, therefore the results are used only to illustrate the potential effect of the frost injuries.

The Shapiro-Wilk test was used to assess the normality of the data. The one-way analysis of variance was used to assess the differences of the height among the clones. The Kruskal-Wallis test was used to assess the differences of the biomass among the clones. The generalized linear model multivariate was used to assess (1) the effect of the clone and age on the phenological stage and level of leaf and stem damage and (2) the effect of the mean grade of leaf and stem damage on the tree height and biomass. The Chi-squared test was used to assess the distribution of the number of damaged trees of clones LV4, LV11 and LV12 among the grades of leaf damage and within the one-year-old and two-year-old trees. All tests were performed at $\alpha = 0.05$. All calculations were done in R 3.0.2. (R Core Team 2013).

In total, 65.4% of trees were in the active phenological stage. All trees in the phenologically dormant stage were found for clones P0114, POP4 and LV10 (Table 2). All trees still growing were denoted for 10 clones, while 6 clones had trees in both phenological stages. The significant ($P < 0.01$) differences of phenological stage that were found between clones are in accordance with the moderate to strong genetic control of the bud set of *Populus spp*. (Hall et al., 2007; Rohde et al., 2011), and the variation of bud set timing may show high (up to ca. 100 days) differences between clones of different origin (Howe et al., 2000; Christersson, 2006; Friedman et al., 2008). The perennial plants in temperate and boreal zone are adapted to the seasonal cycle of the growth and winter dormancy (Howe et al., 2003; Rohde & Bhalerao, 2007). In our study, surviving clones from the earlier introduction (locally collected) demonstrated better fit to environment.The timing of the bud set is an important adaptive trait (Hänninen et al., 1990). At first, growth cessation is induced by decrease of day-length and temperature, than cold acclimation, endodormancy occurs and, finally, plants reach the maximal cold hardiness. Genotypes transferred northward delay the bud set mainly due to the longer daylight, while the genotypes transferred from the northern areas (or high elevations) tend to set bud earlier in the fall, than trees from the local populations (Weber & Stettler, 1985; Skrøppa & Magnussen, 1993).

Table 2. The number of trees according to phenological stage and leaf and stem damage grades

Clone	Phenological stage		Leaf damage Grades					Stem damage Grades					Total
	Dormant	Active	1_L	2_L	3_L	4_L	5_L	1_{ST}	2_{ST}	3_{ST}	4_{ST}	5_{ST}	
AF2	–	27	–	10	17	–	–	27	–	–	–	–	27
AF6	–	28	3	12	13	–	–	28	–	–	–	–	28
AF7	–	27	–	3	24	–	–	27	–	–	–	–	27
AF8	–	29	–	10	19	–	–	29	–	–	–	–	29
P0114	27	–	–	–	–	–	27	27	–	–	–	–	27
POP4	14	–	–	–	–	–	14	14	–	–	–	–	14
LV10	18	–	–	–	–	–	18	18	–	–	–	–	18
LV11	–	48	21	13	14	–	–	48	–	–	–	–	48
LV12	13	101	33	34	4	30	13	114	–	–	–	–	114
LV14	–	43	–	–	43	–	–	23	20	–	–	–	43
LV3	1	11	–	1	–	10	1	10	1	–	1	–	12
LV4	–	55	42	11	1	1	–	55	–	–	–	–	55
LV5	30	1	–	–	1	–	30	31	–	–	–	–	31
LV7	–	23	–	–	–	23	–	23	–	–	–	–	23
LV9	–	29	11	17	–	1	–	29	–	–	–	–	29
LVx	5	21	–	–	–	21	5	26	–	–	–	–	26
Max11	59	67	–	–	–	67	59	126	–	–	–	–	126
Max24	143	48	–	–	5	43	143	142	49	–	–	–	191
OP42	–	27	–	–	1	26	–	27	–	–	–	–	27

Out of the assessed 585 trees, 81% had damaged leaves at various grades (Table 2). Among the actively growing trees, four clones (LV3, LV7, LVX and OP42) had a high proportion (> 80%) of trees with the severely damaged (Grade 4_L) leaves. Clone LV4

showed the highest frost resistance – 76% of trees had intact leaves (Grade 1_L). Similarly, Howe et al. (2000) have reported significant differences and a wide range of the frost damage among clones: in the scale of 10, the least-square means were from –0.8 to 9.5. The frost damage of stem was less common (Table 2). Among the dormant trees, clone LV3 had one tree with the mild stem damage (Grade 2_{ST}). The high susceptibility of stem frost damage was denoted for clones Max24 and LV14, which had 87% and 100% of still growing trees mildly (Grade 2_{ST}) damaged, respectively. The severe (Grade 4_{ST}) stem damage was denoted for one tree (clone LV3). These results confirm that trees that set buds later in the fall are more susceptible to the frost damage (Junttila & Kaurin, 1990; Howe et al., 2000).

The tree age had significant ($P < 0.01$) effect on the level of damaged leaves, but not on the stem damage ($P > 0.05$) at individual tree level. Significant ($P < 0.01$) differences were found also among the clones of the same age. All trees from clones LV4 and LV11 were in the active phenological stage, regardless of the age (Table 2). Also all two-year-old trees and most (87%) of the one-year-old trees from clone LV12 were active. For these three clones, no stem damage was denoted but the damage of leaves differed significantly ($P < 0.01$) between trees of different age. Within clones LV4 and LV11, all two-year-old trees were intact (Grade 1_L) while one-year-old trees were damaged (Grade 2_L and 3_L). In contrast, within clone LV12, most of the two-year-old trees were damaged severely (Grade 4_L) but one-year-old trees had milder damage (Grades 3_L and 4_L). Younger and, consequently, shorter trees might be more damaged by frost. First, a number of physiological changes, including these which are regulating bud activity, are related with maturation (Brunner et al., 2003; Rozi et al., 2010). For instance, the spring phenology of five temperate tree species was found to be ontogenetically determined rather than result from microclimate (Vitasse, 2013). The ontogenetic effect has also been indicated by increased susceptibility to frost damage of one-year-old *Populus × rasumowskyana* shoots that were emerged after the coppicing in the south-western Finland (Ferm et al., 1989). Younger trees tend to emerge leaves earlier than adults (Vitasse et al., 2014), therefore have higher probability to suffer from early spring frosts. However, similar freezing resistance has been observed for leaves at the same developmental stage for seedlings and saplings (< 0.3 m and 2–4 m height, respectively) in comparison to adult trees (25–30 m height) for several temperate broadleaved species during the leaf-flushing (Vitasse et al., 2014). Also the cold hardiness was found to increase with age, and show significant differences between the adult individuals and trees in the juvenile stage for a number of deciduous species (Lim et al., 2014; Hofmann et al., 2014). Second, smaller trees are more exposed to frost. Relatively larger part of smaller trees is located near the ground, where, in open sites, the air temperature is the lowest (Snyder & Melo-Abreu, 2005). For instance, in the southern Sweden in clear-cut area during three growing seasons the observed mean difference between the minimum temperatures in 0.4 and 1.7 m height was 1.6 °C, reaching maximum difference of 3.8 °C (Langvall & Ottosson-Löfvenius, 2002). Consequently, shorter stands have higher probability of frost damage than taller stands. Moreover, the commercial plantations are commonly established on agricultural lands, often situated in open fields. This could lead to uneven distribution of damaged trees within the plantation – heavier damage nears the edge of plantation and less damaged trees in the centre of it or in the border with mature forest where mutual shield is provided (Verwijst et al., 1996).

After the bud set, i.e. phenologically dormant trees, are more tolerant to the frost damage (Junttila & Kaurin, 1990; Frewen et al., 2000; Howe et al., 2000), but too early bud set interferes with the growth and these trees tend to be shorter (Li et al., 1993; Howe et al., 2000).Thus, the trade-off between utilizing the full growing season and the proper frost-tolerance might occur. However, the frost injury depends on the frost event occurrence and severity. For instance, no frost damage of the clones AF2, AF6, AF7 and AF8 were observed during the first three years in Skrīveri (Lazdiņa et al., 2014). But in the study year, 97% of these trees had mild and moderate (Grade 2_L and 3_L, respectively) damage of leaves (Table 2).

The height growth showed temporal differences among the clones (Fig. 3). After the second growing season, the best results were demonstrated by clones AF6, LV3 and LV12: 159.5 ± 10.5, 154.3 ± 14.2 and 143.9 ± 8.5 cm, respectively. The significant ($P < 0.01$) differences between the clones were found, mostly caused by the superiority of clone AF6 and slow growth of clones POP1, POP2 and POP6. It should be noted that most of the other clones had similar or higher height as clones AF2, AF8 and AF7, regardless of the browsing at the end of the previous growing season. This indicates sprouting ability and vigorous growth due to the established root system (Christersson, 1986), and this advantage foster the yield of the second rotation to exceed yield of the first rotation (Dillen et al., 2013). The height differences between clones increased with age. After the second growing season 80 significantly different pairs between clones were found, after the third season 124, while after the fifth growing season this number increased to 169. After the fifth growing season, the height of clones ranged from 273.3 ± 60.2 to 711.0 ± 32.0 cm, and most of the clones LV exceeded those collected in Latvia, as well as AF2, AF7 and AF8. Each of the three highest clones (LV3, LV1 and LV4) was significantly higher than most of the other clones (Fig. 3). The height of these clones was 649.0 ± 21.5, exceeding ($P < 0.01$) others by 34%. The same three clones had the highest biomass and exceeded others by 65%. The fresh above-ground biomass of clones LV3, LV1 and LV4 was 8.47 ± 0.99, 6.40 ± 0.88 and 5.19 ± 0.64 kg (Fig. 4). The corresponding biomass (planting density 6,500 trees ha^{-1}) of these clones was 55.0 ± 6.4, 41.6 ± 5.7 and 33.7 ± 4.2 t$_{fresh}$ ha^{-1}, respectively. In comparison, the mean above-ground biomass of the other clones was 14.8 ± 0.7 t$_{fresh}$ ha^{-1}. The mean biomass increment of the three most productive clones was 8.7 ± 0.7 t$_{fresh}$ ha^{-1} year^{-1}.

The relatively high genetic control of bud set indicates the relatively low microenvironmental effect (Howe et al., 2000). Hence, the relation of growth and frost-tolerance of the same clones in different sites was analysed. Similar (both $P > 0.05$) height and above-ground biomass of clones was found, regardless of the mean grade of leaf damage. In contrast, significant ($P = 0.049$ and $P = 0.026$, respectively) positive relation between both height and biomass with grade of the stem damage was found. This was caused by clones LV14 and LV3 – relatively high and productive clones that had 46.5 and 16.6% of trees with stem damage (Table 2), respectively. The trade-off between growth and bud set is reported by some authors that have noted the tendency of the clones that set bud early to be shorter than others (Li & Adams 1993) and the other way around – trees that set buds later to be higher and have larger diameter (Pliura et al., 2014). Our results are consistent with this belief, regarding the negative effect of stem damage on tree height and biomass. In contrast, no support to the trade-off was showed by similar level of leaf damage. It should be kept in mind,that the relations between

clonal means are demonstrated and further studies should be done to assess these relations at the individual tree level.
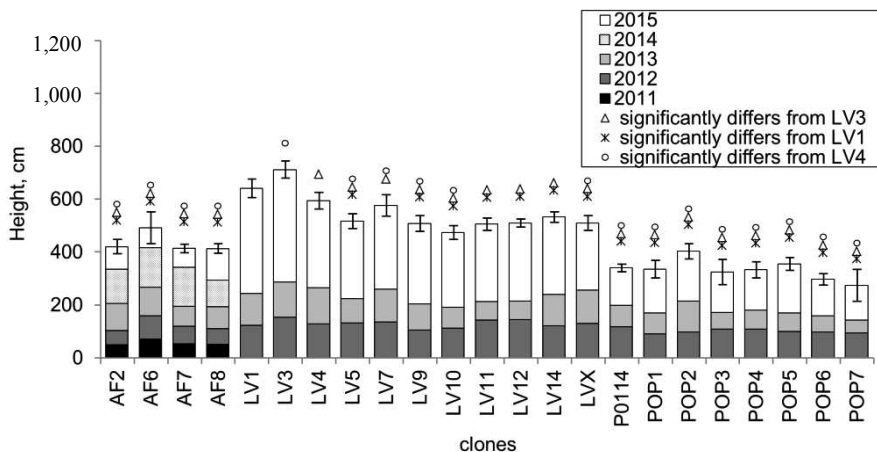
Figure 3. Height of clones after the first to fifth growing season and the confidence interval of height after the fifth growing season. The significant differences of the height after the fifth growing season between the three best (LV3, LV1 and LV4) and the other clones are denoted by symbols.
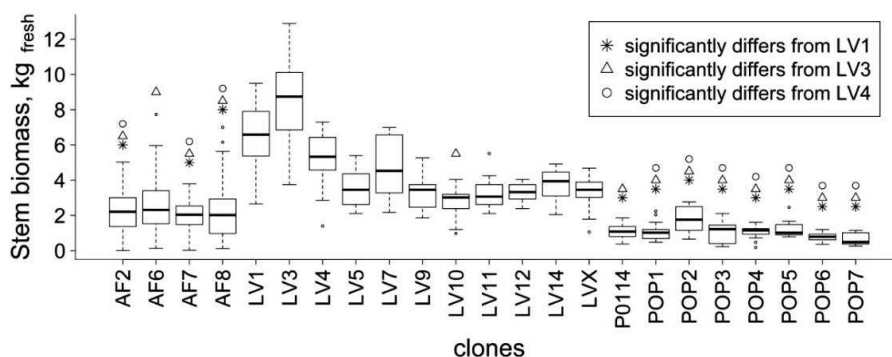
Figure 4. Fresh above-ground biomass of clones in the leafless stage. The significant differences of biomass between the three best (LV3, LV1 and LV4) and the other clones are denoted by symbols. Line shows median, box represents 1st and 3rd quartile, whiskers mark range (not exceeding 150% of interquartile distance) and circles denote outliers of the datasets.

The cold-resistance up to -70° C of the *Populus* species have been reported (Friedman et al., 2008). However, the mortality caused by the cold-injuries is possible if trees are not completely hardened and the sudden drop of temperature occurs (Friedman et al., 2008). Strong negative correlation between the fall frost damage and winter survival has been noted for poplars (Howe et al., 2000), as well as the changes of allometry (lower shoot weight) after the spring frost damage for one of two assessed

Salix hybrids during the first year after the coppicing (Verwijst et al., 1996). The heaviest damaged stand parts had biomass reduction in comparison to undamaged parts for both assessed clones by 47 and 60% (Verwijst et al., 1996). Similarly, Ilstedt (1996) has reported the dieback of ca. 20–60 cm of leading shoots after the fall frost at the age of 2–4 years for most of the poplar hybrid clones that where transferred as far as 10° latitude from the origin of the parental species. The dieback of up to one meter long leading shoot of some 2–3 years old poplar hybrid clones during the winter has mainly resulted with tree death, while other clones had experienced 10–20 cm long shoot dieback and successfully recovered (Christersson, 2006). Dieback of up to three meters long leading shoots of 11-year-old trees (height more than 20 m) were recorded due to the severe winter in 2001–2002 (Christersson, 2006). At the age of 13 years, 15% of the clones were dead due to the frost damage (Christersson, 2006). Nevertheless, frost damage may have indirect negative effect – decreased tree vitality, increased susceptibility to diseases and reduced wood quality. Therefore, we assumed that damaged trees might have biomass reduction, depending on the grade of damage. According to our assumptions (see Materials and Methods), the highest above-ground biomass reduction due to the frost damage caused mortality was expected for clones LVX, LV3 and LV7 (Fig. 5). The potential mortality of these clones resulted in biomass reduction by 80.8, 93.3 and 100%, respectively. Moreover, the clone LV3 would have the absolutely highest above-ground biomass if no frost damage would occur. The loss of biomass of the other clones varied from 0.6 to 29.3%. No biomass reduction was expected for clone P0114, POP4 and LV10. Yet, appropriate frost-tolerance of locally collected clones does not result in higher yield, in comparison to less frost-tolerant but more productive recently introduced clones at the particular frost-event. Further tests in different conditions and age need to be carried out for more comprehensive conclusions.

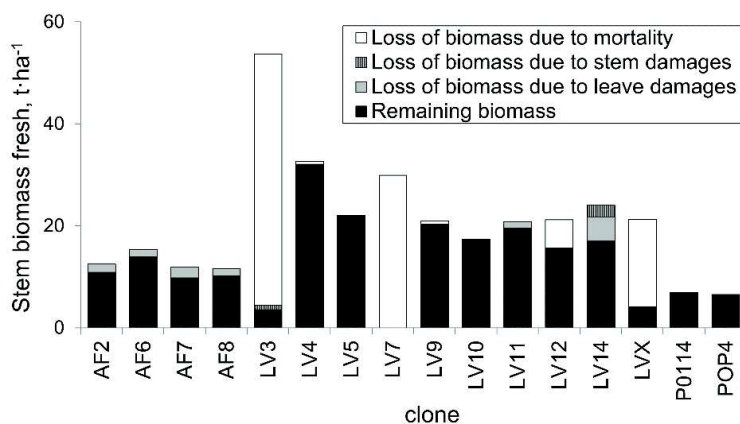**Figure 5.** Potential (modelled) loss of the fresh above-ground biomass in the leafless stage (planting density 6,500 trees ha^{-1}).

Authors are aware that the assumptions placed in the model might not hold. Poplars have good regeneration ability after damage, as demonstrated by results (height growth) after the first-year browsing damage (Fig. 3), and also concluded by other studies (Mulak

et al., 2006; Hamberg et al., 2011; Myking et al., 2011). For instance, 'soon recovery' after fall frost damage has been reported for northward transferred cuttings at the age of 2–4 years in the southern central Sweden (Ilstedt, 1996). Moreover, the frost damage could occur only in the frost years; while, in the absence of fall frost, trees might gain due to the prolonged growing season.

CONCLUSIONS

Frost injuries might result in noticeable biomass reduction and mortality of the most productive clones. Hence, the assessment of productivity, frost-tolerance and their interaction ensures valuable information for further clone tests. Clone had significant (all $P < 0.01$) effect on the phenological stage, leaf and stem frost damage, height and biomass. Our hypothesis was confirmed. Clones (cuttings) which are introduced in the 1969s were less frost-damaged than these which are introduced recently. However, the latter were superior in height and the above-ground biomass production (in the leafless stage). The significant ($P < 0.05$) trend of more stem damage for more productive clones was found. In contrast, the frost damage of leaves had no effect on both tree height and biomass (both $P > 0.05$). Therefore, the results suggest that fast-growing and frost-tolerant clones at the particular age could be selected.

REFERENCES

Brunner, A.M., Goldfarb, B., Busov, V. & Strauss, S.H. 2003. Controlling maturation and flowering for forest tree domestication. In Stewart, C.N. (ed.): *Transgenic Plants: Current Innovations and Future Trends*. Wymondham: Horizon Press, pp. 9–44.

Christersson, L. 1986. High technology biomass production by *Salix* clones on a sandy soil in southern Sweden. *Tree Physiol*., **2**(1-2-3), 261-272.

Christersson, L. 1996. Future research on hybrid aspen and hybrid poplar cultivation in Sweden. *Biomass Bioenerg*. **11**, 109–113.

Christersson, L. 2006. Biomass production of intensively grown poplars in the southernmost part of Sweden: Observations of characters, traits and growth potential. *Biomass Bioenerg*. **30**(6), 497–508.

Community Plant Variety Office. 2014. Official Gazette of the Community Plant Variety Office, 6, 195 pp.

Daugaviete, M., Lazdina, D., Bambe, B., Bardule, A., Bardulis, A. & Daugavietis, U. 2015. Productivity of different tree species in plantations on agricultural soils and related environmental impacts. *Baltic Forestry* **21**(2), 349–358.

DeBell, D.S., Clendenen, G.W., Harrington, C.A. & Zasada, J.C. 1996. Tree growth and stand development in short-rotation Populus plantings: 7-year results for two clones at three spacings. *Biomass Bioenerg* **11**, 253–269.

Diamandis, S. & Koukos, P. 1992. Effect of bacteria on the mechanical and chemical properties of wood in poplars damaged by frost cracks. *Eur. J. For. Pathol*. **22**(6–7), 362–370.

Dillen, S.Y., Djomo, S.N., Al Afas, N., Vanbeveren, S., & Ceulemans, R. 2013. Biomass yield and energy balance of a short-rotation poplar coppice with multiple clones on degraded land during 16 years. *Biomass Bioenerg* **56**, 157–165.

Ferm, A., Hytönen, J. & Vuori, J. 1989. Effect of spacing and nitrogen fertilization on the establishment and biomass production of short rotation poplar in Finland. *Biomass* **18**(2), 95–108.

Frewen, B.E., Chen, T.H.H., Howe, G.T., Davis, J., Rohde, A., Boerjan, W. & Bradshaw, H.D. 2000. Quantitative trait loci and candidate gene mapping of bud set and bud flush in Populus. *Genetics* **154**(2), 837–845.

Friedman, J.M., Roelle, J.E., Gaskin, J.F., Pepper, A.E. & Manhart, J.R. 2008. Latitudinal variation in cold hardiness in introduced *Tamarix* and native *Populus*. *Evol. Appl.* **1**(4), 598–607.

Hall, D., Luquez, V., Garcia, V.M., St Onge, K.R., Jansson, S. & Ingvarsson, P.K. 2007. Adaptive population differentiation in phenology across a latitudinal gradient in European aspen (*Populus tremula*, L.): a comparison of neutral markers, candidate genes and phenotypic traits. *Evolution* **61**(12), 2849–2860.

Hamberg, L., Malmivaara-Lämsä, M., Löfström, I., Vartiamäki, H., Valkonen, S. & Hantula, J. 2011. Sprouting of *Populus tremula* L. in spruce regeneration areas following alternative treatments. *Eur. J. For. Res.* **130**(1), 99–106.

Hänninen, H., Häkkinen, R., Hari, P. & Koski, V. 1990. Timing of growth cessation in relation to climatic adaptation of northern woody plants. *Tree Physiol.,* **6**(1), 29–39.

Heilman, P.E. & Xie, F.G. 1993. Influence of nitrogen on growth and productivity of short-rotation *Populus trichocarpa* x *Populus deltoides* hybrids. *Can. J. For. Res.* **23**, 1863–1869.

Hofmann, M., Jager, M. & Bruelheide, H. 2014. Relationship between frost hardiness of adults and seedlings of different tree species. *iForest* **7**(5), 282–288.

Howe, G.T., Aitken, S.N., Neale, D.B., Jermstad, K.D., Wheeler, N.C. & Chen, T.H. 2003. From genotype to phenotype: unravelling the complexities of cold adaptation in forest trees. *Can. J. Bot.* **81**(12), 1247–1266.

Howe, G.T., Saruul, P., Davis, J. & Chen, T.H.H. 2000. Quantitative genetics of bud phenology, frost damage, and winter survival in an F2 family of hybrid poplars. *Theor. Appl. Genet.* **101**, 632–642.

Hynynen, J., Ahtikoski, A. & Eskelinen, T. 2004. Yield and profitability of aspen plantation. *Metsä tieteen aikakauskirja* **1**, 113–116. (In Finnish.)

Ilstedt, B. 1996. Genetics and performance of Belgian poplar clones tested in Sweden. *For. Genet.*, **3**(4), 183–195.

Ingvarsson, P.K., García, M.V., Hall, D., Luquez, V. & Jansson, S. 2006. Clinal variation in phyB2, a candidate gene for day-length-induced growth cessation and bud set, across a latitudinal gradient in European aspen (*Populus tremula*). *Genetics* **172**(3), 1845–1853.

Jansons, Ā., Zurkova, S., Lazdiņa, D. & Zeps, M. 2014. Productivity of poplar hybrid (*Populus balsamifera* × *P. laurifolia*) in Latvia. *Agronomy Research* **12**(2), 469–478.

Jansons, Ā., Zeps, M., Rieksts-Riekstiņš, J., Matisons, R. & Krišāns, O. 2014. Height increment of hybrid aspen Populus tremuloides × P. tremula as a function of weather conditions in south-western part of Latvia. *Silva Fenn.* **48**(5), pp. 13.

Junttila, O. & Kaurin, Å. 1990. Environmental control of cold acclimation in *Salix pentandra*. *Scand. J. For. Res.*, **5**:(1–4), 195–204.

Kalcsits, L.A., Silim, S. & Tanino, K. 2009. Warm temperature accelerates short photoperiod-induced growth cessation and dormancy induction in hybrid poplar (*Populus × spp.*). *Trees* **23**(5), 971–979.

Karačić, A. & Weih, M. 2006. Variation in growth and resource utilisation among eight poplar clones grown under different irrigation and fertilisation regimes in Sweden. *Biomass Bioenerg* **30**(2), 115–124.

Karačić, A., Verwijst, T. & Weih, M. 2003. Above-ground woody biomass production of short-rotation *Populus* plantations on agricultural land in Sweden. *Scand. J. For. Res.* **18**(5), 427–437.

Langvall, O. & Ottosson-Löfvenius, M. 2002. Effect of shelterwood density on nocturnal near-ground temperature, frost injury risk and budburst date of Norway spruce. *For. Ecol. Manage*. **168**(1), 149–161.

Lazdiņa, D., Bārdulis, A., Bārdule, A. Lazdiņš, A., Zeps, M. & Jansons, Ā. 2014 The first three-year development of ALASIA poplar clones AF2, AF6, AF7, AF8 in biomass short rotation coppice experimental cultures in Latvia. *Agronomy Research* **12**(2), 543–552.

Lazdiņš, A., Lazdiņa, D. & Liepa, I. 2010. Characterization of naturally afforested farmlands in Latvia. In *Annual 16th International Scientific Conference Proceedings*. Jelgava, LLU, 176–182.

Li, C., Puhakainen, T., Welling, A., Viherä-Aarnio, A., Ernstsen, A., Junttila, O., Heino, P. & Palva, E.T. 2002. Cold acclimation in silver birch (*Betula pendula*). Development of freezing tolerance in different tissues and climatic ecotypes. *Physiol. Plant.*, **116**, 478–488.

Li, P. & Adams, W.T. 1993. Genetic control of bud phenology in pole-size trees and seedlings of coastal Douglas-fir. *Can. J. For. Res.* **23**(6), 1043–1051.

Li, P., Beaulieu, J., Corriveau, A. & Bosquet, J. 1993. Genetic variation in juvenile growth and phenology in a white spruce provenance-progeny test. *Silvae Genet*. **42**(1), 52–60.

Lim, C.C., Arora, R. & Krebs, S.L. 2014. Cold hardiness increases with age in juvenile Rhododendron populations. *Front Plant Sci.*, **5**, Article 542, pp. 8.

Mulak, T., Landhäusser, S.M., & Lieffers, V.J. 2006. Effects of timing of cleaning and residual density on regeneration of juvenile aspen stands. *Forest Ecol. Manag*. **232**(1), 198–204.

Myking, T., Bøhler, F., Austrheim, G. & Solberg, E.J. 2011. Life history strategies of aspen (*Populus tremula* L.) and browsing effects: a literature review. *Forestry* **84**(1), 61–71.

Pliura, A., Suchockas, V., Sarsekova, D. & Gudynaitė, V. 2014. Genotypic variation and heritability of growth and adaptive traits, and adaptation of young poplar hybrids at northern margins of natural distribution of *Populus nigra* in Europe. *Biomass Bioenerg*. **70**, 513–529.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Rae, A.M., Robinson, K.M., Street, N.R. & Taylor, G. 2004. Morphological and physiological traits influencing biomass productivity in short-rotation coppice poplar. *Can. J. For. Res.* **34**(7), 1488–1498.

Rohde, A. & Bhalerao, R.P. 2007. Plant dormancy in the perennial context. *Trends Plant Sci.* **12**(5), 217–223.

Rohde, A., Bastien, C. & Boerjan, W. 2011. Temperature signals contribute to the timing of photoperiodic growth cessation and bud set in poplar. *Tree Physiol*. **31**(5), 472–482.

Rozi, M., Wang, C.T., Ma, C., Shevchenko, O., Dye, S.J., Puzey, J.R., Etherington, E., Sheng, X., Meilan, R., Strauss, S.H. & Brunner, A.M. 2010. Populus CEN/TFL1 regulates first onset of flowering, axillary meristem identity and dormancy release in *Populus*. *Plant J*. **62**(4), 674–688.

Rytter, L. & Stener, L.G. 2005. Productivity and thinning effects in hybrid aspen (*Populus tremula* L. x *P. tremuloides* Michx.) stands in southern Sweden. *Forestry* **78**(3), 285–295.

Rytter, L., Andreassen, K., Bergh, J., Ekö, P.M., Grinhölm, T., Kilpeläinen, A., Lazdiņa, D., Muiste, P. & Nord-Larsen, T. 2015. Availability of Biomass for Energy Purposes in Nordic and Baltic Countries: Land Areas and Biomass Amounts. *Baltic Forestry* **21**(2), 375–390.

Saliņš, S. Special types of forest plantations. In Bušs, M. & Mangalis, I. (eds.): *Forest plantations*. Zvaigzne, Rīga, pp. 379–409 (in Latvian).

Scarascia-Mugnozza, G.E., Ceulemans, R., Heilman, P.E., Isebrands, J.G., Stettler, R.F. & Hinckley, T.M. 1997. Production physiology and morphology of *Populus* species and their

hybrids grown under short rotation. II. Biomass components and harvest index of hybrid and parental species clones. *Can. J. For. Res.* **27**(3), 285–294.

Schreiber, S.G. 2012. *Adaptation of trembling aspen and hybrid poplars to frost and drought: implications for selection and movement of planting stock in western Canada*. University of Alberta, Edmonton, Alberta, 134 pp.

Schreiber, S.G., Ding, C., Hamann, A., Hacke, U.G., Thomas, B.R. & Brouard, J.S. 2013. Frost hardiness vs. growth performance in trembling aspen: an experimental test of assisted migration. *J. Appl. Ecol.* **50**(4), 939–949.

Skrøppa, T. & Magnussen, S. 1993. Provenance variation in shoot growth components of Norway spruce. *Silvae Genet.*, **42**, 111–120.

Smilga, J., Zeps, M., Sisenis, L., Kalnins, J., Adamovics, A. & Donis, J. 2015 Profitability of hybrid aspen breeding in Latvia. *Agronomy Research* **13**(2), 430–435.

Snyder, R.L. & Melo₋Abreu, J.P. 2005. *Frost protection: fundamentals, practice and economics. Frost protection: fundamentals, practice and economics*. Food and Agriculture Organization of the United Nations, Rome, 240 pp.

Sykes, M.T., Prentice, I.C. & Cramer, W. 1996. A bioclimatic model for the potential distributions of north European tree species under present and future climates. *J. Biogeogr.* **23**, 203–233.

Telenius, B.F. 1999. Stand growth of deciduous pioneer tree species on fertile agricultural land in southern Sweden. *Biomass Bioenerg* **16**(1), 13–23.

Tullus, A., Rytter, L., Tullus, T., Weih, M. & Tullus, H. 2012. Short-rotation forestry with hybrid aspen (*Populus tremula* L.× *P. tremuloides* Michx.) in Northern Europe. *Scand. J. For. Res.* **27**(1), 10–29.

Verwijst, T., Elowson, S., Li, X. & Leng, G. 1996. Production losses due to a summer frost in a *Salix viminalis* short-rotation forest in southern Sweden. *Scand. J. For. Res.* **11**(1–4), 104–110.

Vitasse, Y. 2013. Ontogenic changes rather than difference in temperature cause understory trees to leaf out earlier. *New Phytol* **198**(1), 149–155.

Vitasse, Y., Lenz, A., Hoch, G. & Körner, C. 2014. Earlier leaf-out rather than difference in freezing resistance puts juvenile trees at greater risk of damage than adult trees. *J. Ecol.* **102**(4), 981–988.

Weber, J.C. & Stettler, R.F. 1985. Genetic variation and production of *Populus trichocarpa* and its hybrids. I. Morphology and phenology of 50 native clones. *Can. J. For. Res.* **15**(2), 376–383.

Xiang, C., Sun, H. & Li, G. 1991. Bacterial swollen stem canker on poplar: the disease and its causes. *J. Northeast For. Univ.* **2**(1), 48–55.

Yu, Q., Tigerstedt, P.M.A. & Haapanen, M. 2001. Growth and Phenology of Hybrid Aspen Clones (*Populus tremula* L. × *Populus tremuloides* Michx.). *Silva Fenn.* **35**(1), 15–25.

Zeps, M., Sisenis, L., Luguza, S., Purins, M., Dzerina, B. & Kalnins, J. 2015. Formation of height increment of hybrid aspen in Latvia. *Agronomy Research* **13**(2) 436–441.

WINTER FROST DAMAGE AND ITS LINK TO EARLY GROWTH AND SURVIVAL IN A POPLAR CLONE COLLECTION

*Silva Šēnhofa, **Dagnija Lazdiņa**, **Mārtiņš Zeps**
Latvian State Forest Research Institute 'Silava', Latvia
*Corresponding author's email: silva.senhofa@silava.lv

Abstract
The Northern European countries largely rely on poplars and their hybrids that are transferred northward from more southern regions, therefore, facing a trade-off between the use of full growth potential and sufficient tolerance of low temperatures. We characterized frost damage and its link to early growth and survival of 33 poplar genotypes at the age of one, three, and four years in a clonal collection on agricultural land. The survival after the first season varied from 42% to 99%. Half of the clones had autumn frost injuries with a maximum of 20% of trees damaged. The autumn frost-damaged trees were significantly ($p < 0.001$) higher before the injury than the undamaged trees with site mean 105.3 ± 7.9 and 72.0 ± 2.5 cm, respectively, but, at the clone mean level, the proportion of autumn frost-damaged trees had no link to survival (rho = 0.53, $p < 0.001$). The observed winter frost damage showed no relation ($p < 0.05$) regarding the proportion of trees with autumn frost damage. Trees with winter frost damage tended to be shorter than undamaged trees ($p < 0.001$) and had lower survival (rho = 0.47, $p < 0.01$). The maximum height difference of the clones among the studied years was in a magnitude from 2.4 to 2.9, and the stability of a clonal ranking increased with the age. The results emphasize the need for further monitoring of the clone performance under the local climatic conditions before recommendations of commercial use of particular clones in Latvia.
Key words: Clonal ranking, cold injury, maladaptation, *Populus* hybrids.

Introduction

Traditional forestry is facing challenges to satisfy expanding global demand for the production of raw materials from sustainable, renewable natural resources. Roundwood and bioenergy production by fast-growing species outside the natural forests pose the potential to produce substantial yield on the limited land area (Jürgensen, Kollert, & Lebedys, 2014; Mola-Yudego *et al*., 2017). This allows to efficiently preserve sequestered CO_2 and substitute fossil fuels thereby mitigating climate change (Sulaiman, Abdul-Rahim, & Ofozor, 2020) and reducing the pressure on natural forests (Pawson *et al*., 2013) that might be not very efficient in providing this ecosystem service (Ķēniņa *et al*., 2018, 2019a, 2019b).

Species and hybrids of the *Populus* genus are shown to be among the most promising fast-growing tree species in the boreal and hemiboreal region (Rytter *et al*., 2013) with a mean annual increment of up to 20 m³ ha⁻¹ year⁻¹ in a rotation of 25 years (Rytter & Stener, 2014). Besides, the assessed species had demonstrated notable resistance to main damaging agent in Northern Europe - wind (Čakša *et al*., 2021; Samariks *et al*., 2020, 2021). The plantation productivity primarily depends on the performance of selected genotypes. Although poplars represent a rather wide genetic basis and are easy to vegetatively propagate, in comparison to other species (Gailis *et al*., 2021), there is very limited adapted planting stock available in Europe. Large areas are established using exclusively a few superior clones, such as OP42 in Denmark (Stener & Westin, 2017) and Sweden (Karacic *et al*., 2020) and I-214 in southern Europe (FAO, 2016), posing concerns related to climate change and pest or disease resistance. Currently, there is a breeding program for

poplars and 16 clones already selected and tested for commercial use in Sweden (Stener & Westin, 2017). Other countries in the north of Europe fully rely on material that is bred and imported from more southern regions, mainly Italy and Germany (Niemczyk *et al*., 2018). The northward transfer, however, might result in a trade-off between the use of full growth potential and sufficient frost tolerance. Too early or late growth onset and cessation leads to suboptimally used growing season (Jansons *et al*., 2014; Gailis *et al*., 2019; Skrøppa & Magnussen, 1993; Zeltiņš *et al*., 2019), meanwhile increasing the risk of cold injuries (Howe *et al*., 2000; Junttila & Kaurin, 1990). Injuries might be affected by genotype (clone) and growth rate (Šēnhofa *et al*., 2016; Zeltiņš *et al*., 2016). Additionally, crossbreeding alters genotypically controlled adaptive traits of a parental species and hybrids from different regions (Gudynaitė-Franckevičienė, Pliūra, & Suchockas, 2020), hence, imposing the importance of genotype testing under local conditions before their application at a commercial scale (Jansons *et al*., 2018; Lazdiņa *et al*., 2016, Senhofa *et al*., 2017; Pliura *et al*., 2014).

This study aimed to characterize susceptibility to frost and its link to early growth and survival of 33 poplar genotypes with a different source of origin for the first four years in a clonal collection on agricultural land. We intended to assess their early performance under low agricultural impact.

Materials and Methods

The study was carried out in a clonal collection in Kalsnava (56°41′ N, 25°58′ E), Latvia, established on abandoned agricultural land (heavy stony clay soil) in the spring 2016. In total, 34 poplar clones from

Silva Šēnhofa, Dagnija Lazdiņa, Mārtiņš Zeps

the *Aigeiros* and *Tacamahaca* sections of the genus *Populus* were represented. Subsets of the clones have Swedish, Italian, and German origin, and together with the clone OP42 (synonym Hybride275 for the same clone), they have been introduced recently, during the last 10 to 15 years. The collection also includes clones collected across Latvia. These are progenies (cuttings) of the poplars that survived after introduction, presumably, in the 1960s, but the origin of these clones is unknown. Per each clone, 97 to 102 cuttings (about 25 cm length) were planted in narrow spacing mono-clonal rows with 350 cm between the rows and 50 cm between individual plants in a row (that makes up 5,714 trees per ha) with no replications within a small area. The site was prepared by inverted soil scarification before the planting but thereafter received minimal agricultural impact with exception of weed control by rotary brush hog mower between tree rows. The plantation was fenced.

In the spring 2017, tree survival and damage (autumn frost injuries, browsing damage, dead or undamaged) were assessed, and the height of all living trees was measured (except for Clone OP42). All trees had developed only a single stem.

In the spring 2018, winter frost damage was assessed. Clones were visually evaluated on a five-scale grade: 0 – dead, 1 – severe damage, 2 – mild damage, tree recovers, 3 – minor damage, and 4 – no visible winter frost damage.

In the spring 2019, the height of all live trees was measured. In the spring 2020, the height was measured for every second tree in a row.

The normality of data was assessed by the Shapiro–Wilk test. The differences in height among the clones and their origins were assessed by nonparametric Kruskal-Wallis, followed by the Dunn test for pairwise comparisons. Mann-Witney U test was used for pairwise clone height comparison for damaged and undamaged trees. Relations between tree and clone parameters were assessed by Spearman's rank correlation. All tests were performed in R (version 4.0.2), at $\alpha = 0.05$. Mean values ± 95% confidence interval are showed throughout the paper.

Results and Discussion

Tree survival after the first season was 82% (site mean), and varied from 42% for clone AF18 to 99% for clones Max1 and Max3 (Figure 1). The average survival of the clonal collection was similar or higher than was found in trials on agricultural land in Denmark at the age of three and Southern Sweden at the age of four years (52 to 89%) for a clonal set that partly overlapped with our study (Stener & Westin, 2017). However, several clones had more than one-third of cuttings dead already after the first growing season. The design of a clonal collection might pose risks of low survival due to microclimatic differences as there was only one replication per clone. However, the studied site was a flat and homogeneous field and no pattern in the spatial distribution of low high mortality was present, suggesting that the microclimatic differences are unlikely to be a cause of mortality.

A high proportion of trees was browsed (site mean 59%). The damage was present for all clones and occurred in the winter when a fence was accidentally left unlocked allowing access for wild ungulates. Browsing is a widespread problem in *Populus* plantations that might contribute to low vitality and hence increase mortality. However, not all *Populus* clones are browsed to the same extent: the proportion of damaged trees varied from 16% to 91%, and 24 out of 33 clones had more than half of the trees browsed. Several feeding experiments have confirmed underlying differences in preference of clones due to plant macronutrient and mineral content (Holeski *et al.*, 2016) and phytochemical defences (Lastra, Kenkel, & Daayf, 2017).

Results at the beginning of the second growing season revealed that several clones might be sensitive to the local climate as half of the clones (16 out of 33) had cold injuries at the beginning of the second growing season. An inappropriate adaptation is a common concern for the low survival of introduced clones (Gudynaitė-Franckevičienė, Pliūra, & Suchockas, 2020; Karacic *et al.*, 2020; Schreiber *et al.*, 2013). The differences in autumn frost damage are likely related to clonal differences in the timing of bud set (Friedman *et al.*, 2008; Howe *et al.*, 2000) that is typically found to be highly heritable (Pliura *et al.*, 2014), thus, differ among the genotypes.

Indeed, while most of the clones were damaged scarcely (median of the proportion of damaged trees 4%), genotypes of certain families were more susceptible to sudden temperature drop than others. In our site progenies of *P. maximowiczii × P. trichocarpa* had suffered from autumn frost substantially more than other clones with the proportion of damaged trees 12% for Hybride275, 14% for Matrix24, and 20% for Matrix11. However, while maladaptation might be related to the high mortality of northward-transferred clones, it seems an incongruous explanation for the high mortality of locally collected clone Pop1. The ortet of this clone was introduced in Latvia decades ago and has shown reasonable growth to be selected for progeny testing; therefore, presumably it should not be severely negatively affected by local climatic conditions.

Neither browsing, nor autumn frost damage was negatively related to survival (rho = −0.02, p > 0.05 and rho = 0.53, p < 0.001). However, only one-fifth (site mean 21%) of trees were alive and undamaged after the first growing season. Clones P0114 and
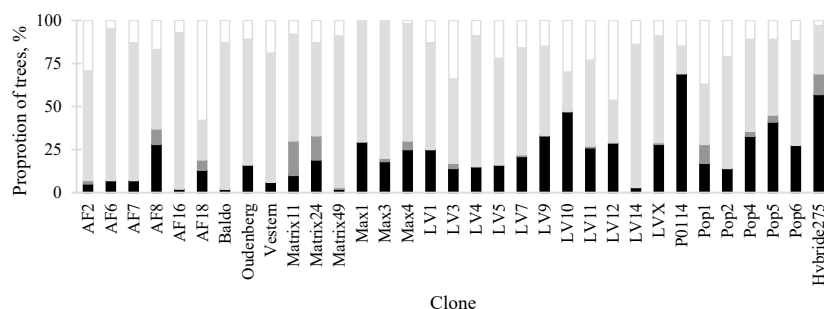
Figure 1. The damage of clones after the first growing season. Colour of the stacked bars: black – undamaged trees, dark grey – autumn frost-damaged trees, light grey – browsed trees, white – dead trees.

Hybride275 had a notably higher proportion (69% and 57%, respectively) of undamaged trees than the others, whereas eight of the clones had less than 10% of such trees.

There was no link between autumn frost damage and survival, suggesting that autumn frost damages unhardened shoots but not to an extent that affects plant survival. However, the effect of frost injuries depends on the timing and severity of frost and might be more severe in case of a more extreme temperature drop. This was shown in a recent study of simulated spring frost where 40% mortality of *P. maximowiczii* × *P. trichocarpa* hybrids and 45% mortality of *P. deltioides* × *P. trichocarpa* hybrids was observed for two-year-old trees (Gudynaitė-Franckevičienė, Pliūra, & Suchockas, 2020).

Tree survival showed a significant positive link to height (rho = 0.67, p < 0.001). At the clone mean level, there was no relationship between height and proportion of autumn frost-damaged (rho = 0.42, p > 0.05) trees. However, the autumn frost-damaged and browsed trees were significantly (both p < 0.001) higher than the undamaged trees with site mean 105.3 ± 7.9, 83.0 ± 1.2, and 72.0 ± 2.5 cm, respectively. The autumn frost-damaged trees were markedly longer compared to the intact trees, suggesting that fast-growing trees are more susceptible to frost at the end of the growing season. It is consistent with previous findings of trees that set buds later are higher, yet, also more prone to frost injuries (Pliura *et al*., 2014). Although we lack repeated assessment of damaged trees, autumn damage might cause stem quality defects due to disrupted apical growth and reduce tree height due to withered shoot top. A study of simulated spring frost showed height reduction by 26% for two-year-old poplars (Gudynaitė-Franckevičienė, Pliūra, & Suchockas, 2020), whereas a study in northern boreal conditions has shown height reduction to exceed 1.35 m length for poor-performing clones while no

or minor reduction for high- and average-performing clones at the age of three years (Schreiber *et al*., 2013).

Overall, the observed damage had a low effect on clone height performance, as there was a relatively tight correlation between the height of the alive trees (pooled undamaged, autumn frost-damaged, and browsed trees) and undamaged trees (rho = 0.82, p < 0.001). Clones significantly (p < 0.001) differed in their height after the first growing season, and their height was from 51 ± 8 to 124 ± 5 cm for alive trees (Figure 2), and 37 ± 9 to 159 ± 25 cm for undamaged trees. However, for a few clones damage significantly affected height: for clone AF16 undamaged trees had by 28% shorter height when all live trees were considered, whereas for clone LV3 undamaged trees were by 39% higher than all live trees.

Poplars in boreal conditions have to deal not only with the mismatching length of the growing season but also with low minimum temperatures and freeze-thaw events (Schreiber *et al*., 2013). The clone survival after the first growing season was positively related to survival (rho = 0.80, p < 0.001) at the age of three years. However, the observed winter frost damage showed no relation regarding the proportion of trees with autumn frost damage observed at the age of one year (Figure 3), indicating different underlying mechanisms for these types of injuries and implications for clone selection. As opposed to results of autumn frost injuries, trees with winter frost damage tended to be shorter than trees with no visible damage (Figure 4) and had lower survival (rho = 0.47, p < 0.01). Such a trend of clones with low survival to be shorter was observed in boreal Canada and was linked to structural traits of wood, namely, xylem vessel size that also affects tree cold tolerance (Schreiber et al., 2013).

The clonal differences in their height were significant at all studied ages (all p < 0.001; Figure 2). Our results of clonal mean at the respective age are in
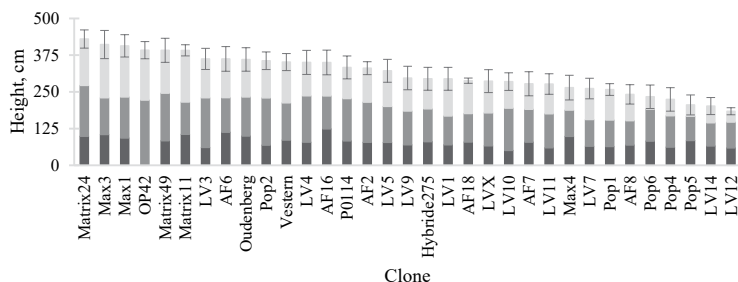
Figure 2. Height at the age of one (dark stacked bars), three (grey stacked bars), and four (light stacked bars; ± 95% confidence interval) years, survival (black bullets) at the age of three years and proportion of autumn frost-damaged trees (white bullets) at the beginning of the second growing season.

a range of mean height of the clone origin groups at the age of three years (166 to 258 cm) in Denmark and the age of four years (32 to 630 cm) in Sweden (Stener & Westin, 2017). Higher height growth was observed in north-eastern Germany (Landgraf, Carl, & Neupert, 2020), where 11 clones overlapped with our studied site. After the first growing season clones had height from 1.09 m to 2.35 m, notably exceeding height performance in our site already after the first season and the difference in height between the studies was even more distant at the age of three years.

The height difference between the highest and lowest clone increased from a magnitude of 2.4 at the age of one year to 2.9 at the age of three years, and such variation across the clones is typically observed in clonal trials (Nielsen *et al.*, 2014; Pliura *et al.*, 2007, 2014). During these two years, clones had moderately

changed their ranking of height (correlation between height measurements rho = 0.61, p < 0.001; Figure 5a). Variation in ranking at the first few years is related to different growth development strategies, such as to clone ability to establish roots (Zalesny, Riemenschneider, & Hall, 2005; Zhao *et al.*, 2014) and allometric differences (Karacic *et al.*, 2020) that are determined by clone parental species. Poor or even adverse relation between height growth at the age of one and four years for 37 poplar clones was observed by Stener and Westin (2017). At the age of four years, the difference in height between the highest and lowest clone was slightly decreased. Additionally, the clonal ranking between the age of three and four years was changed less (maximal difference: 20 positions for clone LV3; Figure 5a) than between one and three years (maximal difference: 10 positions for clone Pop6; Figure 5b).

The poplar performance is also affected by genotype × environment interaction (Pliura *et al.*,
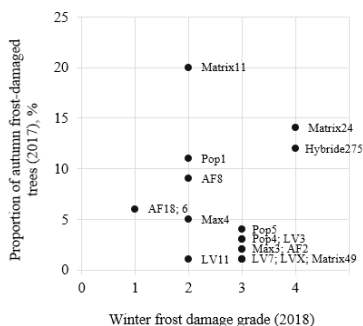
Figure 3. The proportion of autumn frost-damaged trees in the spring 2017 and the winter frost damage grade of the winter 2018. The grades of winter frost damage are as follows: 0 – dead, 1 – severe damage, 2 – mild damage, tree recovers, 3 – minor damage, and 4 – no visible winter frost damage.

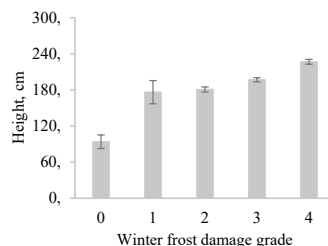
Figure 4. Tree height at the age of three years according to winter frost damage grades of the winter 2018. The grades of winter frost damage are as follows: 0 – dead, 1 – severe damage, 2 – mild damage, tree recovers, 3 – minor damage, and 4 – no visible winter frost damage.
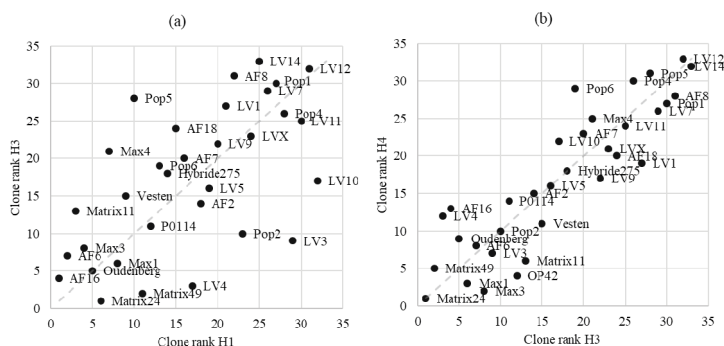
Figure 5. The changes in clone ranking for height (a) between the age of one (H1) and three years (H3) and (b) between the age of three (H3) and four (H4) years. The dashed lines represent the unchanged position of a rank between the different ages. Clones above the line have decreased rank and clones below the line have increased the rank.

2007), which implies a need for clonal testing in various sites also for clones with decent growth. As an example, the clone OP42 was among the best performing clones for height and had reasonable survival in the present study, while in a study of clone OP42 on a frost-prone site all trees had completely withered stems in the spring after the first winter season (Šēnhofa *et al*., 2017). On the other hand, the survival after the winter frost for clone Baldo (*P. deltoides*) was so severe that we removed it from the further measurements. This clone had shown inferior growth also in previous trials in Latvia (Šēnhofa *et al*., 2018), suggesting that further testing and practical use of this particular clone might be inexpedient.

Our results indicate that clones with comparable height growth that are not susceptible to cold injuries might be selected (e.g. clones Max1, Matrix49; Figure 2). Alternatively, for clones Matrix24 and Matrix11, the fast-growth likely compensated the height-loss due to autumn frost damage, as these were among the highest clones at the age of four years. Progenies of the same parental species as clone series Matrix (*P. maximowiczii* × *P. trichocarpa*) have shown similar results by remaining position among the tallest clones regardless of significant height loss due to stem withering (Gudynaitė-Franckevičienė, Pliūra, & Suchockas, 2020). The prevalence of benefits over potential losses in growth and survival due to frost damage was observed for ten-year-old *P. tremuloides* clones that were moved as much as 7° latitude in western Canada (Schreiber *et al*., 2013).

Alternatively, our results also agree with findings from a previous study (Lazdiņa *et al.,* 2016), suggesting that suitable tolerance to cold injuries of locally collected clones has not sufficient advantage to

gain a higher yield, as compared to highly productive, although more sensitive, introduced clones. Attempts to obtain local planting material are also done in the Czech Republic (Novotná, Štochlová, & Benetka, 2020). They tested locally selected *P. nigra* genotypes and crossings among their plus trees selected from natural populations with introduced clone Max4 over three rotations, each by three years. Similarly to our results, locally selected clones were inferior, and the best performing local clone had by the quarter lower yield of dry matter than clone Max4 (Novotná, Štochlová, & Benetka, 2020). The results from a trial in Sweden where 34 clones of different origin were tested showed the most popular 'old' clone in the region, OP42, to exceed growth performance by 30% to 60% at the age of 12 years of other more recently bred varieties (Karacic *et al*., 2020).

Conclusions

The results of this study emphasize the need for clonal testing under the local climatic conditions before recommendations of particular clones for commercial use in Latvia. The results indicate that fast-growing trees (unhardened shoots) are more susceptible to autumn frost damage that reduces height, while trees with poor growth are more likely to be damaged by winter frost that affects survival. Regardless of the large variation among the clones, the best 15% of clones showed comparable height growth (difference less than 10%) and reasonable survival, suggesting that several clones with close performance could be selected for commercial use to mitigate both ecological and financial risks. Yet, further monitoring of the clone performance is needed for recommendations to use particular clones

at least until they have reached half of the expected rotation age.

Acknowledgments

References

Čakša, L., Šēnhofa, S., Šņepsts, G., Elferts, D., Liepa, L., & Jansons, Ā. (2021). Effect of stem snapping on aspen timber assortment recovery in hemiboreal forests. *Forests* 12, 28. DOI: 10.3390/f12010028.

FAO (2016). Poplars and other fast-growing trees – Renewable resources for future green economies. Synthesis of country progress reports. 25th session of the International Poplar Commission, Berlin, Federal Republic of Germany, 13–16 September, 2016. Working Paper IPC/15. Forestry Policy and Resources Division, FAO, Rome.

Friedman, J.M., Roelle, J.E., Gaskin, J.F., Pepper, A.E., & Manhart, J.R. (2008). Latitudinal variation in cold hardiness in introduced *Tamarix* and native *Populus*. *Evol. Appl.* 1(4), 598–607. DOI: 10.1111/j.1752-4571.2008.00044.x.

Gailis, A., Jansone, B., Racenis, E., Sisenis, L., & Jansons, A. (2019). Assessment of silver birch (*Betula pendula* Roth.) geographical provenances in Latvia. In Proceedingas of 19th International Multidisciplinary Scientific GeoConference: SGEM 19(3.2), 625–632. 29 June – 6 July 2019, Albena, Bulgaria. DOI: 10.5593/sgem2019/3.2/S14.081.

Gailis, A., Samsone, I., Šēnhofa, S. Girgžde, E., Kāpostiņš, R., & Jansons, Ā. (2021). Silver birch (*Betula pendula* Roth.) culture initiation in vitro and genotype determined differences in micropropagation. *New Forests* 52(1), 1–16. DOI: 10.1007/s11056-020-09828-9.

Gudynaitė-Franckevičienė, V., Pliūra, A., & Suchockas, V. (2020). Ecogenetic plasticity and genetic variation in *Populus* hybrids under the impact of simulated climate change related stressors. *Balt. For.* 26(2), 462. DOI: 10.46490/BF462.

Holeski, L.M., McKenzie, S.C., Kruger, E.L., Couture, J.J., Rubert-Nason, K., & Lindroth, R.L. (2016). Phytochemical traits underlie genotypic variation in susceptibility of quaking aspen (*Populus tremuloides*) to browsing by a keystone forest ungulate. *J. Ecol.* 104(3), 850–863. DOI: 10.1111/1365-2745.12559.

Howe, G.T., Saruul, P., Davis, J., & Chen, T.H.H. (2000). Quantitative genetics of bud phenology, frost damage, and winter survival in an F2 family of hybrid poplars. *Theor. Appl. Genet.* 101, 632–642. DOI: 10.1007/s001220051525.

Jansons, Ā., Matisons, R., Baliuckas, V., Puriņa, L., Krišāns, O., Jansons, J., & Baumanis, I. (2018). Performance variation of lodgepole pine provenances in Latvia. Silva Fenn. 52(5), 10014. DOI: 10.14214/sf.10014.

Jansons, Ā., Zeps, M., Rieksts-Riekstiņš, J., Matisons, R., & Krišāns, O. (2014). Height increment of hybrid aspen *Populus tremuloides × P. tremula* as a function of weather conditions in south-western part of Latvia. *Silva Fenn*. 48(5), 1124. DOI: 10.14214/sf.1124.

Junttila, O., & Kaurin, A. (1990). Environmental control of cold acclimation in *Salix pentandra*. *Scand. J. For. Res.* 5(1–4), 195–204. DOI: 10.1080/02827589009382605.

Jürgensen, C., Kollert, W., & Lebedys, A. (2014). Assessment of industrial roundwood production from planted forests. FAO Planted Forests and Trees Working Paper FP/48/E. Rome. Retrieved March 10, 2021, from http://www.fao.org/forestry/plantedforests/67508@170537/en/.

Karacic, A., Adler, A., Weih, M., & Christersson, L. (2020). An analysis of poplar growth and quality traits to facilitate identification of climate-adapted plant material for Sweden. *Bioenergy Res.* 1–17. DOI: 10.1007/s12155-020-10210-y.

Ķēniņa, L., Elferts, D., Bāders, E., & Jansons, Ā. (2018). Carbon pools in a hemiboreal over-mature Norway spruce stands. *Forests* 9(7), 435. DOI: 10.3390/f9070435.

Ķēniņa, L., Jaunslaviete, I., Liepa, L., Zute, D., & Jansons, Ā. (2019b). Carbon pools in old-growth Scots pine stands in hemiboreal Latvia. *Forests* 10, 911. DOI: 10.3390/f10100911.

Ķēniņa, L., Mača, S., Jaunslaviete, I., & Jansons, Ā. (2019a). Carbon pools in old-growth Scots pine stands on organic soils and its concentration in deadwood: cases study in Latvia. In A. Raupelienė (Ed.), Proceedings of 9th International Scientific Conference "Rural Development 2019", 26–28 September 2019 (pp. 284–288). VDU, Kaunas, Lithuania. DOI: 10.15544/RD.2019.054.

Landgraf, D., Carl, C., & Neupert, M. (2020). Biomass yield of 37 different SRC poplar varieties grown on a typical site in north eastern Germany. *Forests* 11(10), 1048. DOI: 10.3390/f11101048.

Lastra, R.A., Kenkel, N.C., & Daayf, F. (2017). Phenolic glycosides in *Populus tremuloides* and their effects on long-term ungulate browsing. *J. Chem. Ecol.* 43(10), 1023–1030. DOI: 10.1007/s10886-017-0895-z.

Lazdiņa, D., Šēnhofa, S., Zeps, M., Makovskis, K., Bebre, I., & Jansons, Ā. (2016). The early growth and fall frost damage of poplar clones in Latvia. *Agron. Res.* 14(1), 109–122.

Mola-Yudego, B., Arevalo, J., Díaz-Yáñez, O., Dimitriou, I., Freshwater, E., Haapala, A., Khanam, T., & Selkimäki, M. (2017). Reviewing wood biomass potentials for energy in Europe: the role of forests and fast growing plantations. *Biofuels* 8(4), 401–410. DOI: 10.1080/17597269.2016.1271627.

Nielsen, U.B., Madsen, P., Hansen, J.K., Nord-Larsen, T., & Nielsen, A.T. (2014). Production potential of 36 poplar clones grown at medium length rotation in Denmark. *Biomass Bioenerg* 64, 99–109. DOI: 10.1016/j.biombioe.2014.03.030.

Niemczyk, M., Kaliszewski, A., Jewiarz, M., Wróbel, M., & Mudryk, K. (2018). Productivity and biomass characteristics of selected poplar (*Populus* spp.) cultivars under the climatic conditions of northern Poland. *Biomass Bioenerg* 111, 46–51. DOI: 10.1016/j.biombioe.2018.02.002.

Novotná, K., Štochlová, P., & Benetka, V. (2020). Verification of new *Populus nigra* L. clone improvement based on their performance over three rotations. *iForest* 13(3), 185. DOI: 10.3832/ifor3171-013.

Pawson, S.M., Brin, A., Brockerhoff, E.G., Lamb, D., Payn, T.W., Paquette, A., & Parrotta, J.A. (2013). Plantation forests, climate change and biodiversity. *Biodivers. Conserv.* 22(5), 1203–1227. DOI: 10.1007/s10531-013-0458-8.

Pliura, A., Suchockas, V., Sarsekova, D., & Gudynaitė, V. (2014). Genotypic variation and heritability of growth and adaptive traits, and adaptation of young poplar hybrids at northern margins of natural distribution of *Populus nigra* in Europe. *Biomass Bioenerg* 70, 513–529. DOI: 10.13189/ujps.2015.030602.

Pliura, A., Zhang, S.Y., MacKay, J., & Bousquet, J. (2007). Genotypic variation in wood density and growth traits of poplar hybrids at four clonal trials. *For. Ecol. Manag.* 238(1–3), 92–106. DOI: 10.1016/j.foreco.2006.09.082.

Rytter, L., & Stener, L.G. (2014). Growth and thinning effects during a rotation period of hybrid aspen in southern Sweden. *Scand. J. For. Res.* 29(8), 747–756. DOI: 10.1080/02827581.2014.968202.

Rytter, L., Johansson, K., Karlsson, B., & Stener, L.G. (2013). Tree species, genetics and regeneration for bioenergy feedstock in northern Europe. In S. Kellomäki, A. Kilpeläinen & A. Alam (Eds.), Forest bioenergy production (pp. 7–37). Springer, New York, NY.

Samariks, V, Īstenais, N., Seipuli,s A., Miezīte, O., Krišāns, O., & Jansons, Ā. (2021). Root-soil plate characteristics of silver birch on wet and dry mineral soils in Latvia. *Forests* 12, 20. DOI: 10.3390/f1201002.

Samariks, V., Brizga, D., Rūba, J., Seipulis, A., & Jansons, Ā. (2020). Root-plate characteristics of common aspen in hemiboreal forests of Latvia. *Forests* 12, 32. DOI: 10.3390/f12010032.

Schreiber, S.G., Hamann, A., Hacke, U.G., & Thomas, B.R. (2013). Sixteen years of winter stress: an assessment of cold hardiness, growth performance and survival of hybrid poplar clones at a boreal planting site. *Plant Cell Environ.* 36(2), 419–428. DOI: 10.1111/j.1365-3040.2012.02583.x.

Šēnhofa, S., Neimane, U., Grava, A., Sisenis, L., Lazdiņa, D., & Jansons, A. (2017). Juvenile growth and frost damages of poplar clone OP42 in Latvia. *Agron. Res.* 15(5), 2113–2125.

Šēnhofa, S., Zeps, M., Gailis, A., Kāpostiņš, R., & Jansons, Ā. (2016). Development of stem cracks in young hybrid aspen plantations. For. Stud. 65, 16–23. DOI: 10.1515/fsmu-2016-0008.

Šēnhofa, S., Zeps, M., Ķēniņa, L., Neimane, U., Kāpostiņš, R., Kārkliņa, A., & Jansons, A. (2018). Intra-annual height growth of hybrid poplars in Latvia. Results from the year of establishment. *Agron. Res* 16(1), 254–262.

Skrøppa, T., & Magnussen, S. (1993). Provenance variation in shoot growth components of Norway spruce. *Silvae Genet.* 42, 111–120.

Stener, L.-G., & Westin, J. (2017). Early growth and phenology of hybrid aspen and poplar in clonal field tests in Scandinavia. *Silva Fenn.* 51(3), 5656. DOI: 10.14214/sf.5656.

Sulaiman, C., Abdul-Rahim, A.S., & Ofozor, C.A. (2020). Does wood biomass energy use reduce CO_2 emissions in European Union member countries? Evidence from 27 members. *J. Clean. Prod.* 253, 119996. DOI: 10.1016/j.jclepro.2020.119996.

Zalesny, R.S., Riemenschneider, D.E., & Hall, R.B. (2005). Early rooting of dormant hardwood cuttings of *Populus*: analysis of quantitative genetics and genotype × environment interactions. *Can. J. For. Res.* 35(4), 918–929. DOI: 10.1139/x05-018.

Zeltiņš, P., Katrevičs, J., Gailis, A., Maaten, T., Desaine, I., & Jansons, Ā. (2019). Adaptation capacity of Norway spruce provenances in Western Latvia. *Forests* 10, 840. DOI: 10.3390/f10100840.

Zeltiņš, P., Katrevičs, J., Gailis, A., Maaten, T., Jansons, J., & Jansons, Ā. (2016). Stem cracks of Norway spruce (*Picea abies* (L.) Karst.) provenances in Western Latvia. For. Stud. 65, 57–63. DOI: 10.1515/fsmu-2016-0012.

Zhao, X., Zheng, H., Li, S., Yang, C., Jiang, J., & Liu, G. (2014). The rooting of poplar cuttings: a review. *New For.* 45(1), 21–34. DOI: 10.1007/s11056-013-9389-1.

Juvenile growth and frost damages of poplar clone OP42 in Latvia

S. Sēnhofa[1], U. Neimane[1], A. Grava[1], L. Sisenis[2], D. Lazdina[1] and A. Jansons[1,*]

[1]Latvian State Forest Research Institute 'Silava', Rigas 111, LV 2169 Salaspils, Latvia
[2]Latvia University of Agriculture, Forest Faculty, Akademijas 11, LV3001 Jelgava, Latvia
*Correspondence: aris.jansons@silava.lv

Abstract. Short rotation plantations in the northern Europe are commonly established using poplar clone OP42 (*Populus maximowiczii* Henry × *P. trichocarpa* Torr. and Gray). We assessed its growth and suitability to the climate in central part of Latvia at juvenile age. Trees that had formed single stem were significantly higher (121 ± 2.5 cm), thicker (7.1 ± 0.48 mm) and had longer branches (32 ± 1.5 cm) than trees that had formed multiple stems. In beginning of the second growing season all trees had died stems and 19.6% of them formed new shoots from the ground level. The sprouting trees had random spatial distribution in the field. Regardless of the number of stems, the sprouting trees were significantly lower (110 ± 3.9 cm) than the dead trees (119 ± 2.0 cm). During the repeated assessment about one month later, proportion of the sprouting trees increased up to 44%, but the detected relations between measured traits of sprouting and dead trees remained. Clone OP42 had serious frost induced damages also in autumn phenology experiment (96% trees with severely damaged leaves). Our results suggest that frost prone sites are not suitable for establishment of plantations of OP42 clone.

Key words: *Populus maximowiczii × P. trichocarpa*, clone OP42, sprouting, freeze-thaw, wood dysfunction.

INTRODUCTION

Bioeconomy concept is rapidly gaining popularity in both policy and science (Staffas et al., 2013; Pülzl et al., 2014), and it is closely linked to European Commission goal to develop a resource-efficient and low carbon economy by 2050 (EC, 2011). Bioeconomy emphases use of renewable raw materials (Scarlat et al., 2015), including necessity to increase biomass production in sustainably managed industrial crops (EC, 2012). Woody biomass is one of the largest sources of renewable energy in EU and its consumption is expected to increase in the following decades (Openshaw, 2011; Bentsen & Felby, 2012; Lauri et al., 2014). However native tree species in the Northern Europe (with exception of grey alder) have relatively long rotation period – from ca. 40 years for birch and aspen up to more than 100 years for pine and oak (Rytter et al., 2013); and therefore have limited flexibility to respond to changes in wood demand in a short period of time. Hence, during the last decades fast growing tree species are increasingly used (Gailis & Jansons, 2010; Uri et al., 2010; Jansons et al., 2013), and currently

ca. 50,000 ha of short rotation plantations is established in Europe (Don et al., 2012). *Populus* spp. are among the most energy-efficient perennial energy crops (Djomo et al., 2015), and are commonly used in the Northern Europe (Don et al., 2012) as well as in the Baltic States (Tullus & Vares, 2005; Bardule et al., 2016; Zeps et al., 2016). Poplars are mainly grown for bioenergy under rotation of 8–10 years (Djomo et al., 2015), but could also be grown for solid wood and veneer production in a rotation 20 years (Christersson, 2010). In Latvia, results from poplar trials indicate superior yield than the most productive native species (Jansons et al., 2014); yet results from other Northern Europe countries indicate that even higher yields could be gained (Karačić et al., 2003; Tullus et al., 2013). However, poplars in the Northern Europe are reported to suffer from frost damage at different severity (Ferm et al., 1989; Christersson, 1996; Ilstedt, 1996; Karačić et al., 2003; Christersson, 2006; Pliura et al., 2014). Pliura et al. (2014) studying poplar hybrids in two juvenile clonal trials in Lithuania found out that clones with late growth cessation were of the worse survival, possibly due to delayed shoot maturation and winter damage. In Sweden, two poplar clones had shown high biomass in one of the two experimental sites, while were completely eliminated by frost at the other (Karačić, 2005). One of the most widely used poplar clone worldwide and also in the Northern Europe is hybrid *Populus maximowiczii* (Henry) × *P. trichocarpa* (Torr. and Gray) clone OP42 (Taeroe et al., 2015). It is included in trials as far north as 60°N (Johansson & Karačić, 2011; Johansson & Hjelm, 2012b; Hjelm et al., 2015), indicating its suitability for climate at northern latitudes. Clone OP42 is also included in several trials representing different site conditions in Latvia and considered to be perspective (unpublished data). The hypothesis of the study is that poplar clone OP42 does not suffer from frost damages in Latvia. The objectives are to characterize the meteorological conditions, juvenile growth and frost damages for clone OP42, and compare the autumn phenology of OP42 to other poplar clones as a potential cause of autumn frost damages.

MATERIAL AND METHODS

The study was done in poplar trial located in central part of Latvia (56°34`N, 24°31`E), near Vecumnieki.

Vecumnieki trial was established in spring 2015 on drained peat soil with pH 6,0 using 30 cm long cuttings of clone OP42 (*Populus maximowiczii* (Henry) × *P. trichocarpa* (Torr. and Gray)) obtained from trees grown in western part of Latvia. Trees were planted in 17 rows in a density of 4 × 2 m, total number of planted cuttings 3,393. Weed control (ploughing and herbicide) was carried out once in autumn 2014 (before planting) and manual weed control (ca. 25 cm around the tree) during the growing season of 2015.

In the trial, at the end of the growing season (27/08/2015–18/11/2015) temperature measurements once per hour were done at three different heights – (1) air temperature was measured 20 cm above the ground; (2) soil temperature was measured at the surface level and (3) at the 20 cm depth (Fig. 1). Air temperature first dropped below 0 °C in September 11 and until October 6 negative air temperature recurred occasionally – in nine out of 22 days. During this period, the longest frost (temperature below 0 °C) occurred in September 27 (9 hours, minimal hourly temperature -2 °C) and September 30 (7 hours, minimal hourly temperature -3 °C). In October 7 frost became more intense – air temperature was below 0 °C for 14 hours and dropped down

to -12.5 °C; similar temperatures remained for 10 days – mean minimal hourly temperature was from -9.5 to -13.5 °C, duration of frost was from 11 to 16 hours per day. Similar period of frost occurred in October 28–31. Likewise, on the soil surface two periods of temperature below 0 °C occurred in October, and remained for nine (October 8–16) and three (October 29–31) days. For the first time in the growing season (October 8) soil temperature at the surface level dropped below 0 °C for 2 hours; five days later – for 7 hours (minimal hourly temperature -1 °C). Duration of negative soil surface temperature reached 15 hours per day (-2 °C) in October 30 and 31. However, during the observed period no negative soil temperature at 20 cm depth was recorded.
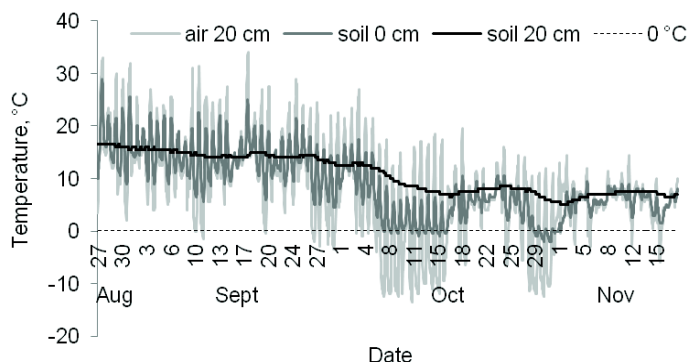

Figure 1. Temperature of air (20 cm above ground) and soil (at surface level – 0 cm – and in 20 cm depth) in Vecumnieki trial during 27/08/2015–18/11/2015.

Data of the long-term (30-year mean) measurements for the respective period were obtained from the nearest (distance ca. 30 km) weather station, located near Bauska (56º22`N, 24º13`E; Latvian Environment, Geology and Meteorology Centre). During the analysed period, mean diurnal air temperature did not decrease below 0 °C; but minimal temperature (30-year mean of the minimal temperature of the date) first dropped below 0 °C in November 11 (Fig. 2) – considerably later than in the study year. As can be seen the study year represent very specific meteorological conditions in the autumn thus authors did not had a chance to repeat the study with larger set of clones and sites during next growing season even so the experimental design was prepared.

In the beginning of June 2016, damage of stems (one-year-old shoots, emerged in the previous growing season) were observed. All trees had completely withered stems (no growth from the previous year shoots occurred), and part of them had new emerging shoots from the ground level. Tree height (± 1 cm) and diameter (± 1 mm; measured for 410 trees in 2 rows) at the stem base (root collar) of the highest one-year-old shoot (emerged in 2015) of trees were measured, number of stems (emerged in 2015) and number of branches (longer than 5 cm) per tree were counted, and length of branches (± 1 cm) was measured. Trees that had more than three stems and more than three branches were pooled into groups 'more than 3 stems' and 'more than 3 branches', respectively. For each tree occurrence (0/1) of browsing damage and occurrence of new emerging shoots (further called 'sprouting' (1) and 'dead' (0) trees) were recorded. In

total, 3,025 trees were measured. In the middle of July, assessment of sprouting/dead trees was repeated in a part of the trial (5 rows, 1,018 trees).
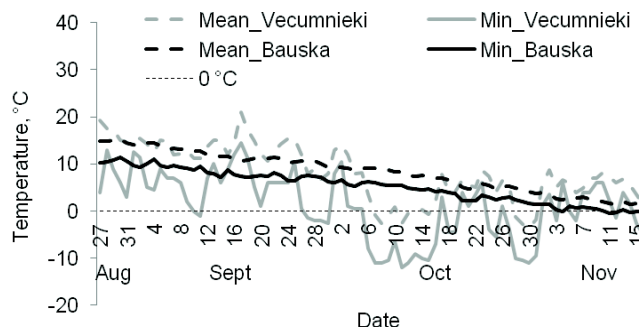

Figure 2. Air temperature in the study year in Vecumnieki trial and long-term measurements of the nearest weather station (Bauska) for the period of 27/08–18/11. 'Mean_Vecumnieki' – mean diurnal temperature, calculated from hourly measurements; 'Min_Vecumnieki' – the lowest recorded diurnal temperature; 'Mean_Bauska' – mean diurnal temperature, calculated from 30-year data of mean temperature of the respective date; 'Min_Bauska' – mean of the 30-year lowest diurnal temperature of the date.

To characterize the frost hardiness of poplars the data obtained in another poplar trial located in eastern part of Latvia (56°41′N, 25°58′E), near Kalsnava, were used additionally. Besides OP42, 17 other clones were included in this trial where autumn phenology observations were made. Frequently recurring freeze-thaw cycles at the same period as in Vecumnieki were observed in Kalsnava; the frost damages for leaves and stems of two-year-old trees were assessed visually (evaluated at five grade scale) in October 15th. The detailed description of methods, as well as the frost hardiness comparison at the clone level was performed by Lazdiņa et al. (2016). In our study, clones were pooled into five groups according to their origin (Sweden, Italy, Germany, Latvia) to estimate the relative frost hardiness of OP42 in comparison to other poplar clones.

The Shapiro-Wilk test was used to assess the normality of the data. Differences of mean height, diameter, and length of branches were assessed using one-way analysis of variance (i) between trees that had formed one or multiple stems, and (ii) between trees that had formed one, two, three or more stems. The Chi-squared test was used to assess (i) distribution of the number of branches, proportion of sprouting trees and proportion of browsed trees between trees that had formed one or multiple stems and among trees that had formed one, two, three or more stems, (ii) distribution of the proportion of sprouting trees between browsed and not browsed trees, (iii) distribution of proportion of sprouting trees among plantation rows. The statistical analysis of differences between proportions of trees among the leaf and stem damage grades was hampered by insufficient number of trees in several of the grades. Pearson's correlation was used to assess relationship between proportion of sprouting trees and mean tree height of the plantation rows. Spearman's correlation was used to assess the relationships between (i) number of branches and number of stems per tree, (ii) length of branches and number of

2116

branches, (iii) length of branches and number of stems per tree. Spatial autocorrelation of the sprouting trees was assessed using Moran's I. All tests were performed at $\alpha = 0.05$. Mean values and their confidence interval are shown both in text and figures.

RESULTS

In Vecumnieki at the end of the first growing season 89% of the planted cuttings had formed shoots. About half (49%) of trees had formed one stem, and about half had formed multiple stems – 31% of trees had formed two, 10% of trees three and 10% of trees four and more stems. Tree height varied from 10 to 251 cm (mean 118 ± 1.8 cm), and trees that had formed multiple stems were significantly ($P < 0.001$) lower (mean height of the highest stem 114 ± 2.6 cm) than trees that had formed one stem (mean height 121 ± 2.5 cm). No overall trend between number of stems and tree height was observed (Fig. 3).
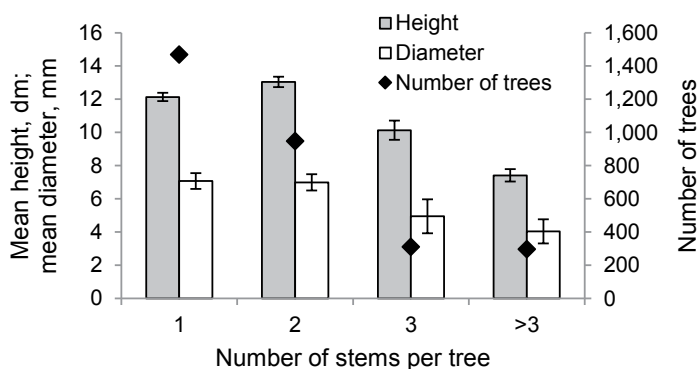

Figure 3. Mean tree height and diameter at root collar (both ± confidence interval) and number of trees according to a number of stems per tree for the clone OP42 in Vecumnieki.

Branches were observed for 30% of trees, mean number of branches was 3.3 (from 1 to 42). One branch was observed for 11% of trees, two branches for 6%, three branches for 4% and more than three branches – for 9% of trees. Proportion of number of branches between trees that had one and trees that had multiple stems was similar ($P = 0.86$). No relation between number of stems and number of branches was observed ($r_s = -0.060$, $P = 0.071$).

Mean length of branches was 30 ± 1.0 cm, and trees that had formed one stem had slightly, but significantly ($P < 0.001$) longer branches (32 ± 1.5 cm) than trees that had formed multiple stems (28 ± 1.4 cm). However, it was similar ($P > 0.05$) for trees that had formed one stem (32 ± 1.5 cm) and trees that had formed two stems (31 ± 2.1 cm), but trees that had formed three (26 ± 2.5 cm) and more (25 ± 2.4 cm) stems had significantly shorter branches. Mean branch length had weak but significant correlation with number of branches ($r_s = 0.089$, $P = 0.007$) and number of stems ($r_s = -0.154$, $P < 0.001$).

Mean diameter at stem base was 6.6 ± 0.32 mm. Similarly to tree height, trees that had formed smaller number of stems were thicker (Fig. 3). Mean diameter of trees that

had formed one and two stems was similar ($P > 0.05$; 7.1 ± 0.48 mm and 7.0 ± 0.49 mm, respectively), and both significantly differed from diameter of trees that had formed three and more stems (4.9 ± 1.0 mm and 4.0 ± 0.73 mm, mutually similar ($P > 0.05$)). Browsing damages were observed for 7.6% of trees. Proportion of browsed trees significantly differed between trees that had formed one, two, three and more stems ($P < 0.001$), and it was 10.2, 6.6, 3.2 and 2.4%, respectively.

In the late June 2016, new emerging (sprouting) shoots from the ground level were found for 19.6% of trees. The sprouting trees had reached slightly, but significantly ($P < 0.001$) lower height in the previous growing season (110 ± 3.9 cm) than the dead trees (119 ± 2.0 cm), regardless of the number of stems (Fig. 4). Among trees that had formed one stem, height of the sprouting and dead trees was 114 ± 5.2 cm and 123 ± 2.8 cm, respectively; among trees that had formed multiple stems – 106 ± 5.7 cm and 116 ± 2.9 cm, respectively.
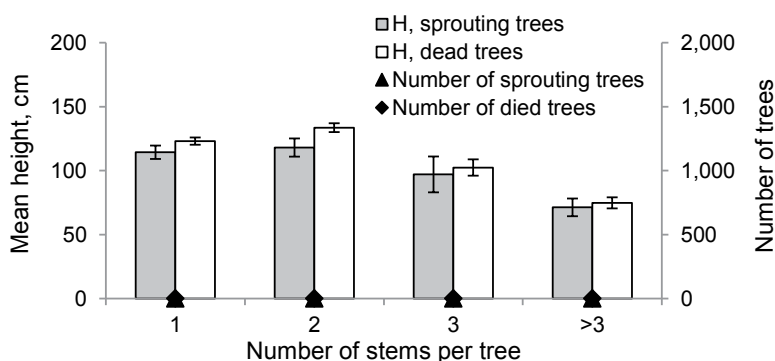

Figure 4. Mean height (H; ± confidence interval) and number (N) of sprouting and dead trees according to number of stems per tree for the clone OP42 in Vecumnieki.

Proportion of the sprouting trees that had formed one, two, three and more stems was similar ($P = 0.89$) – 19.4; 20.1; 20.0 and 18.2%, respectively. Significant ($P = 0.006$) difference of proportion of the sprouting trees was found between browsed (12.6%) and not browsed (20.1%) trees. Proportion of the sprouting trees differed significantly ($P < 0.001$) between the trial rows, but no relation ($P > 0.90$) between proportion of the sprouting trees and mean tree height in the row was found. Spatial distribution of the sprouting trees in the field was random ($P > 0.05$).

During the repeated assessment of sprouting/dead trees, proportion of sprouting trees was notably increased and reached 44%. However, the observed relation between measured traits remained – the sprouting trees were significantly ($P < 0.001$) lower than the dead trees (111 ± 4.6 cm and 123 ± 4.5 cm, respectively). Height of trees that had formed one and multiple stems was similar ($P = 0.058$) – 121 ± 4.5 cm and 115 ± 4.7 cm, respectively. Among trees that had formed one stem, height of the sprouting trees (116 ± 6.2 cm) was significantly ($P = 0.03$) lower than that of the dead trees (126 ± 6.4 cm). Similarly, among trees that had formed multiple stems, height of the sprouting trees (107 ± 6.8 cm) was significantly ($P = 0.002$) lower than that of the dead trees (121 ± 6.4 cm).

Frost damage of the same frost event was assessed in another progeny trial in Kalsnava. Analysis of two-year-old trees reveals differences between clone origins. All trees of clones that were collected across Latvia were dormant (Grade 0L) and had no frost damage of leaves. Clones of Italian origin had all trees still growing, and 66% of trees had moderately damaged (Grade 3L) leaves but no severe damage (Grade 4L) was observed. Clones from Germany had relatively large proportion (64%) of dormant trees; but among still growing trees 96% had severely damaged (Grade 4L) leaves. Similarly to clones of Italian origin, all trees of clone OP42 were still growing at the time of frost event, but in contrast, trees of OP42 were more intensely damaged – 96% of trees had severely (Grade 4L) and 4% of trees had moderately (Grade 3L) damaged leaves (Fig. 5).
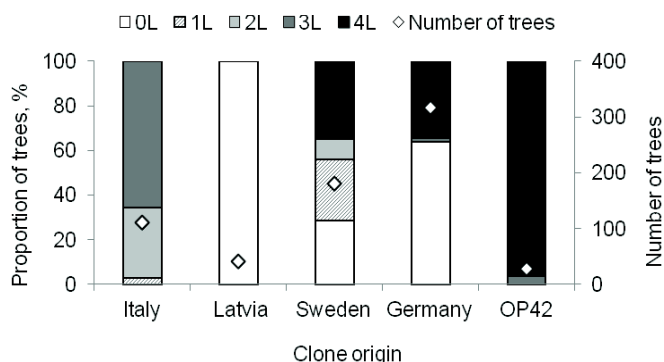

Figure 5. Proportion of two-year-old ramets with different leaf damage grades (0L, 1L, 2L, 3L and 4L) according to clone origin in Kalsnava. Damage grades: '0L' – leaves were already fallen before the freezing event and buds were set; '1L' – visually intact leaves; '2L' – several damaged leaves; '3L' – most of leaves in the current year leading shoot were damaged; '4L' – most of leaves on the whole tree were damaged.

Stem damage was less frequent – in total 8% of trees had stem damage of different intensity. No stem damage was observed for clones from Latvia, which also had no leaf damage, and for clones from Italy, which had moderate leaf damage. Similarly, clones from Sweden and Germany had 1% and 15% of trees with mild stem damage, respectively. Clone OP42 had severely damaged leaves but no stem damage was observed.

DISCUSSION

The results from rather rare combination of meteorological conditions in autumn were reported even so the study design was not initially intended for that. Considering the increasing use of the clone OP42 in Latvia and other Baltic states we did see the necessity to inform about the data so that land owners would have as objective information as possible while selecting the planting material. Although the result from the autumn phenology experiment in Kalsnava is not a direct replication of study in Vecumnieki, still it comes to similar conclusion on the risk of frost damages of the particular clone and provides a plausible reasoning for the observed problem.

Frost induced damage is not exclusively caused by extremely low temperatures; damage type and severity depends on frost event timing, duration and pattern, and the highest risk of frost damage occurs during the transition period between annual cycle of growth and dormancy (Charrier et al., 2015). We studied freeze-thaw damage in the early autumn. The freeze-thaw cycles are common to initiate embolism – bubbles are caused by dissolved air that freezes out of the sap (Tyree & Sperry 1989; Brodersen & McElrone, 2013), and sufficiently large bubbles may fill xylem conduits hampering water transport during the thawing (Pittermann & Sperry, 2006).

The first freeze-thaw cycles of the growing season occurred in the middle of September, and can be characterized by mild frost (ca. -2 to -3 °C). In the middle of October, more intense freeze-thaw occurred (Fig. 1) – temperature dropped below zero for 11–16 hours repeatedly for 10 successive nights, while the maximum temperature at day was from 6.5 to 18 °C. During the studied period the longest thaw period was 13 hours, indicating that trees experienced repeated embolism while the hydraulic conductivity had not recovered from the previous freeze-thaw cycle. Experiments of Just & Sauter (1991) showed that hydraulic conductivity of *P. × canadensis* stem segment decreased by ca. 60% after one freeze-thaw cycle, and almost no recovery was obtained during the first hour after thawing. It took 19 hours at the room temperature (21 °C) to recover 90% of the initial conductivity and about 2 days to recover completely.

Extremely high mortality in the studied site might be explained by timing of the particular freeze-thaw event. At the time of the frost all trees of clone OP42 were actively growing in the Kalsnava trial (Fig. 5), also a study of *P. tremula* × *P. tremuloides* in Latvia has revealed strong relation between height growth intensity and daily mean temperature (Zeps et al., 2015) and many other studies have showed delayed growth cessation for northward transferred species (Howe et al., 2000; Christersson, 2006; Friedman et al., 2008). Hence, most presumably clone OP42 was still growing also in Vecumnieki. During the growing season trees have higher water content than during the dormancy (Mäkinen et al., 2008; Pallardy, 2008), and more severe freeze-thaw damage is showed for trees that have high water content before the freezing occurs (Cox & Zhu, 2003). Also temperature regime before freezing significantly influences damage severity. *Betula* trees that were exposed to longer thaw period before winter freezing had increased percent length of shoot dieback and reduced length of new emerging shoots (Zhu et al., 2000). Longer thawing period was associated with increased dehardening of roots and root damage, thus, reducing root pressure, and resulted in poor recovery of embolism (Zhu et al., 2000).

Timing of the freeze-thaw cycle is also showed to affect tree recovery. *P. balsamifera* had different pattern of recovery after autumn and spring frost (Hacke & Sauter, 1996) – in the autumn when trees still had some leaves, recovery was slow and remained incomplete during the next growing season; in contrast, recovery after spring frost was complete in two months. Tree ability to recover largely depends on its vitality and damage severity. Zhu et al. (2000) have suggested that shoot damage might be directly dependent on ability of the unembolised vessels to maintain water supply for stem and branches. In turn, Cox & Zhu (2003) found that diffuse-porous trees that undergo permanent residual embolism in combination with root and shoot freezing injuries experienced higher bud mortality and shoot dieback than trees that can recover before next freeze-thaw cycle occurs.

Poplars are commonly propagated by cuttings, and trees develop shallow root system with no taproot and most lateral roots found near (within ca. 30 cm) soil surface (Puri et al., 1994; Crow & Houston, 2004; Johansson & Hjelm, 2012a). Fine roots are responsible for water uptake for trees (Block et al., 2006), and the highest biomass of fine roots was found down to 5 cm (Al Afas et al., 2008), 10 cm (Crow & Houston, 2004) depth for several poplar clones. During the studied period only slight temperature drop below zero on soil surface and no negative temperatures at the 20 cm depth was observed during the measurements (Fig. 1), therefore the particular frost event is not likely to cause substantial root damage. However, frequent recurrence of freeze-thaw cycles can cause accumulated embolism during autumn/winter (August–March) season (Sperry & Sullivan, 1992). Most deciduous trees refill frost embolized vessels in spring, and at this time nearly all conduits may be filled with air, causing as much as ca. 90% decrease of hydraulic conductivity (Sperry & Sullivan, 1992). Christensen-Dalsgaard & Tyree (2013) have observed ca. 90% loss of conductivity already after one light frost event, indicating high sensitivity of *P. deltoides* × (*P. laurifolia* × *P. nigra*) clone Walker. Later studies showed that for poplars most of the accumulated embolism occurred after the first few frost events (Christensen-Dalsgaard & Tyree, 2014). Autumn frost damage hamper winter hardening, which in turn increases vulnerability to damage (von Fircks, 1992), thus it could be assumed that root damage might occurred during the following winter when temperature dropped down to -25 °C (data from Latvian Environment, Geology and Meteorology Centre).

Root damage hamper the recovery of the hydraulic conductivity – Sperry (1993) has found that embolism of not-damaged *Betula* trees recovered from 81 to 88% during one month (April to May), while trees with root damage had 75% embolism after two months (in June). Similarly, no recovery of hydraulic conductivity was observed for *P. × canadensis* during more than three months if root pressure was absent (Hacke & Sauter, 1996). The reduced hydraulic conductivity, in turn, is showed to negatively affect timing of bud break – the lower the hydraulic conductivity at the end of the winter, the later the bud break (Wang et al., 1992). The observed emergence of new shoots of the otherwise vigorously sprouting clone OP42 (Johansson & Hjelm, 2012b) in this study was rather late and poorly performed, suggesting that trees were struggling to either rely on the remaining unembolized conduits or try to grow new conduits (Hacke & Sauter, 1996; Améglio et al., 2002).

We found that the sprouting trees were lower than the dead trees, regardless of the number of stems per tree (Fig. 4). Tree height has positive relation to vessel diameter (Martínez-Cabrera et al., 2011), which is the most important wood trait that determine vulnerability to embolism (Sperry & Sullivan, 1992). Plants most efficiently ensures conductivity by forming few, wide and long conduits (Sperry et al., 2008), but for a given tree height many small vessels are more resistant to embolism (Davis et al., 1999). Poplars are associated with high water consumption (Silim et al., 2009), and hence might have trade-off between hydraulic conductivity and resistance to embolism.

CONCLUSIONS

Interest of growing poplars in the Northern Europe is increasing. Yet, limited number of commercial clones is available, and their growth as well as suitability to climate should be thoroughly tested due to northward transfer. We observed reasonable growth of one-year-old poplar clone OP42. However, extremely high mortality occurred due to early autumn frost (freeze-thaw cycles) at the end of the first growing season, suggesting that frost prone sites are not suitable for establishment of plantations of OP42 clone. The results emphasize necessity to include frost risk assessment, especially for the first year of establishment, in site selection and economical calculations. Our experiment was carried out in a single trial and therefore information from other sites needs to be collected before any further generalizations. Resprouting of damaged trees was rather late and poorly performed, and further assessment of vitality and growth of the sprouts is needed.

REFERENCES

Al Afas, N., Marron, N., Zavalloni, C. & Ceulemans, R. 2008. Growth and production of a short-rotation coppice culture of poplar—IV: Fine root characteristics of five poplar clones. *Biomass Bioenerg.* **32**(6), 494–502.

Améglio, T., Bodet, C., Lacointe, A. & Cochard, H. 2002. Winter embolism, mechanisms of xylem hydraulic conductivity recovery and springtime growth patterns in walnut and peach trees. *Tree Physiology* **22**(17), 1211–1220.

Bardule, A., Lazdins, A., Sarkanabols, T. & Lazdina, D. 2016. Fertilized short rotation plantations of hybrid aspen (*Populus tremuloides* Michx. × *Populus tremula* L.) for energy wood or mitigation of GHG emissions. In *Proceedings of 15th International Scientific Conference on Engineering for Rural Development*. Jelgava, Latvia, pp. 248–255.

Bentsen, N.S. & Felby, C. 2012. Biomass for energy in the European Union-a review of bioenergy resource assessments. *Biotechnology for Biofuels* **5**(25), 1–10.

Block, R.M.A., Van Rees, K.C.J. & Knight, J.D. 2006. A review of fine root dynamics in *Populus* plantations. – *Agroforest Syst.* **67**(1), 73–84.

Brodersen, C. & McElrone, A. 2013. Maintenance of xylem network transport capacity: a review of embolism repair in vascular plants. *Front Plant Sci* **4**, article 108.

Charrier, G., Ngao, J., Saudreau, M. & Améglio, T. 2015. Effects of environmental factors and management practices on microclimate, winter physiology, and frost resistance in trees. *Front Plant Sci.* **6**, article 259.

Christensen-Dalsgaard, K.K., Tyree, M.T. 2013. Does freezing and dynamic flexing of frozen branches impact the cavitation resistance of *Malus domestica* and the *Populus* clone Walker? *Oecologia* **173**(3), 665–674.

Christensen-Dalsgaard, K.K. & Tyree, M.T. 2014. Frost fatigue and spring recovery of xylem vessels in three diffuse-porous trees *in situ*. *Plant Cell Environ* **37**, 1074–1085.

Christersson, L. 1996. Future research on hybrid aspen and hybrid poplar cultivation in Sweden. *Biomass Bioenerg.* **11**(2), 109–113.

Christersson, L. 2006. Biomass production of intensively grown poplars in the southernmost part of Sweden: Observations of characters, traits and growth potential. *Biomass Bioenerg.* **30**(6), 497–508.

Christersson, L. 2010. Wood production potential in poplar plantations in Sweden. *Biomass Bioenerg.* **34**(9), 1289–1299.

Cox, R.M. & Zhu, X.B. 2003. Effects of simulated thaw on xylem cavitation, residual embolism, spring dieback and shoot growth in yellow birch. *Tree Physiol.* **23**(9), 615–624.

Crow, P. & Houston, T.J. 2004. The influence of soil and coppice cycle on the rooting habit of short rotation poplar and willow coppice. *Biomass Bioenerg.* **26**(6), 497–505.

Davis, S.D., Sperry, J.S. & Hacke, U.G. 1999. The relationship between xylem conduit diameter and cavitation caused by freezing. *Am J Bot.* **86**(10), 1367–1372.

Djomo, S.N., Ac, A., Zenone, T., De Groote, T., Bergante, S., Facciotto, G., Sixto, H., Ciria Ciria, P., Weger, J. & Ceulemans, R. 2015. Energy performances of intensive and extensive short rotation cropping systems for woody biomass production in the EU. *Renew Sust Energ. Rev.* **41**, 845–854.

Don, A., Osborne, B., Hastings, A., Skiba, U., Carter, M.S., Drewer, J., Flessa, H., Freibauer, A., Hyvönen, N., Jones, M.B., Lanigan, G.J., Mandler, Ü., Monti, A., Djomo, S.N., Valentine, J., Walter, K., Zagadalizarazu, W. & Zenone, T. 2012. Land-use change to bioenergy production in Europe: implications for the greenhouse gas balance and soil carbon. *GCB Bioenergy* **4**(4), 372–391.

EC. 2012. Innovating for Sustainable Growth: A Bioeconomy for Europe. European Commision. 9 pp.

EC. 2011. A Roadmap for moving to a competitive low carbon economy in 2050. European Commision. 16 pp.

Ferm, A., Hytönen, J. & Vuori, J. 1989. Effect of spacing and nitrogen fertilization on the establishment and biomass production of short rotation poplar in Finland. *Biomass* **18**(2), 95–108.

Fircks von, H.A. 1992. Frost hardiness of dormant *Salix* shoots. *Scand J Forest Res* **7**(1–4), 317–323.

Friedman, J.M., Roelle, J.E., Gaskin, J.F., Pepper, A.E. & Manhart, J.R. 2008. Latitudinal variation in cold hardiness in introduced *Tamarix* and native *Populus*. *Evolutionary Applications* **1**(4), 598–607.

Gailis, A. & Jansons, A. 2010. Results of black alder (*Alnus glutinosa* (L.) Gaertn.) improvement in Latvia. In *Proceedings of the Annual 16th International Scientific Conference Research for Rural Development*. Jelgava, Latvia, pp. 266–260.

Hacke, U. & Sauter, J.J. 1996. Xylem dysfunction during winter and recovery of hydraulic conductivity in diffuse-porous and ring-porous trees. *Oecologia* **105**(4), 435–439.

Hjelm, B., Mola-Yudego, B., Dimitriou, I. & Johansson, T. 2015. Diameter–height models for fast-growing poplar plantations on agricultural land in Sweden. *BioEnergy Research* **8**(4), 1759–1768.

Howe, G.T., Saruul, P., Davis, J. & Chen, T.H.H. 2000. Quantitative genetics of bud phenology, frost damage, and winter survival in an F_2 family of hybrid poplars. *Theor Appl Gen.* **101**(4), 632–642.

Ilstedt, B. 1996. Genetics and performance of Belgian poplar clones tested in Sweden. *Forest Genetics* **3**(4), 183–195.

Jansons, A., Sisenis, L., Neimane, U. & Rieksts-Riekstins, J. 2013. Biomass production of young lodgepole pine (*Pinus contorta* var. *latifolia*) stands in Latvia. *iForest* **6**, 10–14.

Jansons, A., Zurkova, S., Lazdina, D. & Zeps, M. 2014. Productivity of poplar hybrid (*Populus balsamifera × P. laurifolia*) in Latvia. *Agronomy Research* **12**(2), 469–478.

Johansson, T. & Hjelm, B. 2012a. Stump and root biomass of poplar stands. *Forests* **3**(2), 166–178.

Johansson, T. & Hjelm, B. 2012b. The sprouting capacity of 8–21-year-old poplars and some practical implications. *Forests* **3**(3), 528–545.

Johansson, T. & Karačić, A. 2011. Increment and biomass in hybrid poplar and some practical implications. *Biomass Bioenerg.* **35**(5), 1925–1934.

Just, J. & Sauter, J.J. 1991. Changes in hydraulic conductivity upon freezing of the xylem of *Populus × canadensis* Moench 'Robusta'. *Trees* **5**(2), 117–121.

Karačić, A. 2005. *Production and ecological aspects of short rotation poplars in Sweden*. Doctoral thesis. Acta Universitatis Agriculturae Sueciae, Uppsala, 42 pp.

Karačić, A., Verwijst, T., Weih, M. 2003. Above-ground woody biomass production of short-rotation *Populus* plantations on agricultural land in Sweden. *Scand J Forest Res.* **18**(5), 427–437.

Lauri, P., Havlík, P., Kindermann, G., Forsell, N., Böttcher, H. & Obersteiner, M. 2014. Woody biomass energy potential in 2050. *Energ Policy* **66**, 19–31.

Lazdiņa, D., Bārdulis, A., Bārdule, A., Lazdiņš, A., Zeps, M. & Jansons, Ā. 2014. The first three-year development of ALASIA poplar clones AF2, AF6, AF7, AF8 in biomass short rotation coppice experimental cultures in Latvia. *Agronomy Research* **12**(2), 543–552.

Lazdiņa, D., Šēnhofa, S., Zeps, M., Makovskis, K., Bebre, I. & Jansons, Ā. 2016. The early growth and fall frost damage of poplar clones in Latvia. *Agronomy Research* **14**(1), 109–122.

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. *Eur J Forest Res.* **127**(3), 235–245.

Martínez-Cabrera, H.I., Schenk, H.J., Cevallos-Ferriz, S.R. & Jones, C.S. 2011. Integration of vessel traits, wood density, and height in angiosperm shrubs and trees. *Am J Bot.* **98**(5), 915–922.

Openshaw, K. 2011. Supply of woody biomass, especially in the tropics: is demand outstripping sustainable supply? *Int Forest Rev.* **13**(4), 487–499.

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

Pittermann, J. & Sperry, J.S. 2006. Analysis of freeze-thaw embolism in conifers. The interaction between cavitation pressure and tracheid size. *Plant Physiol.* **140**(1), 374–382.

Pliura, A., Suchockas, V., Sarsekova, D. & Gudynaitė, V. 2014. Genotypic variation and heritability of growth and adaptive traits, and adaptation of young poplar hybrids at northern margins of natural distribution of *Populus nigra* in Europe. *Biomass Bioenerg.* **70**, 513–529.

Pülzl, H., Kleinschmit, D. & Arts, B. 2014. Bioeconomy–an emerging meta-discourse affecting forest discourses? *Scand Journal Forest Res* **29**(4), 386–393.

Puri, S., Singh, V., Bhushan, B. & Singh, S. 1994. Biomass production and distribution of roots in three stands of *Populus deltoides*. *Forest Ecol Manag* **65**(2), 135–147.

Rytter, L., Johansson, K., Karlsson, B. & Stener, L.G. 2013. Tree species, genetics and regeneration for bioenergy feedstock in Northern Europe. In Kellomäki, S., Kilpeläinen, A. & Alam, A. (eds.): *Forest BioEnergy Production*. Springer, New York, pp. 7–37.

Scarlat, N., Dallemand, J.F., Monforti-Ferrario, F. & Nita, V. 2015. The role of biomass and bioenergy in a future bioeconomy: policies and facts. *Environmental Development* **15**, 3–34.

Silim, S., Nash, R., Reynard, D., White, B. & Schroeder, W. 2009. Leaf gas exchange and water potential responses to drought in nine poplar (*Populus* spp.) clones with contrasting drought tolerance. *Trees* **23**(5), 959–969.

Sperry, J.S. 1993. Winter xylem embolism and spring recovery in *Betula cordifolia*, *Fagus grandifolia*, *Abies balsamea* and *Picea rubens*. In Borghetti, M., Grace, J. & Raschi, A. (eds.): *Water Transport in Plants under Climatic Stress*. Cambridge University Press, Cambridge, UK, pp. 86–98.

Sperry, J.S., Meinzer, F.C. & McCulloh, K.A. 2008. Safety and efficiency conflicts in hydraulic architecture: scaling from tissues to trees. *Plant Cell Environ* **31**(5), 632–645.

Sperry, J.S. & Sullivan, J.E. 1992. Xylem embolism in response to freeze-thaw cycles and water stress in ring-porous, diffuse-porous, and conifer species. *Plant Physiol.* **100**(2), 605–613.

Staffas, L., Gustavsson, M. & McCormick, K. 2013. Strategies and policies for the bioeconomy and bio-based economy: An analysis of official national approaches. *Sustainability* **5**(6), 2751–2769.

Taeroe, A., Nord-Larsen, T., Stupak, I. & Raulund-Rasmussen, K. 2015. Allometric biomass, biomass expansion factor and wood density models for the OP42 hybrid poplar in southern Scandinavia. *BioEnergy Research* **8**(3), 1332–1343.

Tullus, A. & Vares, A. 2005. Early growth of hybrid aspen (*Populus × wettsteinii* Hämet-Ahti) on abandoned agricultural lands in Estonia. *Forestry Studies* **43**, 84–95.

Tullus, H., Tullus, A. & Rytter, L. 2013. Short-rotation forestry for supplying biomass for energy production. In Kellomäki, S., Kilpeläinen, A. & Alam, A. (eds.): *Forest BioEnergy Production*. Springer, New York, pp. 39–56.

Tyree, M.T. & Sperry, J.S. 1989. Vulnerability of xylem to cavitation and embolism. *Annu Rev Plant Phys* **40**(1), 19–36.

Uri, V., Aosaar, J., Varik, M. & Kund, M. 2010. The growth and production of some fast growing deciduous tree species stands on abandoned agricultural land. *Forestry Studies* **52**, 18–29.

Wang, J., Ives, N.E. & Lechowicz, M.J. 1992. The relation of foliar phenology to xylem embolism in trees. *Funct Ecol.* **6**(4), 469–475.

Zeps, M., Gailis, A., Smilga, J., Miezite, O., Sisenis, L. & Zariņa, I. 2016. Hybrid aspen clone wood mechanical properties. *Agronomy Research* **14**(1), 1147–1152.

Zeps, M., Sisenis, L., Luguza, S., Purins, M., Dzerina, B. & Kalnins, J. 2015. Formation of height increment of hybrid aspen in Latvia. *Agronomy Research* **13**(2), 436–441.

Zhu, X.B., Cox, R.M. & Arp, P.A. 2000. Effects of xylem cavitation and freezing injury on dieback of yellow birch (*Betula alleghaniensis*) in relation to a simulated winter thaw. *Tree Physiol.* **20**(8), 541–547.