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

LATVIA UNIVERSITY OF LIFE SCIENCE AND TECHNOLOGY
LATVIJAS BIOZINĀTŅU UN TEHNOLOĢIJU UNIVERSITĀTE

Dr. biol. **ROBERTS MATISONS**

ECOLOGICAL PLASTICITY OF RESPONSES OF RADIAL INCREMENT OF SCOTS PINE AND ITS POTENTIAL FOR BREEDING

PARASTĀS PRIEDES RADIĀLĀ PIEAUGUMA REAKCIJAS EKOLOĢISKAIS PLASTISKUMS UN TĀ SELEKCIJAS POTENCIĀLS

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

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

Salaspils 2024

Supervisor / *Darba vadītājs*:
Dr. silv. Āris JANSONS

The study was carried out in Latvian State Forest Research Institute 'Silava' in 2018–2024 and funded by European Regional Development fund project No. 1.1.1.2.VIAA/1/16/108 'Plasticity of development and xylogenesis of the native and introduced tree species under changing climate', European Social fund project No. 8.2.2.0/20/I/001 'LLU's transition to the new doctoral funding model', JSC 'Latvia's State Forests' project No. 5-5.9.1_007p_101_21_78 'Effect of climate change on forestry and associated risks', and the Latvian Council of Science grant No. lzp-2020/2-0416 'Local specialization and genetic control of plasticity of radial growth responses of Scots pine'.

Darbs izstrādāts Latvijas Valsts Mežzinātnes institūtā "Silava" no 2018. līdz 2024. gadam. Izstrādes finansējums gūts no Eiropas Reģionālās attīstības fonda projekta Nr. 1.1.1.2.VIAA/1/16/108 "Vietējo un introducēto koku sugu attīstības un ksiloģenēzes plastiskums mainīga klimata apstākļos", Eiropas Sociālā fonda projekta Nr. 8.2.2.0/20/I/001 "LLU pāreja uz jauno doktorantūras finansēšanas modeli", a/s "Latvijas valsts meži" atbalstītā projekta Nr. 5-5.9.1_007p_101_21_78 "Klimata pārmaiņu ietekme uz mežsaimniecību un tās riskiem" un Latvijas Zinātnes padomes granta Nr. lzp-2020/2-0416 "Parastās priedes pieauguma reakcijas jutības plastiskums un lokālās specializācijas ģenētiskā kontrole".

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pISBN 978-9934-603-13-6
eISBN 978-9934-603-14-3

DOI: 10.22616/lbtuthesis/2024.013

ABSTRACT

The accelerating climatic changes are challenging the natural adaptability of tree populations, which inevitably leads to economic and ecological consequences, hence proactive adaptive measures appear crucial for sustaining trees and related organisms, as well as their systems. In the eastern Baltic regions, Scots pine (*Pinus sylvestris* L.), which is abundant, stress-tolerant, and economically important, is among the species, whose abundance is projected to decrease due to climatic change. Considering the large-scale nature of climatic changes, the mechanisms of adaptation ought to be robust and self-sustaining, which are largely met by tree breeding. Still, considering the unprecedented pace of environmental changes, comprehensive information on the responses of trees and forests is needed for the asessment of the efficiency of the adaptive measures. Furthermore, mitigating the unprecedented changes apparently requires progressive means (e.g. enhanced application of assisted gene transfer), emphasising the necessity for comprehensive knowledge-based evaluation of the situation and potential solutions to comply with the conservative paradigm of conventional forestry.

Analysis of wood increment is a highly powerful tool for detailed retrospection of growth patterns and the underlying genetic, physiological, and environmental effects. Under rapid environmental changes, information on the environmental and particularly weather/climatic sensitivity of increment can be highly valuable and complementary to the conventional morphometric traits associated with the sustainability of genotypes. Morphometric traits, which are cumulative product of the conditions in the past, might be simply outdated by the environmental changes, which is backed up by the increasing rankings of the north-transferred genotypes in provenance trials. Under such circumstances, the sensitivity of increment, though should be scrutinized accounting for the shifting/ extending environmental gradients, paying attention to the ecological realism of the estimated relationships.

In this thesis, the responsiveness of radial increment of the eastern Baltic Scots pine to weather fluctuations across the regional climatic gradient and the genetic controls over it were assessed by combining methods of time series deconstruction, quantitative wood anatomy, mixed modelling and quantitative genetics. Empirical material was collected in conventionally managed stands and provenance trials spanning from southern Finland to northern Germany. The thesis summarizes the findings of nine peer-reviewed thematically consistent articles mostly published in top-ranked journals. Among the main things, complex meteorological controls of the winter thermal regime and summer moisture regime were estimated over the radial increment across the regional climatic gradient. Still, most of the estimated responses were nonlinear implying their scalability and ecological realism. Regarding the studied genotypes, the sensitivity

of increment to meteorological conditions was phenotypically plastic, while showing signs of local genetic adaptation, thus suggesting the adaptability of the populations. The plasticity of increment and its responsiveness, which arises from the ability to efficiently redistribute assimilates for growth while ensuring hydraulic efficiency of stemwood, was related to the productivity of the genotypes. Accordingly, the more productive provenances, which originated from lowland coastal Germany and Poland, and thus were north-transferred in Latvia, were more sensitive to meteorological fluctuations, while showing low susceptability to frost damage, wven compared to local genotypes. The weather sensitivity of growth has moderate heritability suggesting potential for improvements by tree breeding. Accordingly, the observed results encourage the application of the north-transferred fast-growing genotypes, particularly for supplementing gene pool of breeding populations.

ANOTĀCIJA

Klimata pārmaiņu paātrināšanās ir viens no būtiskākajiem koku populāciju dabiskās adaptēšanās spēju izaicinājumiem, kam neizbēgami sagaidāmas gan ekonomiskas, gan ekoloģiskas sekas. Šo seku mazināšanā proaktīvai un adaptīvai meža apsaimniekošanai ir nozīmīga loma koku un ar tiem saistīto organismu sistēmu ilgtspējas nodrošināšanai. Baltijas jūras reģiona austrumu daļā parastā priede (*Pinus sylvestris* L.) ir plaši izplatīta, stresa toleranta un saimnieciski nozīmīga suga, kuras sastopamībai ir prognozēts samazinājums klimatisko izmaiņu dēļ. Ņemot vērā klimatisko apstākļu ietekmes plašo mērogu, ir nepieciešamība pēc robustām adaptācijas metodēm, starp kurām ir izceļama meža selekcija. Detāla informācija par koku reakciju uz klimatiskajiem apstākļiem un to paātrinātajām izmaiņām, savukārt, ir nozīmīga adaptīvās apsaimniekošanas efektivitātes nodrošināšanai. Progresīvām adaptācijas metodēm (piemēram, genotipu ģeogrāfiskai pārnesei) ir īpaša loma genotipu un vides salāgotības nodrošināšanai, tādējādi uzsverot detālu ekoloģisko saistību izpētes nozīmi mežsaimniecības konservatīvās paradigmas pielāgošanai pieaugošajai apstākļu mainībai.

Koksnes pieauguma analīze ir nozīmīgs augšanas un ar to saistīto ģenētisko, fizioloģisko un vides ietekmju retrospektīvas izziņas avots. Strauju vides izmaiņu apstākļos pieauguma jutība pret klimatiskajiem un meteoroloģiskajiem apstākļiem var nozīmīgi papildināt morfometrisko pazīmju kopu precīzākam genotipu ilgtspējas novērtējumam. Daļa morfometrisko pazīmju, kas ir kumulatīvs pagātnes augšanas apstākļu rezultāts, savukārt, klimata pārmaiņu paātrināšanās ietekmē var zaudēt aktualitāti. To apstiprina uz ziemeļiem pārvietoto provenienču ātraudzības rangu kāpums, nereti pārspējot lokālos genotipus. Tādēļ vispārināmu un/vai uz nākotnes klimatu attiecināmu sakarību konstatēšanai ir nepieciešama pieauguma jutības izzināšana plašākā klimatiskajā gradientā.

Promocijas darbā, izmantojot laika rindu dekonstrukcijas, kvantitatīvās koksnes anatomijas, jaukta tipa modelēšanas un kvantitatīvās ģenētikas metodes, analizēta Baltijas jūras reģiona austrumu daļas parastās priedes populāciju pieauguma reakcija uz meteoroloģiskajiem apstākļiem, kā arī pieauguma jutības ģenētiskā kontrole. Empīriskais materiāls ievākts saimnieciskajos mežos un provenienču stādījumos no Somijas dienvidiem līdz Vācijas ziemeļiem. Promocijas darbs ir deviņu augstas kvalitātes žurnālos publicētu rakstu apkopojums. Konstatēts, ka meteoroloģiskajiem apstākļiem (ziemas temperatūrai un vasaras sausumam) vērtētajā reģionālajā klimatiskajā gradientā raksturīga kompleksa ietekme uz priedes pieaugumu. Vairumam no pieaugumu ietekmējošajiem meteoroloģiskajiem apstākļiem raksturīga nelineāra ietekme, kas norāda uz to atbilstību ekoloģiskajai teorijai. Analizētajiem genotipiem pieauguma reakcijas bija fenotipiski plastiskas, vienlaikus novērotas lokālas ģenētiskas adaptācijas iezīmes, raksturojot populāciju spējas adaptēties vides izmaiņām. Pieauguma un tā reakciju uz vides apstākļiem plastiskums, kas ir asimilātu pārdales un koksnes

hidrauliskās efektivitātes rezultāts, bija saistīts ar genotipu ražību. Ātraudzīgākās provenienceses, kuru izcelsme ir piejūras zemieņu apgabali Vācijas un Polijas ziemeļos (dienvidu izcelsmes no Latvijas perspektīvas), parādīja augstāku pieauguma jutību pret meteoroloģiskajiem apstākļiem un vienlaikus zemu (pat salīdzinoši ar vietējām proveniencēm) salnu bojājumu īpatsvaru. Pieauguma meteoroloģiskajai jutībai novērotās mērenās iedzimstamības koeficientu vērtības norāda uz selekcijas potenciālu uzlabot nākotnes mežaudžu piemērotību klimatam. Konstatētās saistības liecina par labu uz ziemeļiem pārvietotu produktīvāko priedes genotipu plašākai mežsaimnieciskajai izmantošanai, galvenokārt, selekcijas populāciju papildināšanai.

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LIST OF PUBLICATIONS / *PUBLIKĀCIJU SARAKSTS*

I **Matisons, R.**, Elferts, D., Krišāns, O., Schneck, V., Gärtner, H., Bast, A., Wojda, T., Kowalczyk, J., Jansons, Ā. 2021. Non-linear regional weather-growth relationships indicate limited adaptability of the eastern Baltic Scots pine. Forest Ecology and Management, 479, 118600; 10.1016/j.foreco.2020.118600.

II **Matisons, R.**, Dubra, S., Dauškane, I., Bičkovskis, K., Jansons, Ā., Gärtner, H. 2021. Canopy status modulates formation of wood rays in Scots pine under hemiboreal conditions. Dendrochronologia, 67, 125822; 10.1016/j.dendro.2021.125822.

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V **Matisons, R.**, Jansone, D., Elferts, D., Adamovičs, A., Schneck, V., Jansons, Ā. 2019. Plasticity of response of tree-ring width of Scots pine provenances to weather extremes in Latvia. Dendrochronologia, 54, 1–10; 10.1016/j.dendro.2019.01.002.

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VIII **Matisons, R.**, Schneck, V., Jansone, D., Bāders, E., Dubra, S., Zeltiņš, P., Jansons, Ā. 2021. South-eastern Baltic provenances of Scots pine show heritable weather-growth relationships. Forests, 12(8), 1101; 10.3390/f12081101.

IX **Matisons, R.**, Krišāns, O., Jansone, D., Jansons, Ā., Zeltiņš, P. 2024. Genetic and environmental variance of radial increment of southeastern Baltic provenances of Scots pine in response to weather extremes. Baltic Forestry, 30(1), 719; 10.46490/BF719.

Authors' contributions / *Autoru ieguldījums*

Paper / *Raksts*	Idea / *Ideja*	Study design / *Pētījuma dizains*	Data collection / *Datu ievākšana*	Data analysis / *Datu analīze*	Writing / *Rakstīšana*	Share of contribution of RM / *RM relatīvais pienesums*
I	**RM**, ĀJ	**RM**, ĀJ, HG, AB	OK, VS, TW, JK	**RM**, DE, AB	AM, ĀJ, VS, HG, AB, TW	65
II	HG, **RM**	**RM**, SD	SD, ID, KB	**RM**, SD, ID	**RM**, SD, ĀJ, HG	55
III	**RM**, ĀJ	**RM**	AA, DJ, ZB	**RM**, DJ	**RM**, ĀJ	70
IV	**RM**, ĀJ	**RM**, PZ, VS	DJ, EB, SD	**RM**, SD, DJ	**RM**, VS, ĀJ, PZ	70
V	**RM**, ĀJ	**RM**, ĀJ	AA, VS, DJ	DJ, VS, **RM**	**RM**, VS, ĀJ	65
VI	**RM**, GH	**RM**, HG	OK, AK, AA	AK, **RM**, GH	**RM**, ĀJ, HG, AK	60
VII	**RM**, HG	**RM**, HG, ĀJ	AA, **RM**, AK	**RM**, DE	**RM**, HG, DE, ĀJ	55
VIII	**RM**, ĀJ	**RM**, PZ, VS	DJ, EB, SD	**RM**, SD, DJ, PZ	**RM**, VS, ĀJ, PZ	70
IX	**RM**, ĀJ	**RM**, PZ, ĀJ	OK, PZ, DJ	**RM**, DJ, PZ	**RM**, ĀJ, PZ	75

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PRESENTATION IN CONFERENCES / *REZULTĀTU APROBĀCIJA KONFERENCĒS*

1. **Matisons, R.**, Jansone, D., Elferts, D., Adamovičs, A., Jansons, Ā. Pointer years in tree-rings of different provenances of Scots pine in Latvia. BaltDendro 2018, September 5–8, 2018, Liškiava, Lithuania.
2. **Matisons, R.**, Dubra, S., Dauškane, I., Jansons, Ā. Wood rays in tree-rings of Scots pine. BaltDendro 2018, September 5–8, 2018, Liškiava, Lithuania.
3. **Matisons, R.**, Krišāns, O., Kārkliņa, A., Adamovičs, A., Jansons, Ā., Gärtner, H. Tracheid size and cell wall thickness of some provenances of Scots pine in Latvia. TRACE 2019, May 7–10, 2019, Caserta, Italy.
4. **Matisons, R.**, Jansone, D., Elferts, D., Adamovičs, A., Schneck, V., Jansons, Ā. Pointer years in tree-ring width of some provenances of Scots pine in Latvia. TRACE 2019, May 7–10, 2019, Caserta, Italy.
5. **Matisons, R.**, Dubra, S., Dauškane, I., Jansons, Ā. Wood rays in tree-rings of Scots pine. EuroDendro 2019, September 9–13, 2019, Brno, Czech Republic.
6. **Matisons, R.**, Krišāns, O., Kārkliņa, A., Adamovičs, A., Jansons, Ā., Gärtner, H. Tracheid size and cell wall thickness of some provenances of Scots pine in Latvia. EuroDendro 2019, September 9–13, 2019, Brno, Czech Republic.
7. **Matisons, R.** Sensitivity and plasticity of Scots pine increment in changing climate. Knowledge based forest sector, January 26–27, 2021, Riga, Latvia.
8. **Matisons, R.**, Bāders, E., Jansone, D., Zeltiņš, P., Dubra, S., Jansons, A. Provenances of Scots pine – what to expect regarding the plasticity of weather-growth responses? TRACE 2021, June 16–17, 2021, Lund, Sweden.
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10. **Matisons, R.** Sensitivity and plasticity of Scots pine provenances – potential in the changing climate. 6th international conference "Sustainable management of natural resources – a basic condition for successful socio-economic development in the period of implementation of the new environmental policy of the European Union", November 25, 2021, Jelgava, Latvia.
11. **Matisons, R.**, Jansone, D., Ozoliņš, K., Zeltiņš, P., Jansons, A. Non-linear weather-growth relationships of Norway spruce and Scots pine in hemiboreal forests. SNS Growth and Yield Nordic biannual conference "Local solutions for regional and global forest management challenges", June 7–9, 2022, Riga, Latvia.
12. **Matisons, R.**, Jansone, D., Krišāns, O., Jansons, Ā. How plastic are the weather-growth responses of eastern Baltic Scots pine? TRACE 2023, May 8–13, 2023, Coimbra, Portugal.
13. **Matisons, R.**, Jansone, D., Krišāns, O., Jansons, Ā. How plastic is the eastern Baltic Scots pine? BaltDendro 2023, August 14–18, 2023, Saaremaa Island, Estonia.

ABBREVIATIONS / *SAĪSINĀJUMI*

ar1 – First order (lag 1) autocorrelation / *pirmās kārtas autokorelācija*
BR – Blue ring / *gadskārta ar nepilnīgi lignificētām šūnām vēlīnajā koksnē*
CVP – Provenance coefficient of variation / *provenience*s *ģenētiskais variācijas koeficients*
CWT – tracheid cell wall thickness / *traheīdu šūnapvalka biezums*
DIP – Dippoldiswalde provenance / *Dippoldisvaldes provenience*
EBN – Eibenstock provenance / *Eibenstokas provenience*
EPS – Expressed Populations Signal / *populācijas signāla stiprums*
EW – earlywood / *agrīnā koksne*
FR – Frost ring /*gadskārta ar salnu bojājumu*
G × E – genotype by trial interaction / *genotipa-vides mijiedarbība*
GDR – German Democratic Republic / *Vācijas Demokrātiskā republika*
GUS – Güstrow provenance / *Gustrovas provenience*
H^2 – Broad sense heritability / *iedzimstamības indekss sensu lato*
KA – Kalsnava provenance trial / *Kalsnavas provenienču izmēģinājuma stādījums*
KAL – Kalsnava provenance / *Kalsnavas (Jaunkalsnavas) provenience*
LA – tracheid lumen cross-section area / *traheīdu lūmena laukums*
LI – Liepāja provenance trial / *Liepājas provenienču izmēģinājuma stādījums*
LW – latewood / *vēlīnā koksne*
NBD – Neubrandenburg provenance / *Jaunbrandenburgas provenience*
NL – Nedlitz provenance trial / *Nedlicas provenienču izmēģinājuma stādījums*
PY – Pointer year / *"zīmīgais" (izlecošais) gads gadskārtu mērījumu sērijā*
r-bar – Mean interseries correlation / *vidējā starpsēriju korelācija*
RST – Rostock provenance / *Rostokas provenience*
RYT – Rytel Provenance / *Riteles provenience*
SENS – Mean sensitivity / *vidējā gadskārtu sēriju jutība*
SNR – Signal-to-noise ratio / *signāla-trokšņa attiecība*
SPEI – Standardized precipitation evapotranspiration index / *standartizētais nokrišņu un evapotranspirācijas indekss*
TRW – tree-ring width / *gadskārtu platums*
USSR – Union of Socialistic Soviet Republics / *Padomju Sociālistisko Republiku Savienība*
WR – wood rays / *koksnes stari*
WS – Waldsieversdorf provenance trial / *Valdsīversdorfas provenienču izmēģinājuma stādījums*
ZV – Zvirgzde provenance trial / *Zvirgzdes provenienču izmēģinājuma stādījums*

1 INTRODUCTION

1.1 Background

In the eastern Baltic region, the accelerating climatic changes are forcing shifts in the distribution of vegetation zones and tree species, hence altering the composition of forests (Buras and Menzel, 2019). In combination with the anticipated changes in climate, which can extend vegetation season while concomitantly causing additional stresses (Allen et al., 2015; Reyer et al., 2017), the projected changes in forest growth are expected to result in substantial ecological and economic consequences (Hanewinkel et al., 2012). This is enhanced by the growing demand for timber and forest-related products (Routa et al., 2019). The effects of environmental changes can vary regionally and locally (Reyer et al., 2014); however, the increasing variability of environmental conditions is likely to add stresses to tree growth and subsequently challenge forestry (Allen et al., 2015; Reyer et al., 2017), hence highlighting the necessity for adaptive climate-smart management for sustaining productivity of forests (Lindner et al., 2014; Reyer et al., 2014).

The warming of climate appears positive for the net productivity within the region due to the extension of vegetation and growth periods (Lindner et al., 2014; Reyer et al., 2014); still, it also increases diverse risks, such as damage by frost (Gu et al., 2008; Augspurger, 2009), which can hamper the increment (Piermattei et al., 2015). Furthermore, the observed and anticipated increase in variability of the summer moisture regime (Allen et al., 2015), intensifies drought conditions, to which forests are becoming increasingly vulnerable (Choat et al., 2012), including at high latitudes (Isaac-Renton et al., 2018). The edaphic conditions modulate the magnitude of drought, as forests on freely draining mineral soils with low water table, which are a considerable part of the commercial forests in Northern Europe (Lindner et al., 2014), can be particularly sensitive (Wang et al., 2021). The shift and extension of local climatic gradients (Meier et al., 2022) are subjecting local populations to the increasing frequency of weather extremes, which are testing the adaptive capacity of the genotypes (Valladares et al., 2014; Schwarz et al., 2020; Leites and Benito Garzon, 2023). Due to warming, cold hardening can be affected, thus subjecting trees to additional stresses during the dormancy period (Ögren, 1997; Vuosku et al., 2022), though the resistance to frost and cold is a multifactorial process (Beck et al., 2004; Baniulis et al., 2020).

The large-scale nature of the anticipated climatic risks highlights the necessity for climate-smart management and sustainable long-term solutions (Nabuurs et al., 2018; Chmura et al., 2021). Considering the accelerating rate of environmental changes, the evolutionary adaptation of local populations is lagging, hence proactive management and assisted migrations/gene flow is advantageous for sustainable forestry (Aitken and Bemmels, 2016), emphasizing the estimation of optimal transfer distance of reproductive material (Chauvin et al., 2019; Chmura et al., 2021). Accordingly, tree breeding particularly in a synergy with the assisted gene flow appears as the most promising means of adaptive management to increase the sustainability of forests (O'Neill et al., 2014; MacLachlan et al., 2017; Breed et al., 2018). For this, information on genetic control over the traits contributing to sustainability in addition to productivity is crucial for successful long-term improvements of forest reproductive material (MacLachlan et al., 2017; Matias et al., 2017; Grattapaglia et al., 2018; Ahrens et al., 2020). Considering the intensification and emergence of environmental hazards, the agility of the breeding programmes is crucial to minimize damage and gain advantages from environmental changes (Jansson et al., 2017; Ansarifar et al., 2020). Hence, the flow of up-to-date information on the performance of genotypes allowing agile adjustments in selection indices is highly advantageous (Li et al., 2017; Breed et al., 2018; Grattapaglia et al., 2018). As a result, tree breeding is becoming knowledge intensive, with comprehensive information on the genetic controls of diverse traits becoming paramount for the sustainability of the results (Li et al., 2017; Housset et al., 2018; Burdon and Klapste, 2019).

Populations of widely distributed species, such as Scots pine (*Pinus sylvestris* L.), adapt to local conditions, and for the traits important for survival and reproduction, as well as competitiveness, the adaptation can be genetic (Martin et al., 2010; Wojkiewicz et al., 2016; Yeaman et al., 2016; Chauvin et al., 2019; Ahrens et al., 2020). This supports the heritability of diverse traits and the potential for their improvements by breeding (Li et al., 2017; Li et al., 2018; Chauvin et al., 2019). As long-lived and sessile organisms, trees encounter a spectrum of environmental conditions during their life, hence they have evolved phenotypic plasticity to cope with the environmental fluctuations (Corcuera et al., 2011; Arnold et al., 2019; Cuny et al., 2019). Though, to maximize survival and competitiveness under certain conditions, phenotypic plasticity can be subjected to local adaptation (Yeaman et al., 2016; Li et al., 2017; Alakärppä et al., 2018; Ahrens et al., 2020), which persists under intensive gene flow (Moran et al., 2017; Li et al., 2018) and restricts the ability cope with extensive/rapid changes in environment (Valladares et al., 2014; Aitken and Bemmels, 2016). Hence phenotypic plasticity and local genetic adaptation are the indicators of the adaptability of populations/genotypes (Eckert et al., 2015; Moran et al., 2017; Chauvin et al., 2019; Ahrens et al., 2020; Ansarifar et al., 2020).

The phenotypic plasticity is a result of the G × E, which can be specific for populations, thus contributing to the differences in adaptivity (Valladares et al., 2014; Chmura et al., 2021; de la Mata et al., 2022). Though considering the multifactorial regulation of free growth, the G × E are complex (Li et al., 2017) and hence burden wide-scale prediction of the results of breeding (Li et al., 2017; Ansarifar et al., 2020). On the other hand, the G × E can be used to predict the local performance of genotypes and their adaptability in the medium- and long-term, which can serve as a powerful tool for adaptive management (Li et al., 2017; Chmura et al., 2021). This is particular considering the increasing local diversification of responses to environmental changes (Lindner et al., 2014; Reyer et al., 2014), which, if matched by compatible genotype, can add to the field performance (Ansarifar et al., 2020). The information on the genetic effects (genotype and G × E) on diverse traits can be assessed by means of quantitative genetics, which can provide highly detailed estimates (Falconer and MacKay, 1996; Loha et al., 2006). Accordingly, both individual and interacted genetic effects are crucial for breeding the forest reproductive material best suited for the increasing variability of environmental conditions (Li et al., 2017; Grattapaglia et al., 2018; Ansarifar et al., 2020).

Provenance trials provide opportunities for assessment of performance and risks for diverse genotypes under future and past climates depending on the direction of the assisted gene flow (Leites et al., 2012; Taeger et al., 2013; Nabais et al., 2018). Considering the occurring and projected northward shift of climatic zones in the eastern Baltic region, moderate northward transfer of genotypes has been advised to sustain forest productivity and reduce emerging consequences of drought (O'Neill et al., 2014; Berlin et al., 2016; Hayatgheibi et al., 2020). However, the north-transferred genotypes usually have longer vegetation period, increasing the possibility of frost/cold damage (Schreiber et al., 2013; Berlin et al., 2016; Montwe et al., 2018), while southwards transfer increases susceptibility to drought (Isaac-Renton et al., 2018; Chauvin et al., 2019), which can reduce the overall productivity (O'Neill et al., 2014). Additionally, provenance trials can act as a source of tested genotypes for the supplementation of local breeding populations according to the semiconservative breeding strategy (O'Neill et al., 2014; MacLachlan et al., 2017).

Under the increasing scrutiny of the ecological plasticity of trees (Corcuera et al., 2011; Valladares et al., 2014; Arnold et al., 2019), provenance trials have regained interest as the models for the analysis of genetic controls over the traits crucial for sustainability of genotypes (Leites et al., 2012; Nabais et al., 2018), particularly under shifting and/or extending climatic gradients (Valladares et al., 2014; Wilmking et al., 2020; Meier et al., 2022). Application of molecular and functional ecology methods on the provenance material has enabled direct and detailed evaluation of the genetic mechanisms determining traits affecting sustainability (Housset et al., 2018; Zhang et al., 2018; Ahrens et al., 2020). Such information has been proven to be complementary to the field performance estimates, which has been the initial goal for the establishment of provenance trials (Jansons and Baumanis, 2005; Konig, 2005; Leites et al., 2012), hence is crucial for adaptive management (Bolte et al., 2009; Nabuurs et al., 2018; Arnold et al., 2019). Still, due to the complexity of G × E (Li et al., 2017), which affects phenotypic and ecological plasticity (Arnold et al., 2019; Ansarifar et al., 2020; de la Mata et al., 2022), local information on the performance of diverse genotypes and populations (provenances) is crucial (Berlin et al., 2016; Breed et al., 2018; Chmura et al., 2021). Though, provenance trials provide limited information on the genetic effect, as the origin (parental structure) of the genotypes is unknown (Falconer and MacKay, 1996; Loha et al., 2006; Hayatgheibi et al., 2019).

In the majority of breeding programmes, the selection of genotypes is based on selection indices, which incorporate a variable set of economically important traits, among which those indicative of productivity (dimensions and stem quality) have a central role (Baliuckas et al., 2004; Jansson et al., 2017; Burdon and Klapste, 2019; Lenz et al., 2020). Though, tree dimensions and stem quality are cumulative indicators of the conformity of genotypes with the growing conditions in the past (Burdon and Klapste, 2019; Hayatgheibi et al., 2019), which, considering the accelerating pace of environmental changes, appear outdated (Aitken and Bemmels, 2016; de Villemereuil et al., 2016). Accordingly, shifts in the rankings of genotypes and provenance according to the allometrics have been observed across vast territories in the eastern Baltic region and elsewhere, as the climatic gradient shifts (Jansons and Baumanis, 2005; Berlin et al., 2016; Hayatgheibi et al., 2020; Chmura et al., 2021; Szeligowski et al., 2023).

For more accurate projections of field performance under future climates and hence more relevant breeding indices, information on growth responses to the extending spectrum of meteorological conditions can be highly informative (Zhang et al., 2018; Wilmking et al., 2020), substantially complementing data on the morphological traits (Xu et al., 2017; Heer et al., 2018; Housset et al., 2018). As the climate is one of the principal determinants of tree growth (Speer, 2010; Hayatgheibi et al., 2020; Wilmking et al., 2020), accurate projections of growth responses to meteorological and climatic conditions appear crucial for climate-smart and adaptive management (Bolte et al., 2009; Tei et al., 2017; Zhang et al., 2018). Thus, assessment of the genetic control over the sensitivity of growth/increment, and inclusion of such information in selection indices can contribute to the sustainability of breeding (Burdon and Klapste, 2019; Ahrens et al., 2020; Chmura et al., 2021).

Under temperate climate, tree growth is periodic, hence clear borders between increments of subsequent years can be distinguished, thus enabling retrospective analysis (Speer, 2010; Gärtner et al., 2015; Xu et al., 2017; Gennaretti et al., 2022). Due to the convenience of sampling and high informativity regarding the environmental effects, radial increment, TRW was been the overwhelming proxy of free growth globally (Babst et al., 2018). Despite the sensitivity to local effects, TRW is a highly relevant proxy for the productivity of tree and forest growth, implying sufficiency for the assessment of a wide spectrum of environmental questions (Xu et al., 2017; de Micco et al., 2019; Wilmking et al., 2020). The formation of increment is a complex process, and hence TRW is a composite of several environmental and intrinsic effects (Cook, 1987; Speer, 2010), which are highly topical, particularly regarding the adaptability of trees and forests to accelerating environmental changes (Housset et al., 2018; Zhang et al., 2018; Schwarz et al., 2020). Accordingly, diverse mathematical methods have been developed for the separation of the underlying effects, among which time series analysis and variance deconstruction is among the most efficient (Cook, 1987; Bunn, 2008; Stoffel et al., 2010; Jetschke et al., 2019).

The TRW as a cumulative quantitative proxy of growth is summarizing the conformity of genotypes with the conditions during the xylogenesis, as well as prior to it (Hacket-Pain et al., 2018; Montwe et al., 2018; Cuny et al., 2019; de Micco et al., 2019; Wilmking et al., 2020), hence the disentanglement of their individual contributions can be challenging (Fonti et al., 2010; Gärtner et al., 2015; Babst et al., 2018). To gain deeper insight into environmental forcing and regulation of xylogenesis, analysis of wood anatomy can provide highly detailed quantifiable data on the properties of wood (Fonti et al., 2010; Cuny et al., 2019; Gennaretti et al., 2022). According to the pipe theory, wood primarily acts as the water transpose system consisting of numerous pipes connecting roots with leaves (Tyree and Zimmermann, 2002; Martinez-Vilalta et al., 2004). The set and properties of the pipes largely determine the efficiency of the transport, as well as hydraulic safety, i.e., resistance to cavitation and embolism, which causes physiological water deficit (Sperry and Tyree, 1990; Anderegg et al., 2015; Prendin et al., 2018).

The lumen area of vessels/tracheids is a proxy of the efficiency of water transport and risk of embolism, while the cell wall thickness is largely determining the mechanical properties of wood, as well as resistance to embolism (Sperry and Tyree, 1990; Tyree and Zimmermann, 2002; Martin et al., 2010). Under the globally intensifying drought effects on forests, such information is becoming increasingly topical (Gennaretti et al., 2022). Besides the vertical water transport, stemwood acts as a storage silo for water, nutrients and minerals, indicating the relevance of horizontal substance transfer between and within heartwood and sapwood (Tyree and Zimmermann, 2002; Richardson et al., 2013). These functions are largely maintained by WR, the quantification of which indicates the storage capacity of wood and hence acts as an indirect proxy for assimilation (von Arx et al., 2017).

The extending vegetation period is increasing the risk and severity of frost damages (Lee et al., 2007; Augspurger, 2009; Kidd et al., 2014), which burdens and disrupts xylogenesis, and the imprints of such events are archived in wood as anomalies, allowing retrospective assessment of their causality (Payette et al., 2010; Gennaretti et al., 2022). Severe late frosts, particularly as the xylogenesis has already been initiated, shatter unmatured wood cells resulting in the formation of FR in EW (Lee et al., 2007; Payette et al., 2010). In contrast, early frosts disrupt lignification, hence cell walls contain an increased amount of cellulose, which, in the case of double staining of wood by Astra blue and safranin (Gärtner and Schweingruber, 2013), causes LW to appear blue or bluish, thus signifying a BR (Piermattei et al., 2015). Both these anomalies are becoming increasingly promising proxies for assessment of conformity of genotypes (particularly transferred) with local climates and weather anomalies (Payette et al., 2010; Piermattei et al., 2015; Gennaretti et al., 2022). Also, these anomalies might affect the mechanics and strength of wood, as the optimal structure of wood is distracted and causing mechanical weak spots (Berry et al., 1983; Lee et al., 2007).

The deconstructed variance of components of increment and related proxies, particularly if coupled with advanced regression and modelling techniques (Cavin and Jump, 2017; Zhang et al., 2018; Wilmking et al., 2020), enables highly detailed assessment of both short- and long-term effects on growth under normal and extreme conditions (Sass-Klaassen et al., 2016; McCullough et al., 2017; Xu et al., 2017; Babst et al., 2018). Considering weather and climate as a principal determinant of tree growth, the assessment of climate- and weather-growth relationships has been a substantial field of application of the in-depth analysis of increment (Cook, 1987; Ohse et al., 2012; Lloyd et al., 2013; Harvey et al., 2020; Wilmking et al., 2020). Though, for the scalability of such knowledge under increasing environmental variability, analysis of increment across reasonable climatic gradient is essential, as the locally observed relationships can already be outdated (Lloyd et al., 2013; Henttonen et al., 2014; Restaino et al., 2016; Cavin and Jump, 2017).

The ecological relationships across the environmental gradients are bell-shaped, while linear relationships can be estimated if a limited part of a gradient is considered (Way and Oren, 2010; Lloyd et al., 2013; Restaino et al., 2016). Hence, the shift of the limited window of observation, as in the case of local data, inevitably leads to biased extrapolation of the linear relationships (Valladares et al., 2014; Wilmking et al., 2020; Wu et al., 2022). To solve such an issue, the estimation of nonlinear ecological responses across a reasonable part of the climatic gradient is crucial (Lloyd et al., 2013; Cavin and Jump, 2017). In this regard, time series of tree-ring proxies are advantageous, as even at a local scale, they represent a temporal gradient of conditions (McCullough et al., 2017; Xu et al., 2017; Babst et al., 2018). Furthermore, a dataset representing reasonable parts of spatiotemporal gradients can be obtained by regional sampling (Restaino et al., 2016; Cavin and Jump, 2017; Harvey et al., 2020).

In the eastern Baltic region, Scots pine is a common and economically highly important coniferous tree species (Routa et al., 2019) projected to decrease in abundance within the region during the 21st century (Buras and Menzel, 2019). It is ecologically plastic and grows on a variety of sites, while being particularly important under oligotrophic and mesotrophic conditions with freely draining mineral soils (Berlin et al., 2016; Jansson et al., 2017). As for a widespread species, its local populations have undergone genetic adaptation (Martin et al., 2010; Wojkiewicz et al., 2016; Alakärppä et al., 2018), implying differing adaptability to environmental changes (Valladares et al., 2014; Li et al., 2017; Moran et al., 2017). The local adaptation of Scots pine has been related to anatomical and physiological adaptations to cope with drought stress and wind loading, as well as with competition (Martin et al., 2010; Wojkiewicz et al., 2016; Tyrmi et al., 2020). Furthermore, a local small-scale adaptation of pine is known in response to contrasting edaphic conditions (Eckert et al., 2015; Zadworny et al., 2016). Hence, the local genetic adaptation of the populations implies that the projections of the bioclimatic models could be biased, overestimating the reduction of the abundance of Scots pine, particularly under adaptive management (Valladares et al., 2014; Wu et al., 2022). Concomitantly, local genetic adaptation is the basis for successful breeding programmes within the region, which is largely based on the morphometric traits related to stand productivity and stem (timber) quality (Baliuckas et al., 2004; Eckert et al., 2015; Jansson et al., 2017), while sensitivity traits are still being underrepresented (Fries, 2012; O'Neill et al., 2014; Wojkiewicz et al., 2016; Ahrens et al., 2020).

The growth of Scots pine has been shown to be sensitive to weather conditions and its extremes, though the relationships exhibit local features (Elferts, 2007; Zunde et al., 2008; Jansons et al., 2016; Harvey et al., 2020). Across the eastern Baltic regions, the increment of Scots pine shows a gradual shift of local linear weather-growth relationships from growth limitation by summer warmth in Finland to spring temperature and summer drought limitation in Poland and Germany (Henttonen et al., 2014; Harvey et al., 2020). Accordingly, the Baltics appear as the transition zone where the weather limitation shifts, implying complex controls over the increment (Harvey et al., 2020), allowing scrutiny of the stationarity of weather-growth relationships (Wilmking et al., 2020). Considering location under a cold climate, winter temperature can have contrasting effects on increment, likely via cold damage of respiratory losses of sugars (Ögren, 1997; Beck et al., 2004), supporting the carryover effects of weather conditions. The regional weather-growth relationships also imply the effects of growth-reproduction tradeoffs, which are suggested by the negative effects of thermal conditions in the preceding summer (Hacket-Pain et al., 2018). The effects of climatic factors on the growth of Scots pine have also been supported by the gradual shifts in rankings of provenances, as the north transferred genotypes rise with warming (Jansons and Baumanis, 2005; Berlin et al., 2016).

The stemwood of Scots pine is rather primitive and is mostly formed of tracheids, which surround scarce resin ducts (Carlquist, 2001; Martinez-Vilalta et al., 2004) and axial parenchyma (Olano et al., 2013; von Arx et al., 2017). The CWT and LA vary greatly, though the transition between LW and EW is abrupt and forms a distinct border (Mencuccini et al., 1997; Carlquist, 2001). The CWT and LA within EW and LW can vary greatly according to environmental conditions during their formation (Cuny et al., 2019), as well as due to local genetic adaptation (Martin et al., 2010). Though, the plasticity of xylogenesis, which mitigates the effects of shifting conditions on the functioning of the xylem (Cuny et al., 2019), appears restricted (Seo et al., 2020), presuming susceptibility to the hydraulic risks, particularly in the latter part of the growing/vegetation season (Piermattei et al., 2015; Cuny et al., 2019). Considering hydraulic architecture (wood anatomy) important for survival and competitiveness, it is subject of genetic adaptation (Lenz et al., 2010; Fries, 2012; Carvalho et al., 2017).

1.2 Aim

The aim of the study was to assess the plasticity of the response of radial increment of eastern Baltic Scots pine to meteorological/climatic conditions and evaluate the climatic adaptability of the species and the potential for its improvements by tree breeding.

1.3 Objectives

The subordinate objectives were to assess:

1) The responsiveness of radial increment of the eastern Baltic populations of Scots pine to the principal meteorological and climatic drivers across the regional climatic gradient;
2) The effects of local genetic adaptation (genetic factors) on the sensitivity of increment to meteorological conditions and their extremes and its phenotypic plasticity at the regional level in relation to productivity;
3) The effects of local adaptation on xylogenesis and wood anatomy of Eastern Baltic populations of Scots pine and hence susceptibility to water shortage;
4) The genetic effects (heritability) and breeding potential for radial growth sensitivity of eastern Baltic provenance of Scots pine.

1.4 Theses

The proposed theses are:

1) Radial increment of the eastern Baltic Scots pine is subjected to complex controls of meteorological (thermal and moisture) conditions during and prior to its formation;
2) The nonlinear effects of the principal weather drivers of increment show climate-dependant weather controls over the increment, projecting disproportional effects of climatic changes on growth;
3) Weather sensitivity of increment and its plasticity relate to the field performance of the genotypes indicating adaptability of regional populations/provenances;
4) Weather sensitivity of increment and its plasticity is at least partially genetically determined, implying potential for improving climatic adaptability by targeted breeding.

1.5 Thesis structure

The thesis consists of nine thematically consistent papers scrutinizing plasticity and principal drivers of radial increment of Scots pine in the eastern Baltic region. The first two papers address the plasticity of responses of genotypes *in situ*, thus evaluating the principal regional climatic and weather drivers of radial growth. Three papers investigate local adaptation and plasticity of weather-growth responses of regional provenances differing by field performance, thus assessing the sensitivity-productivity relationships. Two papers analyse wood anatomical properties of the provenances as the proxies for susceptibility to increasing climatic risks. The last two papers quantify the heritability of weather-growth sensitivity and its breeding potential.

1.6 Topicality

The study focusses on local specifics of weather controls over the formation of wood increment and its plasticity by quantification of the underlying environmental and genetic effects. The relationships between the environmental sensitivity of genotypes and their productivity highlighted favourable tradeoffs (more productive genotypes are sensitive) suggesting sensitivity of increment as an adaptation to fluctuating conditions. Accordingly, the ability to promptly adjust growth contributes to the resilience and productivity of genotypes in the long term. Such relationships are backed by the genotype-specific differences in wood anatomy. The results demonstrate a comparison regarding the scalability of linear and nonlinear weather-growth relationships recognizable at local/regional scales. Analysis of inter- and intra-annual variability of WR is suggested as a proxy for the adaptive capacity of trees of different social strata.

Methodologically, the thesis explores the application of wood anomalies (FR and BR) in retrospection of the effects of frosts for the characterisation of genotypes. This is supplemented by the approbation of quantitative wood anatomy methods for comparative studies of genotypes, thus allowing more comprehensive evaluation based on limited empirical material. The synergy of time series deconstruction and mixed additive modelling has been tested for local ecological studies under accelerating environmental changes. The results of the thesis are particularly relevant to the eastern Baltic region; however, the algorithms of research are universal for studies of comparable spatiotemporal scales. The obtained results provide a solid background for further research based on an expanded set of genotypes thus confirming the scalability and applicability of the proposed relationships within local populations.

2 MATERIAL AND METHODS

2.1 Sites and trials

A regional transect stretching from Southern Finland to northern Germany was used to represent the regional spatiotemporal climatic gradient (Fig. 1A) (Paper I). Along the transect, 22 open-pollinated conventionally managed maturing or mature stands (69–129 years) of Scots pine with an area exceeding one ha

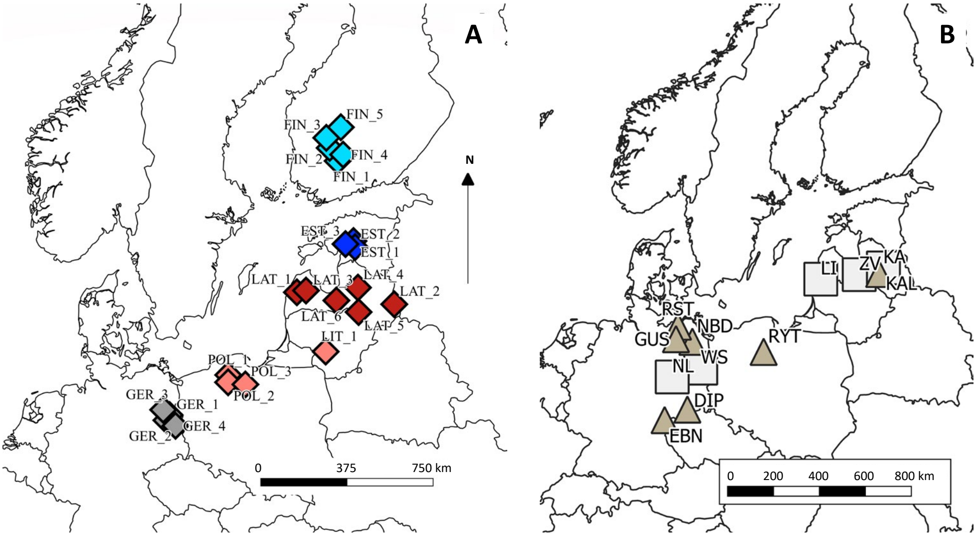

Figure 1. **Location of the studied mature commercial stands of Scots pine on mineral freely draining soils representing the local populations *in situ* (A), as well as the location of the studied provenance trials and origin of studied provenances (shown by triangles and squares, respectively; B)**

1. attēls. ***Pētīto parastās priedes saimniecisko audžu uz drenētām augsnēm, kas reprezentē lokālās populācijas in situ (A), kā arī provenienču stādījumu un izcelsmju (attiecīgi trijstūri un kvadrāti; B) atrašanās vietas***

occurring on freely draining mesotrophic soils were selected from the national inventories. The selection was done for the assessment of principal regional weather drivers affecting conventionally managed populations *in situ*. The locations were represented by one to six stands to account for local specifics in radial growth. The stands were situated in sites with generally flat topography at low elevation, representing coastal and inland conditions. An admixture of Norway spruce (*Picea abies*) and silver birch (*Betula pendula*) was quite common. Additionally, a managed mature well-draining mesotrophic Scots pine stand with scarce spruce understory in the central part of Latvia (56.799 °N; 24.498 °E) was randomly selected from forest inventory for sampling for the estimation of differences in WR among pines of different canopy status (Paper II).

The selected stands/locations represented climates from cold humid continental in Finland to temperate oceanic in northern Germany (Kottek et al., 2006), where the mean annual temperature ranged from 4.3 to 10.1°C, respectively. Across the transect, the winter thermal regime was more variable than that in summer. The mean annual precipitation, though was comparable among the sites, ranging 542–771 mm year^{-1} in the stands in Finland and Latvia, respectively (Harris et al., 2020). The annual precipitation regime was also comparable among the stands with half of the annual precipitation occurring during the active vegetation season, thus generally balancing evapotranspiration. The main changes in climate have been expressed as explicit warming during the dormancy period, which extended vegetation season, as well as increasing variability of summer precipitation and temperature regime, which has been increasing the incidence the hot drought conditions (Allen et al., 2015; Meier et al., 2022).

To assess the local adaptation of populations in terms of sensitivity of increment, five provenance trials representing a truncated climatic gradient between Latvia and northern Germany were studied (Fig. 1B) (Papers III–IX). The provenance trials were established in 1975 under the international collaboration of the USSR and GDR under the IUFRO framework for the assessment of the performance of the (eastern) European provenances of Scots pine (Kohlstock and Schneck, 1992; Jansons and Baumanis, 2005). The tested provenances originated from the region spreading between 46 and 56 °N, and 11 and 30 °E; a set of 36 provenances was common for all trials. Such a region includes the spectrum of climatic conditions predicted for Baltic states by the end of the 21st century (Buras and Menzel, 2019; Meier et al., 2022). The seed material has been collected from the plus-trees within each of the provenances thus representing the top-performing genotypes. The trials were established by planting one-year-old seedlings raised in local nurseries. The initial spacing of the planting was 2 × 1 and 2 × 0.5 m for the respective trials in Latvia and Germany.

The provenances were planted according to a randomized block design, yet the size and number of the blocks differed between the countries. In the trials in Latvia, the provenances were represented by six blocks (replications) of 35 (5 × 7) trees, while in Germany by for blocks of 100 (10 × 10) trees. The trials grew on freely draining oligotrophic sandy soils in Latvia and mesotrophic silty podzolic soils in Germany; the topography of all sites was flat and elevation was low, as typical for the lowland region. Initially, tending of all trials was implemented if necessary, yet the thinning regimes differed. In Latvia, the trials have undergone a single thinning from below to 1,800 trees ha^{-1} at the age of 21 years, while in Germany a year prior to sampling NL trial was thinned from below 1,100 trees ha^{-1}. In the WS trial, three thinnings have been implemented with the last one in the winter of 2013–2014, thus decreasing the stand density to 900–1,200 trees ha^{-1}.

2.2 Provenance selection

To assess local adaptation of genotypes in terms of growth sensitivity and plasticity, seven provenances with differing field performance, represented in all of the studied trials were selected according to the consolidated ranking of field performance according to recent inventories (Fig. 1B) (Papers III–IX). Previous studies have shown a significant effect of provenance on both the productivity and stem quality of trees (Jansons and Baumanis, 2005; Taeger et al., 2013), with the selected provenances having consistent rankings. Such selection also allowed the assessment of sensitivity-productivity relationships (Leites et al., 2012; Valladares et al., 2014; Matias et al., 2017; Housset et al., 2018) and conditions underlying plastic responses (de Villemereuil et al., 2016; Nabais et al., 2018).

Two low-performing provenances (DIP and EBN), which originated for the Ore Mountains, one local (from the Latvia perspective, KAL), which excelled in stem quality and had above average performance, and two top-performing provenances (GUS and RYT), which originated from coastal lowland areas in northern Poland and northern Germany were selected. Additionally, for the estimation of heritability, two top-performing provenances from the same lowland region (NBD and RST) were selected (Papers VII, IX). Generally, the top- and low-performing provenances represented the higher and lower quartiles of productivity and stem quality traits of the trials.

2.3 Data acquisition

2.3.1 Sampling

Within the maturing conventionally managed stands across the international transect (Fig. 1A), from 15–30 healthy dominant non-leaning trees without visual damage and signs of disease were selected for sampling (Paper I). Two increment cores per tree from randomly oriented opposite sides of the stem were collected at the breast height using a 5 mm increment corer. For the quantification of wood parenchyma (WR) and its relationships to canopy status (Paper II), in a mature conventionally managed stand, seven dominant trees (with wide, well-developed crowns) and six intermediate trees (reaching canopy, yet with narrow and reduced crown) were selected. Edge trees, as well as tilted trees, were avoided. From each of the trees, two increment cores at the breast height from random opposite directions were collected using a 5 mm increment corer. Special attention was paid to the sharpness of the corer, so the increment cores were collected and maintained unbroken. For the assessment of growth pattern, a single core per tree was additionally sampled form from five dominant and five intermediate trees within the stand.

In the provenance trials, sampling was done considering the randomized plot design (Papers III–IX). From each block, two or three dominant or co-dominant visually healthy trees without visible damages were selected. Block edge and tilted trees were avoided if possible. Two increment cores from randomly oriented opposite sides of the stem were collected from each tree at breast height using a 5 mm increment corer. It was ensured that the corer was clean and freshly sharpened, hence the cores were not broken.

2.3.2 Tree-ring width measurements

The collected increment cores (except those for WR, Paper II) were permanently mounted (glued) into single-row wooden mounts. It was ensured, that the axial direction of tracheids was perpendicular to the surface of the mounts. In the case of twisted cores, a hot steam jet was used to soften and untwist the cores (Speer, 2010). Softening of samples also prevented their breakage during the mounting. The surface of the mounted samples was levelled using progressive sanding by a handheld orbital grinder or cut using the WSL core microtome (Gärtner and Nievergelt, 2010). The measurements of TRW were made manually using the LINTAB 6 measurement table and TSAP software (RinnTech, Heidelberg, Germany). The measurements were done by the same person. The accuracy of the measurements was 0.01 mm.

2.3.3 Quantitative wood anatomy

For estimation of WR (Paper II), the increment cores were soaked in water for a day to completely refill the xylem and thus soften it. The cores were cut tangentially by hand sledge microtome GSL1 (Gärtner et al., 2014). The thickness of the section was 15–35 µm. Two sections (from middle EW and LW) per 30–35 outermost tree-rings. The older tree-rings were not sampled, as the parenchyma would likely died off and hence would not be distinguishable in the stained samples. To assess the anatomical structure of wood and the effects of local adaptation (Papers VI, VII), thin cross-sections (14–18 µm) of the increment cores were cut using the WSL core microtome (Gärtner and Nievergelt, 2010) according to the protocol by Gärtner and Schweingruber (2013).

The sections were double stained by Astra blue and safranin (Gärtner and Schweingruber, 2013), thus enhancing the contrast between the parts of tree-rings, as well as lignified and nonlignified wood elements (parenchyma). Samples were embedded in Canada balsam or in glycerine. High-resolution distortion-free microscopic images of the samples were acquired with a transparent light

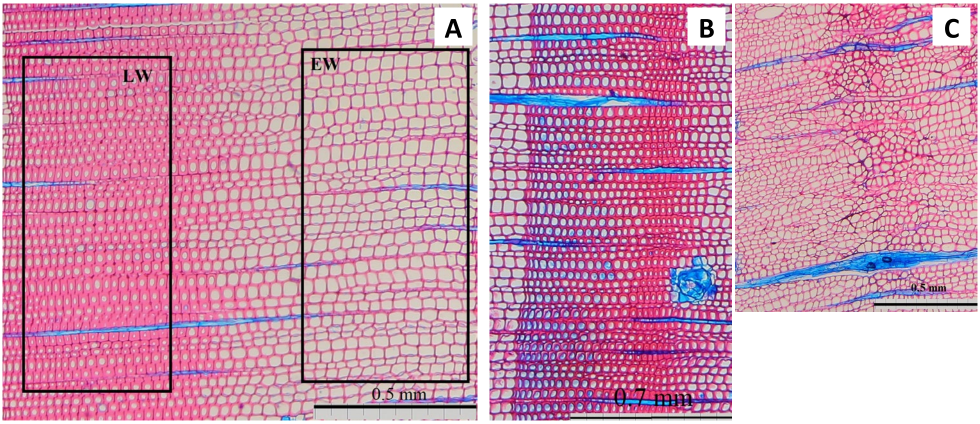

Figure 2. **Measurement area of tracheid cell wall thickness and lumen within a tree-ring (A), example of a 'blue' (B) and frost (C) rings**

The thin cross-sections of wood are double stained by Astra blue and safranin.

2. attēls. ***Traheīdu šūnapvalku biezuma un lūmena laukuma mērīšanas apgabali gadskārtas attēlā (A), kā arī gadskārtu ar priekšlaicīgu lignifikācijas pārtraukumu (B) un vēlu salnu bojājumu (C) piemēri***

Mikroskopiskais koksnes preparāts ir krāsots ar Astra zilo un safranīnu.

microscope equipped with a digital camera with an 18 Mpx cropped matrix at 40× magnification. The images were stitched using the PTGui program (New House Internet Services, Rotterdam). The recognition and measurements of WR (Paper II) and CWT and LA (Paper VI) were made using WinCELL 2007a (Regent Instruments, Canada) software. The estimation of wood anomalies related to frosts (FR, BR; Piermattei et al., 2015) was done by visual inspection of the images (Fig. 2).

2.3.4 Climatic data and arrangements

To assess the weather-growth relationships (Papers I–IX), as well as the weather effects on wood anatomy and its anomalies, gridded climatic data (CRU TS4; Harris et al., 2020) were acquired for the grid points closest to the sampling locations. The monthly precipitation, temperature, and potential evapotranspiration estimates were acquired for the period 1901–2017. To evaluate the severity of drought conditions, SPEI was calculated as the proxy of the moisture regime (Vicente-Serrano et al., 2010). For the weather-growth analysis, the monthly climatic data were arranged according to the climatic windows extending from May/June of the year of the preceding formation of increment to September of the year of increment, thus assessing the carryover effects of meteorological conditions (Beck et al., 2004; Hacket-Pain et al., 2018; Harvey et al., 2020).

2.4 Data analysis

To ensure the quality of the measurements and reliability of the dating of increment, which is paramount for growth sensitivity analysis (Speer, 2010), graphical and statistical crossdating was performed (Papers I–IX). Time series were corrected or omitted if necessary. The sufficiency of crossdating and strength of the environmental signals within the datasets was described by several time series agreement metrics, e.g., r-bar, ar1, SENS, EPS, SNR, etc (Wigley et al., 1984; Bunn, 2008; Speer, 2010). The metrics were calculated for the high-frequency (i.e., annual) variation component of the increment.

The time series of TRW were double detrended using a modified negative exponential curve and flexible cubic spline with the wavelength of two thirds of the series length (Papers I and III) or comparable wavelengths (other papers), which is a strict detrending approach explicitly highlighting the inter-annual variation. Considering that the increment proxies often contain high ar1 (Cook, 1987), time series were prewhitened using the first-order autoregressive function (Bunn, 2008). For the estimation of local linear relationships (Wilmking et al., 2020), the detrended time series of trees were averaged into stand/provenance chronologies using the biweight robust mean (Cook, 1987; Bunn, 2008).

Specific standardization based on the relative growth changes was applied to estimate PY (Jetschke et al., 2019), when the growth of a considerable part of the dataset or data subset expresses abrupt changes in increment

(Paper III and IX). Considering the location of the sampled sites under temperate climates, as well as non-suppressed growth, the criteria for the estimation of event years and subsequently PY was generally low (Elferts, 2007; Jetschke et al., 2019). The weather drivers of the PY were analysed according to van der Maaten-Theunissen et al. (2021) and Schwarz et al. (2020). The resilience analysis was conducted to assess the tolerance of increment to weather anomalies (Paper III). Resistance (PY/pre-PY), recovery (post-PY/PY), resilience (post-PY/pre-PY), and relative resilience ((post-PRPY)/pre-PY) indices (Lloret et al., 2011) were calculated based on TRW.

Bootstrapped Pearson correlation analysis between the chronologies and PY time series and the weather data was used to screen the local linear weather-growth relationships for the proxies of the radial increment (Papers I–VIII). Moving-window bootstrapped correlation analysis was used to assess the stationarity of local linear weather-growth relationships (Zang and Biondi, 2015; Hofgaard et al., 2019). Considering that the studied trees grew in the mid-part of the distribution area under presumedly favourable site conditions, multiple regression techniques were used to estimate the principal weather drivers of the increment (Papers I and IV). Considering that ecological responses across the environmental (both spatial and temporal) gradients are bell-shaped (Way and Oren, 2010; Lloyd et al., 2013), thus nonlinear, generalized additive mixed models were, which allow estimation of response splines, were used for the regression (Wood, 2011). Residual chronology index values of sands (Paper I) or trees (Paper IV) were used as the response variable, with the meteorological variables tested as the predictors. The set of predictors was selected according to the arbitrary selection principle considering the result of local screening by correlation analysis, as well as several fit metrics. Year and spatial hierarchical structures in data (tree, trial, stand, etc) were included in the models as nested random effects to account for the dependencies in data.

Linear mixed effects models were used to evaluate the effects of canopy statue on the quantity and properties of WR (Paper II), and the effects of provenance on resilience components in response to PY, as well as on the wood anatomy (CWT and LA). The structure of random effects as described above was used to account for the dependencies in the data. The significance of the fixed effects was evaluated using Wald's χ^2 test. Conformity with model assumptions was checked using the diagnostic plots.

To quantify site and genetic (incl. G × E) effects of the weather-growth sensitivity and responsiveness of increment to weather anomalies in PY, the variance was separated by linear mixed effects model according to Loha et al. (2006) and Falconer and MacKay (1996) based on the studied provenances (Fig. 1B). The response variable was the local weather-growth correlation (based on detrended basal area increment) and the event year values (relative growth changes; Jetschke et al., 2019; Papers VIII and IX, respectively). Heritability (H^2) and CVP were calculated for the depiction of the genetic effects. Data analysis was conducted in R v. 4.2.2 using the libraries dplR (Bunn, 2008), pointRes (van der Maaten-Theunissen et al., 2021), treeclim (Zang and Biondi, 2015), lme4 (Bates et al., 2015), and mgcv (Wood, 2011).

3 RESULTS AND DISCUSSION

3.1 The quality of datasets

The time series of TRW generally showed good quality, and the vast majority of them passed quality checking and crossdating, providing the basis for the estimation of weather-growth relationships (Papers I, III–IX). The informativity of the datasets of TRW was supported by the estimated metrics of agreement, with the EPS exceeding the arbitrary threshold of 0.85, which denotes sufficiency for climatic analyses (Wigley et al., 1984). Hence, SNR mostly exceeded 5.0 indicating environmental signals in TRW to be of reasonable strength, though according to the provenance data (Paper IV, V), it tended to be higher for the more productive genotypes. The SENS and Gini coefficient of the time series (Papers I, III–IX), which show the extent of the inter-annual variability of growth (Bunn et al., 2013), was intermediate, which is optimal for weather-growth analysis (Speer, 2010). The effect of previous growth on increment across the international transect (Paper I) and in the provenance trials (Papers III–V, VIII–IX) was explicit, as indicated by high ar1, which implies a conservative growth strategy (Way and Oren, 2010; Isaac-Renton et al., 2018). Though, the ar1 tended to be lower and mean sensitivity slightly higher in the provenance trials in northern Germany, likely indicating higher marginality of local climates from the perspective of the genotypes (Taeger et al., 2013; Cavin and Jump, 2017; Cuny et al., 2019).

The time series of wood anatomical proxies (Paper II, VI) were shorter than TRW, and they were often disrupted due to shifts in the orientation of wood fibbers within a stem (von Arx et al., 2016; Gennaretti et al., 2022). Hence the agreement metrics calculated for them were biased. Nevertheless, the measurements of wood anatomical proxies contained reasonable variance enabling ecological investigation. The distributions of wood anatomical anomalies (BR, FR) were zero-inflated implying low incidence, hence they were analysed in a simplified manner (Paper VII). All of the accounted 126 BR occurred in LW, yet the majority of the 97 FR accounted occurred in the mid-part of EW, thus supporting relationships with late and early frosts (Gu et al., 2008; Kidd et al., 2014; Piermattei et al., 2015). The quantity and dimensions of WR (Paper II), showed low variation implying conservative behaviour in terms of nonstructural carbohydrate storage capacity (Olano et al., 2013; Richardson et al., 2013; von Arx et al., 2017). The quantity and characteristics of wood elements are restricted to ensure structural wood integrity (Mencuccini et al., 1997; Cuny et al., 2019). Nevertheless, the measured dimensions of WR varied unevenly, presuming differing environmental constraints, and hence sensitivity to fluctuating conditions (Olano et al., 2013).

3.2 Regional and local growth responses of native populations

Radial increment of the eastern Baltic populations of Scots pine showed complex effects of meteorological conditions in the native locations (Paper I). The local weather-growth correlations, which represent local linear relationships between the TRW chronology indices (i.e., annual relative additional increment) and weather conditions (Lloyd et al., 2013; Tei et al., 2017; Babst et al., 2018) showed a gradual shift along the transect, hence spatial nonstationarity (Hofgaard et al., 2019; Wilmking et al., 2020). In southern Finland, the weather-growth correlations showed local effects of the thermal regime during and prior to xylogenesis, hence the proportion of sites showing common tendencies was low. Still, the correlations supported low temperature limitations of growth (Henttonen et al., 2014; Montwe et al., 2018). In the sites southwards from Finland, a pattern of weather-growth correlations emerged with the effects of winter temperature and particularly summer moisture regime becoming common. Still, in Latvia, where sampled stands were more scattered (Fig. 1), the local weather-growth relationships appeared most diverse, although correlations with winter temperature were common. Also, negative correlations with temperature in the preceding summer were common in Latvia, and to a lesser extent, in northern Germany. In the southern part of the transect, increment showed common correlations with meteorological conditions related to drought conditions, which adheres to the globally emerging effects (Choat et al., 2012; Allen et al., 2015).

The moving window correlations analysis, however, showed that most of the local weather-growth correlations were temporarily nonstationary (Hofgaard et al., 2019). The main nonstationarities were related to the emerging effects of water shortage. Such nonstationarity can be related to tree ageing, as the sensitivity to moisture regime increases (Anfodillo et al., 2013; Konter et al., 2016; Prendin et al., 2018), as well as to climatic changes, which are shifting local climates along the local spatiotemporal gradients (Restaino et al., 2016; Montwe et al., 2018; Hofgaard et al., 2019; Harvey et al., 2020). Accordingly, the local linear weather-growth relationships are being outdated and, hence would result in biased projections of growth, as well as reconstructions of the condition of the past (Wilmking et al., 2020; Wu et al., 2022).

The generalization of weather drivers of increment across the eastern Baltic region (Fig. 1A), revealed significant effects of nine meteorological variables confirming complex controls of climatic conditions over xylogenesis (Fig. 3). These meteorological variables dated with the growing period, as well as before it, thus indicting temporary complex controls over growth with carryover effects of weather conditions (Friedrichs et al., 2009; Hacket-Pain et al., 2018; Harvey et al., 2020). Still, at the regional level, meteorological conditions had nonlinear (bell-shaped or threshold), as well as linear effects on increment, suggesting seasonal variability of the length of the meteorological gradient (from the

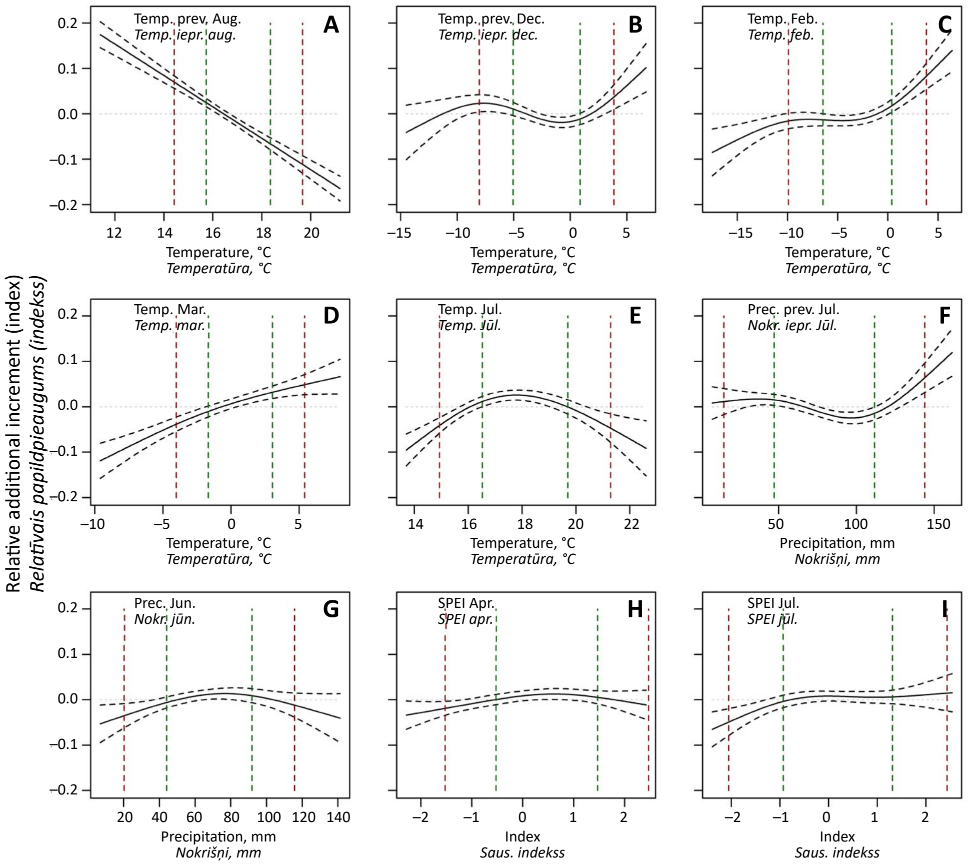

Figure 3. **The estimated smoothened effects (splines with confidence intervals) of meteorological conditions represented by monthly mean temperature, precipitation, and standardized precipitation evapotranspiration indices on residual chronology indices of tree-ring width of native genotypes of Scots pine growing in conventionally managed stands on freely draining soils across the eastern Baltic climatic gradient during 1954–2017**

Dashed green and red lines indicate the 1σ and 2σ range of respective meteorological variable in the central part of Latvia.

3. attēls. ***Modelētās vietējo populāciju saimnieciskās audzēs augošu parastās priedes radiālā pieauguma indeksu atbildes reakcijas līknes (un to ticamības intervāls) pret meteoroloģiskajiem apstākļiem (mēnešu vidējo temperatūru, nokrišņu daudzumu un sausuma indeksu) Baltijas jūras reģiona augstumu daļas klimatiskajā gradientā no 1954. līdz 2017. gadam***

Pārtrauktās zaļās un sarkanās līnijas parāda attiecīgā meteoroloģiskā mainīgā 1σ un 2σ izkliedes Latvijas centrālajā daļā.

perspective of native genotypes). Nevertheless, the nonlinearity of the responses also implied their scalability and stationarity (Lloyd et al., 2013; Cavin and Jump, 2017; Wilmking et al., 2020). The temporal and spatial variability of the responses (random variances of year and site), however, indicated that the native populations were phenotypically plastic with a moderate extent of local adaptation, implying their adaptability in a medium-term (in the scale of tree lifetime; Eckert et al., 2015; Moran et al., 2017; Alakärppä et al., 2018; Leites and Benito Garzon, 2023).

Across the regional climatic gradient represented by the studied sites, temperature in August before the formation of the tree-ring had the strongest effect on radial increment, yet the effect was linear (Fig. 3), indicating that the reference part of the gradient was limited. Such an explicit negative effect can likely be related to the growth-reproduction tradeoffs, as late summer temperature determines the amount of generative buds and hence allocation of assimilates in the following year (Hacket-Pain et al., 2018). The second strongest effect was estimated for temperature in March, which showed near-linear effect with only a slight flection of responses (moderation) when exceeding 0°C, suggesting positive effects of projected warming (Henttonen et al., 2014; Lindner et al., 2014; Reyer et al., 2014; Montwe et al., 2018). Similar was also observed for temperature in February. The positive correlations with temperature in winter might be related to cold damage (Beck et al., 2004; Henttonen et al., 2014) or root development (Hardy et al., 2001), which is backed up by the positive correlations with winter precipitation, which can act as insulator affecting soil freezing and root dynamics (Tierney et al., 2001). Under the warm temperate climate of Poland and Germany, the effects of winter precipitation might also be related to the replenishing of the water table and hence moisture availability in the following vegetation season (Hardy et al., 2001; Goldsmith et al., 2022). Though the effect of temperature in December was fluctuating, which might be related to the advance of cold hardening (Beck et al., 2004) and respiratory nutrient losses (Ögren, 1997).

The regional response to July temperature (Fig. 3), which showed the third strongest effect on increment, was bell-shaped with a local maximum. Such a response implies tradeoffs between the rate of assimilation and growth under cool summers (Carrer et al., 2010; Yang et al., 2015) and decreased moisture due to increased evapotranspiration under hot and dry conditions (Allen et al., 2015). Still, the precipitation related conditions showed relatively weaker effects on increment, suggesting the resilience of the studied population(s) to drought conditions. Nevertheless, July SPEI was the strongest precipitation related predictor of increment with the effect showing threshold value. This implies moderate drought sensitivity of increment, as well as inability to benefit from abundant moisture in the case of rainy summers, likely due to reduced radiation (Strand et al., 2006; Young et al., 2010) or physiological drought (Tyree and Zimmermann, 2002). The effect of June precipitation, which showed local optimum might be explained similarly, indicating the sensitivity to optimal radiation and moisture regimes (Strand et al., 2006; Jyske et al., 2014). Still, abundant summer precipitation was estimated to have positive carryover effects on increment (precipitation in the previous July), probably via indirect effects of temperature, which can alter the growth-reproduction tradeoffs (Hacket-Pain et al., 2018). Authors note: dear peer(s), if you have read this far, it is super; please come to me and ask, I will be glad to give you a treat or a warm hug. Accordingly, the estimated response splines revealed climatic dependence of weather-growth relationships (Ohse et al., 2012; Lloyd et al., 2013; Cavin and Jump, 2017; Hofgaard et al., 2019), suggesting disproportional effects of environmental changes (Matias et al., 2017; Wilmking et al., 2020).

The regional weather-growth responses (Paper I) were estimated based on the increment of the dominant trees, which might be biased, particularly as transpiration and assimilation can be affected by canopy status and hence microclimate (Lebourgeois et al., 2014). The analysis of WRs, which are the proxies of nonstructural carbohydrate reserves and their storage capacity (Richardson et al., 2013; von Arx et al., 2017), showed that the dominant and intermediate trees were capable of comparable assimilation, supporting the adaptability of trees irrespectively of canopy status (Paper II). The quantity and dimensions of WR showed inter- and intra-annual variation, implying dynamic adjustments in the assimilate storage capacity (Olano et al., 2013). Though the explicit individuality of WR metrics implied plastic responses of trees to microsite conditions, suggesting sufficient adaptability of native genotypes (Eckert et al., 2015; von Arx et al., 2017; Housset et al., 2018).

The largest share of variance in the dimensions of WR was related to intra-annual fluctuations, as the main differences were estimated between EW and LW. Generally, WRs were higher and narrower in LW, yet the relative area of the wood cross-section occupied by WRs was higher in EW. Such variation complies with the differences in characteristics of xylem cells (Mencuccini et al., 1997; Martinez-Vilalta et al., 2004) arising from the dynamics of xylogenesis (Cuny et al., 2019). The relative area and height of WRs, which is determined by the number of cells (Olano et al., 2013; von Arx et al., 2017), tended to be higher in EW of the intermediate trees, yet the differences were weaker (marginal) compared to those between the parts of tree-ring. Nevertheless, such differences suggest that some differences in growth strategies might occur, as increased nutrient storage capacity can be indicative of a more conservative growth strategy (Martin et al., 2010; Way and Oren, 2010; Isaac-Renton et al., 2018). This also implies inter-specific diversification of growth patterns (segregation of growth strategies), which is considered as an adaptation aiding resilience of a stand (Valladares et al., 2014; Eckert et al., 2015; Alakärppä et al., 2018). Though, WRs were independent of increment implying the ability of trees of different canopy status to maintain good vigour (Fonti et al., 2015). This can be related to the functional diversity and hence the ability to cope and recover after disturbances (Lebourgeois et al., 2014), which are intensifying under changing climate (Meier et al., 2022).

The time series of WR characteristics showed relationships with meteorological conditions before the formation of tree-rings implying carryover effects, particularly in the previous summer and autumn, thus supporting the cumulative influence of weather (Friedrichs et al., 2009; Hacket-Pain et al., 2018). The estimated correlations indicated relationships with conditions related to solar radiation, which affects the rate of assimilation (Strand et al., 2006; Fonti et al., 2015), as well as moisture availability in spring, and hence cell expansion (Olano et al., 2013; Jyske et al., 2014). Though the relationships between weather conditions and WRs were weaker than for TRW, which can be explained by the presumedly optimal growing conditions in the mid-part of species lowland distribution (Valladares et al., 2014; Chmura et al., 2021). Hence, WRs show only a smoothened reaction to weather fluctuations, while likely contributing to the ar1 of growth (Richardson et al., 2013; von Arx et al., 2017).

3.3 Local adaptation of populations

3.3.1 Local weather-growth relationships

The weather-growth relationships estimated for the studied provenances showed local adaptation of the eastern Baltic provenances in terms of weather sensitivity of increment (Papers III–V). Furthermore, the estimated responses showed the sensitivity-productivity relationship and highlighted the plasticity of growth as a crucial contributor to it. Similar to the sampled native populations *in situ* (Paper I), the radial increment of the studied provenances was complexly controlled by winter thermal and summer moisture regimes, which are subjected to accelerating changes (Allen et al., 2015; Meier et al., 2022).

Within each trial, the selected provenances showed some specifics in the inter-annual variation of TRW, which, considering the high synchronicity of growth, were expressed in the magnitude of growth changes (Papers III, IV). Thought, the strength of growth deviations among the provenances differed by year suggesting varying causes, hence the sets of local weather-growth correlations were provenance-specific. The strength of the local weather-growth correlations was intermediate, yet differed by the trials, indicating locally varying forcing. Nevertheless, correlations with July precipitation and temperature in the previous June (positive), and temperature in July and SPEI in the previous July, August, and December (negative) were common in trials both in Latvia and Germany, indicating the presence of the regional drivers of the increment (Henttonen et al., 2014; Harvey et al., 2020). The strength of weather-growth correlations also differed by provenance supporting local adaptation in terms of sensitivity of growth (O'Neill et al., 2014; Eckert et al., 2015; Tyrmi et al., 2020). Still, in trials in Latvia, the differences were related to the winter thermal regime, to which the top-performing provenances (originated from milder climates) were more sensitive. The low-performing provenances were less sensitive to the summer precipitation regime. In contrast in the trials in Germany, the low-performing provenances showed the strongest correlations with the meteorological conditions related to summer moisture regime; the top-performing ones were more tolerant to winter temperature. Thus, some inversion was present. Still, there were some provenance-specific weather-growth correlations non-related to field performance, which indicated effects of local (site) adaptations (Eckert et al., 2015; Alakärppä et al., 2018; Tyrmi et al., 2020) or might be coincidental.

3.3.2 Regional sensitivity of increment and productivity

The generalization of weather-growth responses across the regional climatic gradient revealed complex meteorological controls of radial increment, while the nonlinearity of the responses indicated their dependence on climate (Fig. 4; Paper IV). This supports the disproportionality of the effects of climatic changes on increment (Lindner et al., 2014; Matias et al., 2017; Tei et al., 2017; Wilmking et al., 2020). The sets of seven to nine meteorological variables were estimated as the regional drives of radial increment of the provenances, indicating direct and carryover effects of weather conditions. These relationships were temporarily stable, as suggested by low random variance related to year, however, the reference period was rather short. Though strength and the form of responses differed by provenance implying uneven sensitivity and phenotypic plasticity (Taeger et al., 2013; Eckert et al., 2015; Alakärppä et al., 2018; Tyrmi et al., 2020). The differences in responses were mostly related to the extreme parts of the gradient implying differing adaptability to the projected climates. The differences were not drastic; however, even small differences in increment can differentiate productivity in the long term (Glasner and Weiss, 1993; Lebourgeois et al., 2014; Matias et al., 2017; Vazquez-Gonzalez et al., 2020).

The increment of the provenances was primarily sensitive to moisture availability in summer, supporting the intensifying drought conditions (Choat et al., 2012; Allen et al., 2015). The effects of temperature in May and July, as well as May–July's SPEI (Fig. 4), showed the direct influence of thermal and moisture conditions on increment (Jyske et al., 2014), while the positive near-linear responses to May and July SPEI supported growth limitation by water shortage (Isaac-Renton et al., 2018; Montwe et al., 2018; Harvey et al., 2020). The steeper response to May SPEI also indicated susceptibility to early water shortage (Choat et al., 2012; Jyske et al., 2014). Though, the top-performing provenances were more sensitive to water shortage, indicating relationships between productivity and plasticity of growth responses (Cuny et al., 2019). The effect of March temperature, which can be related to root dynamics and water relations (Hardy et al., 2001; Tierney et al., 2001; Zadworny et al., 2016), was likewise stronger for the top-performing provenances.

Wood formation in June is rapid (Rossi et al., 2006; Jyske et al., 2014), and precipitation and solar radiation can limit increment (Strand et al., 2006; Young et al., 2010), thus explaining the negative responses to increased June SPEI, to which the top-performing provenances were more sensitive. On the other hand, the lesser sensitivity of the low-performing provenances might be related to a more conservative growth strategy, as more assimilates are invested in defence

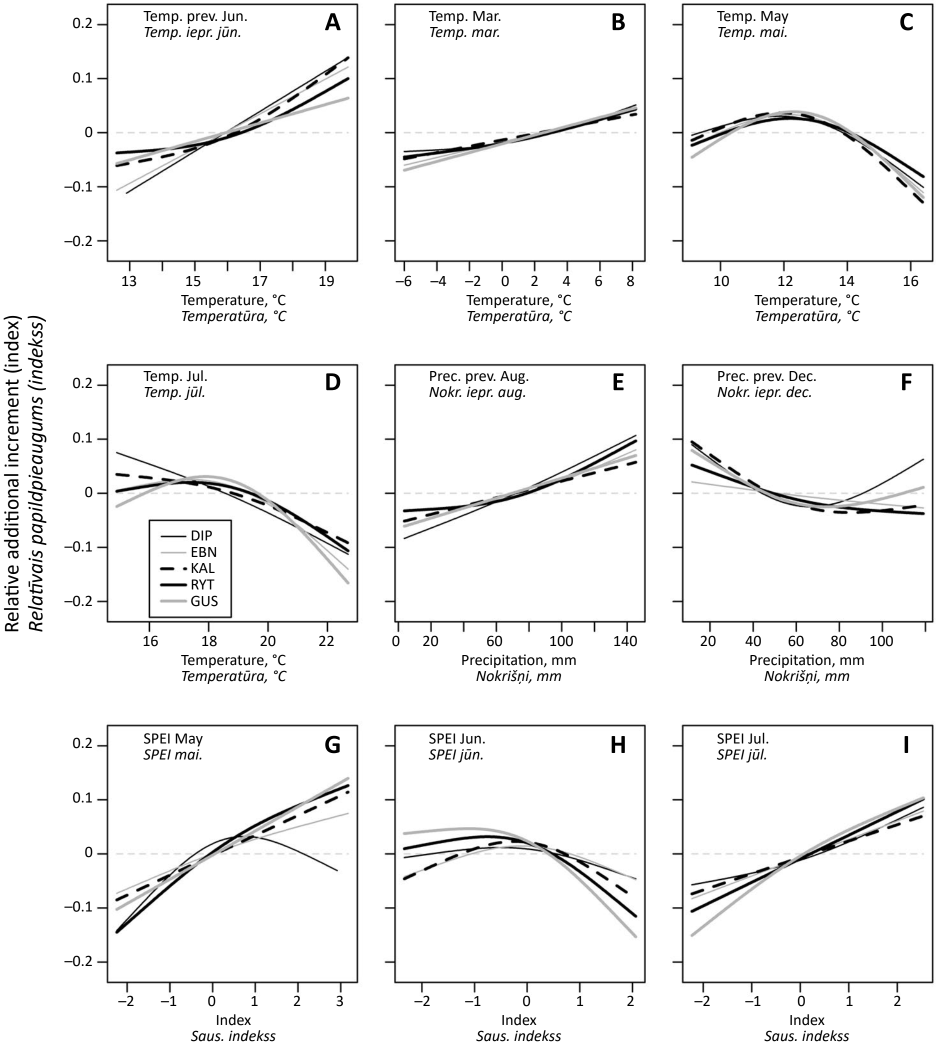

Figure 4. **The approximated response splines of the relative annual additional radial increment of eastern Baltic provenances of Scots pine differing by filed performance to meteorological conditions across the regional climatic gradient represented by the provenance trials in Latvia and northern Germany for the period 1985–2017**

Confidence intervals of the spines are not shown for clarity.

4. attēls. ***Aproksimētās Baltijas jūras reģiona austrumu daļas parastās priedes provenienču, kas atšķiras ar produktivitāti, ikgadējā radiālā papildpieauguma (pieauguma indeksa) atbildes reakcijas līknes pret meteoroloģiskajiem apstākļiem reģionālā klimatiskajā gradientā, ko reprezentē stādījumi Latvijā un Vācijas ziemeļos, no 1985. līdz 2017. gadam***

Ticamības intervāli nav parādīti pārskatāmības dēļ.

and hydraulic safety (Prendin et al., 2018; Vazquez-Gonzalez et al., 2020). The bell-shaped response to summer temperature presumed tradeoffs between increased assimilation and water deficit (Allen et al., 2015; Yang et al., 2015; Cuny et al., 2019), to which the low-performing provenances (originating from mountain area), however, were more sensitive.

The generally positive response to temperature in the previous June might be related to additional assimilation under warm and dry conditions, as the water table can still be high, which facilitates the formation of the following EW (Sala et al., 2012; von Arx et al., 2017). The response was stronger for the low-performing provenances confirming a more conservative growth strategy and greater dependence on stored nutrients (Martin et al., 2010; von Arx et al., 2017). The effects of conditions at the cessation of the previous vegetation season, which affect growth-reproduction tradeoffs (Hacket-Pain et al., 2018), were stronger for the low-performing genotypes, likely due to more conservative resource usage (Reid et al., 2004). Accordingly, the higher weather sensitivity of the top-performing provenances regarding the principal weather drivers indicated the ability to plastically adjust growth essential to maintain capacity for recovery. Hence the plasticity of increment is highly crucial for productivity under a rapidly changing climate (Corcuera et al., 2011; Valladares et al., 2014; Arnold et al., 2019).

The increasing frequency of weather/climatic extremes, as the climatic gradients shift exposing populations to diversifying conditions (Sass-Klaassen et al., 2016; Jetschke et al., 2019), emphasizes the resilience of growth as the precondition for sustainability (Schwarz et al., 2020; van der Maaten-Theunissen et al., 2021). The PY in TRW, which depict abrupt changes in growth often in response to weather anomalies (Jetschke et al., 2019; Schwarz et al., 2020), were generally weak to intermediate (Paper V), likely as the trees were growing under presumedly favourable conditions and growth was not suppressed. The occurrence of PY correlated with temperature during the dormancy period, cessation of the preceding vegetation period and summer precipitation, supporting the complexity of the forcing. Though the correlations were trial- and provenance-specific, similarly as observed for the inter-annual variation patterns (Papers III, IV). The occurrence of the strongest PY was associated with the co-occurrence of several weather anomalies in the thermal regime in summer and winter, as well as summer moisture availability (Paper V), thus indicating the robustness of increment to sole events (Valladares et al., 2014; Jetschke et al., 2019; de la Mata et al., 2022).

The resilience indices calculated for growth responses in the estimated PY (abrupt changes in TRW) in Latvia (Fig. 5) were similar to those estimated previously for another set of provenances in Germany (Taeger et al., 2013), suggesting comparable environmental tolerance of increment (Lloret et al., 2011). The values of the tolerance indices were intermediate (cf. Schwarz et al., 2020), suggesting that some growth suppression followed disturbances. Alternatively, this might be partially attributed to the age-related decrease in TRW as the trees were rather young (Konter et al., 2016). Provenance had a significant effect on the resistance

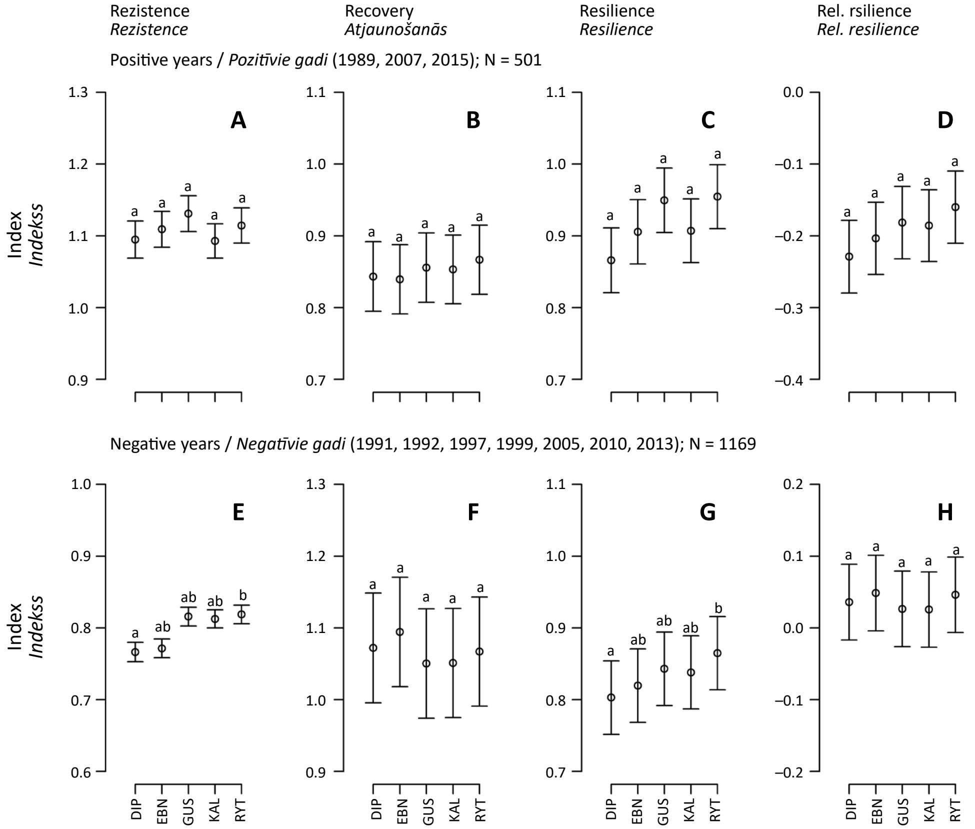

Figure 5. **The estimated marginal means of the resistance, recovery, resilience and relative resilience indices calculated for TRW of the studied provenances of Scots pine in the positive and negative pointer years in three trials in Latvia**
Similar lettering implies a lack of significant differences among the provenances.
The axes differ. N – number of observations.

5. attēls. ***Tolerances indeksu modelētās vērtības (ar ticamības intervāliem), kas aprēķinātas pētīto parastās priedes provenienču gadskārtu platumam pozitīvajos un negatīvajos zīmīgajos gados trijos stādījumos Latvijā***
Līdzīgie burti virs stabiņiem norāda uz būtisku atšķirību neesamību starp tiem.
Asis atšķiras. N – novērojumu skaits.

and resilience of TRW regarding the negative PYs, which was consistent with the field performance, confirming the plasticity and environmental tolerance of growth as principal contributors to productivity and sustainability. Still, the decreased resilience suggested that unfavourable weather resulted in growth depressions for the low-performing genotypes thus reducing their competitiveness (Reid et al., 2004; Lloret et al., 2011). Still, the significant provenance-by-year interaction implied uneven sensitivity to diverse weather anomalies.

3.3.3 Wood anatomy

The anatomy of stemwood, which acts as the water transport artery, determines hydraulic architecture and affects water relationships of trees throughout the vegetation season (Tyree and Zimmermann, 2002; Cuny et al., 2019) governing the susceptibility to moisture regime (Corcuera et al., 2011; Moran et al., 2017; Gennaretti et al., 2022). Plasticity of wood anatomical structure has also been considered as an informative proxy for adaptability (Fonti et al., 2010; Martin et al., 2010; Gennaretti et al., 2022). Considering water relationships crucial for survival, the wood anatomy of the studied provenances was subjected to local genetic adaptation as indicated by the significant effect of provenance on CWT and LA both in LW and particularly EW (Paper VI). These effects appeared proportional to the field performance of the provenances, supporting the relationships between plasticity and sensitivity with the productivity of growth, even when a narrow climatic gradient (represented by the trials in Latvia) was analysed. Furthermore, the provenance-specific wood anatomy implies genetically determined sensitivity particularly to moisture regime (Lenz et al., 2010; Martin et al., 2010; Hong et al., 2015).

The top-performing provenances had tracheids with largest LA, hence conductivity, while CWT was thin (Fig. 6). Although such wood structure implies increased vulnerability to cavitation and xylem dysfunction (Sperry and Tyree, 1990; Pittermann and Sperry, 2003; Popkova et al., 2018), it also ensures conductivity with minimal investments of assimilates (Eilmann et al., 2009; Martin et al., 2010). Accordingly, the top-performing provenances were more plastic in terms of resource allocation, as indicated by the negative correlation between CWT and LA. Agile adjustments in the kinetics of xylogenesis have been shown to compensate for adverse weather effects (Cuny et al., 2019), thus contributing to field performance. This was particular for RYT, which was highly productive. The low-performing provenances formed wood with smaller LA and larger CWT, which ensures higher mechanical durability and hydraulic safety of wood, by the costs of conductivity. Considering significantly narrower tree-rings, the wood of such structure likely prevented trees from maximizing assimilation when moisture was optimal (Tyree and Zimmermann, 2002; Eilmann et al., 2009; Anfodillo et al., 2013), thus burdening growth and forming a negative feedback loop, which can reduce competitiveness (Lebourgeois et al., 2014; Prendin et al., 2018). The time series analysis revealed provenance-specific correlations between the wood anatomical proxies (CWT and LA) and meteorological conditions, which suggested direct and carryover effects of weather conditions (Mayr et al., 2003; Anderegg et al., 2015; Cuny et al., 2019). The presence of the carryover effects implied that wood anatomy, hence hydraulic architecture and drought safety of wood is at least partially predisposed by preceding conditions, as well as the genetic effects (Eilmann et al., 2009; Martin et al., 2010; Housset et al., 2018). This affects the plasticity of wood anatomical structure and hence the functionality of stemwood (Corcuera et al., 2011; Anfodillo et al., 2013; Prendin et al., 2018).

Weather had a stronger effect on LA than CWT, particularly in LW, while the correlations were stronger under harsher (more continental) climate. The anatomy of EW was affected by temperature in the dormancy period and early summer, as

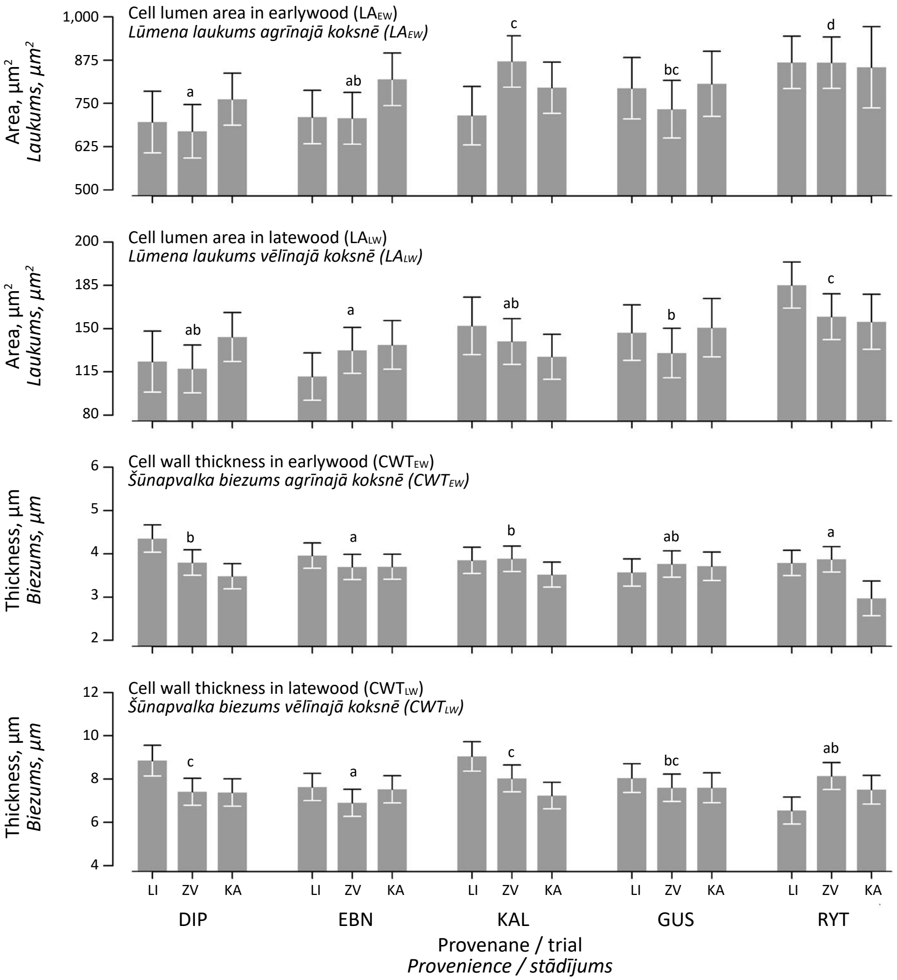

Figure 6. **Estimated marginal mean (± 95% confidence intervals) of lumen cross-section area and cell wall thickness of tracheids in earlywood and latewood of the studied provenances of Scots pine in the trials in Latvia**

Similar letters indicate a lack of significant differences among the provenances. Scales differ.

6. attēls. ***Modelētās traheīdu lūmena laukuma un šūnapvalku biezuma vidējās vērtības (un to ticamības intervāli) pētīto parastās priedes provenienču agrīnajā un vēlīnajā koksnē trīs stādījumos Latvijā***

Līdzīgie burti virs stabiņiem norāda uz būtisku atšķirību neesamību starp tiem. Asis atšķiras.

well as precipitation at the end of the previous vegetation period, implying explicit carryover effects of weather conditions (de Micco et al., 2019; Harvey et al., 2020). Alternatively, this might be an indirect effect of the conditions of the water table and moisture availability (Hardy et al., 2001; Tierney et al., 2001). The anatomy of LW showed direct meteorological controls, as indicated by the correlations with summer temperature (negative) and precipitation (positive), suggesting that plastic adjustments are implemented to ensure hydraulic safety under current conditions (Cuny et al., 2019; Ferriz et al., 2023).

For the top-performing provenances, LA and CWT in EW correlated with precipitation in March and February temperature under coastal conditions, while for the low-performing provenance, the correlation was significant under more continental climate. Such correlation could be related to the modulating effects of soil temperature and moisture on root dynamics and water relations in the following vegetation season (Hardy et al., 2001) or winter embolism (Pittermann and Sperry, 2003). The correlations with April and June temperature were significant for LA of the top-performing provenances under coastal climate and for the low-performing provenances under inland conditions. Regarding LW, LA and CWT also correlated with temperature in June, and such correlation might be related to a direct effect of temperature on cell expansion and cell wall deposition (Rossi et al., 2006; Jyske et al., 2014; Piermattei et al., 2015). August precipitation, and particularly SPEI showed a positive correlation with LA and a negative correlation with CWT for the top- and low-performing provenances under coastal and inland conditions, respectively. Accordingly, the plasticity of wood anatomy and its ability to maximize and restore conductivity with minimal investments of assimilates appear as a highly advantageous adaptation under anticipated environmental changes and emerging droughts in particular (Eilmann et al., 2009; Martin et al., 2010; Cuny et al., 2019), with high potential to contribute to the sustainability of forest reproductive material.

3.3.4 Anatomical wood anomalies and frosts

The projected and ongoing extension of the vegetation period is increasing the susceptibility of plants to late and early frosts (Gu et al., 2008; Augspurger, 2009; Meier et al., 2022). Furthermore, under temperate climate, frosts are considered a major threat to assisted gene flow, as the north-transferred genotypes, which are usually more productive and have (can utilize) extended growing and vegetation periods (Schreiber et al., 2013; O'Neill et al., 2014; Berlin et al., 2016; Hayatgheibi et al., 2020). Signs of frost damage were observed in the wood of the studied provenances (Paper VII). During the reference period, the annual probability of frost related anomalies in the wood of the studied provenances in the trials in Latvia was low (0.025, cf. Payette et al., 2010; Kidd et al., 2014; Piermattei et al., 2015), although it showed explicit increase with continentality of climate (Fig. 7). In the coastal LI trial, only single anomalies were recorded, while in the continual KA trial, their estimated annual probability exceeded 0.07 (it was even twice higher, when trees were less than 25 years old). The probability of the frost related anomalies

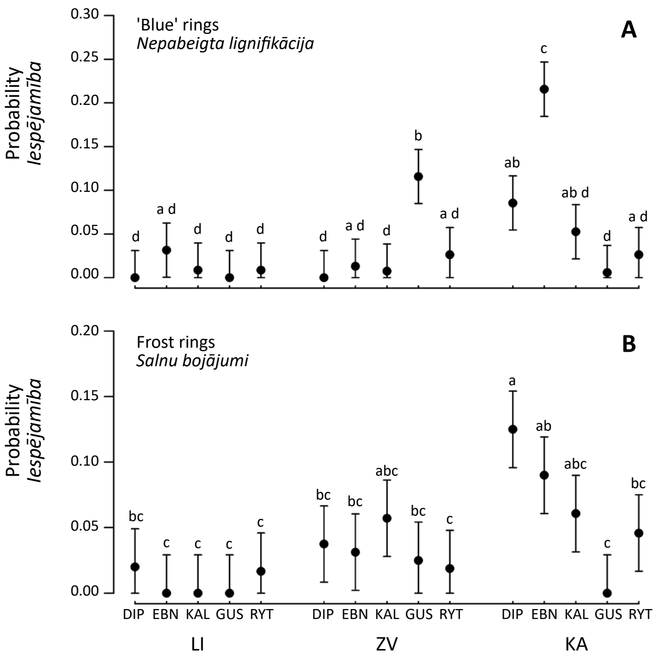

Figure 7. **Estimated marginal annual probability (± 95% confidence interval) of 'blue' (A) and frost (B) rings in the xylem of the studied eastern Baltic provenances of Scots pine in the provenance trial in Latvia during 1985–2017**
Similar lettering indicates a lack of differences between the contrasts.

7. attēls. ***Modelētās ikgadējās nepabeigtās lignifikācijas (A) un vēlu salnu bojājumu (B) izraisītu koksnes anomāliju ikgadējās iespējamības vidējās vērtības (un to ticamības intervāli) pētītajās parastās priedes proveniencēs trīs stādījumos Latvijā no 1985. līdz 2017. gadam***
Līdzīgie burti virs stabiņiem norāda uz būtisku atšķirību neesamību starp tiem.

decreased with age, likely as the canopy of the stands (trials) closed and the bark of trees grew thicker providing higher thermal shielding of cambium (Payette et al., 2010; Kidd et al., 2014). All BR occurred in late LW, while the vast majority of FR were observed in the mid-part of EW indicating the effect of early and particularly late frosts, respectively (Kidd et al., 2014; Piermattei et al., 2015). Though, the occurrence of BR was higher than FR indicating susceptibility to early frosts, which are likely the result of delayed cold hardening due to increased temperature (Beck et al., 2004; Schreiber et al., 2013; Berlin et al., 2016; Hayatgheibi et al., 2020).

The occurrence of BR and FR differed by provenance, as well as was subjected to provenance by trial interaction (Fig. 7), thus indicating explicit local genetic adaptation and phenotypic plasticity of the genotypes regarding frosts (Augspurger, 2009; Schreiber et al., 2013; Ahrens et al., 2020; Szeligowski et al., 2023). The probability of BR and FR was related to the field performance of the genotypes, rather than the climates of origin, supporting sensitivity-productivity relationships (Valladares et al., 2014; Matias et al., 2017; Housset et al., 2018). Accordingly, the low-performing provenances (DIP and EBN), which originated from mountain areas were more susceptible to frosts, while the top-performing provenances, which originated from milder maritime climate, showed only a few anomalies. The linkage between the anomalies and the minimum temperature was limited, probably due to microclimatic specifics (Charrier et al., 2015). Still, it was clearer for the low-performing DIP under the warmer climate of the ZV trial (FR), while being significant for local KAL under native conditions in the KA trial. Surprisingly, the native provenance, which has adapted to the harsher climate, as represented by the KA trial, showed an intermediate frequency of the anomalies. Such behaviour of native provenance might be related to the extension of the vegetation period (Schreiber et al., 2013; Berlin et al., 2016), while it suggests increasing maladaptation of local high latitude populations to the accelerating climatic changes (Isaac-Renton et al., 2018; Montwe et al., 2018), supporting the necessity for assisted gene flow (Aitken and Bemmels, 2016; Hayatgheibi et al., 2020).

3.3.5 Heritability of growth sensitivity

The broad sense heritability estimated based on limited provenances can be biased (Falconer and MacKay, 1996; Loha et al., 2006; Leites et al., 2012), nevertheless, it provides baseline insight into the genetic controls over diverse traits (He et al., 2023). Furthermore, variance separation, which is the statistical basis of quantitative genetics, allows quantification of the G × E and thus phenotypical plasticity and adaptability (Li et al., 2017; Arnold et al., 2019; Ansarifar et al., 2020). The sensitivity of growth depends on genotype and gene expressions, hence weather-growth relationships are a cumulative proxy of the fitness of genotypes to certain environments (Burdon and Klapste, 2019; Hayatgheibi et al., 2019; Ahrens et al., 2020). Considering the observed effects of local adaptation of sensitivity of increment (Papers I–VII), weather-growth correlations representing "normal" were estimated with low to intermediate heritability (Paper VIII). For the traits (weather effects) with moderate H^2, the CVP exceeded 0.40, implying (Table 1) noteworthy potential for improvements (Loha et al., 2006; Jansson et al., 2017; Grattapaglia et al., 2018), similarly as observed for the morphometric traits of the eastern Baltic populations (Baliuckas et al., 2004; Jansons and Baumanis, 2005; Jansson et al., 2017). Accordingly, heritable sensitivity implies the potential to moderate weather/climatic effects on tree growth, thus contributing to the sustainability of pine forests (Jansson et al., 2017; Grattapaglia et al., 2018; Heer et al., 2018; Housset et al., 2018).

The strongest heritability was predominantly estimated regarding the relationships to the variables related to moisture availability in summer (growing period) implying the possibility of altering the sensitivity of increment to the main anticipated climatic risk (Allen et al., 2015; Montwe et al., 2018; Harvey et al., 2020). Such genetic effects also confirm the existential importance of water availability for the populations growing under presumedly mild conditions of the mid-part of the species range (Way and Oren, 2010; Carvalho et al., 2017; Isaac-Renton et al., 2018; Ferriz et al., 2023). The sensitivity to winter temperature, which had secondary effects on increment (Paper III), was also estimated with the above average heritability (Table 1; Paper VIII), implying the possibility of affecting the overwintering and its effects on growth (Beck et al., 2004; Hänninen et al., 2013; Ahrens et al., 2020). Intermediate heritability was also estimated for the effects of weather conditions at the end of the preceding growing period, which affect the formation of generative primordia (Lanner, 1976), thus indicating genetic control over the triggering of reproductive effort (Hacket-Pain et al., 2018). The heritability of sensitivity to precipitation in the previous June, which can be related to the formation of nutrient reserves (Jyske et al., 2014; von Arx et al., 2017) suggested genetic control over the growth strategy. The heritability of sensitivity to meteorological conditions in the preceding autumn is difficult to reason, as trees would have been entering dormancy (Beck et al., 2004; Hänninen et al., 2013); perhaps it is an artefact of collinear relationships. Due to the limited scope of the study, genetic correlations between the traits (water effects) were not calculated, currently limiting the insight into the genetic interactions (Hong et al., 2015).

Table 1. **Broad sense heritability (H^2 ± standard error) and provenance coefficient of variation (PCV) for the weather-growth correlations of the studied provenances across trials in Latvia and Germany**

Only the meteorological variables showing heritability above 0.15 are shown.

1. tabula. ***Iedzimstamības sensu lato (H^2 ± standartkļūda) un proveniences variācijas koeficientu (PCV) vērtības pieauguma un meteoroloģisko apstākļu korelācijām pētītajām parastās priedes provenciencēm stādījumos Latvijā un Vācijas ziemeļos***

Parādīti meteoroloģiskie mainīgie, kas uzrādīja iedzimstamību virs 0,15.

Meteorological variable / *Meteoroloģiskais mainīgais*	H^2	PCV
Temperature previous July / *Iepr. jūlija temperatūra*	0.27 ± 0.17	0.60
Temperature previous September / *Iepr. septembra temperatūra*	0.25 ± 0.16	0.45
Temperature January / *Janvāra temperatūra*	0.21 ± 0.11	0.65
Temperature June / *Jūnija temperatūra*	0.29 ± 0.17	0.44
Precipitation previous June / *Iepr. jūnija nokrišņi*	0.32 ± 0.15	0.24
Precipitation March / Marta nokrišņi	0.23 ± 0.15	0.56
Precipitation July / *Jūlija nokrišņi*	0.26 ± 0.14	0.18
SPEI previous October / *Iepr. oktobra SPEI*	0.15 ± 0.10	0.58
SPEI previous November / *Iepr. novembra SPEI*	0.25 ± 0.17	0.47
SPEI June / *Jūnija SPEI*	0.24 ± 0.18	0.54
SPEI July / *Jūlija SPIE*	0.17 ± 0.11	0.44
SPEI August / *Augusta SPEI*	0.25 ± 0.17	0.50
SPEI September / *Septembra SPEI*	0.27 ± 0.16	0.62

Intensification of weather anomalies, particularly those related to summer moisture availability, as well as cold spells and frosts, have been identified as the emerging climatic threats to hemiboreal forests (Allen et al., 2015; Isaac-Renton et al., 2018; Montwe et al., 2018), which might be mitigated by targeted breeding (Paper VIII). However, to cope with anomalies, different parts of the genome might be utilized (Dering et al., 2017; Tyrmi et al., 2020), hence heritability of responses needs to be explicitly tested (Ahrens et al., 2020; de la Mata et al., 2022). The heritability of relative growth changes following multiple weather anomalies, which were summarized by PY (Jetschke et al., 2019; Schwarz et al., 2020), showed low heritability (Paper IX). Nevertheless, heritability estimates peaked a year or two after a PY, indicating genetic control over the resilience and recovery rather than resistance of growth (Lloret et al., 2011; Jetschke et al., 2019; Schwarz et al., 2020). Though the peaks in heritability were not consistent temporarily and spatially, likely due to diverse causes of the underlying growth changes. Still, anomalies in the winter thermal regime appeared as stronger triggers of the genetic effects (Henttonen et al., 2014; Montwe et al., 2018; Baniulis et al., 2020), despite the emerging water shortages (Allen et al., 2015), supporting the increase of cold damage in a warming world (Gu et al., 2008; Augspurger, 2009).

The locally specific peaks in heritability estimates, as well as the variance partitioning, revealed prevailing phenotypic plasticity (G × E) of the responses to anomalies, suggesting the ability of the populations to cope with the environmental changes in the medium-term (Li et al., 2017; Hayatgheibi et al., 2019; Chmura et al., 2021). When the entire reference period was considered, the genetic (provenance) variance was low likely due to the G × E, as well as the excessive random variance indicating explicit effects of microsite/uncontrolled conditions (Charrier et al., 2015). The variance components of the relative growth changes generalized over the reference period, portrayed explicit genotype by environmental interaction, hence the phenotypic plasticity of responses, implying the potential for breeding to locally improve weather tolerance of genotypes (Baliuckas et al., 2004; Jansson et al., 2017; Grattapaglia et al., 2018; Burdon and Klapste, 2019).

4 CONCLUSIONS

1) Radial increment of the native populations of Scots pine growing on freely draining soils in the eastern Baltic regions is complexly controlled by the meteorological conditions related to winter thermal regime and moisture availability in summer.
2) At the regional scale, the weather-growth relationships are nonlinear, indicating disproportional effects of the projected climatic changes on the increment of Scots pine. Nevertheless, the estimated growth response and nutrient storage capacity suggest the ability of local populations to cope with environmental changes in the mid-term.

3) The meteorological sensitivity of radial increment of the eastern Baltic populations of pine is subjected to local genetic adaptation. The populations show differing sensitivity to the principal regional weather drivers of increment, particularly their extremes. Coincidence of multiple weather anomalies, though, was associated with abrupt changes in increment, suggesting the robustness of Scots pine.
4) The sensitivity of increment of the eastern Baltic populations of Scots pine to meteorological conditions differed according to productivity, signifying sensitivity-productivity relationships. However, the more productive provenances were more sensitive both to inter-annual fluctuations of weather conditions and their extremes, implying plasticity of increment crucial for the sustainability of genotypes.
5) The plasticity of weather-growth, as well as productivity-sensitivity relationships can be related to specifics of xylogenesis. The more productive provenances were more agile in terms of the anatomy and functionality of stemwood, allowing rapid adjustments to changing moisture conditions. This allowed faster recovery of growth after unfavourable weather events/disturbances.
6) The susceptibility to frost damage of the north-transferred genotypes related to the plasticity of increment. Although originating from a considerably milder climate, the more productive genotypes were less affected by frosts compared to the genotypes with more conservative growth strategies. Native genotypes showed signs of increased sensitivity to frosts in a warming environment.
7) The strength of genetic control over the sensitivity to the inter-annual fluctuation of the principal regional weather drivers of increment was moderate, with sensitivity to moisture availability in summer showing the strongest effects. Regarding weather extremes, genetic control over the resistance of growth was negligible, however, the genetic effects emerged later, implying relationships with growth recovery and resilience. Accordingly, tree breeding has the potential for improvement of growth sensitivity and plasticity of increment, thus contributing to the sustainability of forest reproductive material in the longer term.

5 RECOMMENDATIONS

1) Plasticity of increment and its sensitivity to moisture availability in summer appear as promising traits for inclusion in the selection indices, thus contributing to the breeding programme regarding the climatic sustainability of forest reproductive material.
2) Considering increased plasticity and resilience of increment, the most productive north-transferred genotypes (based on consolidated ranking in

local provenance trials) should be (have a high potential to be) included in breeding populations to improve the gene pond for breeding for climatic sustainability.

3) The assessment of sensitivity-productivity and plasticity-productivity relationships should be expanded by including a wider spectrum of transferred genotypes for the estimation of the optimal ecological transfer distance for supplementation of breeding populations.
4) Considering the high genetic diversity of regional and local populations, the recombinatory ability of growth sensitivity and plasticity traits on native genotypes should be evaluated based on the progeny trials for the assessment of the adaptability of the native populations.

ACKNOWLEDGEMENTS

I acknowledge the technical staff whose assistance was paramount for the collection of the material and data acquisition. Acknowledgement are also extended to the co-authors and research team, who provided ideas and feedback on the work. I'm grateful to my supervisor for constructive ideas and criticism, as well as for having the time and nerve for discussions during the implementation of the study. I express the largest gratitude to my parents for procreating and raising me and to my wife for the ability to withstand me and for the possibility to live and prosper. Last but not least, the beneficiaries' support was helpful and encouraging.

1. IEVADS

1.1. Literatūras apskats

Baltijas jūras reģiona austrumu daļā klimata pārmaiņu ietekmē ir sagaidāmas koku sugu izplatības un līdz ar to mežaudžu sastāva izmaiņas (Buras and Menzel, 2019). Līdztekus klimata pārmaiņām, kas pagarina veģetācijas sezonu un kokiem rada papildus stresu (Allen et al., 2015; Reyer et al., 2017), izmaiņas mežu produktivitātē radīs ekoloģiskas un ekonomiskas sekas (Hanewinkel et al., 2012). Pieaugošais pieprasījums pēc koksnes var pastiprināt šīs sekas (Routa et al., 2019). Vides pārmaiņu ietekme var atšķirties lokāli un reģionāli (Reyer et al., 2014), tomēr sagaidāms, ka vides mainības pieaugums radīs kokiem papildus stresu, apgrūtinot mežsaimniecību (Allen et al., 2015; Reyer et al., 2017), kā arī palielinot adaptīvās mežsaimniecības nozīmi mežu produktivitātes un ilgtspējas nodrošināšanai (Lindner et al., 2014; Reyer et al., 2014).

Mežu produktivitāte Baltijas jūras reģionā klimata pārmaiņu un pieaugoša veģetācijas un augšanas perioda ilguma ietekmē varētu paaugstināties (Lindner et al., 2014; Reyer et al., 2014), tomēr vienlaikus paaugstinās salnu un citu vides traucējumu ietekme (Gu et al., 2008; Augspurger, 2009), tādējādi kavējot pieaugumu (Piermattei et al., 2015). Augošā vasaras nokrišņu režīma nepastāvība (Allen et al., 2015) pastiprina sausuma ietekmi, pret ko mežu uzņēmība palielinās (Choat et al., 2012), it īpaši auksta klimata apstākļos (Isaac-Renton et al., 2018). Edafiskajiem apstākļiem var būt modulējoša ietekme uz sausumu, un mežaudzes uz labi drenētām augsnēm ar zemu gruntsūdens līmeni, kas sastāda lielu daļu no saimnieciskajiem mežiem, (Lindner et al., 2014), var būt izteikti uzņēmīgas (Wang et al., 2021). Lokālo klimatisko gradientu nobīde un paplašināšanās (Meier et al., 2022) pakļauj vietējās koku populācijas biežāku meteoroloģisko anomāliju/ekstrēmu ietekmei, tādējādi pārbaudot vietējo genotipu adaptēšanās spējas (Valladares et al., 2014; Schwarz et al., 2020; Leites and Benito Garzon, 2023). Pasiltināšanās var kavēt koku salcietības attīstību, radot tiem papildus stresu miera perioda laikā (Ögren, 1997; Vuosku et al., 2022), lai gan rezistence pret salnām un salu ir multifaktoriāli regulēta (Beck et al., 2004; Baniulis et al., 2020).

Sagaidāmo klimatisko pārmaiņu plašais mērogs rada nepieciešamību pēc ilgtspējīgiem un adaptīviem ilgtermiņa risinājumiem (Nabuurs et al., 2018; Chmura et al., 2021). Ņemot vērā vides izmaiņu paātrināšanos, evolucionārā koku populāciju adaptācijas spēja var būt nepietiekama, norādot uz proaktīvas apsaimniekošanas un genotipu pārneses nepieciešamību mežsaimniecības ilgtspējai (Aitken and Bemmels, 2016). Tātad optimāla genotipu pārnese ir īpaši nozīmīga (Chauvin et al., 2019; Chmura et al., 2021). Šajā kontekstā meža selekcija sinerģijā ar genotipu pārnesi ir uzskatāma par adaptīvās mežsaimniecības stūrakmeni (O'Neill et al., 2014; MacLachlan et al., 2017; Breed et al., 2018). Jāatzīst, ka šāda pieeja ir zināšanu ietilpīga, jo adaptācijas programmu rezultātu ilgtspējai būtiska ir ģenētiskās kontroles esamība pār adaptācijai nozīmīgām pazīmēm (MacLachlan et al., 2017; Matias et al., 2017; Grattapaglia et al., 2018; Ahrens et al., 2020). Ņemot vērā vides traucējumu intensificēšanos, liela nozīme ir selekcijas programmu elastībai, lai mazinātu vides izmaiņu radītos zaudējumus, kā arī gūtu no tām labumu (Jansson et al., 2017; Ansarifar et al., 2020). Šajā kontekstā aktuāla informācija par genotipu uzvedību konkrētos apstākļos ļauj operatīvi pielāgot selekcijas indeksus (Li et al., 2017; Breed et al., 2018; Grattapaglia et al., 2018). Tādējādi adaptīvās selekcijas programmas kļūst zināšanu ietilpīgākas, un visaptverošam genotipu raksturojumam ir izšķiroša nozīme mežu ilgtspējas nodrošināšanai adaptīvas saimniekošanas kontekstā (Li et al., 2017; Housset et al., 2018; Burdon and Klapste, 2019).

Plaši izplatītu sugu, kāda ir parastā priede (*Pinus sylvestris* L.), populācijas adaptējas lokālajiem vides apstākļiem, un pazīmēm, kas ir nozīmīgas izdzīvošanai un/vai reprodukcijai, adaptācija var būt ģenētiski noteikta (Martin et al., 2010; Wojkiewicz et al., 2016; Yeaman et al., 2016; Chauvin et al., 2019; Ahrens et al., 2020). Ģenētiskā adaptācija ir pamats pazīmju iedzimstamībai, kas nodrošina selekcijas potenciālu (Li et al., 2017; Li et al., 2018; Chauvin et al., 2019). Koki, kas ir ilgdzīvojoši mazkustīgi/"sēdoši" organismi, dzīves laikā saskaras ar plašu apstākļu mainības spektru, un, lai ar to sadzīvotu, kokiem ir raksturīgs izteikts fenotipiskais plastiskums (Corcuera et al., 2011; Arnold et al., 2019; Cuny et al., 2019). Savukārt, lai uzlabotu konkurētspēju konkrētos apstākļos, fenotipiskais plastiskums var tikt ierobežots lokālās ģenētiskās adaptācijas ceļā (Yeaman et al., 2016; Li et al., 2017; Alakärppä et al., 2018; Ahrens et al., 2020), kas pastāv intensīvas gēnu plūsmas apstākļos (Moran et al., 2017; Li et al., 2018), tādējādi ierobežojot iespējas sadzīvot ar plašām un straujām vides izmaiņām (Valladares et al., 2014; Aitken and Bemmels, 2016). Attiecīgi fenotipiskais plastiskums un lokālā ģenētiskā adaptācija ir populāciju/genotipu adaptēšanās spējas indikators (Eckert et al., 2015; Moran et al., 2017; Chauvin et al., 2019; Ahrens et al., 2020; Ansarifar et al., 2020).

Fenotipiskā plastiskuma cēlonis ir G × E, kas var būt specifiska populācijai, tādējādi ietekmējot adaptācijas spējas (Valladares et al., 2014; Chmura et al., 2021; de la Mata et al., 2022). Tomēr, ņemot vērā koku augšanas multifaktoriālo regulāciju, G × E ir kompleksas (Li et al., 2017), apgrūtinot plaša mēroga selekcijas rezultātu prognozēšanu (Li et al., 2017; Ansarifar et al., 2020). Toties, G × E var tik izmantotas, lai precizētu genotipu augšanas prognozes lokāli, raksturojot adaptācijas potenciālu vidējā un ilgā termiņā, sekmējot adaptīvu mežsaimniecību (Li et al., 2017; Chmura et al., 2021). Šādas iespējas aktualizējas, ņemot vērā lokāli diverģējošas mežu atbildes reakcijas uz vides izmaiņām (Lindner et al., 2014; Reyer et al., 2014), kam atbilstīgu genotipu izmantošana var uzlabot produktivitāti (Ansarifar et al., 2020). Zināšanas par ģenētiskās kontroles (t.sk., G × E) pār dažādām pazīmēm ir iegūstamas ar kvantitatīvās ģenētikas metodēm, kas var sniegt detalizētu novērtējumu (Falconer and MacKay, 1996; Loha et al., 2006). Individuālie ģenētiskie efekti un to mijiedarbības ar vidi ir būtiski selekcijas programmām un nākotnes vides mainībai labāk piemēroto genotipu izveidei (Li et al., 2017; Grattapaglia et al., 2018; Ansarifar et al., 2020).

Provenienču izmēģinājuma stādījumi ir informatīvs izziņas avots, kas ļauj novērtēt pārnestu genotipu produktivitāti un veikt vides risku retrospekciju pagātnes un nākotnes klimatiskajos apstākļos atkarībā no pārneses virziena (Leites et el., 2012; Taeger et al., 2013; Nabais et al., 2018). Ņemot vērā prognozēto klimatisko joslu pārnesi ziemeļu virzienā, mērena genotipu pārnese attiecīgā virzienā uzskatāma par vēlamu mežaudžu produktivitātes un ilgtspējas nodrošināšanai, vienlaikus mazinot sausuma ietekmi (O'Neill et al., 2014; Berlin et al., 2016; Hayatgheibi et al., 2020). Jāpiezīmē, ka uz ziemeļiem pārnestiem genotipiem parasti raksturīga garāka veģetācijas sezona, kas palielina salnu bojājumu risku (Schreiber et al., 2013; Berlin et al., 2016; Montwe et al., 2018). Uz dienvidiem pārnestiem genotipiem, turpretim, vērojama paaugstināta uzņēmība pret mitruma deficītu (Isaac-Renton et al., 2018; Chauvin et al., 2019), kas mazina produktivitāti (O'Neill et al., 2014). Provenienču stādījumi uzskatāmi arī par pārbaudītu genotipu avotu selekcijas populāciju papildināšanai puskonservatīvas mežsaimniecības paradigmā (O'Neill et al., 2014; MacLachlan et al., 2017).

Pieaugot nepieciešamībai apzināt koku ekoloģisko plastiskumu un adaptēšanās spējas (Corcuera et al., 2011; Valladares et al., 2014; Arnold et al., 2019), provenienču izmēģinājumu stādījumi ir uzskatāmi par modeļobjektiem, kas ļauj raksturot ģenētisko kontroli pār adaptācijai un ilgtspējai nozīmīgām pazīmēm (Leites et al., 2012; Nabais et al., 2018) mainīga klimata apstākļos (Valladares et al., 2014; Wilmking et al., 2020; Meier et al., 2022). Molekulārās bioloģijas un funkcionālas ekoloģijas metožu pielietojums ļauj veikt tiešu detālu provenienču materiāla ilgtspēju nodrošinošo mehānismu izpēti (Housset et al., 2018; Zhang et al., 2018; Ahrens et al., 2020). Šāda informācija ir komplementāra morfometriskajam un produktivitātes vērtējumam, kas ir sākotnējais provenienču izmēģinājumu stādījumu izveides mērķis (Jansons and Baumanis, 2005; Konig, 2005; Leites et al., 2012), tādējādi sekmējot adaptīvās saimniekošanas metožu ieviešanu (Bolte et al., 2009; Nabuurs et al., 2018; Arnold et al., 2019). Tomēr G × E kompleksās dabas dēļ (Li et al., 2017), kas ietekmē fenotipisko un līdz ar to ekoloģisko plastiskumu (Arnold et al., 2019; Ansarifar et al., 2020; de la Mata et al., 2022), lokāla informācija par dažādu genotipu produktivitāti un jutību joprojām ir aktuāla (Berlin et al., 2016; Breed et al., 2018; Chmura et al., 2021). Jāatzīst, ka provenienču stādījumi ir uzskatāmi par ierobežoti informatīviem iedzimstamības izziņas avotiem, nezināmas ģimeņu struktūras dēļ (Falconer and MacKay, 1996; Loha et al., 2006; Hayatgheibi et al., 2019).

Vairumā selekcijas programmu genotipu atlasei izmanto selekcijas indeksus, kas apvieno ekonomiski nozīmīgu pazīmju kopumu, starp kuriem produktivitātei ir centrāla loma (Baliuckas et al., 2004; Jansson et al., 2017; Burdon and Klapste, 2019; Lenz et al., 2020). Tomēr kokaugu dimensijas un stumbra kvalitāte ir kumulatīvi genotipu un pagātnes apstākļu saderības indikatori (Burdon and Klapste, 2019; Hayatgheibi et al., 2019), kas pieaugošas vides mainības apstākļos ir novecojuši to apzināšanas brīdī (Aitken and Bemmels, 2016; de Villemereuil et al., 2016). Attiecīgi, genotipu/provenienču ranžējumam ir izteikta tendence mainīties Baltijas jūras reģionā un citviet līdz ar izmaiņām klimatiskajos gradientos (Jansons and

Baumanis, 2005; Berlin et al., 2016; Hayatgheibi et al., 2020; Chmura et al., 2021; Szeligowski et al., 2023).

Pieauguma reakcija uz vides apstākļiem un to mainību var būt ļoti informatīva pazīme, lai prognozētu produktivitāti un ilgtspēju vides izmaiņu apstākļos (Zhang et al., 2018; Wilmking et al., 2020), papildinot atziņas, kas gūtas no morfometriskām pazīmēm (Xu et al., 2017; Heer et al., 2018; Housset et al., 2018). Klimatam esot vienam no galvenajiem koku augšanas noteicējiem (Speer, 2010; Hayatgheibi et al., 2020; Wilmking et al., 2020), precīzas pieauguma reakcijas uz meteoroloģiskajiem apstākļiem prognozes ir nozīmīgas adaptīvās mežsaimniecības ilgtspējas mērķu sasniegšanai (Bolte et al., 2009; Tei et al., 2017; Zhang et al., 2018). Tādējādi pieauguma jutības ģenētiskās kontroles novērtējums un šādas informācijas iekļaušana/izmantošana selekcijas indeksu papildināšanai ir vēlama selekcijas programmu ilgtspējas sekmēšanai (Burdon and Klapste, 2019; Ahrens et al., 2020; Chmura et al., 2021).

Mērenā klimata apstākļos koku pieaugums ir periodisks, un izteiktas pieauguma robežas ir izšķiramas, kā rezultātā ir iespējama ticama augšanas retrospekcija (Speer, 2010; Gärtner et al., 2015; Xu et al., 2017; Gennaretti et al., 2022). Datu ieguves efektivitātes un vides ietekmes informativitātes dēļ radiālais pieaugums, TRW ir izteikti populārākais koku pieauguma raksturlielums (Babst et al., 2018). Neskatoties uz jutību pret lokālajiem apstākļiem, TRW ir uz kokaugu un mežaudžu produktivitāti attiecināms mērījums, kas nodrošina efektīvu dažādu vides ietekmju novērtējumu (Xu et al., 2017; de Micco et al., 2019; Wilmking et al., 2020). Pieauguma veidošanās ir komplekss process, un TRW ir vairāku vides un iekšējo faktoru ietekmes rezultāts (Cook, 1987; Speer, 2010), kas ir aktuāls koku un mežu adaptācijas potenciāla novērtējumam strauju vides izmaiņu kontekstā (Housset et al., 2018; Zhang et al., 2018; Schwarz et al., 2020). Lai nodalītu vides ietekmes, ir izstrādātas specifiskas matemātiskās metodes, ļaujot veikt uzticamu dispersijas komponenšu dekonstrukciju, piemēram, laika rindu analīzes ceļā (Cook, 1987; Bunn, 2008; Stoffel et al., 2010; Jetschke et al., 2019).

Kā pieauguma raksturlielums, TRW kumulatīvi raksturo genotipa un vides stāvokļa (ksiloģenēzes laikā un pirms tā) saderību (Hacket-Pain et al., 2018; Montwe et al., 2018; Cuny et al., 2019; de Micco et al., 2019; Wilmking et al., 2020), līdz ar to šo ietekmju atšķetināšana, raksturojot individuālo pienesumu, var būt sarežģīta (Fonti et al., 2010; Gärtner et al., 2015; Babst et al., 2018). Dziļākas ksiloģenēzi ietekmējošo apstākļu kopas izpratnei koksnes anatomijas retrospekcija ir detālas un kvantitatīvas informācijas avots, kas arīdzan saistāms ar koksnes īpašībām (Fonti et al., 2010; Cuny et al., 2019; Gennaretti et al., 2022). Cauruļu teorija (*pipe theory*) postulē, ka koksne ir no mikroskopiskām caurulītēm veidota ūdens transporta sistēma, kas savieno konkrētu uzsūcošo sakni ar lapu (Tyree and Zimmermann, 2002; Martinez-Vilalta et al., 2004). Attiecīgi, caurulīšu kopums un to īpašības nosaka ūdens transporta efektivitāti, kā arī hidraulisko drošību, t.i., rezistenci pret kavitāciju un embolizāciju, kas ir fizioloģiskā sausuma cēlonis (Sperry and Tyree, 1990; Anderegg et al., 2015; Prendin et al., 2018).

Traheīdu lūmena laukums ir ūdens vadītspējas efektivitātes un kavitācijas riska raksturlielums, savukārt šūnapvalka biezums raksturo koksnes mehāniskās īpašības un rezistenci pret embolizēšanos (Sperry and Tyree, 1990; Tyree and Zimmermann, 2002; Martin et al., 2010). Pieaugošas sausuma ietekmes apstākļos šāda informācija kļūst īpaši nozīmīga (Gennaretti et al., 2022). Papildus vertikālajam ūdens transportam, stumbra koksne nodrošina horizontālo ūdens transportu, kā arī ir ūdens un barības vielu glabātuve, nodrošinot vielu pārnesi starp aplievu un kodolkoksi (Tyree and Zimmermann, 2002; Richardson et al., 2013). Šīs funkcijas lielā mērā nodrošina WR, kuru daudzums un izmēri nosaka koksnes spēju uzglabāt asimilātus, tādējādi esot par netiešu asimilācijas raksturlielumu (von Arx et al., 2017).

Veģetācijas sezonas pagarināšanās palielina salnu bojājumu risku un intensitāti (Lee et al., 2007; Augspurger, 2009; Kidd et al., 2014), kas apgrūtina un pārtrauc ksiloģenēzi, kā rezultātā rodas koksnes anomālijas, kas tiek arhivētas koksnē, pieļaujot to cēloņu raksturošanu retrospekcijas ceļā (Payette et al., 2010; Gennaretti et al., 2022). Stipras vēlas salnas, it īpaši pēc ksiloģenēzes iniciācijas, saplēš jaunveidotās EW šūnas, radot FR (Lee et al., 2007; Payette et al., 2010). Turpretī agras salnas augšanas sezonas izskaņā pārtrauc lignifikāciju, līdz ar to šūnapvalkos saglabājas augstāks celulozes īpatsvars, kas pēc dubultas krāsošanas ar Astra zilo un safranīnu (Gärtner and Schweingruber, 2013) liek LW izskatīties zilganai, parādot BR (Piermattei et al., 2015). Abas šīs koksnes anomālijas kļūst par populāriem genotipu un vides (lokālā klimata un meteoroloģisko anomāliju) saderības izziņas avotiem (Payette et al., 2010; Piermattei et al., 2015; Gennaretti et al., 2022). Šīs anomālijas var mazināt koksnes mehānisko izturību, jo ir izjaukta optimālā struktūra (Berry et al., 1983; Lee et al., 2007).

Pieauguma un saistīto raksturlielumu dispersijas komponenšu dekonstrukcija kopā ar multiplās regresijas analīzi (Cavin and Jump, 2017; Zhang et al., 2018; Wilmking et al., 2020) nodrošina detālu īstermiņa un ilgtermiņa vides apstākļu normālu un ekstrēmu ietekmju vērtējumu (Sass-Klaassen et al., 2016; McCullough et al., 2017; Xu et al., 2017; Babst et al., 2018). Pieņemot laikapstākļus un klimatu kā nozīmīgus koku augšanu ietekmējošus vides faktorus, attiecīgo koku atbildes reakciju novērtējums ir centrālā pieauguma pielietojuma joma (Cook, 1987; Ohse et al., 2012; Lloyd et al., 2013; Harvey et al., 2020; Wilmking et al., 2020). Pieauguma reakcijas mērogojamības nodrošināšanai klimata pārmaiņu apstākļos ir nepieciešama paraugošana, kas aptver nozīmīgu klimatiskā gradienta daļu, tā ka lokālās saistības var strauji kļūt neaktuālas (Lloyd et al., 2013; Henttonen et al., 2014; Restaino et al., 2016; Cavin and Jump, 2017).

Ekoloģiskās reakcijas pret vides gradientu ir zvanveida sakarības, bet lineāras saistības ir vērojamas tikai ierobežotā gradienta daļā (Way and Oren, 2010; Lloyd et al., 2013; Restaino et al., 2016). Attiecīgi, ierobežota references loga pārvietošanās gradientā, piemēram, lokālas analīzes gadījumā, nenovēršami noved pie tendenciozas lokālu lineāru saistību interpretācijas (Valladares et al., 2014; Wilmking et al., 2020; Wu et al., 2022). Līdz ar to nelineāru ekoloģiski reālistisku atbildes reakciju apzināšana, analizējot nozīmīgu gradienta daļu, ir kritiski svarīga (Lloyd et al., 2013; Cavin and Jump, 2017). Šajā kontekstā gadskārtu raksturlielumu laika rindas ir nozīmīgas, jo tās sniedz ieskatu par reakciju uz klimatisko gradientu laikā (McCullough et al., 2017; Xu et al., 2017; Babst et al., 2018). Datu kopas, kas reprezentē telpisku klimatisko gradientu, ir iegūstamas reģionālas paraugošanas ceļā (Restaino et al., 2016; Cavin and Jump, 2017; Harvey et al., 2020).

Baltijas jūras reģiona austrumu daļā parastā priede ir bieži sastopama un ekonomiski nozīmīga suga (Routa et al., 2019), kurai prognozēts īpatsvara sarukums 21. gs. laikā (Buras and Menzel, 2019). Suga ir ekoloģiski plastiska, tā spēj augt dažādos edafiskajos un klimatiskajos apstākļos; saimnieciski nozīmīgākie edafiskie apstākļi ir oligotrofas un mezotrofas audzes ar labi drenētām augsnēm (Berlin et al., 2016; Jansson et al., 2017). Ņemot vērā plašo sugas izplatību, tās populācijas ir ģenētiski adaptējušās lokāliem apstākļiem (Martin et al., 2010; Wojkiewicz et al., 2016; Alakärppä et al., 2018), norādot uz atšķirīgām adaptēšanās spējām (Valladares et al., 2014; Li et al., 2017; Moran et al., 2017). Priedes lokālās adaptācijas ir saistāmas ar izmaiņām koksnes anatomijā, kā arī fizioloģiskajās funkcijās, kas saistāmas ar sausuma un vēja ietekmi, kā arī konkurences apstākļiem (Martin et al., 2010; Wojkiewicz et al., 2016; Tyrmi et al., 2020). Maza mēroga lokālas adaptācijas ir novērotas saistībā ar edafiskajiem apstākļiem (Eckert et al., 2015; Zadworny et al., 2016). Attiecīgi lokālā ģenētiskā adaptācija norāda uz bioklimatisko modeļu prognožu neprecizitātēm, proti, izplatības un pārstāvētības samazinājuma pārvērtējumu, it īpaši ņemot vērā mežsaimniecības adaptīvo ietekmi (Valladares et al., 2014; Wu et al., 2022). Lokālās ģenētiskās adaptācijas ir arīdzan pamats veiksmīgām selekcijas programmām, kas lielā mērā ir balstītas uz koku morfometriju un produktivitāti, kā arī stumbra īpašībām (Baliuckas et al., 2004; Eckert et al., 2015; Jansson et al., 2017), nepieciekami apskatot augšanas uzņēmības pret vidi pazīmes (Fries, 2012; O'Neill et al., 2014; Wojkiewicz et al., 2016; Ahrens et al., 2020).

Parastās priedes pieaugums ir jutīgs pret meteoroloģiskajiem apstākļiem un to ekstrēmiem, bet saistībām ir raksturīgas lokālas iezīmes (Elferts, 2007; Zunde et al., 2008; Jansons et al., 2016; Harvey et al., 2020). Baltijas jūras reģiona austrumu daļā priedes pieaugums parāda pakāpenisku jutības nomaiņu no zemas temperatūras limitācijas Somijā uz pavasara temperatūras un vasaras sausuma limitāciju Polijā un Vācijā (Henttonen et al., 2014; Harvey et al., 2020). Attiecīgi, Baltijas valstis ir pārejas zona, kurā meteoroloģisko apstākļu limitējošās ietekmes maiņa norāda uz kompleksu pieauguma kontroli (Harvey et al., 2020), kas ļauj novērtēt šo saistību stacionaritāti (Wilmking et al., 2020). Ņemot vērā vēso klimatu, ziemas temperatūrai var būt kontrastējošas ietekmes, ko nosaka sala bojājumu un barības vielu zudumu mijiedarbība (Ögren, 1997; Beck et al., 2004), tādējādi norādot uz vides ietekmes pārnesi laikā. Reģionālā līmenī novērotās pieauguma un meteoroloģisko apstākļu saistības attiecināmas uz augšanas un reprodukcijas mijiedarbību, uz ko norāda negatīvās pieauguma saistības ar temperatūru iepriekšējās vasaras izskaņā (Hacket-Pain et al., 2018). Klimatisko apstākļu ietekmi uz parastās priedes augšanu parāda graduālas provenienču ranžējuma izmaiņas, uz ziemeļiem pārnestajiem genotipiem kļūstot produktīvākiem (Jansons and Baumanis, 2005; Berlin et al., 2016).

Parastās priedes stumbra koksne ir primitīva un sastāv galvenokārt no traheīdām, kas apņem retas sveķu ailes (Carlquist, 2001; Martinez-Vilalta et al., 2004), un aksiālās parenhīmas (Olano et al., 2013; von Arx et al., 2017). Traheīdu CWT un LA ir variabli, bet robežas starp LW un EW ir izteiktas (Mencuccini et al., 1997; Carlquist, 2001). Traheīdu CWT un LA gan EW gan LW var būt variabli atbilstoši apstākļiem to veidošanās laikā (Cuny et al., 2019), kā arī lokālas ģenētiskās adaptācijas dēļ (Martin et al., 2010). Ksiloģenēzes plastiskums, kas mazina meteoroloģisko apstākļu ietekmi uz koksnes funkcionalitāti (Cuny et al., 2019), ir ierobežots (Seo et al., 2020), norādot uz uzņēmību pret hidrauliskiem riskiem, it īpaši augšanas sezonas izskaņā (Piermattei et al., 2015; Cuny et al., 2019). Koksnes hidrauliskajai arhitektūrai, kas ir nozīmīga izdzīvošanai un konkurētspējai, novērojamas izteiktas lokālās adaptācijas iezīmes (Lenz et al., 2010; Fries, 2012; Carvalho et al., 2017).

1.2. Mērķis

Darba mērķis ir apzināt Baltijas jūras reģiona austrumu daļas parastās priedes radiālā pieauguma reakcijas plastiskumu pret meteoroloģisko/klimatisko apstākļu mainību, raksturot sugas klimatiskās adaptācijas spējas un to uzlabošanas potenciālu selekcijas ceļā.

1.3. Uzdevumi

Mērķim pakārtotie uzdevumi bija:

1) raksturot Baltijas jūras reģiona austrumu daļas parastās priedes pieauguma jutību pret meteoroloģiskajiem un klimatiskajiem apstākļiem reģionālajā klimatiskajā gradientā;
2) novērtēt lokālās ģenētiskās adaptācijas (ģenētisko faktoru) un populāciju fenotipiskā plastiskuma ietekmi uz pieauguma jutību pret meteoroloģiskajiem apstākļiem un to ekstrēmiem reģionālā līmenī, un to saistību ar produktivitāti;
3) raksturot lokālas ģenētiskās adaptācijas ietekmi uz Baltijas jūras reģiona austrumu daļas parastās priedes populāciju ksiloģenēzi un koksnes anatomiju, kā arī jutību pret mitruma deficītu;
4) salīdzināt pieauguma meteoroloģiskās jutības iedzimstamību un selekcijas potenciālu Baltijas jūras reģiona austrumu daļas parastās priedes proveniencēm.

1.4. Tēzes

Darbā izvirzītas tēzes:

1) Baltijas jūras reģiona austrumu daļas parastās priedes radiālais pieaugums ir pakļauts kompleksai meteoroloģisko apstākļu (temperatūra un mitruma apstākļi) ietekmei gan pieauguma veidošanās laikā, gan pirms tā;

2) nelineārās galveno meteoroloģisko apstākļu ietekmes parāda uz klimata atkarīgu radiālā pieauguma meteoroloģisko limitāciju, liecinot par neproporcionālām klimata pārmaiņu sekām uz augšanu;
3) pieauguma meteoroloģiskā jutība un tās plastiskums ir saistāmi ar genotipu produktivitāti, norādot uz reģiona populāciju/provenienču adaptācijas potenciālu;
4) pieauguma meteoroloģiskā jutība un tās plastiskums ir ģenētiski determinēti, liecinot par iespējamiem uzlabojumiem selekcijas ceļā.

1.5. Promocijas darba struktūra

Promocijas darbs sastāv no deviņām tematiski vienotām publikācijām (zinātniskiem rakstiem), kas apskata galvenās Baltijas jūras reģiona austrumu daļas parastās priedes pieauguma meteoroloģisko apstākļu ietekmes. Pirmie divi raksti ir veltīti vietējo genotipu augšanas reakcijas uz meteoroloģiskajam apstākļiem raksturošanai *in situ*. Trīs raksti ir veltīti pieauguma reakcijas lokālās adaptācijas un fenotipiskā plastiskuma izpētei, raksturojot jutības un produktivitātes saistības. Divi raksti analizē koksnes anatomijas raksturlielumus, novērtējot provenienču jutību un uzņēmību pret klimatiskajiem riskiem. Pēdējie divi raksti kvantificē pieauguma meteoroloģiskās jutības iedzimstamību un selekcijas potenciālu.

1.6. Aktualitāte

Pētījums liek uzsvaru uz meteoroloģisko faktoru ietekmi uz parastās priedes pieaugumu, kvantificē tā plastiskumu, kā arī vides un ģenētisko faktoru ietekmi uz to. Saistības starp genotipu vides jutību un produktivitāti norāda uz vēlamām mijiedarbībām (produktīvākie genotipi ir jutīgākie), atklājot pieauguma jutību kā nozīmīgu adaptāciju nepastāvīgiem apstākļiem. Attiecīgi, spēja operatīvi kontrolēt ksiloģenēzi dod artavu genotipu konkurētspējai ilgtermiņā. Šo faktu apliecina genotipiem specifiska koksnes anatomiskā struktūra. Iegūtie rezultāti salīdzina lineāru un nelineāru pieauguma-vides saistību mērogojamību reģiona līmenī. Iekšgada un starpgadu analīze norāda uz WR kā adaptīvās kapacitātes raksturlielumu dažādu Krafta klašu kokiem.

Metodoloģiski promocijas darbs iedziļinās koksnes anatomisko anomāliju (FR un BR) pielietojamībā genotipu uzņēmības pret salnām raksturošanai. To papildina kvantitatīvās koksnes anatomijas metožu veiksmīgā aprobācija genotipu salīdzināšanai, kas ļauj veikt padziļinātu analīzi, balstoties uz ierobežotu empīrisko materiālu. Pārbaudītas laika rindu dekonstrukcijas un jaukta tipa aditīvās modelēšanas priekšrocības ekoloģiskos pētījumos pieaugošas vides mainības apstākļos. Pētījuma rezultāti ir īpaši aktuāli Baltijas jūras reģionam, bet izpētes algoritmiem ir universāls raksturs un izmantojamība salīdzināmu vides gradientu gadījumā. Iegūtās atziņas ir pamats turpmākajiem pētījumiem, kas apskata lielāku genotipu izlasi, lai apliecinātu to mērogojamību un praktisko nozīmi.

2. MATERIĀLS UN METODES

2.1. Audzes un izmēģinājumu stādījumi

Reģionālā klimatiskā gradienta raksturošanai izmantota transekte, kas stiepās no Somijas dienvidiem līdz Vācijas ziemeļiem (1A. attēls; Raksts I). Gar transekti saimnieciskajos mežos izvēlētas 22 brīvapputes parastās priedes audzes (69– 129 gadus vecas), kuru platība bija lielāka par vienu hektāru un kurās bija automorfas, labi drenētas minerālaugsnes. Atlase veikta no nacionālajiem meža reģistriem. Šāda atlase veikta, lai apzinātu galvenos pieaugumu ietekmējošos apstākļus *in situ*. Sešos apakšreģionos (valstīs) atlasītas viena līdz sešas audzes, tādējādi raksturojot lokālo pieauguma specifiku. Pētītajās audzēs reljefs bija pārsvarā līdzens, tās atradās zemieņu līdzenumos piekrastes un iekšzemes apvidos. Audzēs bija parastās egles (*Picea abies* Karst.) un āra bērza (*Betula pendula* Roth.) piemistrojums. Papildus Latvijas centrālajā daļā (56,799° Z. pl.; 24,498° A. gar.) izvēlēta parastās priedes briestaudze ar retu parastās egles paaugu, lai ievāktu paraugus WR raksturošanai dažādu Krafta klašu kokos (Raksts II).

Pētītās audzes reprezentēja apvidus ar klimatisko apstākļu spektru no auksta mitra kontinentāla klimata (Somijas dienvidos) līdz mērenam okeāniskam (Vācijas ziemeļos) (Kottek et al., 2006), kur gada vidējā temperatūra bija robežās, attiecīgi, no 4,3 līdz 10,1°C. Visos apvidos temperatūras režīms ziemā bija mainīgāks nekā vasarā. Gada nokrišņu daudzums starp pētījuma teritorijām bija salīdzināms un svārstījās no 542 līdz 771 mm gadā, attiecīgi, Somijā un Latvijā (Harris et al., 2020). Nokrišņu sadalījums pētītajos apvidos bija līdzīgs – lielākā daļa no gada nokrišņiem bija vasaras mēnešos, kopumā līdzsvarojot palielināto evapotranpirāciju. Klimata pārmaiņas galvenokārt izpaudās kā pasiltināšanās miera periodā un līdz ar to – veģetācijas sezonas pagarināšanās, kā arī vasaras nokrišņu režīma heterogenitātes pieaugums un karstu sausuma periodu paildzināšanās, un to biežuma pieaugums (Allen et al., 2015; Meier et al., 2022).

Reģionālo parastās priedes populāciju pieauguma jutības lokālās ģenētiskās adaptācijas raksturošanai analizēti pieci provenienču izmēģinājumu stādījumi, kas reprezentē saīsinātu reģionālo klimatisko gradientu starp Latviju un Vāciju (1B. attēls; Raksti III–IX). Šie stādījumi ierīkoti IUFRO organizētas pētījuma ietvaros 1975. gadā, sadarbojoties USSR un GDR, ar mērķi salīdzināt Austrumeiropas populācijas (Kohlstock and Schneck, 1992; Jansons and Baumanis, 2005). Pētījumā iekļautas proveniences no apgabala, ko ierobežo 46 un 56° Z. pl., un 11 un 30° A. gar.; 36 proveniences pārstāvētas visos pētītajos stādījumos. Šāda telpiskā populāciju pārstāvētība reprezentē Baltijai prognozēto klimatisko apstākļu spektru uz 21. gs. beigām (Buras and Menzel, 2019; Meier et al., 2022). Provenienču sēklas ievāktas no pluskokiem, tādējādi reprezentējot produktīvākos genotipus. Stādījumi ierīkoti, stādot viengadīgus konteinerstādus, kas izaudzēti tuvējās stādaudzētavās.

Sākotnējais stādījumu biezums Latvijā un Vācijā bija, attiecīgi, 5000 koki ha^{-1} un 10 000 koki ha^{-1} (2 × 0,5 m).

Provenieces stādītas randomizētu bloku (parceļu) veidā, bet bloku izmērs un skaits atšķīrās starp valstīm. Stādījumos Latvijā provenieces reprezentētas sešos atkārtojumos pa 35 kokiem katrā, bet Vācijā – četros atkārtojumos pa 100 kokiem. Stādījumi izveidoti apgabalos ar labi drenētām ologotrofām smilšainām podzolaugsnēm Latvijā un mezotrofām mālsmilts podzolaugsnēm Vācijā; visi stādījumi izveidoti līdzenumos ar augstumu zem 250 m v.j.l. Sākotnēja agrotehniskā kopšana (konkurējošās veģetācijas novākšana) veikta pēc vajadzības, bet jaunaudžu kopšana (stādīto priežu retināšana) atšķīrās starp valstīm. Latvijā stādījumi kopti vienreiz 21 gada vecumā, izvācot neproduktīvākos kokus, līdz ~ 1800 koki ha^{-1} biezumam. Vācijā NL stādījumā veikta intensīvāka kopšana līdzīgā vecumā (līdz biezumam 1100 koki ha^{-1}); WS stādījumā veiktas trīs kopšanas (pēdējā 2013. un 2014. gados), samazinot biezumu līdz 900–1200 koki ha^{-1}.

2.2. Provenienču atlase

Pieauguma plastiskuma un jutības lokālās ģenētiskās adaptācijas novērtējumam atlasītas septiņas provenieces, kas atšķīrās ar produktivitāti un bija pārstāvētas visos stādījumos; atlase veikta, balstoties uz konsolidētu ranžējumu atbilstoši aktuālākajai inventarizācijai (1B. attēls; Raksti III–IX). Līdz šim proveniencei novērota būtiska ietekme uz produktivitāti un stumbra kvalitātes rādītājiem (Jansons and Baumanis, 2005; Taeger et al., 2013), pētītajām proveniencēm parādot līdzīgu ranžējumu starp stādījumiem. Šāda atlase ļauj novērtēt genotipu-vides jutības un produktivitātes saistības (Leites et al., 2012; Valladares et al., 2014; Matias et al., 2017; Housset et al., 2018), kā arī atbildes reakcijas plastiskuma cēloņus (de Villemereuil et al., 2016; Nabais et al., 2018).

Starp atlasītajām proveniencēm divas bija neproduktīvas (DIP un EBN), kuru izcelsme ir Rūdu kalni, viena lokālā (no Latvijas perspektīvas, KAL), kas izceļas ar stumbra īpašībām un produktivitāti virs vidējās, un divas produktīvākās (GUS un RYT), kuru izcelsme ir piekrastes zemienes Vācijas un Polijas ziemeļos. Papildus iedzimstamības raksturošanai atlasītas vēl divas produktīvākās provenieces no tā paša reģiona (NBD un RST; Raksti VII, IX). Kopumā produktīvās un neproduktīvās provenieces reprezentēja attiecīgi augstāko un zemāko produktivitātes un stumbra kvalitātes kvartiles neatkarīgi no stādījuma.

2.3. Datu ieguve

2.3.1. Paraugošana

Saimnieciskajās audzēs, kas atlasītas gar starptautisko transekti (1A. attēls), izvēlēti no 15 līdz 30 vizuāli veseli dominanti nebojāti koki (Raksts I). Katram no atlasītajiem kokiem krūšu augstumā no nejauši izvēlētām pretējām stumbra pusēm ar Preslera svārpstu ievākti 5 mm urbumi. Koksnes parenhīmas (WR) kvantificēšanai un tās saistībām ar Krafta klasi analizēšanai, (Raksts II) briestaudzē no septiņiem dominējošiem (I un II Krafta klase) un sešiem nomāktiem (III un IV Krafta klase) kokiem analoģiski ievākti koksnes paraugi. Papildus no pieciem dominējošiem un pieciem nomāktiem kokiem tajā paša audzē ievākti koksnes paraugi augšanas gaitas raksturošanai.

Provenienču izmēģinājumu stādījumos paraugošana veikta atbilstoši koku pārstāvētībai atkārtojumos (Raksti III–IX). Katrā atkārtojumā no diviem vai trim dominējošiem vai ko-dominējošiem vizuāli veseliem nebojātiem kokiem ar Preslera svārpstu krūšu augstumā ievākti divi paraugi no nejaušām pretējām stumbra pusēm. Visas paraugošanas laikā svārpsta asumam un tīrībai pievērsta pastiprināta uzmanība, lai nodrošinātu augstu paraugu kvalitāti.

2.3.2. Gadskārtu platuma mērīšana

Ievāktie koksnes paraugi (izņemot tos, kas paredzēti WR kvantificēšanai; Raksts II) ielīmēti unitārās planšetēs. Fiksēšanas laikā uzmanība pievērsta korektai paraugu orientācijai, lai nodrošinātu, ka traheīdas ir perpendikulāras planšetes virsmai. Karsta tvaika strūkla izmantota, lai pirms līmēšanas mīkstinātu un iztaisnotu savērpušos paraugus (Speer, 2010), kā arī mazinātu paraugu lūšanu fiksēšanas laikā. Paraugu virsmu sagatavoja mērīšanai, progresīvi slīpējot vai griežot ar urbumu mikrotomu (Gärtner and Nievergelt, 2010). Gadskārtu platumi mērīti, manuāli izmantojot LINTAB 6 mērgaldu un TSAP programmatūru (RinnTech, Heidelberg, Vācija). Mērījumus veica viena persona. Mērījumi veikti ar 0,01 mm precizitāti.

2.3.3. Kvantitatīvā koksnes anatomija

Lai novērtētu WR (Raksts II), pieauguma urbumi (koksnes paraugi) vienu diennakti mērcēti ūdenī, rehidrējot un tādējādi mīkstinot koksni. Urbumi tangenciāli (šķērseniski) sagriezti 15 līdz 35 µm biezos griezumos, izmantojot GSL1 mikrotomu (Gärtner et al., 2014). Katrai no ārējām 30 līdz 35 gadskārtām no EW un LE ievākts viens labas kvalitātes griezums. Vecākās gadskārtas nav analizētas parenhīmas atmiršanas un līdz ar to neizšķiramības dēļ. Koksnes šķērseniskās anatomiskās struktūras raksturošanai un lokālās adaptācijas iezīmju tajā novērtējumam (Raksti VI, VII), mikroskopiskie griezumi (14 līdz 18 µm biezi) sagatavoti ar urbumu mikrotomu (Gärtner and Nievergelt, 2010) atbilstoši Gärtner and Schweingruber (2013) protokolam.

Plānie griezumi krāsoti ar Astra zilā un safranīna maisījumu (Gärtner and Schweingruber, 2013), tādējādi izceļot kontrastu starp gadskārtu daļām, kā arī starp lignificētajiem (koksne) un nelignificētajiem (parenhīma, WR) elementiem. Griezumus fiksēja Kanādas balzamā vai glicerīnā. Augstas izšķirtspējas nesagrozīti mikroskopiski griezumu attēli uzņemti ar caurejošās gaismas mikroskopu, kas aprīkots ar 18 Mpx spoguļkameru pie attēlu 40× palielinājuma. Atsevišķie paraugu attēli apvienoti, izmantojot PTGui programmu (New House Internet Services, Rotterdam). Lai atpazītu un nomērītu WR (Raksts II), kā arī CWT un LA (Raksts VI), izmantota WinCELL 2007a programma (Regent Instruments, Kanāda). Ar salnām saistīto koksnes anatomisko anomāliju (FR, BR; Piermattei et al., 2015) reģistrēšana veikta vizuāli, izmantojot griezumu attēlus (2. attēls).

2.3.4. Klimatiskie dati

Lai novērtētu pieauguma un meteoroloģisko apstākļu saistības (Raksti I–IX), kā arī saistību ar koksnes anatomiju un tās anomālijām, no CRU TS4 klimatiskās datu kopas (Harris et al., 2020) atlasītas tās daļas, kas raksturoja novērojama punktus, kas bija vistuvāk pētītajām audzēm un stādījumiem. Mēnešu vidējā temperatūra, nokrišņu summa, potenciālā evapotranspirācija iegūtas periodam no 1901. līdz 2017. gadam. Sausuma apstākļu raksturošanai aprēķināts standartizētais nokrišņu evapotranspirācijas indekss (SPEI; Vicente-Serrano et al., 2010). Pieauguma un meteoroloģisko apstākļu saistību analīzei klimatiskie dati sakārtoti atbilstoši klimatiskajam gadam no maija/jūnija gadā pirms pieauguma līdz septembrim pieauguma gadā, tādējādi testējot meteoroloģijas ietekmes pārnesi (Beck et al., 2004; Hacket-Pain et al., 2018; Harvey et al., 2020).

2.4. Datu analīze

Mērījumu kvalitātes un datējuma kontrolei, kas ir kritiska pieauguma jutības analīzei (Speer, 2010), mērījuma laika rindas šķērsdatētas, izmantojot grafiskās un statistiskās metodes (Raksti I–IX). Korekcijas mērījumu sērijās ieviestas pēc nepieciešamības. Datējuma un vides signālu reprezentativitātes raksturošanai laika rindu kopām aprēķināti informativitātes un saskanības indeksi r-bar, ar1, SENS, EPS, SNR u.c. (Wigley et al., 1984; Bunn, 2008; Speer, 2010). Šie indeksi aprēķināti laika rindu ikgadējās mainības komponentei.

Ikgadējās pieauguma mainības komponentes izcelšanai TRW laika rindas divkārši detrendētas, izmantojot modificēto negatīvi eksponenciālo līkni un fleksiblu kubisku spailnu ar viļņa garumu, kas sastāda ⅔ no mērījumu sērijas garuma (Raksti I, III), vai salīdzināmu garumu (pārējie raksti). Tādējādi veikta strikta detrendēšana, izceļot ikgadējo mainību. Ņemot vērā, ka TRW raksturīga augsta autokorelācija (Cook, 1987), tā noņemta, izmantojot autoregresīvu modeli. Lokālo lineāro saistību novērtējumam (Wilmking et al., 2020) detrendētās laika rindas apvienotas audžu/provenienču hronoloģijās (Cook, 1987; Bunn, 2008).

Specifiskas standartizēšanas metodes, kas balstās uz relatīvajām pieauguma izmaiņām, izmatotas, lai identificētu PY (Jetschke et al., 2019), gadus, kad nozīmīga laika rindu daļa parāda krasas izmaiņas (Raksti III, IX). Ņemot vērā, ka pētītie koki auga mērenā klimatā un to augšana nebija izteikti apgrūtināta, PY identificēšanā izmantoto parametru pielaides bija lielas (Elferts, 2007; Jetschke et al., 2019). Meteoroloģisko apstākļu saikne ar PY analizēta atbilstoši van der Maaten-Theunissen et al. (2021) un Schwarz et al. (2020). Tolerances analīze veikta, lai raksturotu koku atbildi uz meteoroloģiskajām anomālijām (Raksts III). Rezistences (PY/pre-PY), atkopšanās (post-PY/PY), resiliences (post-PY/pre-PY) un relatīvās resiliences ((post-PRPY)/pre-PY) indeksi (Lloret et al., 2011) aprēķināti, balstoties uz TRW.

Būtstrapota Pīrsona korelācijas analīze starp hronoloģijām un PY laika rindām, un meteoroloģiskajiem mainīgajiem izmantota lokālo lineāro saistību ar pieauguma raksturlielumiem apzināšanai (Raksti I–VIII). Būtstrapota slīdošā korelācijas analīze izmantota lokālo lineāro saistību stacionaritātes novērtējumam (Zang and Biondi, 2015; Hofgaard et al., 2019). Ņemot vērā, ka pētītie koki auga sugas izplatības areāla vidus daļā, kur apstākļi izskatāmi par optimāliem, multiplās regresijas pieeja izmantota, lai noskaidrotu pieaugumu ietekmējošos galvenos meteoroloģiskos apstākļus (Raksti I, IV). Tā kā ekoloģiskās atbildes reakcijas plašākā gradientā ir zvanveida (Way and Oren, 2010; Lloyd et al., 2013), tātad nelineāras, jaukta tipa vispārināti aditīvi modeļi, kas ļauj novērtēt atbildes reakcijas splainus, izmantoti regresijas veikšanai (Wood, 2011). Atlikumu hronoloģiju indeksi audzēm (Raksts I) vai kokiem (Raksts IV) analizēti kā atkarīgais mainīgais, bet meteoroloģiskie mainīgie – kā ietekmējošie. Ietekmējošo mainīgo kopums atlasīts atbilstoši arbitrārās atlases principiem, daļēji pamatojoties uz korelācijas analīzi un modeļa informativitāti. Gads un telpiskās atkarības struktūra (koks, atkārtojums, stādījums, audze utt.) iekļauti modelī kā randomie efekti, tādējādi novēršot neatkarības problēmu.

Lineāri jaukta tipa modeļi izmantoti, lai novērtētu Krafta klases ietekmi uz WR dimensijām un daudzumu koksnē (Raksts II), kā arī provenienences ietekmi uz pieauguma tolerances rādītājiem un koksnes anatomiju (CWT un LA). Randomo efektu struktūra, kas aprakstīta iepriekš, izmantota, lai novērstu neatkarības problēmu. Fiksēto efektu būtiskums novērtēts ar Wald's χ^2 testu. Modeļu atbilstība statistiskajiem pieņēmumiem pārbaudīta ar diagnostiskajiem grafikiem.

Audzes un ģenētisko (t.sk., G × E) efektu kvantificēšanai pieauguma meteoroloģiskajai jutībai, kā arī pieauguma reakcijai PY, dispersijas komponentes atdalītas ar jaukta tipa modeli atbilstoši Loha et al. (2006) un Falconer and MacKay (1996), par pamatu ņemot provenienču datus (1B. attēls). Kā atkarīgais mainīgais izmantotas lokālās pieauguma un meteoroloģisko mainīgo korelācijas (aprēķinātas detrendētām pieauguma līknēm) un individuālu koku pieauguma relatīvās izmaiņas PY (Jetschke et al., 2019; attiecīgi Raksti VIII, IX). Plašas nozīmes iedzimstamības indekss (H^2) un CVP aprēķināti ģenētisko faktoru ietekmes raksturošanai. Datu analīze veikta R v. 4.2.2 vidē, izmantojot pakotnes dplR (Bunn, 2008), pointRes (van der Maaten-Theunissen et al., 2021), treeclim (Zang and Biondi, 2015), lme4 (Bates et al., 2015) un mgcv (Wood, 2011).

3. REZULTĀTI UN DISKUSIJA

3.1. Mērījumu kvalitāte

Lielākā daļa no TRW laika rindām bija kvalitatīvas un tika veiksmīgi šķērsdatētas, nodrošinot ticamu pieauguma un meteoroloģisko apstākļu saistību retrospekciju (Raksti I, III–IX). Datu kopu informativitāti apliecināja aprēķinātie vides signālu reprezentācijas rādītāji, EPS pārsniedzot pieņemto 0,85 slieksni, un tādējādi norādot uz atbilstību klimatiskas ietekmes analīzei (Wigley et al., 1984). Līdzīgi, SNR vairumā no datu kopām pārsniedz 5,0, norādot uz izteiktu vides mainības komponenti TRW, kas, salīdzinot provenieces, bija stiprāka produktīvākajiem genotipiem (Raksti IV, V). Vidējās SENS un gini koeficientu vērtības (Raksti I, III–IX), kas parāda pieauguma ikgadējās mainības pakāpi (Bunn et al., 2013), bija mērenas, kas ir optimāli pieauguma un vides mainības saistību analīzei (Speer, 2010). Iepriekšējās augšanas ietekme uz pieaugumu audzēs gar transekti (Raksts I), kā arī provenienču izmēģinājumu stādījumos (Raksti III–V, VIII–IX) bija izteikta, uz ko norādīja augsta ar1 vērtība, liecinot par salīdzinoši konservatīvu augšanas stratēģiju (Way and Oren, 2010; Isaac-Renton et al., 2018). Tomēr stādījumos Vācijā ar1 bija nedaudz zemāka un SENS bija augstāka, liecinot par augstāku klimatisko apstākļu marginalitāti no analizēto genotipu perspektīvas (Taeger et al., 2013; Cavin and Jump, 2017; Cuny et al., 2019).

Koksnes anatomisko mērījumu laika rindas bija īsākas, salīdzinot ar TRW (Raksti II, VI), un tām bija iztrūkumi, kas saistāmi ar dabisko koksnes šķiedras orientācijas mainību (von Arx et al., 2016; Gennaretti et al., 2022). Attiecīgi, laika rindu saskanības reprezentācijas rādītāji bija zemāki un neprecīzi, bet mērījumi parādīja ekoloģisko saistību analīzei pietiekamu dispersiju. Koksnes anatomijas anomālijas (BR, FR) bija retas, un to sadalījums bija novirzīts nulles virzienā, pieļaujot tikai vienkāršotu statistisko analīzi (Raksts VII). Visi 126 BR novēroti LW, bet vairums no 97 konstatētajiem FR bija EW vidusdaļā, attiecīgi liecinot par agru un vēlu salnu ietekmi (Gu et al., 2008; Kidd et al., 2014; Piermattei et al., 2015). Gan WR daudzums, gan to dimensijas (Raksts II) bija līdzīgas starp analizētajiem kokiem, norādot uz konservatīvu augšanas stratēģiju asimilātu uzglabāšanas kapacitātes ziņā (Olano et al., 2013; Richardson et al., 2013; von Arx et al., 2017). Koksnes elementu daudzums un īpašības ir strikti limitētas, lai nodrošinātu koksnes fizioloģisko integritāti un funkcionalitāti (Mencuccini et al., 1997; Cuny et al., 2019). Tomēr jāatzīmē, ka WR dimensiju variācija bija atšķirīga starp dažādu Krafta klašu kokiem, norādot uz atšķirīgu vides limitāciju un jutību pret vides mainību (Olano et al., 2013; Lebourgeois et al., 2014).

3.2. Reģionālās un lokālās vietējo populāciju pieauguma reakcijas

Meteoroloģiskajiem apstākļiem novērota kompleksa ietekme uz Baltijas jūras reģiona austrumu daļas parastās priedes lokālo populāciju pieaugumu (Raksts I). Lokālās pieauguma un meteoroloģisko apstākļu korelācijas, kas reprezentē lineāras saistības ar ikgadējā pieauguma komponenti (Lloyd et al., 2013; Tei et al., 2017; Babst et al., 2018), parādīja graduālas izmaiņas gar transekti, norādot uz telpisko nestacionaritāti (Hofgaard et al., 2019; Wilmking et al., 2020). Somijā pieaugums korelēja ar temperatūras apstākļiem pieauguma veidošanās laikā un pirms tā, bet saistībām bija lokāls raksturs un kopīgo iezīmju izpausme zema. Neskatoties uz to, korelācijas norādīja, ka augšanu limitēja zemas temperatūras (Henttonen et al., 2014; Montwe et al., 2018). Audzēs, kas atradās uz dienvidiem no Somijas, novērota ar sausumu saistāmo meteoroloģisko apstākļu ietekmes pastiprināšanās, vienlaikus nezūdot ziemas temperatūras ietekmei. Latvijā, kur audzes bija telpiski izkliedētākas (1A. attēls), lokālās korelācijas bija daudzveidīgākas, bet korelācijas ar ziemas temperatūru bija kopīgas vairumam audžu. Negatīvās korelācijas ar temperatūru iepriekšējā gada vasaras izskaņā bija biežas Latvijā, kā arī Vācijas ziemeļos. Transektes dienvidu daļā parastās priedes pieaugums visbiežāk korelēja ar meteoroloģiskajiem apstākļiem, kas raksturo vasaras sausuma intensitāti, kas saskan ar globālu sausuma ietekmes uz mežiem pastiprināšanos (Choat et al., 2012; Allen et al., 2015).

Slīdošās korelācijas parādīja, ka lokālās pieauguma un meteoroloģisko apstākļu korelācijas bija nestacionāras (Hofgaard et al., 2019). Galvenokārt nestacionaritāte saistīta ar sausuma ietekmes pastiprināšanos, kas var būt saistītas ar koku novecošanos un jutības pieaugumu (Anfodillo et al., 2013; Konter et al., 2016; Prendin et al., 2018), reģionālajam klimatiskajam gradientam pārvietojoties un pagarinoties klimata pārmaiņu rezultātā (Restaino et al., 2016; Montwe et al., 2018; Hofgaard et al., 2019; Harvey et al., 2020). Attiecīgi, lokālās korelācijas ir acīmredzami strauji novecojošas, norādot uz to neatbilstību meteoroloģisko apstākļu retrospekcijai un augšanas prognozēm (Wilmking et al., 2020; Wu et al., 2022).

Vispārinot meteoroloģisko apstākļu ietekmes uz pieaugumu reģionālajā klimatiskajā gradientā (1A. attēls), novērtēta deviņu meteoroloģisko mainīgo kompleksa ietekme uz pieauguma ikgadējo mainību (3. attēls). Šie meteoroloģiskie apstākļi saistīti ar augšanas periodu, kā arī periodu pirms tā, norādot uz laikā kompleksām ietekmēm un to pārnesi (Friedrichs et al., 2009; Hacket-Pain et al., 2018; Harvey et al., 2020). Reģionālā līmenī novērtētajiem būtiskajiem meteoroloģiskajiem mainīgajiem novērotas galvenokārt nelineāras ietekmes uz pieaugumu, norādot uz sezonāli nevienlīdzīgu meteoroloģiskā gradienta garumu (no vietējo genotipu perspektīvas). Vienlaikus nelineārās ietekmes norādīja uz novērtēto saistību mērogojamību un stacionaritāti (Lloyd et al., 2013; Cavin and Jump, 2017; Wilmking et al., 2020). Novērtēto ietekmju mainība laikā un telpā (randomo gada un audzes efektu dispersijas) norādīja uz pētīto lokālo populāciju fenotipisko plastiskumu un adaptācijas potenciālu vidējā termiņā (attiecībā pret koka dzīvildzi; Eckert et al., 2015; Moran et al., 2017; Alakärppä et al., 2018; Leites and Benito Garzon, 2023).

Analizētajā klimatiskajā gradientā stiprākā ietekme uz lokālo populāciju pieaugumu konstatēta iepriekšējā augusta temperatūrai, bet saistības bija lineāras un negatīvas (3. attēls), norādot, ka ir bijusi reprezentēta ierobežota mainība. Šādas saistības skaidrojamas ar resursu pārdali starp reprodukciju un augšanu, proti, augšanas sezonas izskaņa ir laiks, kad veidojas pieauguma aizmetņi, un temperatūra nosaka ģeneratīvo un veģetatīvo aizmetņu sadalījumu (Hacket-Pain et al., 2018). Marta temperatūra novērtēta ar otro stiprāko ietekmi (pozitīvu) uz pieaugumu, bet saistības bija nelineāras, lai gan tikai ar nelielu pārliekumu virs 0°C, norādot uz pozitīvu pasiltināšanās ietekmi (Henttonen et al., 2014; Lindner et al., 2014; Reyer et al., 2014; Montwe et al., 2018). Līdzīga aina vērojama pieauguma saistībām ar temperatūru februārī. Pozitīvās saistības ar temperatūru ziemā skaidrojamas ar sala bojājumiem (Beck et al., 2004; Henttonen et al., 2014), kā arī augsnes temperatūras ietekmi uz sakņu attīstību (Hardy et al., 2001), par ko liecina pozitīvās korelācijas ar ziemas nokrišņiem, kas ietekmē augsnes sasalšanu (Tierney et al., 2001). Siltāka klimata apstākļos Polijā un Vācijā ziemas nokrišņu ietekme savukārt ir saistāma ar gruntsūdens līmeņa apjaunošanos un mitruma apstākļiem augšanas sezonas laikā (Hardy et al., 2001; Goldsmith et al., 2022). Decembra temperatūras ietekme savukārt bija mainīga, kas būtu skaidrojams ar dinamisku līdzsvaru starp salcietības attīstību/uzturēšanu (Beck et al., 2004) un barības vielu rezervju zudumu elpošanas procesā (Ögren, 1997).

Pieauguma atbildes reakcija uz temperatūru jūlijā (3. attēls), kuras ietekme bija trešā stiprākā, bija zvanveida un uzrādīja lokālu maksimumu, ka saistāms ar līdzsvaru starp pazeminātu asimilāciju vēsās vasarās (Carrer et al., 2010; Yang et al., 2015) un mitruma deficītu sausos un karstos apstākļos (Allen et al., 2015). Tomēr ar nokrišņiem saistītie mainīgie parādīja salīdzinoši vājāku ietekmi uz pieaugumu, liecinot par pētīto populāciju resilienci. Ūdens bilancei (SPEI) jūlijā bija spēcīgākā ietekme no visiem ar nokrišņiem saistītajiem mainīgajiem, liecinot par mērenu uzņēmību pret sausumu, kā arī nespēju izmantot augšanas priekšrocības mitrās vasarās samazināta gaismas daudzuma (Strand et al., 2006; Young et al., 2010) vai fizioloģiskā sausuma (Tyree and Zimmermann, 2002) dēļ. Jūnija temperatūras ietekme, kam novērots lokāls optimums, skaidrojama ar līdzsvaru starp saules radiācijas un siltuma daudzumu, un mitruma apstākļiem (Strand et al., 2006; Jyske et al., 2014). Paaugstinātam vasaras mitrumam novērtēta pozitīvas ietekmes pārnese, par ko liecināja atbildes reakcija uz iepriekšējā jūlija nokrišņiem, kas skaidrojama ar veģetatīvo un ģeneratīvo aizmetņu īpatsvara izmaiņām (Hacket-Pain et al., 2018). Autora piezīme: dārgo recenzent, ja izlasījāt tik tālu, tas ir brīnišķīgi; griezieties pie autora pēc sirsnīga cienasta un/vai apskāviena. Attiecīgi novērtētās atbildes reakciju līknes parādīja pieauguma reakcijas uz meteoroloģiskajiem apstākļiem atkarību no klimata (Ohse et al., 2012; Lloyd et al., 2013; Cavin and Jump, 2017; Hofgaard et al., 2019), norādot uz neproporcionālām vides pārmaiņu sekām (Matias et al., 2017; Wilmking et al., 2020).

Reģionālās pieauguma atbildes reakcijas (Raksts I) vērtētas dominantajiem kokiem, kas var pilnībā nereprezentēt zemāku Krafta klašu kokus un līdz ar to visas audzes pieaugumu, atšķirīgas asimilācijas un evapotranspirācijas/mikroklimatisko apstākļu dēļ (Lebourgeois et al., 2014). Šajā kontekstā WR, kas ir rezerves barības vielu uzglabāšanas kapacitātes raksturlielums (Richardson et al., 2013; von Arx et al., 2017), parādīja, ka dominantie un nomāktie koki ir spējīgi būt līdzvērtīgi produktīvi (primārā produktivitāte), norādot uz to adaptēšanās spējām neatkarīgi no Krafta klases (Raksts II). Tomēr analizētie koki bija spējīgi dinamiski pielāgot barības vielu rezervju kapacitāti (Olano et al., 2013), par ko liecināja WR daudzuma un dimensiju ikgadējā mainība. Izteikti individuālās WR dimensiju iezīmes norādīja uz pieauguma un asimilācijas plastiskumu pret mikroklimatiskajiem apstākļiem, liecinot par labu vietējo genotipu adaptēšanās spējai (Eckert et al., 2015; von Arx et al., 2017; Housset et al., 2018).

Lielākā WR mainības daļa ir saistāma ar iekšgada mainību, jo izteiktākās atšķirības novērotas starp EW un LW, nevis secīgām gadskārtām. Kopumā WR bija augstāki un šaurāki LW, bet kopējais WR daudzums bija augstāks EW. Šāda mainība atbilst koksnes šūnu īpašībām (Mencuccini et al., 1997; Martinez-Vilalta et al., 2004), kas ir augšanas dinamikas rezultāts (Cuny et al., 2019). Relatīvais WR augstums un šķērsgriezuma laukums, ko nosaka parenhīmas šūnu skaits (Olano et al., 2013; von Arx et al., 2017), bija augstāks vidējo Krafta klašu kokiem EW, salīdzinot ar dominantajiem kokiem, lai arī atšķirības bija marginālas. Šādas atšķirības norāda uz dažādu augšanas stratēģiju iespējamību, tā kā palielinātas barības vielu rezerves ir konservatīvas stratēģijas iezīmes (Martin et al., 2010; Way and Oren, 2010; Isaac-Renton et al., 2018). Šis arīdzan norāda uz iekšsugas augšanas stratēģiju segregāciju, kas ir uzskatāma par adaptāciju, kura uzlabo audzes resilienci (Valladares et al., 2014; Eckert et al., 2015; Alakärppä et al., 2018). Analizētās WR dimensijas un daudzums bija neatkarīgs no TRW, norādot uz koku spēju uzturēt vitalitāti neatkarīgi no Krafta klases (Fonti et al., 2015), kas saistāms ar audzes funkcionālo daudzveidību, kura ir nozīmīga noturībai pret pieaugošajiem traucējumiem (Lebourgeois et al., 2014).

Iegūtās WR laika rindas parādīja korelācijas ar meteoroloģiskajiem apstākļiem pirms gadskārtas veidošanās, norādot uz ietekmes pārnesi, it īpaši attiecībā uz iepriekšējās vasaras un rudens apstākļiem, vienlaikus liecinot par kumulatīvu vides mainības ietekmi (Friedrichs et al., 2009; Hacket-Pain et al., 2018). Aprēķinātās korelācijas parādīja saistības ar saules radiācijas daudzumu un līdz ar to ar asimilācijas intensitāti (Strand et al., 2006; Fonti et al., 2015), kā arī ar pieejamo ūdens daudzumu pavasarī, kas ietekmē koksnes šūnu izplešanos (Olano et al., 2013; Jyske et al., 2014). Jāpiezīmē, ka WR saistības ar meteoroloģiskajiem apstākļiem ir vājākas nekā TRW, kas skaidrojams ar optimāliem augšanas apstākļiem izplatības areāla vidusdaļā (Valladares et al., 2014; Chmura et al., 2021). Attiecīgi WR parāda izlīdzinātu reakciju pret meteoroloģisko mainību, vienlaikus dodot pienesumu ar1 izpausmei TRW (Richardson et al., 2013; von Arx et al., 2017).

3.3. Populāciju lokālās adaptācijas

3.3.1. Lokālās pieauguma un meteoroloģisko apstākļu saistības

Novērtētās pieauguma un meteoroloģisko apstākļu saistības analizētajām proveniencēm parādīja reģiona parastās priedes lokālās adaptācijas iezīmes attiecībā uz augšanas jutību (Raksti III–V). Novērotas jutības saistības ar produktivitāti, kā arī pieauguma plastiskuma pienesums tai. Līdzīgi kā novērots populācijām *in situ* (Raksts I), radiālais pieaugums bija pakļauts kompleksai meteoroloģisko apstākļu – ziemas temperatūras un vasaras sausuma, kas ir galvenās klimata pārmaiņu izpausmes (Allen et al., 2015; Meier et al., 2022) – kontrolei.

Katrā izmēģinājumu stādījumā pētītās provenienčes parādīja specifisku ikgadējo TRW mainību, kas, ņemot vērā augsto pieauguma sinhronitāti, izpaudās kā atšķirības reakcijas stiprumā (Raksti III, IV). Reakcijas stipruma atšķirības starp proveniencēm atšķīrās pa gadiem, norādot uz pieauguma jutības atšķirībām un specifikām saiknēm ar meteoroloģiskajiem apstākļiem. Lokālo pieauguma un meteoroloģisko apstākļu korelācijas bija mēreni stipras, taču konstatētās atšķirības starp stādījumiem norādīja uz lokālām iezīmēm. Tomēr korelācijas ar jūlija nokrišņiem un iepriekšējā jūnija temperatūru (pozitīvas), kā arī ar jūlija temperatūru un iepriekšējā jūlija, augusta un decembra SPEI (negatīvas) bija kopīgas stādījumos Latvijā un Vācijā, atklājot reģionālas jutības iezīmes (Henttonen et al., 2014; Harvey et al., 2020). Pieauguma un meteoroloģisko mainīgo korelācijas uzrādīja atšķirības starp proveniencēm, liecinot par lokālām ģenētiskām jutības adaptācijām (O'Neill et al., 2014; Eckert et al., 2015; Tyrmi et al., 2020).

Atšķirības starp proveniencēm Latvijā galvenokārt bija saistītas ar jutību pret ziemas temperatūru, ātraudzīgākās provenences (ar izcelsmi no maigāka klimata) bija visjutīgākās. Lēnaudzīgākajām proveniencēm konstatētas zemākas korelācijas starp pieaugumu un vasaras nokrišņu daudzumu. Pretstatā, stādījumos Vācijā lēnaudzīgākās provenences parādīja stiprāku korelāciju ar vasaras sausumu raksturojošajiem mainīgajiem, bet ātraudzīgās provenences bija tolerantākas pret ziemas temperatūru. Attiecīgi, bija vērojama telpiska inversija. Provenences parādīja arī atsevišķas specifiskas korelācijas, norādot uz lokālām ar produktivitāti nesaistītām adaptācijām (Eckert et al., 2015; Alakärppä et al., 2018; Tyrmi et al., 2020), vai arī – tās var būt sakritība.

3.3.2. Pieauguma reģionāla jutība un produktivitāte

Pieauguma reakcijas uz meteoroloģiskajiem apstākļiem reģionālais vispārinājums parādīja kompleksu pieauguma kontroli, bet atbildes reakciju nelinearitāte norādīja uz šo saistību atkarībā no klimata (4. attēls; Raksts IV). Šāda reakcija apliecina neproporcionālu klimata pārmaiņu ietekmi uz pētītā reģiona priedes populāciju pieaugumu (Lindner et al., 2014; Matias et al., 2017; Tei et al., 2017; Wilmking et al., 2020). Provenienču pieaugums bija saistīts ar septiņiem līdz deviņiem meteoroloģiskajiem mainīgajiem, norādot uz tiešām un pārnestām apstākļu ietekmēm. Novērotās saistības uzskatāmas par stacionārām, par ko liecināja zemā ar pieauguma gadu saistītā dispersija, lai gan references periods bija salīdzinoši īss. Atbildes reakcijas stiprums un forma atšķīrās starp proveniencēm, norādot uz atšķirīgu jutību un pieauguma plastiskumu (Taeger et al., 2013; Eckert et al., 2015; Alakärppä et al., 2018; Tyrmi et al., 2020). Reakciju atšķirības galvenokārt saistāmas ar meteoroloģisko apstākļu ekstrēmu vērtībām, liecinot par nevienlīdzīgu spēju adaptēties sagaidāmajām klimatiskajām izmaiņām. Lai gan atšķirības nebija drastiskas, arī nelielām ietekmēm ilgtermiņā var būt nozīmīgas sekas (Glasner and Weiss, 1993; Lebourgeois et al., 2014; Matias et al., 2017; Vazquez-Gonzalez et al., 2020).

Pētīto provenienču pieaugums bija primāri jutīgs pret vasaras mitruma apstākļiem, apliecinot sausuma ietekmes pieaugumu (Choat et al., 2012; Allen et al., 2015). Maija un jūlija temperatūras un SPEI ietekmes (4. attēls) norādīja uz tiešu meteoroloģisko apstākļu ietekmi uz pieauguma veidošanos (Jyske et al., 2014), vienlaikus liecinot, ka ūdens trūkumam bija izteikta limitējoša ietekme (Isaac-Renton et al., 2018; Montwe et al., 2018; Harvey et al., 2020). Reakcija uz SPEI maijā bija krasa, atspoguļojot agrīna ūdens deficīta nozīmi (Choat et al., 2012; Jyske et al., 2014). Jāatzīmē, ka ātraudzīgākās provenieces bija jutīgākas pret mitruma apstākļiem, atainojot saikni starp produktivitāti un pieauguma plastiskumu (Cuny et al., 2019). Marta temperatūras ietekme, kas skaidrojama ar sakņu attīstību (Hardy et al., 2001; Tierney et al., 2001; Zadworny et al., 2016), arī bija stiprāka ātraudzīgākajām proveniencēm.

Jūnijā noris strauja pieauguma veidošanās (Rossi et al., 2006; Jyske et al., 2014), ko ierobežo nokrišņi un pieejamā saules radiācija (Strand et al., 2006; Young et al., 2010). Tas izskaidro novēroto reakciju uz paaugstinātu SPEI, kas bija izteikta ātraudzīgākajām proveniencēm. No otras puses, lēnaudzīgāko provenienču zemākā jutība uz jūnija apstākļiem saistāma ar konservatīvāku augšanas stratēģiju, kad koki asimilātus iegulda aizsardzības mehānismos (Prendin et al., 2018; Vazquez-Gonzalez et al., 2020). Reakcija uz vasaras temperatūru bija zvanveida, kas liecina par līdzsvaru starp asimilācijas intensitāti un mitruma pieejamību (Allen et al., 2015; Yang et al., 2015; Cuny et al., 2019), pret ko mazproduktīvas provenieces (ar izcelsmi no kalnu reģiona) bija jutīgākas.

Kopumā pozitīvā pieauguma atbildes reakcija uz iepriekšējā gada jūnija temperatūru ir skaidrojama ar papildu barības vielu asimilāciju un rezervju veidošanos, kas sekmē EW veidošanos nākamajā gadā (Sala et al., 2012; von Arx et al., 2017). Šāda atbildes reakcija bija izteiktāka lēnaudzīgajām proveniencēm, norādot uz konservatīvāku augšanas stratēģiju un lielāku atkarību no rezerves barības vielām (Martin et al., 2010; von Arx et al., 2017). Apstākļi iepriekšējās veģetācijas sezonas izskaņā ietekmēja augšanas reprodukcijas līdzsvaru (Hacket-Pain et al., 2018), un šāda saikne konservatīvisma dēļ bija izteiktāka lēnaudzīgākajām proveniencēm (Reid et al., 2004). Attiecīgi, augstāka pieauguma jutība pret galvenajiem meteoroloģiskajiem mainīgajiem norāda uz ātraudzīgāko provenienču spēju plastiski pielāgot augšanu tekošajiem apstākļiem, vienlaikus saglabājot atkopšanās kapacitāti. Tādējādi pieauguma plastiskums ir būtisks paātrinošos klimata pārmaiņu kontekstā (Corcuera et al., 2011; Valladares et al., 2014; Arnold et al., 2019).

Laikapstākļu klimatisko ekstrēmu biežuma pieaugums, klimatiskajiem gradientiem mainoties (Sass-Klaassen et al., 2016; Jetschke et al., 2019), uzsver augšanas resilienci kā priekšnosacījumu genotipu ilgtspējai (Schwarz et al., 2020; van der Maaten-Theunissen et al., 2021). Identificētie PY, kas reprezentē krasas pieauguma izmaiņas saistībā ar meteoroloģiskām anomālijām (Jetschke et al., 2019; Schwarz et al., 2020), kopumā bija maz izteikti (Raksts V), pētītajiem kokiem augot labvēlīgos apstākļos. Identificētie PY korelēja ar miera perioda temperatūras, iepriekšējā veģetācijas perioda beigu un vasaras nokrišņu daudzuma anomālijām, norādot uz kompleksām ietekmēm. Tomēr novērotās korelācijas bija specifiskas stādījumiem, līdzīgi, kā novērots ikgadējai mainībai (Raksti III, IV). Stiprākie PY, savukārt, ir saistāmi ar vairāku temperatūras un nokrišņu anomāliju līdziestāšanos (Raksts V), liecinot par neuzņēmību pret individuālām anomālijām (Valladares et al., 2014; Jetschke et al., 2019; de la Mata et al., 2022).

Aprēķinātie resiliences indeksi pieaugumam PY Latvijā (5. attēls) bija salīdzināmi ar aprēķinātajiem pieaugumiem citām provenicencēm Vācijā (Taeger et al., 2013), norādot uz saildzināmu pieauguma toleranci pret vides mainību (Lloret et al., 2011). Aprēķināto indeksu vērtības bija mērenas (*cf*. Schwarz et al., 2020), liecinot par pieauguma samazinājumu pēc traucējuma. Šāds novērojums varētu būt arī saistītas ar vecuma trendu TRW, jo analizētie koki bija jauni (Konter et al., 2016). Proveniencei bija būtiska ietekme uz pieauguma rezistenci un resilienci negatīvajos PY, kas saskanēja ar produktivitāti, apliecinot pieauguma plastiskumu kā nozīmīgu genotipu produktivitātei un ilgtspējas nodrošināšanai. Samazināta resilience norāda, ka nelabvēlīgi apstākļi spēj samazināt pieaugumu uz vairākiem gadiem tieši lēnaudzīgajām provenicencēm, mazinot to konkurētspēju (Reid et al., 2004; Lloret et al., 2011). Tomēr būtiskā provenieces un gada mijiedarbība norādīja uz provenienču specifisku jutību/uzņēmību pret vides meteoroloģiskajām anomālijām.

3.3.3. *Koksnes anatomija*

Stumbra koksnes, kas ir ūdens transporta artērija, anatomija nosaka koka hidraulisko arhitektūru un funkcionēšanu dzīves laikā (Tyree and Zimmermann, 2002; Cuny et al., 2019), raksturojot jutību pret mitruma apstākļu izmaiņām (Corcuera et al., 2011; Moran et al., 2017; Gennaretti et al., 2022). Anatomiskās struktūras pielāgošanas plastiskums ir saistāms ar genotipu adaptācijas spējām (Fonti et al., 2010; Martin et al., 2010; Gennaretti et al., 2022). Ņemot vērā, ka hidrauliskā arhitektūra ir nozīmīga izdzīvošanai ilgtermiņā, pētīto provenienču koksnes anatomija parādīja lokālas ģenētiskās adaptācijas iezīmes, par ko liecināja būtiska provenieces ietekme uz CWT un LA gan LW, un it īpaši EW (Raksts VI). Šīs ietekmes bija proporcionālas produktivitātei, apliecinot plastiskuma saiknes ar produktivitāti pat šaurākā (Latvijas) klimatiskajā gradientā. Provenicencēm specifiska koksnes anatomija apliecina ģenētiski noteiktu jutību pret mitruma režīmu (Lenz et al., 2010; Martin et al., 2010; Hong et al., 2015).

Ātraudzīgākajām provenicencēm traheīdām bija lielāks LA un konduktivitāte, bet CWT bija zemāks (6. attēls). Lai arī šāda koksnes struktūra veicina uzņēmību pret kavitāciju un funkciju zudumu (Sperry and Tyree, 1990; Pittermann and Sperry, 2003; Popkova et al., 2018), tā ļauj nodrošināt konduktivitāti ar minimālu ogļhidrātu izmantošanu (Eilmann et al., 2009; Martin et al., 2010). Attiecīgi, ātraudzīgākas provenieces spēja efektīvāk izmantot asimilātus, par ko liecināja negatīva korelācija starp CWT un LA. Savlaicīga ksiloģenēzes pielāgošana ļauj kompensēt nelabvēlīgu apstākļu izraisītus bojājumus (Cuny et al., 2019), uzlabojot produktivitāti, kas bija izteikti vērojams produktīvajai RYT. Lēnaudzīgākās provenieces veidoja koksni ar mazāku LA un biezāku CWT, kas nodrošina augstāku mehānisko izturību un hidraulisko integritāti, vienlaikus mazinot konduktivitāti. Ņemot vērā mazāku TRW, šāda koksnes struktūra neļāva izmantot vides potenciālu augšanai pie optimāliem apstākļiem (Tyree and Zimmermann, 2002;

Eilmann et al., 2009; Anfodillo et al., 2013), kavējot augšanu, veidojot negatīvu atbildes cilpu un tādējādi mazinot konkurētspēju (Lebourgeois et al., 2014; Prendin et al., 2018). Laika rindu analīze parādīja proveniencēm specifiskas korelācijas starp koksnes anatomijas raksturlielumiem un meteoroloģiskajiem mainīgajiem, kas liecina par tiešu un pārneses ietekmi (Mayr et al., 2003; Anderegg et al., 2015; Cuny et al., 2019). Meteoroloģisko apstākļu ietekmes pārnese norāda, ka koksnes anatomija un līdz ar to uzņēmība pret mitruma apstākļiem vismaz daļēji ir atkarīga no iepriekšējiem apstākļiem, kā arī ģenētiskajiem faktoriem (Eilmann et al., 2009; Martin et al., 2010; Housset et al., 2018). Šāda ietekmes pārnese, savukārt, ietekmē koksnes anatomijas plastiskumu un funkcionalitāti (Corcuera et al., 2011; Anfodillo et al., 2013; Prendin et al., 2018).

Meteoroloģiskajiem mainīgajiem novērota izteiktāka saikne ar LA nekā ar CWT (galvenokārt LW), it īpaši skarbāka klimata apstākļos. Iepriekšējās vasaras, miera perioda un vasaras sākuma temperatūrai, savukārt, bija saistības ar EW anatomiju, norādot uz tiešu ietekmi un tās pārnesi (de Micco et al., 2019; Harvey et al., 2020). Šādas saistības var būt arī gruntsūdens līmeņa mainības artefakts (Hardy et al., 2001; Tierney et al., 2001). Tieša meteoroloģisko apstākļu ietekme vērojama uz LW anatomiju, kas bija jutīga pret vasaras temperatūru un nokrišņiem, liecinot par plastisku ksiloģenēzes pielāgošanu augšanas sezonas gaitā (Cuny et al., 2019; Ferriz et al., 2023).

Ātraudzīgākajām proveniencēm piekrastes klimatā LA un CWT, kas veidojās EW, korelēja ar nokrišņu daudzumu martā, temperatūru februārī, bet lēnaudzīgajām proveniencēm šādas korelācijas novērotas skarbākā (kontinentālākā) klimatā. Šādas saistības ir skaidrojamas ar augsnes temperatūras ietekmi uz sakņu attīstību, kas nosaka uzņēmību pret mitruma apstākļiem (Hardy et al., 2001), kā arī ziemas embolizēšanos (Pittermann and Sperry, 2003). Ātraudzīgāko provenienču LA korelēja ar temperatūru aprīlī un jūnijā piekrastes klimatā, bet lēnaudzīgajām proveniencēm – arī kontinentālā klimatā. Jūnija temperatūrai bija būtiska ietekme uz LA un CWT, kas atradās LW, kas skaidrojama ar tiešu temperatūras ietekmi uz koksnes šūnu izplešanos (Rossi et al., 2006; Jyske et al., 2014). Piekrastes un iekšzemes klimatā nokrišņiem un SPEI augustā novērota korelācija ar LA ātraudzīgajām proveniencēm, bet ar CWT – lēnaudzīgajām proveniencēm. Novērotās saistības liecina, ka koksnes anatomijas fenotipiskais plastiskums un genotipu spēja ar minimālu asimilātu izmantošanu nodrošināt maksimālu koksnes konduktivitāti ir īpaši nozīmīgi pielāgojumi pieaugošas vides mainības apstākļos (Eilmann et al., 2009; Martin et al., 2010; Cuny et al., 2019), kam ir potenciāls uzlabot mežu ilgtspēju nodrošinot adaptēties spējīgāku reproduktīvo materiālu.

3.3.4. Koksnes anatomijas anomālijas un salnas

Veģetācijas perioda pagarināšanās paaugstina vēlu un agru salnu ietekmi (Gu et al., 2008; Augspurger, 2009; Meier et al., 2022). Mērenā klimata apstākļos salnas ir uzskatāmas par nozīmīgu klimatisko risku genotipu pārnesei, jo uz ziemeļiem pārnestajiem genotipiem, kas ir produktīvāki, ir ilgāka veģetācijas sezona

(Schreiber et al., 2013; O'Neill et al., 2014; Berlin et al., 2016; Hayatgheibi et al., 2020). Salnu bojājumu iezīmes bija novērotas pētīto provenienču koksnē (Raksts VII). References periodā sala bojājumu ikgadējā iespējamība stādījumos Latvijā bija zema (0,025, *cf*. Payette et al., 2010; Kidd et al., 2014; Piermattei et al., 2015), lai arī tā bija izteikti augstāka kontinentālākā klimatā (7. attēls). Piekrastes LI stādījumā novērotas vien retas ar salnām saistītas koksnes anomālijas, bet kontinentālākajā KA stādījumā to ikgadējā iespējamība pārsniedza 0,07 (kas bija pat divas reizes augstāka, īpaši kamēr koki bija jaunāki par 25 gadiem). Ar salnām saistīto koksnes anomāliju iespējamība samazinājās, kokiem novecojot, līdz ar vainagu saslēgšanos un kreves veidošanos, kas aizsargā kambiju (Payette et al., 2010; Kidd et al., 2014). Visas BR novērotas vēlajā LW, bet vairums no FR bija vidējā EW, izceļot agru un vēlu salnu ietekmes (Kidd et al., 2014; Piermattei et al., 2015). Jāpiezīmē, ka BR bija biežāk nekā FR, norādot uz augstāku uzņēmību pret agrām salnām, kas saistāms ar vēlāku salcietības attīstību pasiltināšanās ietekmē (Beck et al., 2004; Schreiber et al., 2013; Berlin et al., 2016; Hayatgheibi et al., 2020).

Provenience, kā arī provenieces un stādījuma mijiedarbība ietekmēja BR un FR (7. attēls), norādot uz genotipu salnu uzņēmības ģenētisko adaptāciju un fenotipisko plastiskumu (Augspurger, 2009; Schreiber et al., 2013; Ahrens et al., 2020; Szeligowski et al., 2023). Koksnes anomāliju iespējamība bija saistīta ar produktivitāti, bet ne izcelsmes vietas klimatiskajiem apstākļiem, apliecinot jutības-produktivitātes saistības (Valladares et al., 2014; Matias et al., 2017; Housset et al., 2018). Lēnaudzīgākās provenieces (DIP un EBN), kuru izcelsme ir no kalnu apgabaliem, bija uzņēmīgākas pret salnām, bet ātraudzīgākajās proveniencēs, kuru izcelsme ir no piejūras klimata, novērotas vien dažas anomālijas. Saistības starp koksnes anomālijām un temperatūras minimumiem bija neizteiktas, visticamāk, mikroklimatisko apstākļu dēļ (Charrier et al., 2015). Tomēr šādas saistības bija izteiktākas lēnaudzīgākajām proveniencēm (DIP) siltāka klimata (ZV stādījums) apstākļos. Šīs saistības būtiskas bija vietējai KAL proveniencei tās izcelsmes apvidū, ko reprezentēja KA stādījums, kur savukārt pārnestās provenieces bija mazāk ietekmētas. Lokālā provenience, kas tiek uzskatīta par adaptējušos vietējiem apstākļiem, parādīja vidēju koksnes anomāliju biežumu. Šādas saistības skaidrojamas ar veģetācijas sezonas paildzināšanos (Schreiber et al., 2013; Berlin et al., 2016), vienlaikus norādot uz izteikto ziemeļu populāciju uzņēmību pret klimata pārmaiņām (Isaac-Renton et al., 2018; Montwe et al., 2018), kā arī uz nepieciešamību pēc genotipu pārneses (Aitken and Bemmels, 2016; Hayatgheibi et al., 2020).

3.3.5. Augšanas jutības iedzimstamība

Plašās nozīmes iedzimstamības novērtējums, kas balstīts ierobežotā genotipu/provenienču izlasē, var būt neprecīzs (Falconer and MacKay, 1996; Loha et al., 2006; Leites et al., 2012), tomēr tas uzskatāms par pazīmju ģenētiskās kontroles izziņas sākumposmu (He et al., 2023). Pazīmju dispersijas atdalīšana, kas ir kvantitatīvās ģenētikas statistiskais pamats, ļauj kvantificēt ģenētiskās, t.s., G × E ietekmes, ļaujot novērtēt fenotipisko plastiskumu un adaptācijas spējas (Li et al., 2017; Arnold et al., 2019; Ansarifar et al., 2020). Pieauguma jutība ir atkarīga no gēnu ekspresijas un genotipa, līdz ar to pieauguma un meteoroloģisko apstākļu saistības ir kumulatīvs genotipa un vides saderības raksturlielums (Burdon and Klapste, 2019; Hayatgheibi et al., 2019; Ahrens et al., 2020). Ņemot vērā radiālajā pieaugumā novērotās lokālās adaptācijas iezīmes (Raksti I–VII), pieauguma un meteoroloģisko apstākļu korelācijām, kas reprezentē "normālo" pieauguma mainību, aprēķināti iedzimstamības rādītāji (Raksts VIII). Korelācijām ar mērenu H^2 CVP pārsniedza 0,40 (1. tabula), norādot uz vērā ņemamu pieauguma jutības uzlabošanas potenciālu (Loha et al., 2006; Jansson et al., 2017; Grattapaglia et al., 2018), līdzīgi kā novērots morfometriskajām pazīmēm reģionā (Baliuckas et al., 2004; Jansons and Baumanis, 2005; Jansson et al., 2017). Jutības iedzimstamība norāda uz potenciālu mazināt pieauguma atkarību no klimata, uzlabojot parastās priedes audžu ilgtspēju (Jansson et al., 2017; Grattapaglia et al., 2018; Heer et al., 2018; Housset et al., 2018).

Augstākie iedzimstamības rādītāji kopumā konstatēti galvenokārt pieauguma saistībām ar meteoroloģiskajiem mainīgajiem, kas raksturo vasaras mitruma apstākļus, liecinot par selekcijas potenciālu mazināt galvenos klimatiskos riskus (Allen et al., 2015; Montwe et al., 2018; Harvey et al., 2020). Novērotā ģenētiskā ietekme apliecina mitruma režīma eksistenciālo nozīmi izplatības vidusdaļā augošajām populācijām (Way and Oren, 2010; Carvalho et al., 2017; Isaac-Renton et al., 2018; Ferriz et al., 2023). Pieauguma jutībai pret ziemas temperatūru, kam bija sekundāra ietekme uz pieaugumu (Raksts III), konstatēta par vidējo rādītāju augstāka iedzimstamība (1. tabula; Raksts VIII), norādot uz iespēju uzlabot genotipu pārziemošanas efektivitāti (Beck et al., 2004; Hänninen et al., 2013; Ahrens et al., 2020). Mērena iedzimstamība novērtēta jutībai pret iepriekšējās vasaras beigu apstākļiem, kas nosaka pieauguma aizmetņu veidošanos (Lanner, 1976), liecinot par sēklu gadu iniciējošo mehānismu ģenētisku kontroli (Hacket-Pain et al., 2018). Jutība pret iepriekšējā jūnija nokrišņiem, kas var tikt saistīti ar barības vielu rezervi (Sala et al., 2012; von Arx et al., 2017), norāda uz augšanas stratēģijas iedzimstamību. Attiecībā uz iepriekšējā rudens nokrišņiem, iedzimstamību ir grūti pamatot, jo koki, visticamāk, ir miera periodā (Beck et al., 2004; Hänninen et al., 2013); iespējams, tas ir kolineāru saistību artefakts. Jāatzīst, ka ierobežotās genotipu kopas dēļ, ģenētiskās korelācijas starp pieauguma jutības pazīmēm netika aprēķinātas, tādējādi ierobežojot ģenētisko mijiedarbību apzināšanu (Hong et al., 2015).

Meteoroloģisko anomāliju, it īpaši to, kas ir saistītas ar vasaras mitruma apstākļiem, salu un salnām, pastiprināšanās un ar to saistītie mežsaimniecības riski (Allen et al., 2015; Isaac-Renton et al., 2018; Montwe et al., 2018) var tikt mazināti mērķtiecīgas selekcijas ceļā (Raksts VIII). Tomēr, lai pārciestu anomālijas, var tikt izmantoti specifiski genoma apgabali (Dering et al., 2017; Tyrmi et al., 2020), tādēļ šo atbildes reakciju iedzimstamība ir jāvērtē tieši (Ahrens et al., 2020; de la Mata et al., 2022). Pieauguma relatīvās izmaiņas, ko apraksta PY (Jetschke et al., 2019; Schwarz et al., 2020), gados ar vairāku anomāliju sakritību, uzrādīja zemu iedzimstamību (Raksts IX). Tomēr iedzimstamībai bija tendence paaugstināties gadu vai divus pēc PY, norādot uz pieauguma resilences un atkopšanās, bet ne noturības ģenētisku kontroli (Lloret et al., 2011; Jetschke et al., 2019; Schwarz et al., 2020). Iedzimstamības izpausmes nebija telpiski un laikā stacionāras, kas skaidrojams ar atšķirīgajiem pieauguma izmaiņu (PY) cēloņiem. Ziemas temperatūras anomālijas bija izteiktāki ģenētisko ietekmju palaideļēji (Henttonen et al., 2014; Montwe et al., 2018; Baniulis et al., 2020), neskatoties uz palielinošos sausuma nozīmi priedes pieaugumam (Allen et al., 2015), liecinot par augošiem sala riskiem, klimatam pasiltinoties (Gu et al., 2008; Augspurger, 2009).

Lokālās iedzimstamības izpausmju iezīmes, kā arī dispersijas komponentes parādīja izteiktas pieauguma atbildes reakcijas uz meteoroloģiskajām anomālijām fenotipisko plastiskumu (G × E), liecinot par populāciju spēju adaptēties vides pārmaiņām vidējā termiņā (Li et al., 2017; Hayatgheibi et al., 2019; Chmura et al., 2021). Apskatot visu references periodu kopumā, provenieces dispersijas komponente bija zema, kas skaidrojams ar G × E, kā arī izteikto lokālo apstākļu ietekmi (Charrier et al., 2015). Relatīvo pieauguma izmaiņu dispersijas komponentes parādīja izteiktāku G × E, un līdz ar to pazīmes fenotipisko plastiskumu, norādot uz selekcijas potenciālu lokāli uzlabot augšanas toleranci (Baliuckas et al., 2004; Jansson et al., 2017; Grattapaglia et al., 2018; Burdon and Klapste, 2019).

4. SECINĀJUMI

1) Meteoroloģiskajiem apstākļiem, kas saistīti ar ziemas temperatūras un vasaras nokrišņu režīmu, ir kompleksa ietekme uz Baltijas jūras reģiona austrumu daļas parastās priedes vietējo populāciju pieaugumu audzēs ar labi drenētām minerālaugsnēm.
2) Reģionālā mērogā pieauguma saistības ar meteoroloģiskajiem apstākļiem ir nelineāras, norādot uz neproporcionālu sagaidāmo klimata pārmaiņu ietekmi uz parastās priedes augšanu. Novērtētās pieauguma atbildes reakcijas un barības vielu rezervju apjoms liecina par lokālo populāciju potenciālu vidējā termiņā pielāgoties vides izmaiņām.
3) Baltijas jūras reģiona austrumu daļas parastās priedes pieauguma jutība pret meteoroloģiskajiem apstākļiem ir saistīta ar lokālu ģenētisku adaptāciju. Populācijas parāda atšķirīgu jutību pret galvenajiem pieaugumu ietekmējošajiem meteoroloģiskajiem apstākļiem un to ekstrēmiem. Tikai vairāku meteoroloģisku anomāliju sinerģija izraisa straujas pieauguma izmaiņas, apliecinot sugas toleranci.
4) Genotipu ātraudzība ietekmēja pieauguma jutību, norādot uz Baltijas jūras reģiona austrumu daļas parastās priedes populāciju jutības un produktivitātes saistībām. Ātraudzīgākajām proveniencēm novērota augstāka jutība pret ikgadējo laikapstākļu mainību, kā arī to ekstrēmiem, norādot uz pieauguma plastiskuma nozīmi genotipu ilgtspējai.

5) Pieauguma un meteoroloģisko apstākļu, kā arī jutības un produktivitātes mijiedarbības ir saistāmas ar koksnes veidošanās specifiku. Ātraudzīgākās proveniences ir plastiskākas koksnes anatomijas un, līdz ar to, arī koksnes funkcionalitātes ziņā, kas nodrošina operatīvu augšanas regulāciju atbilstoši mitruma apstākļiem. Šādas īpašības nodrošina ātru atjaunošanos pēc nelabvēlīgiem traucējumiem.

6) Uz ziemeļiem pārnesto genotipu uzņēmība pret salnu bojājumiem ir atkarīga no pieauguma plastiskuma. Lai arī ātraudzīgāko provenienču izcelsmes vietā ir maigāks klimats, tās bija mazāk pakļautas salnu bojājumiem, salīdzinot ar genotipiem, kuru augšanas stratēģija ir konservatīvāka. Vietējie genotipi, klimatam kļūstot siltākam, parādīja paaugstinātas jutības pret salnām iezīmes.

7) Pieauguma jutībai pret nozīmīgāko meteoroloģisko apstākļu ikgadējo mainību konstatēta mērena ģenētiska kontrole, kas visizteiktāk izpaužas saistībā ar vasaras mitrumu noteicošajiem apstākļiem. Jutībai pret meteoroloģisko apstākļu ekstrēmiem bija vāja ģenētiskā kontrole, bet ģenētiskās ietekmes izpaudās nākamajos gados, parādot saistību ar augšanas atjaunošanos un resilienci. Tātad kokaugu selekcijai ir potenciāls uzlabot pieauguma plastiskumu un meteoroloģisko toleranci, tādējādi sekmējot sekmējot mežu ilgtspēju nodrošinot adaptēties spējīgāku reproduktīvo materiālu.

5. REKOMENDĀCIJAS

1) Pieauguma plastiskums un jutība pret vasaras mitruma apstākļiem ir selekcijas indeksā perspektīvi iekļaujamas pazīmes, kas var sekmēt reproduktīvā materiāla adaptīvo potenciālu pieaugošas vides mainības apstākļos.

2) Ņemot vērā pieauguma plastiskumu un resilienci, produktīvākie uz ziemeļiem pārnestie genotipi, atbilstoši vairāku stādījumu konsolidētajam vērtējumam, uzrāda augstu potenciālu un būtu iekļaujami selekcijas populācijā, tādējādi sekmējot tās ilgtspēju.

3) Jutības-produktivitātes saistību izpēti vēlams paplašināt, iekļaujot lielāku pārnesto genotipu kopu, tādējādi nodrošinot optimālās pārneses attāluma novērtējumu selekcijas populācijas papildināšanai.

4) Reģiona un lokālo populāciju ģenētiskās daudzveidības adaptīvās selekcijas potenciāla novērtējumam, pieauguma jutības un plastiskuma rekombinācijas īpašību raksturošanai vēlama pēcnācēju pārbaužu stādījumu analīze, tādējādi raksturojot lokālo populāciju adaptēšanās spēju robežas.

PATEICĪBAS

Autors pateicas tehniskajam personālam, kas palīdzēja ievākt materiālu un iegūt pētījuma datu kopas. Pateicība arī līdzautoriem un zinātniskajai komandai par ieteikumiem un konstruktīvo kritiku. Autors izsaka atzinību darba vadītājam par konstruktīvajām idejām un kritiku, kā arī veltīto laiku un mentālajiem resursiem pētījuma realizācijas gaitā. Autors ir pateicīgs saviem vecākiem par radību un audzināšanu, kā arī sievai par spējām viņu paciest radošā procesa laikā, kā arī ikdienā. Visbeidzot, mecenāta atbalsts bija noderīgs un iedrošinošs.

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I **Matisons, R.**, Elferts, D., Krišāns, O., Schneck, V., Gärtner, H., Bast, A., Wojda, T., Kowalczyk, J., Jansons, Ā. 2021. Non-linear regional weather-growth relationships indicate limited adaptability of the eastern Baltic Scots pine. Forest Ecology and Management, 479, 118600; 10.1016/j.foreco.2020.118600.

II **Matisons, R.**, Dubra, S., Dauškane, I., Bičkovskis, K., Jansons, Ā., Gärtner, H. 2021. Canopy status modulates formation of wood rays in Scots pine under hemiboreal conditions. Dendrochronologia, 67, 125822; 10.1016/j.dendro.2021.125822.

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Forest Ecology and Management 479 (2021) 118600

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Non-linear regional weather-growth relationships indicate limited adaptability of the eastern Baltic Scots pine

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ARTICLE INFO

Keywords:
Pinus sylvestris
Climate-growth relationships
Phenotypic plasticity
Radial increment
Climatic gradient

ABSTRACT

Under changing climate, temporal and spatial stability (stationarity) of growth responses of trees to weather and climate, which has often been presumed without explicit testing, is crucial for prediction of productivity and sustainability of forests. However, considering evolutionary adaptation of tree populations to wide spatio-temporal ecological gradients, extrapolation of linear responses, which could be observed in limited parts of the gradients (certain locality), can result in biased results. Accordingly, the plasticity of responses of tree-ring width of the eastern Baltic populations of Scots pine (*Pinus sylvestris* L.) to meteorological conditions across the regional climatic gradient was assessed using a mixed generalized additive model. The linear responses were assessed using a bootstrapped correlation analysis for comparison. The radial growth responses of the eastern Baltic population of Scots pine showed explicit regional gradients according to the local climates, indicating gradual shifts in the effects of winter temperature and summer moisture regime. Accordingly, temperature in late-winter and summer, as well as summer water deficit were identified as the main regional drivers of tree-ring width. Their effects were generally non-linear, indicating explicit spatiotemporal gradients in growth responses in the mid-part of species distribution. This also implied limited efficiency of simple linear models for the assessment of radial growth under moderate conditions. The responses to summer temperature indicated local optima, while the responses to drought index showed threshold values. The responses to winter temperature indicated positive effect of warming on growth. In some stands, specific non-stationary responses though were evident, suggesting that trees have adapted (specialized) to certain local climatic conditions, which are changing and thus explaining temporal shifts in growth responses. Nevertheless, the estimated responses suggested phenotypical adaptability limits of the eastern Baltic populations of Scots pine in a longer term, supporting the necessity of climate-smart management for sustainability of forest in the region in the future.

1. Introduction

The effects of climate and weather as the major determinants of tree growth have been extensively studied during the recent decades, yet they are still topical in the context of the ongoing global changes (Wilmking et al, 2020; Zhang et al., 2018; Cavin and Jump, 2017; Matias et al., 2017; Restaino et al., 2016). Due to convenience, tree-ring width (TRW) has been a widely applied proxy in such studies (Zhang et al., 2018; Heer et al., 2018; Housset et al., 2018; McCullough et al., 2017; Henttonen et al., 2014). The information about growth responses to meteorological conditions has been widely applied for the reconstructions of environments in the past, as well as for the predictions of future forest growth (Buras and Menzel, 2019; Zhang et al., 2018; Wilmking et al., 2017; Fonti and Jansen, 2012), thus assessing dynamics of ecosystems (Seddon et al., 2016). Such estimates are based on the uniformitarianism principle, which implies that the reaction of trees is constant (i.e., uniform) in time and space (Wilmking et al., 2017), sometimes even presuming linearity of growth responses due to simplicity of interpolations (Wilmking et al., 2020). However, the ecological and physiological responses are prevailingly non-linear, e.g., bell-

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https://doi.org/10.1016/j.foreco.2020.118600
Received 23 July 2020; Received in revised form 7 September 2020; Accepted 8 September 2020

shaped, etc. (Wilmking et al., 2020; Hofgaard et al., 2019; Billings et al., 2015; Lloyd et al., 2013), which also adhere to the uniformitarianism principle (Wilmking et al., 2017).

Close-to-linear responses can be observed in distinct parts of ecological gradients (Lloyd et al., 2013; Way and Oren, 2010; Loehle, 1998). Accordingly, the non-linearity of population response, which is observable across a wider gradient, might be interpreted as the non-stationarity of local linear responses, if the gradient is shifting, as in the case of climate, thus biasing extrapolation (Wilmking et al., 2020; Fei et al., 2017; Konter et al., 2016). Therefore, generalization of growth responses presuming their plasticity based on extensive datasets across spatiotemporal gradients, as in regional tree-ring datasets (Harvey et al., 2020; Hofgaard et al., 2019; Cavin and Jump, 2017; Restaino et al., 2016; Lloyd et al., 2011), can greatly improve the accuracy of extrapolations under shifting conditions (Wilmking et al., 2020; McCullough et al., 2017; Valladares et al., 2014; Lloyd et al., 2013; Wang et al., 2010). Such extrapolations are concurring on increasing and disproportional consequences of warming, in marginal as well as core areas of species' ranges (Wilmking et al., 2020; Cavin and Jump, 2017; Restaino et al., 2016; Seddon et al., 2016). Accordingly, presumption of simple linear weather-growth relationships appear outdated, particularly when assessing tree growth under rapidly changing climate.

As long lived organisms, trees have evolutionary adapted to a greatly fluctuating environments via phenotypical plasticity of structural and physiological responses (Nabais et al., 2018; Aitken and Bemmels, 2016), which modulate sensitivity of growth (Cuny et al., 2019; Matisons et al., 2019, 2017; Cavin and Jump, 2017). Being of adaptive importance, the plasticity of responses is often genetically determined, resulting in local specialization of (meta)populations (Chauvin et al., 2019; Nabais et al., 2018; Valladares et al., 2014; Lloyd et al., 2011). For the wide-spread tree species, the genetically determined specialization of populations, which persists under high gene flow (Chauvin et al., 2019; Moran et al., 2017), can restrict plasticity to match certain environments (Li et al., 2018; Cavin and Jump, 2017; Lloyd et al., 2011), resulting in uneven adaptability (Cavin and Jump, 2017; Dering et al., 2017; Valladares et al., 2014; Martin et al., 2010). This also presumes existence of local optimum conditions.

Due to the accelerating climatic changes, the rate of evolutionary adaptation of local populations appears to be lagging behind (Bolte et al., 2009), subjecting trees to 'extreme' conditions *in situ* (Aitken and Bemmels, 2016). Accordingly, adaptive climate-smart management appears necessary to sustain forests (they productivity) in the future (Nabuurs et al., 2018). This is particularly under intensifying meteorological extremes (Hartmann et al., 2013), which shape species distribution (Bolte et al., 2009; Loehle, 1998). Under such circumstances, information about the plasticity of responses of native tree populations is crucial for assessment of their adaptability limits and local-scale performance in the future (Cavin and Jump, 2017; Booth, 2016; Mina et al., 2016; Restaino et al., 2016; Wang et al., 2010).

Shifts in sensitivity (plasticity of linear relationships) of tree growth to meteorological conditions have been generally related to tree ageing (Trouillier et al., 2019; Konter et al., 2016; Wu et al., 2013) and climatic changes (Matias et al., 2017; Matisons et al., 2017; Ohse et al., 2012; Carrer and Urbinati, 2006), thus representing temporal gradient (plasticity). The age-related changes in sensitivity of trees have been related to the increase in size and the adjustments in wood architecture to support the ascending and growing foliage (Trouillier et al., 2019; Matisons et al., 2017; Vieira et al., 2009). The age/size-related growth responses, however, are adding noise to reconstructions and growth predictions, which could be accounted by producing more complex statistical models (Trouillier et al., 2019; Konter et al., 2016). Such shifts can also modulate interactions between certain environmental factors (Hofgaard et al., 2019; Fei et al., 2017).

The effects of climatic changes on growth responses have been often related to the temperature stress and moisture deficit, particularly in dry environments, as warmer temperature increases evapotranspiration and thus water loss, especially in anisohydric species (Restaino et al., 2016; Ohse et al., 2012; Carrer et al., 2010). For instance, negative growth reaction to temperature is intensified by water deficit, as trees cannot transpire sufficiently; however, under cold conditions, temperature can have a positive effect (Cavin and Jump, 2017; Ohse et al., 2012; Lloyd et al., 2011). This highlights the non-linear effects of meteorological conditions on growth across a climatic gradient (Wilmking et al., 2020). Furthermore, due to the warming, such interactions have been observed also in the regions where tree growth is considered to be limited by low temperature and trees have genetically specialized to local conditions (e.g., boreal forests) (Henttonen et al., 2014; Lloyd et al., 2013; Ohse et al., 2012), highlighting complexity of weather-growth interactions (Harvey et al., 2020; Jansons et al., 2016; Friedrichs et al., 2009).

Weather-growth interactions have been considered complex particularly in the core-part of species' range, where climate is not considered strictly limiting, yet local or micro-site conditions modulate growth responses (Cuny et al., 2019; Weigel et al., 2018; Friedrichs et al., 2009). Contrastingly, high sensitivity to meteorological variables (particularly extremes) has also been shown for core populations due to local specialization (Cavin and Jump, 2017; Restaino et al., 2016). Nevertheless, this emphases presence of explicit, yet diverse gradients of tree growth responses to meteorological conditions (Harvey et al., 2020; Hofgaard et al., 2019; Restaino et al., 2016; Henttonen et al., 2014). In this respect, analysis of climatic rather than geographic gradients contributes to a better understanding of responses to tree populations to climatic changes, particularly at the regional scale (Cavin and Jump, 2017; Restaino et al., 2016; Henttonen et al., 2014).

Scots pine (*Pinus sylvestris* L.) is a wide-spread ecologically plastic and economically important species in Eurasia (Hytteborn et al., 2005). It has high genetic diversity and locally specialized, yet phenotypically plastic populations (Nabais et al., 2018; Dering et al., 2017; Martin et al., 2010), particularly in the Baltic region (Dering et al., 2017). Nevertheless, the abundance of the species has been predicted to decrease in the Eastern and Northern Europe (Buras and Menzel, 2019) due to the loss of competitiveness under intensifying environmental stresses (Loehle, 1998). In this regard, the eastern Baltic region is among the areas where decreases in the abundance of Scots pine have been predicted regardless of the mild climate and location in the mid-part of specie's range (Buras and Menzel, 2019), thus providing the possibility to estimate plasticity and adaptability of local populations (Harvey et al., 2020; Cavin and Jump, 2017; Aitken and Bemmels, 2016; Taeger et al., 2015; Valladares et al., 2014). Such regional scale analysis can also aid to the assessment of changes in growth under short-range assisted gene flow (Nabuurs et al., 2018; Matias et al., 2017; Aitken and Bemmels, 2016; Berlin et al., 2016).

This study aimed to assess the plasticity of TRW responses of maturing eastern Baltic Scots pine to main regional meteorological variables (temperature and precipitation related ones), accounting for the climatic gradients. We hypothesized that the effects of meteorological conditions affecting TRW were non-linear and were modulated by the local climates. We assumed that the responses to temperature showed a local maximum, while the responses to precipitation-related variables showed threshold values. We also hypothesized that ageing affected responses of the studied trees.

2. Material and methods

2.1. Study sites, sampling and measurements

To assess the spatiotemporal gradients in responses of TRW of the open-pollinated eastern Baltic Scots pine to the main regional climatic/weather drivers, 22 sites (forest stands with area > 1 ha) from five locations distributed at 400–700 km distance along a transect were selected for sampling (Fig. 1). The transect spread from southern

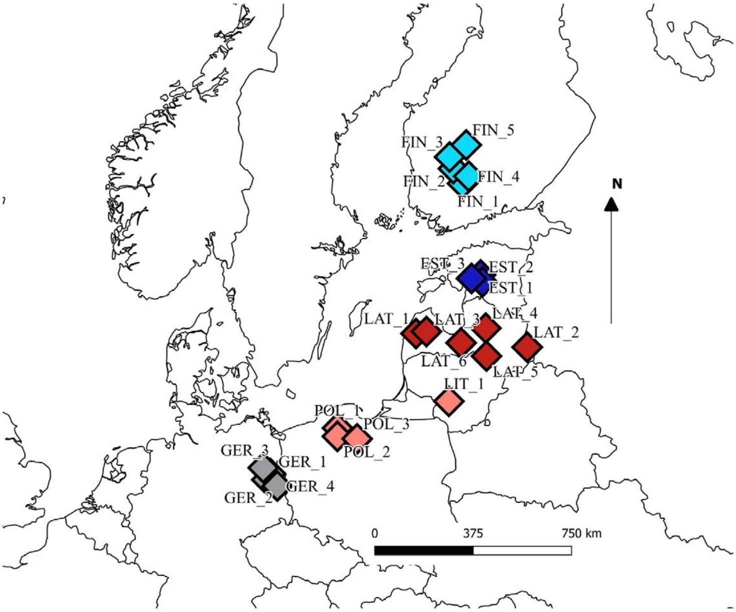

Fig. 1. Location of the studied eastern Baltics stands of Scots pine.

Table 1
Location, composition, and age of the studied stands of Scots pine.

Site	Latitude, ˚N	Longitude, ˚E	Admixture	Stand age	Main soil texture
FIN_1	61.81	24.31	–	129	Silty
FIN_2	61.81	24.31	–	97	Sand
FIN_3	61.83	24.21	Spruce, 10%	100	Sand
FIN_4	61.83	24.21	–	124	Silty
FIN_5	61.83	24.21	–	96	Silty
EST_1	58.79	25.38	–	90	Sand
EST_2	58.78	25.39	–	69	Sand
EST_3	58.79	25.39	–	83	Sand
LAT_1	56.99	21.76	–	83	Sand
LAT_2	56.58	27.85	Spruce, 30%	98	Silty
LAT_3	57.05	22.33	Spruce, 20%	102	Sand
LAT_4	57.15	25.58	–	95	Sand
LAT_5	56.31	25.62	Birch, 10%	109	Sand
LAT_6	56.71	24.23	–	113	Silty
LIT_1	54.91	23.56	–	94	Sand
POL_1	53.76	17.47	Birch, 20%	91	Silty
POL_2	53.79	17.46	Spruce, 10%	81	Sand
POL_3	53.71	18.54	–	103	Sand
GER_1	52.56	14.13	Birch, 30%	77	Silty
GER_2	52.55	14.14	–	93	Silty
GER_3	52.55	14.15	Spruce, 20%	120	Sand
GER_4	52.59	14.17	Birch, 10%	96	Silty

Finland to northern Germany, thus represented the hemiboreal and nemoral forest zones. One to six stands per location were sampled to account for the stand specifics of radial growth (Harvey et al., 2020; Weigel et al., 2018; Friedrichs et al., 2009). The selected stands (close canopy woodlands) were naturally regenerated and conventionally managed, and mostly represented inland conditions. The topography of the sites was flat, and they were growing in mesotrophic conditions on well-drained sandy or silty podzols (Table 1). The age of the stands ranged 69–129 years, which in Northern Europe corresponds to a maturing or mature Scots pine. The stands were dominated by Scots pine, yet some of them had a slight admixture of birch (*Betula* spp. L.) or Norway spruce (*Picea abies* Karst.).

The selected stands represented the regional climatic gradient from cold humid continental (southern Finland and the Baltic states) to temperate oceanic (northern Germany and Poland). The long-term (1988–2017) mean annual temperature ranged from 4.3 to 10.1 ˚C in the sites in the Southern Finland and Northern Germany, respectively (Table 2). February and July generally were the coldest and the warmest months, respectively; yet winter temperature regime generally expressed higher inter-annual variability compared to that in summer months (Harris et al., 2014). The mean annual precipitation was comparable among the sites, ranging 542–771 mm in sites in Southern Finland and Latvia, respectively. The intra-annual distribution of precipitation was similar among the sites; the highest monthly precipitation occurred during the vegetation period, and summer precipitation (May–September) comprised approximately half of the annual. During the last decades in the study region, the climatic changes were expressed as warming, particularly during the dormant period, resulting in an extension of the vegetation period; annual and summer precipitation showed a decreasing trend in Poland and Germany (Hartmann et al., 2013).

In each stand, wood samples (increment cores) from 15 to 30 healthy undamaged (i.e. without visual damage of crown and stem) dominant trees were collected using a 5-mm increment corer at 1.3 m height. Two increment cores were collected per tree from randomly oriented opposite sides of the stems avoiding reaction wood (tilted trees). In total, 620 trees (1240 cores) were sampled during the winter-spring period of 2017–2018. In the laboratory, samples (cores) were

Table 2
Climatic description of the studied sites by country (range of values is given). Data represents period 1988–2017. February and July are the coldest and warmest months, respectively. May–September period corresponds to vegetation period. Number of brackets indicate number of study sites.

	FIN (5)	EST (3)	LAT (6)	LIT (1)	POL (3)	GER (4)
Temperature, °C						
Mean annual	4.3–4.6	6.3–6.4	6.1–7.4	7.5	8.4–8.7	9.8–10.1
Mean annual, st. dev.	0.7–0.8	0.6–0.7	0.6–0.7	0.6	0.6–0.7	0.7–0.8
Mean February	–6.8 to –6.4	–3.9 to –3.7	–4.5 to –1.5	–2.4	0.4–0.5	1.9–2.1
Mean monthly minimum February	–10.5 to –9.8	−6.8 to –6.4	−7.5 to –3.8	−5.1	−2.3 to –2.0	–1.3 to –0.9
Mean monthly maximum February	–3.1 to –2.8	–1.1 to –1.0	–1.6–0.8	0.3	3.1–3.2	5.0–5.2
Mean July	16.7–17.2	17.9–18.0	17.5–18.2	18.6	17.7–18.3	19.3–19.7
Mean monthly minimum July	11.4–12.1	13.3–13.6	12.5–13.7	13.4	13.4–13.7	14.1–14.4
Mean monthly maximum July	22.1–22.5	22.4–22.7	21.4–23.6	23.7	22.1–23.1	24.5–25.2
Mean May-September	13.1–13.4	14.5–14.6	14.4–15.2	15.8	15.2–15.8	16.9–17.3
Mean monthly minimum May-September	7.9–8.5	10.0–10.3	9.4–10.8	10.7	10.8–11.2	11.7–12.1
Mean monthly maximum May-September	18.3–18.5	18.9–19.2	18.5–20.5	20.9	19.6–20.5	22.0–22.5
***Precipitation,* mm**						
Mean annual	542–587	698–703	640–771	634	584–682	562–593
Mean annual, st. dev.	60–66	81–82	74–90	71	71–81	76–78
Mean May-September	294–303	320–327	310–356	334	322–348	288–300
Mean May-September, st. dev.	57–59	61–65	58–70	63	62–70	65–66

fixed on wooden mounts using a water solvent glue. The surface of the fixed samples was prepared for TRW measurements using the WSL core microtome (Gärtner and Nievergelt, 2010) or by progressive grinding. Measurements were done manually, using the LINTAB 5 measurement system (RinnTECH, Heidelberg, Germany) with the 0.01 mm accuracy.

2.2. *Data analysis*

The quality of the TRW time-series was evaluated by a visual and statistical crossdating. Most of the time-series ($\geq 87\%$ per stand) were crossdated successfully and were used for the analysis. Mean sensitivity, first order (lag-1) autocorrelation, mean interseries correlation (r-bar), expressed population signal, and signal to noise ratio were calculated for description of the high-frequency variation of TRW based on detrended time-series (Bunn, 2008; Wigley et al., 1984). To assess the high-frequency variation of TRW (with the effects of ageing and disturbances removed), a residual chronology was produced for each stand (Cavin and Jump, 2017; Bunn, 2008). Double detrending with a negative exponential curve and a cubic spline (30% cut-off and wavelength of 2/3 of series length) followed by the prewhitening by an autoregressive model ('AR1') removing the effect of autocorrelation (previous growth; von Arx et al., 2017) was performed for individual time-series of trees. To produce TRW chronologies for stands, detrended time series of trees were pooled by the biweight robust mean (Bunn, 2008). Chronologies were analysed for the common period of 1954–2017, when the expressed population signal (calculated for 30-year moving windows) exceeded 0.85 (cf. Wigley et al., 1984).

To assess the linear relationships between high-frequency variation of TRW captured by the residual chronologies and meteorological variables, bootstrapped Pearson correlation analysis (nonparametric percentile interval bootstrapping with replication; 1000 iterations; Zang and Biondi, 2013) was performed for each stand. Temporal stability of the correlations was estimated using a moving bootstrapped correlation analysis with the 30-year time windows (lagged by one year, Zang and Biondi, 2013). The tested meteorological variables were monthly mean temperature, precipitation sums, and standardized precipitation evapotranspiration index (SPEI; Vicente-Serrano et al., 2010). These meteorological variables were arranged according to the time window from the previous June (preceding formation of tree-ring) to October in the year of tree-ring formation.

To assess the non-linearity and plasticity of the main responses of high-frequency variation of TRW to meteorological variables captured by the residual chronologies across the spatiotemporal gradients represented by the studied sites, a generalized additive mixed model was used (Wood, 2011). Such models are highly sufficient for the analysis of heterogenic ecological data representing wide spatiotemporal gradients (e.g., climate), assessing plasticity of the responses (Hofgaard et al., 2019; Cavin and Jump, 2017, Lloyd et al., 2013). The index values of the residual chronologies, which represent the relative additional radial wood increment, were used as the response variable. Different combinations of meteorological variables (used in the correlation analysis) were tested as the predictors, allowing fourth power of the smoothing function (i.e. basis dimension was set to four) to avoid overfitting. The amount of data, however, did not allow testing of the interactions between the predictors. Year and site were used as nested random effects to account for the dependencies in the data due to the phenotypic plasticity and local specialization of the populations (Heer et al., 2018; Housset et al., 2018; Valladares et al., 2014). Tree age was used to account for the temporal correlation (ρ) caused by ageing (Konter et al., 2016; Wu et al., 2013). Models were fit using the restricted likelihood approach (Wood, 2011). Generalized cross-validation procedure was used for estimation of the smoothing parameters. Regression spline with shrinkage was used to smoothen the results. The Akaike Information Criterion (AIC) was used for selection of the best performing set of meteorological variables (according to arbitrarily selection principle); model residuals were checked for normality and homogeneity (by diagnostic plots). The predictors were checked for collinearity using the variance inflation factor (predictors with the criterion > 5 were excluded from the model). To verify the absence of overfitting for the refined model, cross-validation based on independent tree-ring data with similar characteristics from the studied region (Supplementary material, Table S1) was performed. Data analysis was performed in R (v. 3.6.1; R Core Team, 2019), using the packages 'mgcv' (Wood, 2011), 'dplR' (Bunn, 2008), 'car' (Fox and Weisberg, 2011), and 'bootRes' (Zang and Biondi, 2013). The meteorological data were obtained from the online repository of CRU (Harris et al., 2014) for the grid points located at ≤ 35 km distance from the studied stands.

3. Results

3.1. *Linear weather-growth relationships*

Time-series from 13 to 30 trees per stand were successfully crossdated (559 trees in total), indicating conformity of individual growth patterns and quality of the measurements (Table 3; Supplementary material, Figs. S1, S2). During the common period (1954–2017), variation of TRW among trees within a stand was generally similar (r-bar $\geq$ 0.33), yet the mean r-bar tended to decrease southwards, ranging

Table 3
General statistics of the datasets of crossdated tree-ring width time-series of the stands of Scots pine from the eastern Baltic region for period 1954–2017. SENS – mean sensitivity, AC1 – first order autocorrelation, N- number of crossdated time-series, r-bar – mean interseries correlation, EPS – expressed population signal, and SNR – signal to noise ratio.

Stand code	Begin	End	Mean, mm	St. dev., mm	SENS	AC1	N	r-bar	EPS	SNR
FIN_1	1892	2017	1.85	0.52	0.18	0.81	30	0.54	0.961	24.61
FIN_2	1924	2017	2.07	0.50	0.17	0.76	29	0.48	0.957	22.44
FIN_3	1921	2017	1.98	0.69	0.19	0.85	30	0.46	0.959	23.42
FIN_4	1897	2017	1.62	0.38	0.19	0.79	27	0.51	0.963	25.76
FIN_5	1925	2017	2.20	0.53	0.17	0.79	27	0.48	0.953	20.38
EST_1	1932	2018	1.97	0.53	0.19	0.76	27	0.52	0.964	26.54
EST_2	1952	2017	2.47	0.80	0.19	0.82	29	0.53	0.967	29.46
EST_3	1939	2018	2.18	0.87	0.17	0.87	29	0.37	0.943	16.41
LAT_1	1930	2017	0.78	0.02	0.19	0.77	26	0.43	0.949	18.49
LAT_2	1915	2017	1.11	0.03	0.21	0.85	18	0.38	0.902	9.17
LAT_3	1911	2017	0.91	0.02	0.19	0.82	22	0.49	0.953	20.41
LAT_4	1918	2017	0.91	0.02	0.19	0.80	22	0.41	0.931	13.53
LAT_5	1904	2017	1.10	0.03	0.22	0.82	18	0.34	0.899	8.95
LAT_6	1900	2017	2.25	0.57	0.19	0.80	20	0.33	0.900	9.00
LIT_1	1927	2017	3.39	0.87	0.20	0.72	13	0.37	0.878	7.21
POL_1	1931	2018	2.18	0.96	0.20	0.82	30	0.47	0.963	26.28
POL_2	1941	2018	2.36	0.93	0.22	0.82	29	0.59	0.976	40.20
POL_3	1919	2018	1.62	0.46	0.24	0.70	30	0.51	0.968	30.72
GER_1	1944	2017	2.54	0.73	0.22	0.71	30	0.58	0.972	35.19
GER_2	1928	2017	2.40	0.69	0.20	0.71	30	0.39	0.949	18.46
GER_3	1901	2017	2.73	0.58	0.23	0.68	13	0.38	0.852	5.57
GER_4	1925	2017	2.30	0.80	0.23	0.70	30	0.43	0.958	22.88

from 0.49 to 0.40 for sites in Southern Finland and Latvia, respectively (Table 3). In contrast, the mean sensitivity of the time-series for the sites increased southwards indicating regional shift in inter-annual variability of increment, ranging 0.18–0.22 in Southern Finland and Northern Germany, respectively. The first order autocorrelation was high ($\geq$0.68) indicating dependence of TRW on previous growth; signal to noise ratio ranged 5.57–40.20, indicating varying individuality of TRW patterns.

During the analysed period of 1954–2017, regionally and locally specific linear correlations between the residual chronologies and studied meteorological variables were estimated (Fig. 2), indicating differences in responsiveness of growth. Radial increment of the studied trees generally showed sensitivity to temperature in dormant period and water availability in summer, suggesting direct and carry-over effects of meteorological conditions under temperate climate. Nevertheless, the effects of common limiting factors were clearer in the central and southern part of the transect, while they were relaxed under cooler climates in Southern Finland and Estonia. Temperature in the winter months and, particularly, March showed frequent significant (*p*-value < 0.05) positive correlations with TRW across the transect, particularly in its south- and mid-part (in Latvia). The positive correlations with precipitation and SPEI in summer (June–August), as well as precipitation in February were common under a warmer climate in Lithuania, Poland, and Germany (Table 2). The negative correlation with temperature in the previous August with low frequency was detected along the transect, yet it was most common in Latvia (Fig. 2). Some stands in the northern part of the transect showed contrasting correlations between TRW and precipitation in the previous August, indicating local specifics.

The moving-window correlation analysis, which splits the timescale providing a finer resolution of the linear relationships, indicated temporal shifts in the linear weather-growth relationships (Supplementary material, Figs. S4–S8), suggesting their non-stationarity along the transect. These changes in the linear correlations also showed local specifics, implying some stand effects irrespectively of the location, and suggesting relaxation of a common limiting factor(s). Under cooler climate in Southern Finland and Estonia, February and July temperatures have been losing effect around the 1980s and 1990s (intervals ending after ca. 1990 and 2000), respectively. In some stands, however, the effect of temperature in April and in the previous August has intensified in the intervals ending after 2000. Concomitantly, the negative effects of summer precipitation have been intensifying around that time. Nevertheless, in a stand in Estonia (EST_3), positive correlation with June temperature has been significant during most of the studied period. In some stands in Latvia, the correlation with temperature in March has been weakening since the mid-part of the analysed period (LAT_1 and LAT_5), yet the effect of temperature in January/February and April has intensified (in LAT_3, LAT_4, and LAT_6). Concomitantly, the negative correlations with precipitation and SPEI in summer have intensified (in LAT_4, LAT_5, and LAT_6) or remained stable (LAT_2). The correlation with winter precipitation has intensified and become significant since the mid-part of the studied period, indicating alterations in responsiveness of trees.

The variability of shifts in weather-growth relationships was even clearer in the southern part of the transect. Under warmer climate in Lithuania and Poland, February/March temperature showed a continuous, yet weakening correlation with TRW (Supplementary material, Fig. S7). The negative correlation with July temperature and the positive effect of summer precipitation have become significant and intensified since the 1980s. In POL_3 stand, correlation with February precipitation has been significant at the beginning and at the ending of the analysed period; the effect of precipitation in the previous July was observed in some intervals ending before 1993. In the Northern Germany, the shifts of the correlations appeared complex (Supplementary material, Fig. S8). Since the 1980s, the effect of June precipitation showed contrasting patterns, intensification in GER_2 and GER_3, yet weakening in GER_1 and, particularly, GER_4 stands, thus highlighting local specifics. The correlation with temperature in late-summer of the previous year has been losing significance in all stands, while the effects of temperature and/or precipitation in the dormant period, particularly December, have intensified, indicating shifts in periods of responsiveness of tree growth.

3.2. Non-linear weather-growth relationships

The application of a mixed additive model accounting for the random effects of stand and year allowed identification of the main meteorological drivers of TRW of the eastern Baltic Scots pine across the regional climatic gradient. Generalization over a wide spatio-temporal scale (length of the transect ca. 1500 km and timespan of

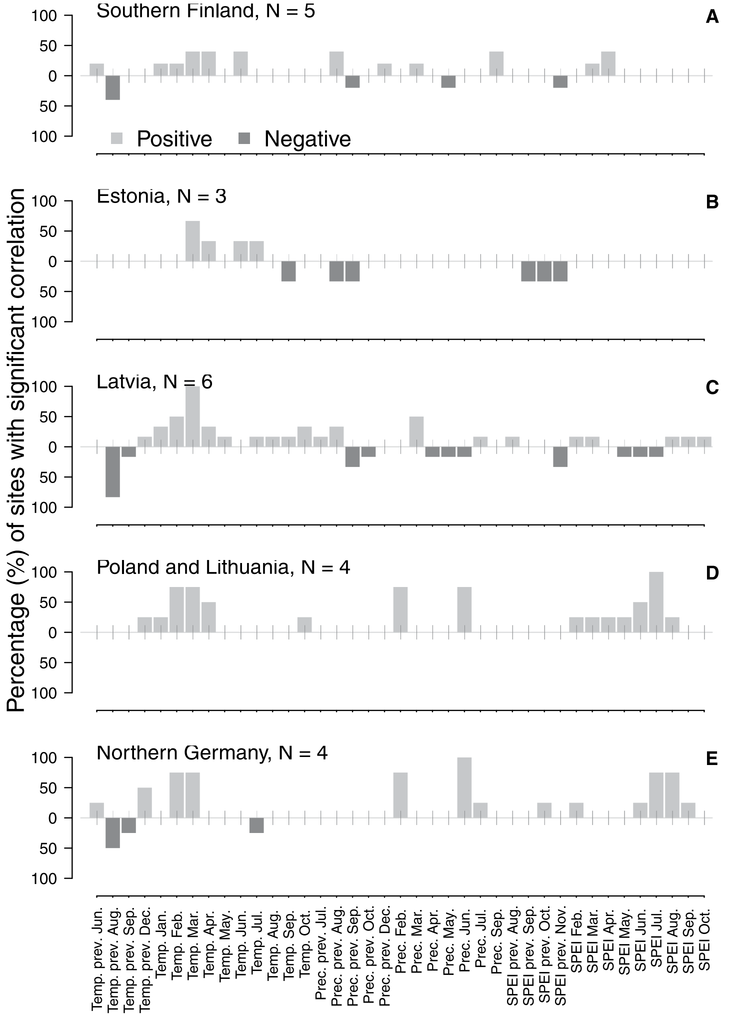

Fig. 2. The proportion of stands of Scots pine showing significant (p-value < 0.05) Pearson correlation between the residual chronologies of tree-ring width and meteorological variables: monthly mean temperature (Temp.), precipitation sums (Prec.) and standardized precipitation evapotranspiration index (SPEI) by countries. The negative correlations are represented by the bars below zero. The analysis is based on the period 1954–2017. Only the meteorological variables showing significant correlations are presented on the x-axis.

63 years) highlighted the effect of climate on the response (reaction) of TRW to the inter-annual variability of meteorological conditions (Fig. 3). Though local specialization might have mediated growth responses. The refined model was significant (p-value < 0.001) and included nine of the 51 tested meteorological variables. The adjusted-R^2 for the fixed part of the model was intermediate ca. 0.22 (cf. Cavin and Jump, 2017), as the dataset represented a regional gradient (Table 4). The marginal pseudo-R^2 for the random part of the model was 0.47. Such intermediate R^2 values indicated that the model was not overfitted. The included meteorological variables (fixed effects) were significant (p-value < 0.02; F-values ≥ 6.32). Although the flexibility of the smoothing splines (basis dimension) up to the fourth degree was allowed, for all meteorological variables the effective degree of freedom was < 3.0, indicating responses with up to two inflection points. The estimated effect of tree age on TRW variation was generally low (correlation term $\rho = 0.16$), implying weak age-effects on growth during

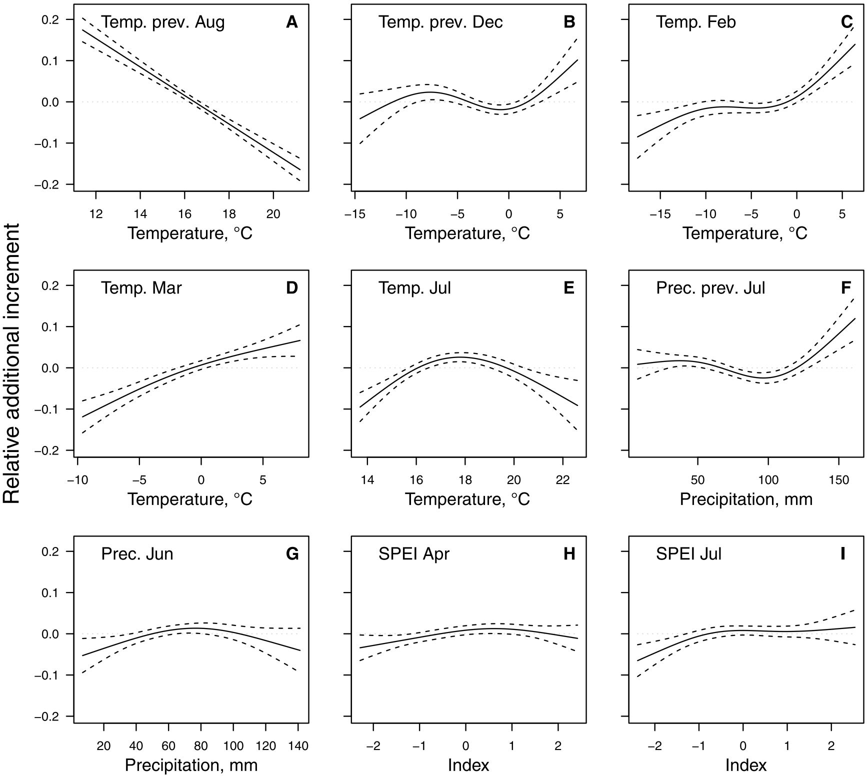

Fig. 3. The estimated approximate smoothing splines (dashed lines denote 95% confidence intervals) of the responses of high-frequency variation (relative additional increment, which is dimensionless) of tree-ring width of eastern Baltic Scots pine to meteorological variables (monthly mean temperature, precipitation sum, and standardized precipitation evapotranspiration index SPEI) during 1954–2017.

the analysed period, as the trees were maturing. Among the random effects, year had a thrice higher variance compared to stand. This suggests that phenotypic plasticity prevailed over the local (e.g., site level) genetic specialization of the studied trees, which constrain plasticity of the responses to meteorological conditions. The cross-validation based on independent data verified that the refined model was not overfitted, as the root-mean-square-errors according to the calibration and verification datasets were comparable (0.131 and 0.128, respectively).

The meteorological variables included in the refined model (Table 4) were similar to those identified by the linear correlation analysis (Fig. 2; supplementary material S4–S8), yet the estimated responses of TRW (relative additional increment represented by the residual chronologies) were mostly quadratic or cubic (Fig. 3). Accordingly, this highlighted the biasness of a simple linear model for the assessment of weather-growth relationships across spatiotemporal gradient of tree growth. Temperature in the previous August showed the highest *F*-value (Table 4); however, it was the only variable estimated with a linear effect, indicating stationarity across the studied gradient (Fig. 3A). Temperature in March showed the second highest effect (*F*-value), yet the response to it was only close-to-linear (Fig. 3D), as suggested by the common linear correlations (Fig. 2), with a slight decrease at ca. –1 °C. In contrast, the response to July temperature was bell-shaped, with a local maximum between 16 and 19 °C, when positive additional increment was estimated (Fig. 3E). The response to February temperature (Fig. 3C) displayed an effective threshold, as a positive response of TRW was triggered by the mean temperature exceeding ca. –2 °C. Nonetheless, a positive effect of increasing February temperature was estimated under cold conditions (< –10 °C). The response to temperature in the previous December (Fig. 3B), which had the weakest effect (Table 4), showed some fluctuation with a local maximum around –7 °C and local minimum at –1 °C (Fig. 3B), which resulted in slight changes in radial growth. Previous December temperature above 2.5 °C resulted in a larger additional increment of TRW.

The precipitation-related variables showed weaker effect on high-frequency variation of TRW than most of the temperature variables (Table 4), and the range of estimated relative additional increment was lower (Fig. 3). Among the precipitation-related variables, July SPEI was estimated with the strongest effect (*F*-value = 12.10; Table 4); the estimated response curve indicated a clear threshold of sensitivity at ca. 0.3 (Fig. 3I). This implied sensitivity of TRW to water deficit, yet irresponsiveness (zero additional increment) to a positive water balance

Table 4

Statistics of the smoothing splines from the generalized additive mixed model describing the main relationships between high frequency variation of tree-ring width of Scots pine from the eastern Baltic region and meteorological variables: month mean temperature, precipitation, and precipitation evapotranspiration index (SPEI) for 1954–2017 period.

Fixed effects			
Smoothening term	Effective degree of freedom	*F*-value	*p*-value
Temperature in previous August	1.00	68.28	< 0.001
Temperature March	1.97	26.49	< 0.001
Temperature July	2.79	22.60	< 0.001
Temperature February	2.85	14.15	< 0.001
SPEI July	2.50	12.10	< 0.001
Precipitation previous July	2.88	11.73	< 0.001
Precipitation June	2.43	9.46	< 0.002
SPEI April	2.23	7.80	< 0.01
Temperature previous December	2.89	6.32	< 0.02
Random effects			
Term	Variance	Standard error	
Year	1.52	0.97	
Stand	0.56	0.48	
Residual (scale)	0.38		

(SPEI > 0; cf. Vicente-Serrano et al., 2010). Positive effect of abundant summer precipitation (> 120 mm/month) was indicated by the estimated response to precipitation in the previous July (Fig. 3F). Nonetheless, the response to this variable showed a local minimum at ca. 100 mm/month, resulting in negative additional increment. This indicated a negative effect of precipitation within the range 40–80 mm/month, which corresponds to dry or moderate years (Table 2). The responses to April SPEI and June precipitation were bell-shaped (Fig. 3G, H), showing a local maximum (optimum) of the available moisture in spring and early summer, which, however, were estimated with a slight (ca. 0.03) positive additional increment. The local maximum of these variables was estimated at ca. 80 mm/month and 0.7 for June precipitation and April SPEI, respectively, suggesting a limited interval of optimal, yet slightly excessive (e.g. SPEI > 0) moisture conditions.

4. Discussion

4.1. Plasticity of growth responses

The shifts in the linear correlations across the transect (Fig. 2) and in time (Figs. S4–S8), as well as the estimated response splines (Fig. 3), portrayed the non-linearity and plasticity of the TRW-weather relationships (Hofgaard et al., 2019; McCullough et al., 2017; Wilmking et al., 2020) of the eastern Baltic Scots pine. Such responses are indicative of high phenotypic plasticity and regional genetic specialization (Heer et al., 2018; Housset et al., 2018; Moran et al., 2017; Booth, 2016), which are crucial for adaptability of trees, allowing them to survive increasingly variable weather conditions (Chauvin et al., 2019; Mina et al., 2016; Valladares et al., 2014). For the studied (meta)population, phenotypic plasticity exceeded genetic specialization (higher variance of year than site; Table 4), which suggests high adaptability of the trees in medium term (Housset et al., 2018; Mina et al., 2016; Valladares et al., 2014; Wang et al., 2010). A lower variance related to the genetic specialization (Table 4) could be related to relatively high genetic diversity of the eastern Baltic populations of Scots pine (Dering et al., 2017; Neimane et al., 2009). Still, genetic specialization in terms of growth resilience has been observed for the provenances of Scots pine from the studied region (Matisons et al., 2019; Matias et al., 2017; Berlin et al., 2016), which can mediate growth responses (Restaino et al., 2016).

The estimation of significant response curves (Fig. 3) implied presence of uniformitarian and stationary, though non-linear regional growth responses to meteorological conditions (Wilmking et al., 2020) for the studied eastern Baltic Scots pine. Accordingly, the regional and temporal shifts in the linear correlations (Fig. 2, S4–S8) can be related to the location along the climatic gradient and warming-induced shifts in it (Cavin and Jump, 2017; Restaino et al., 2016). The effects of local specialization, though estimated with low influence (Table 4), were evidenced by the locally varying responsiveness of TRW (Fig. 2) and contrasting temporal shifts of the responses (Supplementary material, Figs. S4–S8). Such explicit local characteristics apparently highlighted the non-stationarity of the responses (Wilmking et al., 2020). One could argue about the presence of triggers of such local responses, which, however, are often complex and difficult to assess (Wilmking et al., 2017). Trees growing in the core areas of their range adapt to regional climates to maximize growth (competitiveness), while in the marginal areas, strong local specialization and habitat selection occurs to ensure survival (Cavin and Jump, 2017). Accordingly, the effect of a common limiting factor appears relaxed in the marginal-areas of species range, while in the core areas, the opposite can be observed (Cavin and Jump, 2017; Restaino et al., 2016). This, apparently, adheres also to the population scale, as similar pattern could be spotted for the studied trees, which represent Baltic climatype (metapopulation) of Scots pine (Giertych and Matyas, 1991). Accordingly, analysis of a wide (with the regard to species range) climatic gradient assuming non-linearity of responses aids evaluation of uniform and stationary weather-growth relationships (Wilmking et al., 2020).

The effect of meteorological conditions on TRW is modulated by their intensity (Restaino et al., 2016; Henttonen et al., 2014; Ohse et al., 2012; Carrer and Urbinati, 2006), as well as the tree size/age-related changes in physiological processes (Cuny et al., 2019; Trouillier et al., 2019; Konter et al., 2016; Wu et al., 2013). This relates the temporal non-stationarity of the linear response (Supplementary material, Figs. S4–S8) to ageing and particularly climate (low age-related correlation, $\rho = 0.16$), suggesting disproportional effects of climatic changes (Way and Oren, 2010; Loehle, 1998). Considering the location of the studied stands in a region with cold/moderate climates (Table 2; cf. Harris et al., 2014), winter-spring temperature were the primary drivers of TRW (Harvey et al., 2020, Weigel et al., 2018). The secondary role of summer moisture (precipitation) regime (Fig. 3F, G, I) might be related to climatic changes and intensifying water deficit in temperate and hemiboreal forests (Harvey et al., 2020; Lloyd et al., 2013; Ohse et al., 2012; Friedrichs et al., 2009). This also implies interactions between the effects of winter temperature regime and summer water deficit (Fei et al., 2017; Matisons et al., 2017; Ohse et al., 2012), which diversify growth responses (Hofgaard et al., 2019; Wilmking et al., 2017).

4.2. Regional weather drivers of radial growth

As hypothesized, the prevailingly non-linear weather-TRW relationships were revealed by the generalized additive model (Fig. 3), indicating presence of regional weather drivers of radial increment (Cavin and Jump, 2017; Restaino et al., 2016; Matias et al., 2017; Lloyd et al., 2011, 2013), which however, were similar to those identified by the linear correlation analysis (Fig. 2). The identified non-linear responses mostly followed quadratic or cubic curves (Fig. 3), as expected across ecological gradients (Way and Oren, 2010), revealing local optimum or threshold values of meteorological variables (Hofgaard et al., 2019; Aitken and Bemmels, 2016; Lloyd et al., 2013). Such curves also implied responsiveness of TRW to the main weather drivers under supposedly moderate conditions (Cavin and Jump, 2017; Way and Oren, 2010), which could not be detected by the linear correlation analysis (Billings et al., 2015). Accordingly, presumption of a linear response hampers the assessment of growth under warming induced shifts in climatic gradient (Wilmking et al., 2020; Hartmann et al., 2013). The age-effects in the responses of TRW to meteorological conditions (Vieira et al., 2009) were rather weak, as the trees were mostly in the maturing phase, when the increase of canopy and water demand is balanced by root and stem growth (Trouillier et al., 2019; Konter et al., 2016). This confirmed shifts in the weather-TRW relationships (Fig. 2, S4–S8) to be primarily warming-related (Matisons et al., 2017; Ohse et al., 2012; Carrer and Urbinati, 2006).

The responses of TRW to the conditions prior to xylogenesis (Figs. 2 and 3) indicated the importance of the carryover effects for tree growth (Cuny et al., 2019; Castagneri et al., 2017; Sass-Klaassen et al., 2016; Lloyd et al., 2013). The response to temperature in the previous August (Fig. 3A), which had the strongest, yet the only linear effect among the significant variables (Table 4), can be explained by the trade-offs in allocation of nutrients for seed production and increment (Hacket-Pain et al., 2019). Increased late-summer temperature facilitates formation of primordia of the generative buds (reproductive effort), thus explaining the negative effect on growth (Hacket-Pain et al., 2018, 2019). Still, the linear or near-linear effect of a variable (Fig. 3A, D) might also suggest that the studied gradient was too short to assess the plasticity of the response (Lloyd et al., 2013; Way and Oren, 2010).

Temperature in the dormant period and, particularly in March (Figs. 2 and 3B, C, D), showed the second strongest effects on TRW (Table 4). These relationships, which are common for Scots pine under hemiboreal conditions (Harvey et al., 2020), indicated mostly positive effects of the warming of the dormant period on increment (Ohse et al., 2012; Lloyd et al., 2011; Carrer and Urbinati, 2006). The effects of temperature in the dormant period under seasonal climate (Fig. 3B, C, D) might be related to root activity (Hansen and Beck, 1994), which depends on soil temperature and affects water absorption in the following season (Tierney et al., 2001). Such mechanism could also explain the effects of winter precipitation (snow) as suggested by the linear correlation (Fig. 2), which acts as a thermal insulator and affects soil moisture regime (Tierney et al., 2001). The fluctuating responses to December and February temperature (Fig. 3B, C), might also be related to the complex controls of dormancy (Beck et al., 2004), and utilization of carbohydrate reserves in trees (Ögren, 1997). Under cold conditions (< –10 °C) trees apparently suffered some cold damage (Pearce, 2001), as indicated by the overall positive responses to temperature (Fig. 3B, C, D). Particularly in December, a temperature increase between –8 and 0 °C caused a slight negative response, likely due to insufficient cold hardening or dehardening (Beck et al., 2004) and respiratory nutrient losses (Ögren, 1997), whereas the above-zero temperatures, obviously improved the overwintering (Pearce, 2001).

The effect of moisture availability (SPEI) in April (Fig. 3H) suggested the carryover effects of spring precipitation (Cuny et al., 2019; Lloyd et al., 2013; Way and Oren, 2010), yet the effect was weak. The response curve (Fig. 3H) indicated positive water balance (SPEI = ca. 0.8; cf. Vicente-Serrano et al., 2010) to result in positive additional increment, likely due to reduced atmospheric demand for water (Jyske et al., 2014) or frost damage under cloudy conditions (Beck et al., 2004; Ögren, 1997). Nevertheless, the moving linear correlation analysis (Supplementary material, Figs. S4–S8) indicated alterations in the periods of responsiveness of trees to temperature in winter/spring months (Ohse et al., 2012) due to extension of vegetation period (Hartmann et al., 2013).

Direct effects of weather on radial growth were illustrated by the non-linear TRW responses to variables related to summer water availability (Fig. 3). The observed response highlighted contrasting effects of increasing variability of precipitation on growth in the nemoral, as well as boreal zones (Harvey et al., 2020; Hofgaard et al., 2019; Jansons et al., 2016; Ohse et al., 2012; Friedrichs et al., 2009). Under temperate climate, xylogenesis is rapid in June, and sufficient supply of water (ca. 60–90 mm/month; Fig. 3G) is crucial for cell expansion (Castagneri et al., 2017; Jyske et al., 2014), as well as assimilation (Pallardy, 2008), explaining the positive growth response to precipitation. In contrast, excessive precipitation in June (> 100 mm/month) caused a negative trend in response, probably due to decreased assimilation in rainy days (Jyske et al., 2014; Strand et al., 2006).

Under temperate lowland conditions in Europe, July is the warmest period when the highest assimilation in trees occurs (Yang et al., 2015; Jyske et al., 2014). The response to July temperature was bell-shaped (Fig. 3E), which can be explained by the trade-offs between favourable temperature and sufficient water supply under increased transpiration (Yang et al., 2015; Carrer et al., 2010). However, the estimated positive additional increment under the optimal conditions was low (Fig. 3E), which might be explained by specialization of the studied populations to certain temperature regime (Aitken and Bemmels, 2016), or, alternatively, by formation of latewood, which comprises a smaller part of TRW (Cuny et al., 2019). A positive linear effect of July temperature was evident only in the Southern Finland (Fig. 2), likely due to a delayed xylogenesis under cooler climate (Jyske et al., 2014; Henttonen et al., 2014). The response of TRW to July SPEI < 0 (Fig. 3I), when evapotranspiration exceeded precipitation (Vicente-Serrano et al., 2010), illustrated the effect of summer water deficit (Carrer et al., 2010), particularly under warmer climate in Poland and Northern Germany (Fig. 2). Nevertheless, trees appeared irresponsive to moist conditions (SPEI > 1; Fig. 3I), probably due to decreased assimilation under cloudy conditions (Strand et al., 2006). Still, formation of additional increment occurred if preceding July was precipitation rich (> 100 mm; Fig. 3F), which might be related to carryover effects of nutrient reserves (von Arx et al., 2017; Sass-Klaassen et al., 2016). The negative response of TRW to preceding year with moderately dry July (Fig. 3F) could be explained by the reallocation of assimilates to root rather than stem growth to improve water uptake (Brunner et al., 2015), or by increased reproduction effort (Hacket-Pain et al., 2019). Still, despite the high phenotypic plasticity, the observed temporal shifts in correlation and non-linear responses (Fig. 3E, S6–S8) suggested warming-induced increase of water stress for Scots pine in summer (von Arx et al., 2017). Scots pine is considered susceptible to water deficit among other pines (Martinez-Vilalta et al., 2004), supporting the necessity for the adaptive climate-smart management (Nabuurs et al., 2018; Taeger et al., 2015) in the eastern Baltic region.

5. Conclusions

Generalization across the spatiotemporal gradients highlighted ecological plasticity of radial growth of the eastern Baltic Scots pine. As hypothesized, the responses of TRW to the main regional weather drivers across the studied climatic gradient were non-linear, indicating plasticity of growth. The non-linear responses also explained (at least partially) the non-stationarities of climatic signals due to climatic changes. This also highlighted the effect of local climates on weather-growth relationships. Local specialization, particularly in the marginal parts of the studied (meta)populations of pine, resulted in some specific responses and their temporal shifts, adding uncertainties for the regional responses. Accordingly, analysis of wide climatic gradient (at the population scale), presuming non-linearity, aids the assessment of stationarity of growth responses, while simple linear models are losing sufficiency for the description of weather-growth relationships and growth predictions, under moderate, yet changing conditions. Due to location in temperate climate, winter-spring temperature showed generally positive effect on growth, while negative effects of increasing variability of summer weather was indicated by the responses showing stationary maxima (optimum). The observed temporal shifts in the responses to weather variability were prevailingly due to the climatic changes, while tree aging only slightly affected growth responses. High phenotypical plasticity, yet lower genetic differentiation (local specialization) indicated high adaptability of the studied populations in a medium term, presuming restricted adaptability in a longer term. This supports the necessity of climate-smart management to sustain the productivity of pine forest in the eastern Baltic region in the future.

CRediT authorship contribution statement

Roberts Matisons: Conceptualization, Methodology, Investigation, Formal analysis, Visualization, Writing - original draft, Writing - review & editing, Supervision, Data curation. **Didzis Elferts:** Methodology, Data curation, Formal analysis, Supervision, Validation. **Oskars Krišāns:** Visualization, Investigation, Data curation, Resources. **Volker Schneck:** Methodology, Writing - review & editing, Supervision, Data curation. **Holger Gärtner:** Conceptualization, Methodology, Writing - original draft, Supervision. **Alexander Bast:** Conceptualization, Methodology, Writing - original draft, Supervision. **Tomasz Wojda:** Investigation, Data curation. **Jan Kowalczyk:** Investigation, Data curation. **Āris Jansons:** Conceptualization, Writing - original draft, Writing - review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

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

Acknowledgements

The study was conducted under the framework of the post-doctoral studies in Latvia ('Plasticity of development and xylogenesis of the native and introduced tree species under changing climate', project No.: 1.1.1.2.VIAA/1/16/108) financed by the European Regional Development Fund. We would like to thank Martin Wilmking and his team for the inspiration. We also acknowledge the technical staff, who helped during selection of the territories and sampling. Authors declare no conflict of interests.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118600.

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Dendrochronologia 67 (2021) 125822

Contents lists available at ScienceDirect

Dendrochronologia

journal homepage: www.elsevier.com/locate/dendro

Canopy status modulates formation of wood rays in scots pine under hemiboreal conditions

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ARTICLE INFO

Keywords:
Xylem parenchyma
Time series analysis
Growth plasticity
Wood anatomy
Tangential cut
Eastern baltic region

ABSTRACT

Non-structural carbohydrates (NSC) reserves are crucial for trees to cope with weather extremes, thus to ensure their survival and ecological plasticity. The NSC reserves can depend on social status, suggesting uneven plasticity of trees at the stand level. In stemwood of Scots pine (*Pinus sylvestris* L.), which is a widespread and important species, NSC reserves are stored in parenchyma in wood rays (WR). The quantity of WRs is adjusted intra-annually, allowing retrospective analysis of factors affecting their formation. Accordingly, the differences in WR quantity in stemwood of dominant and intermediate (canopy trees with reduced and narrow crowns) maturing Scots pine were assessed by quantitative wood anatomy. Tangential cuts from the outermost 30 tree-rings were analysed. The relative ray area was intermediate, i.e. covering about 5% of the tangential cut, yet expressed high individuality among the trees. The size and amount of WR mainly differed between the earlywood and latewood; WRs in latewood were higher although narrower in comparison to earlywood, yet their total amount was higher in earlywood. Canopy status had only a slight effect, as quantity and height of WR tended to be higher for the intermediate trees, particularly in earlywood. The size and quantity of WR expressed inter-annual variation, which was mainly related to the meteorological conditions prior to the formation of the tree-ring (previous summer and autumn) indicating legacy effects of climatic factors on NSC and susceptibility of trees to cumulative effects of weather extremes. However, the climatic signals in the inter-annual variation of WR were weaker than observed before, likely due to location of the studied stand in the mid-part of the species range. Nevertheless, the observed differences in mean values and inter-annual variation of WR suggested a within-species diversity of carbon allocation patterns, supporting adaptability of the species.

1. Introduction

Adaptability of trees and stands to the changing environments, which has been identified as the key issue for sustainability of forests (Nabuurs et al., 2018; Aitken and Bemmels, 2016), is determined by phenotypical plasticity and genetic specialization, which persists also under high gene flow (Housset et al., 2018; Moran et al., 2017). This indicates the necessity for proactive management under the increasing rates of climatic change (Nabuurs et al., 2018). Nevertheless, sustainability of forests has also been related to the diversity of stands, which can improve the adaptability of native populations via inter-species facilitation of growth and survival; though such mechanisms can differ locally (Sheil and Bongers, 2020; Forrester and Bauhus, 2016; Jucker et al., 2014). Furthermore, structural diversity in monocultures can facilitate their sustainability, as trees of diverse age/size are playing complementary roles in regard to physical stability, microclimate, nutrient turnover, etc. (Bohn and Huth, 2017; Forrester and Pretzsch, 2015). Such effects appear particularly advantageous under the growing impacts of weather extremes (e.g., storm, drought) on forests (Seidl et al., 2014), which can have long-term legacy effects on the vigour and functioning of trees (Zweifel et al., 2020; Bonnesoeur et al., 2016).

Quantification of tree responses to environmental fluctuation has been among the most studied issues in forestry, particularly in relation to climatic change (Zhang et al., 2018; Matias et al., 2017). Most of these studies focus on proxies related to wood increment, considering them as the measure of tree vigour and productivity in a certain period of time

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https://doi.org/10.1016/j.dendro.2021.125822
Received 3 September 2020; Received in revised form 18 February 2021; Accepted 2 March 2021

(Housset et al., 2018; Zhang et al., 2018). Tree-ring width has been widely used as a highly informative proxy for studies of tree increment (De Micco et al., 2019; Housset et al., 2018), as it is a product of the conditions before and during its formation (Zhang et al., 2018). In addition, species and/or provenances can show diverse reaction of increment to similar conditions due to e.g. specific patterns of carbon allocation (growth vs. deposition of reserves; Trouve et al., 2015; Vanninen and Mäkelä, 2000) and xylogenesis (Lebourgeois et al., 2014; Sheil and Bongers, 2020). In this regard, quantitative wood anatomy, which focuses on the basic structural elements of wood, as tracheids, parenchyma, vessels, or fibers, can provide more detailed insights in the specific processes of xylogenesis and their reaction to environmental conditions, thus aiding for a better understanding of growth and field performance of trees (Forrester and Bauhus, 2016; von Arx et al., 2015; Olano et al., 2013; Fonti and Jansen, 2012; Vanninen and Mäkelä, 2000).

The most frequently measured wood anatomical proxies applied in environmental studies are the dimensions of conduits, which determine wood properties and hydraulic architecture (conductivity) (De Micco et al., 2019; Fonti and Jansen, 2012). Wood rays (WRs), which consist of parenchyma and bordering tracheid cells (depending on species), are essential for the storage and transfer of nutrients in the form of non-structural carbohydrates (NSC) (Hartmann and Trumbore, 2016). The WRs occur in the stem, branches and roots, providing a dynamic complex of functions and support the survival of trees (Spicer, 2014; Olano et al., 2013; Sala et al., 2012). The NSC are key players in plant responses to drought, and they are suspected to have an effect on the regulation of xylem water transport (Tomasella et al., 2020; Plavcova and Jansen, 2015; Spicer, 2014). Accordingly, the quantity of WRs in the stem can be indicative for the adaptive capacity and plasticity of trees (Klein et al., 2014; Spicer, 2014), particularly in relation to environmental extremes (von Arx et al., 2017). In this regard, the ability to mobilize NSC stored in the rays enables trees to survive these extremes and their legacy effects (Zweifel et al., 2020; Bonnesoeur et al., 2016; Fonti et al., 2015). Still, this wood anatomical proxy has received limited attention, most likely due to the laborious acquisition of data (von Arx et al., 2017; Olano et al., 2013).

The quantity of WRs, which act as storage reservoirs for the NSC of a certain capacity (von Arx et al., 2017; Plavcova and Jansen, 2015), expresses multi-annual, annual, as well as intra-annual variation between earlywood (EW) and latewood (LW) in response to meteorological fluctuations (Fonti et al., 2015; Olano et al., 2013). Such relationships also highlight the key moments for xylogenesis and formation of wood parenchyma (Guerin et al., 2020; Zweifel et al., 2020; Castagneri et al., 2019). The involvement of NSC in the formation of EW (Fisher and Holl, 1991; Lanner, 1978) affects water relations and current assimilation, which in turn can modulate formation of LW (Castagneri et al., 2019) and NSC, thus providing a feedback loop. Accordingly, the quantity of WRs can vary within a tree-ring while simultaneously showing delayed reaction (long-term legacy effects) to environmental fluctuation (von Arx et al., 2017; Richardson et al., 2013). This is also supported by the formation of WR initials in the preceding year (Morris and Jansen, 2016; Spicer, 2014; Mauseth, 1988). These issues also support local specifics in variation of WR proxies (e.g., due to stand history), as suggested by the varying climate-growth relationships (von Arx et al., 2015; Olano et al., 2013). As the assimilation rate is affected by the canopy (social) status of trees (Wegiel and Polowy, 2020; Fonti et al., 2015; Reid et al., 2004), differences in WR quantity within a stand are expectable (Richardson et al., 2013; Vanninen and Mäkelä, 2000), thus adding complexity of the ecophysiological interpretation of the variation in this proxy.

The aim of this study was to assess quantity of WRs in EW and LW of dominant and co-dominant Scots pine (*Pinus sylvestris* L.) in a commercial oligotrophic stand in the hemiboreal zone. This conifer species has been chosen due to its simple wood anatomical structure (Mauseth, 1988) and high ecological and economic importance in Northern Europe (Hytteborn et al., 2005), as well as due to the explicitly projected changes in its abundance and growth within the region (Buras and Menzel, 2019). We hypothesized that the quantity of WRs was higher in the dominant trees providing higher capacity for NSC storage. We also assumed that larger WRs occurred in LW, thus providing capacity for storage of NSC as reserves for early xylogenesis in the following year, though this process is affected by weather conditions.

2. Material and methods

2.1. Study area and sampling

A 115-year-old commercial stand of Scots pine growing in the central part of Latvia (56.799 °N; 24.498 °E) on well-drained oligotrophic sandy soil was sampled. According to stand inventory, the mean (± standard deviation) diameter at breast height (DBH) and height of the trees was 28.6 ± 7.6 cm and 24.4 ± 1.0 m, respectively; the total basal area was 29.6 m^2 ha^{-1}. The stand was formed by Scots pine with a slight admixture (ca. 10 % of basal area) of Norway spruce in the advance growth. The last thinning, removing ca. 30 % of the standing stock was performed at the age of 90 years (according to national forest inventory data).

The climate at the study site is temperate. The mean annual temperature (± standard deviation) during the 1990–2019 was 7.2 ± 0.7 °C, with July (18.2 ± 1.6 °C) and January (3.2 ± 2.5 °C) being the warmest and coldest months, respectively (Supplementary material, Fig. S1; Harris et al., 2014). The mean annual precipitation was 657 ± 79 mm. The highest monthly precipitation occurred during the summer months (June–August, ca. 77 ± 26 mm). The vegetation period (mean daily temperature >5 °C) lasts from mid-April to October, while the growing period for Scots pine extends from May to August (Mäkinen et al., 2018). Climatic changes are mainly expressed as a warming during the dormant period and as an increase in the variability of the summer precipitation regime (Avotniece et al., 2012).

Within the stand, seven dominant (canopy trees with wide and well developed crowns; DBH = 36.5 ± 5.2 cm) and six intermediate (canopy trees with reduced and narrow crowns; DBH = 25.3 ± 2.9 cm) trees were sampled. Two increment cores from the opposite sides of stem were collected with a 5-mm Pressler increment corer at the breast height. To avoid reaction wood, tilted trees were not sampled. Additionally, from five dominant and five intermediate trees, one core per stem was collected for the analysis of radial increment. The sampling was done in September 2018.

2.2. Sample preparation and measurements

To analyse the intra- and inter-annual variation of WRs in stems of Scots pine differing by canopy status, each core was cut into tangential thin sections using a hand sledge microtome GSL1 (Gärtner et al., 2014), which was equipped with Leica Surgipath DB80 LX disposable blades. The thickness of the thin sections ranged 15–35 μm. A thin section from EW and LW from each of the outermost 30–35 tree-rings was collected. Older samples were not taken as they were impossible to double stain due to the die-off of parenchyma cells (Richardson et al., 2013; Gartner et al., 2000). The thin sections were double stained in Astra blue and Safranin to enhance the contrast between the lignified (tracheids including those at the upper and lower ends of WRs) and the non-lignified cells (WR parenchyma) according to Gärtner and Schweingruber (2013).

To measure WR proxies on the tangential cuts (i.e., the height and width of an entire ray including all parenchyma and ray tracheids at the upper and lower ends), high resolution (0.6–0.9 pixels μm^{-1}) distortion free microscopic images were acquired at ×40 optical resolution using a light microscope (Gärtner et al., 2015), which was equipped with a digital camera with an 18 Mpx cropped matrix. The measurements of WR proxies were made using the WinCELL 2007a software (Regent Instrument, Inc.); the image analysis was based on colour. The cross-sections of WRs on the tangential cut was considered as the lumen of a measurement unit (object). The dimensions of the WR cross-section were measured in a free direction (maximum height and width acquired). So, height, width, and area of the WRs on the tangential cuts, as well as relative area of WR (proportion of area of the tangential cut), were measured. Additionally, ray density, i.e. the number of rays per unit of area of the tangential cut (mm^2) was calculated. Unfortunately, it was not possible to obtain high quality thin sections, and hence images (insufficient contrasts) from each tree-ring, likely due to varying cell properties among tree-rings (von Arx et al., 2015; Richardson et al., 2013), which resulted in interruptions of the measurement time series. To assess the inter-annual variation in radial increment, surface of the additional increment cores (glued in wooden mounts) was grinded with a sandpaper, and tree-ring widths were measured manually, using the Lintab 5 measurement table and the TSAP software (RinnTech Inc., Heidelberg, Germany).

2.3. Data analysis

The quality of the measurements was checked by a graphical inspection. Datasets for the common period 1989–2018 were analysed. The differences in WR proxies according to canopy status of a tree (two levels: dominant and intermediate), part of tree-ring (two levels: EW and LW), as well as their interaction (as fixed effects), were estimated using liner mixed models (Bates et al., 2015), accounting for the hierarchical structure and any unbalancedness in the data. Core nested within tree, and year of tree-ring formation were included in the models as crossed random effects. Restricted maximum likelihood approach was used to fit the models. Models were based on the mean values of RW proxies for each tangential cut to normalize the data and emphasize the environmental signal (Olano et al., 2013; Font and Jansen, 2012, Matisons et al., 2012). Tree-ring index of each group (dominant and intermediate trees) was included in the model as a numeric covariate to account for the linkage between formation of WR and wood increment (Olano et al., 2013). For this, the biweight robust mean was used to calculate tree-ring indices based on the double detrended time series (by a modified negative exponential function and flexible cubic spline with 32-year wavelength and 50 % cut-off frequency) for each group of trees. The significance of the tested effects (fixed, as well as random) was evaluated using the maximum likelihood approach and the χ^2 criterion. The levels of the significant factors were compared using the Tukey HSD test.

Time series analysis was applied to assess the inter-annual variation of WR and the involvement of meteorological conditions in it. For each tree, time series of WR proxies were produced and scaled (cantered to the mean and expressed in standard deviation) to avoid the explicit effects of tree-related differences in the mean values, while maintaining trends in the data. Due to missing values in the measurement time series (detrending of individual time series was not possible), classic chronology building was not performed. Instead, the scaled times series were simply averaged for EW and LW of dominant and intermediate trees, thus producing a simple “standard” chronology. The similarity among the chronologies of different proxies representing EW and LW of dominant and intermediate trees was assessed using the Principal Component Analysis based on the correlation matrix; years were treated as individuals and proxies for each group were considered as variables. The significance of the principal components (PCs) was determined by a randomization (Monte-Carlo) test performing 1000 iterations.

The relationships of the chronologies of WR proxies, as well as the scores of the first two PCs of their variation with meteorological variables: monthly mean temperature, precipitation sums, and standardized precipitation evapotranspiration indices (SPEI; Vicente-Serrano et al., 2010) were estimated using a bootstrapped Pearson correlation analysis (performing 1500 iterations). To account for the carryover effects of weather conditions on growth of Scots pine (Lanner, 1978), the climatic data were arranged into climatic window from June in the year preceding formation of tree-ring (previous June) to July and September for EW and LW, respectively. Gridded climatic data were used in the analyses (Harris et al., 2014). Collinearity of the significant variables was checked, and only the non-collinear variables are reported. Data analysis was performed in program R (v. 3.6.2) using packages ‘lme4′ (Bates et al., 2015), ‘dplR’ (Bunn, 2008), and ‘emmeans’ (Lenth, 2019).

3. Results

3.1. Variation of WR proxies among trees

In total, WR proxies from 683 thin sections (349 and 334 for EW and LW, respectively) representing the common period 1989–2018 were analysed. The mean relative ray area (tangential surface) of 5% is implying an average amount of WR in the stem wood of the studied Scots pine. Nevertheless, the quantity and size of WR was varying among trees as well as in time. The coefficients of variation ranged 0.21–0.47 for width and relative area of WR, respectively (Table 1), indicating uneven constrains of the proxies. The studied proxies showed high individuality among trees – from the analysed random effects, tree caused the highest variance in all proxies. The variances associated with core was lower, yet significant for WR height, width, and relative area; the variances related to the year of tree-ring formation was considerably lower. Nevertheless, the studied models accounting for individuality of trees were sufficient for the description of the differences in the WR proxies according to the study design, as the conditional R^2 values ranged 0.43–0.76. The statistical models were strictly significant for most proxies (p-value $<$0.001), except for density (Table 2).

Canopy status and part of tree-ring generally showed a complex effect on the size of WR, as indicated by the significant (p-value < 0.05) interaction between these factors for WR height, cross-section area, and relative area (Table 2). The WR tended to be higher for the intermediate than for the dominant trees, particularly in EW (Fig. 1 A). Nevertheless, despite the individuality of trees, significant differences in estimated means were observed only between the strongest contrasts. Significantly (p-value < 0.01) lower WRs were observed in EW of the dominant as well as intermediate trees compared to their respective LW, though for the intermediate trees the differences might have been coincidental. Concerning mean cross-section and relative areas, hence size and quantity of WR (Fig. 1 C, D), the means were significantly (p-value $<$ 0.01) higher in EW than in LW for both the dominant and intermediate trees. Still, some slight differences between the dominant and intermediate trees were observed, particularly in EW. The WR width differed intra-seasonally according to timing of their formation; it was by ca. 31 % higher in EW than in LW, irrespectively of tree status (Fig. 1 B), as indicated by the explicit non-interacted effect of the part of tree-ring (Fig. 1). In contrast to WR size, the number of ray initials was highly similar for the studied trees (ca. 12.4 mm^{-2} on tangential cut; not shown), as WR density was estimated independent of canopy status of trees and part of tree-ring (Table 2).

Table 1

General statistics of the datasets of the studied anatomical wood ray proxies for stemwood at the breast height of a mature Scots pine from a managed stand for the period 1989–2018 (for stand age ca. from 85 to 115 years).

	Height, μm	Width, μm	Cross-section area, μm^2	Density, n mm^{-2}	Relative area, %
Minimum	48.05	16.50	646.31	1.56	1.42
Maximum	310.00	59.08	5241.81	47.70	13.15
Mean	149.27	32.32	2750.03	11.94	5.18
St. deviation	44.13	6.77	779.02	3.20	2.41
Coef. of variation	0.30	0.21	0.28	0.27	0.47
Total variance	1947.65	45.83	606877.23	10.26	5.82

Table 2
Variance of random effects of year and core nested within tree, and χ^2 values of tree status, part of a tree-ring and their interaction on the studied proxies of wood rays for stemwood at the breast height of a mature Scots pine from a managed stand for the period 1989–2018 (for stand age ca. from 85 to 115 years). Significance codes, p-value: * - <0.05, ** - < 0.01, *** - < 0.001.

	Height	Width	Cross-section area	Density	Relative area
Random effects, variance					
Year	0.59	0.06	2624	0.01	0.02
Tree/core	**91.26*****	**1.23***	2	0.14	**0.207****
Tree	**1279.65*****	**7.52****	345,241***	**4.44*****	**3.726*****
Residual	784.35	18.72	338,145	6.49	2.79
Fixed effects, χ2					
Tree status	0.69	0.02	0.03	1.33	0.33
Part of tree-ring	**61.32*****	**681.81*****	**30.15*****	1.87	**19.19*****
Tree status by part of tree-ring interaction	**16.29*****	0.51	**3.74***	0.10	**7.10****
Tree-ring index (covariate)	0.21	0.27	1.32	0.16	1.33
Model statistics					
Overall significance, *p*-value	<0.001	<0.001	<0.001	0.26	<0.001
Conditional pseudo-R^2	0.67	0.60	0.54	0.43	0.61

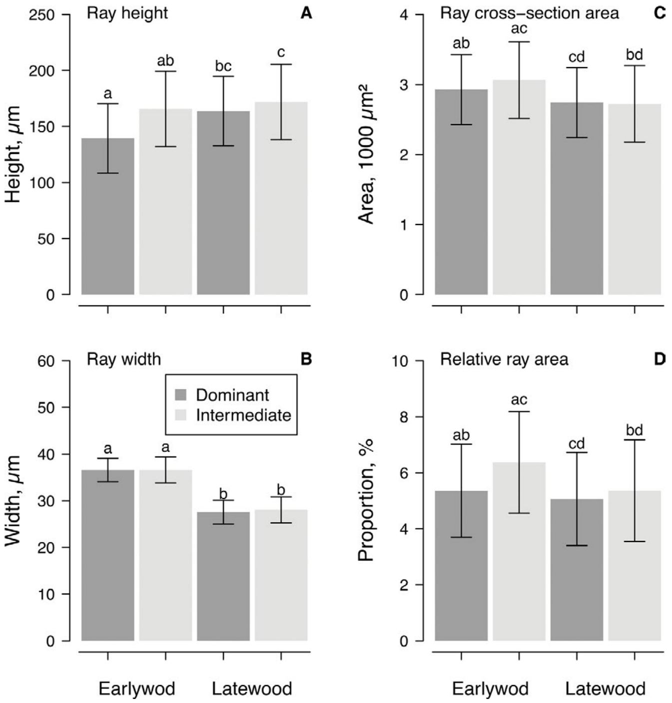

Fig. 1. Estimated marginal means for wood ray height (A), width (B), cross-section area (C), and relative area (D) according to canopy status of tree and part of tree-ring for stemwood at the breast height of mature Scots pine from a managed stand for the period 1989–2018 (for stand age ca. from 85 to 115 years). Whiskers denote the estimated 95 % confidence intervals. Similar letters above the bars indicate lack of significant differences in means (p-value > 0.05), as determined by the Tukey HSD test.

3.2. Inter-annual variation

The established chronologies indicated individuality of intra-annual variation of WR proxies, although some group specifications were evident, particularly for EW and LW (Supplementary material Fig. S2). Accordingly, the amount of common variation in the data extracted by the first two PCs was limited (ca. 37 % of the total variance). Nevertheless, both PCs were significant (*p*-value < 0.01; Fig. 2 A), indicating temporal complexity of formation of WR. Canopy status, apparently, affected the plasticity of WR in terms of inter-annual variation. The first two PCs (Fig. 2 B) revealed distinct grouping of the chronologies of WR proxies, distinguishing those representing LW of the dominant trees, as well as EW and LW of intermediate trees. The chronologies representing EW of the dominant trees showed an overlap with

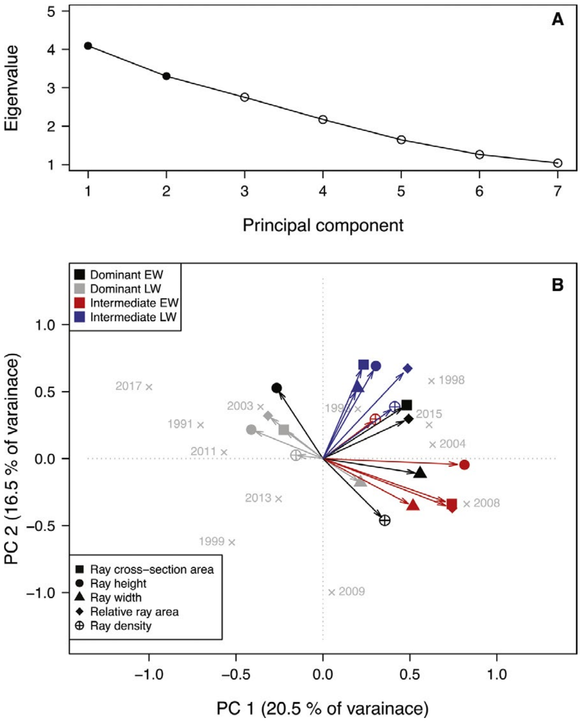

Fig. 2. Eigenvalues of the first seven principal components of wood ray proxies for stemwood at the breast height according to canopy status of tree and part of tree-ring of mature Scots pine from a managed stand for the period 1989–2018 (for stand age ca. from 85 to 115) and their significance (p-value < 0.05, filled dots), as determined by the randomization test (A); and ordination of the wood ray proxies according to the first two principal components of their variation (B). In (B), grey crosses indicate scores of years (scaled for clarity); years showing explicit values of scores are shown for clarity. EW-earlywood, LW-latewood.

others, particularly with those representing the intermediate trees. This also suggested the presence of common environmental signals among the groups.

The inter-annual variation of WR and its main patterns were related to meteorological variables. The first PC was particularly associated with the variation of WR proxies in 1991, 1998, 2004, 2008, 2011, 2015, and 2017 (Fig. 2 B), years in which July was cooler than usual, as well as extremes in precipitation occurred in February, June, July, and in previous October (not shown). The scores of the first PC significantly (p-value < 0.05) correlated with the meteorological variables related to water deficit – precipitation sum in previous July and SPEI in March and previous August (r = -0.38, 0.28, and -0.37, respectively). The linkage with conditions in previous year indicated carryover effects of meteorological conditions on WR. Direct effect of meteorological conditions on formation of WR, though, was indicated by the second PC, which was particularly associated with the variation of WR proxies in 1993, 1999, and 2009, years when extremes in precipitation and temperature occurred in May. Nevertheless, the scores of the second PC significantly correlated with mean monthly temperature in July and previous October (r = -0.33 and –0.34, respectively).

Carryover effects of meteorological conditions were demonstrated by the correlations between the chronologies of WR proxies and six of the tested meteorological variables mostly related to conditions prior to growing season (Fig. 3). The estimated correlations were specific to EW and LW, and social status of trees, indicating complex climatic control of formation and anatomy of WR. The inter-annual variation in WR height in EW and LW of the intermediate trees was correlated with precipitation in previous July and SPEI in previous September. Concerning the dominant trees, WR height appeared less sensitive to the studied meteorological variables, although negative correlation with temperature in the previous October was estimated for LW. The WR width showed the lowest sensitivity to the studied meteorological variables, as only that from EW of the dominant trees showed correlation with temperature and SPEI in the previous August/September. Similarly, WR cross-section area in LW of the intermediate trees showed positive correlation with temperature in the previous August, while in the dominant trees, it was positively correlated to precipitation in May and negatively to temperature in the previous October. The WR density showed sensitivity to meteorological conditions only in the LW of the intermediate trees; a positive correlation with temperature in the previous August and negative correlations with precipitation and SPEI in previous summer was estimated. The relative ray area showed the same correlations for LW of the intermediate trees. Additionally, significant correlations between relative ray area and temperature in previous October and precipitation in May were observed for LW and EW of the dominant trees, respectively.

4. Discussion

4.1. Tree canopy status and intra-seasonal variability of WR

The means and the ranges of the WR proxies were comparable to

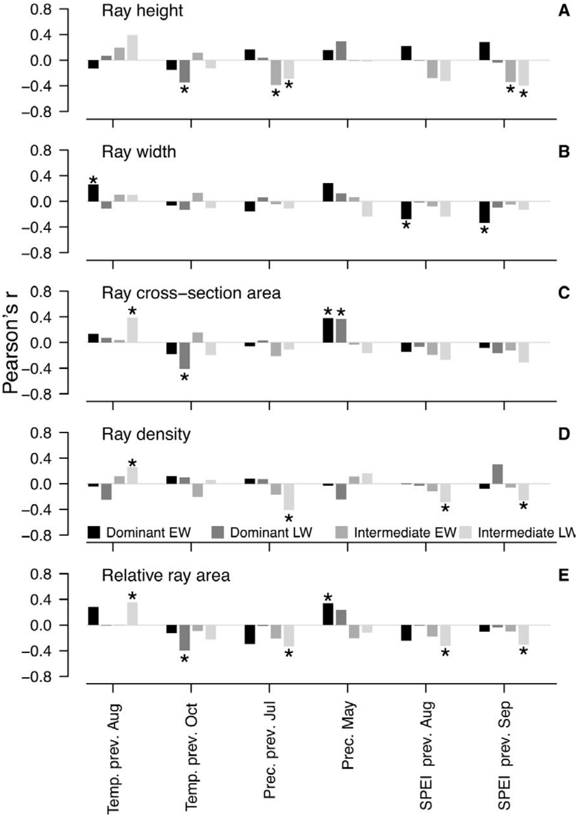

Fig. 3. Bootstrapped Pearson correlation coefficients between the chronologies of wood ray height (A), width (B), cross-section area (C), density (number per area) (D), and relative area (E) and meteorological variables according to canopy status of tree and part of tree-ring for stemwood at the breast height of mature Scots pine from a managed stand for the period 1989–2018 (for stand age ca. from 85 to 115). Only the non-collinear meteorological variables showing significant correlations with chronologies are shown. Asterisks indicate the statistical significance of the correlations (p-value < 0.05). EW-earlywood, LW-latewood.

those observed in other studies, which, however, investigated sites with contrasting climate (von Arx et al., 2017; Fonti et al., 2015; Olano et al., 2013). This implies strict physiological constrains for formation of WR to provide hydraulic integrity and functioning of stems, as well as to ensure storage capacity for assimilates (Fonti et al., 2015; Sala et al., 2012; Gartner et al., 2000). In line with other studies (von Arx et al., 2017; Fonti et al., 2015; Olano et al., 2013), WR proxies expressed explicit individuality among trees (Table 2) under presumably optimal growing conditions in the mid-part of Scots pine distribution range (Hytteborn et al., 2005). High individuality of WR characteristics among trees appears to be genetically determined (Fichot et al., 2009), as hinted by high genetic diversity of Scots pine within the region (Dering et al., 2017). Such effect might be related to the positive effects of structural and functional diversity on sustainability of a stand via within-species segregation of growth strategies (Bonnesoeur et al., 2016; Forrester and Bauhus, 2016). The dimensions and quantity of WR has been related to provenance, hence reflect adaptations to moisture, temperature, as well as to stand conditions (Martin et al., 2010).

Alternatively, high individuality in the quantity of WR has been related to the differences in leaf area and size of the crown (Gartner et al., 2000). Competition for light and water, which can differ locally based on micro-site conditions, diversify assimilation of trees (Jucker et al., 2014), thus supporting the individuality in formation of NSC reserves portrayed by the WR proxies (Table 2). Nevertheless, structural and functional diversity of trees has been related to the ability of stands to recover after intense natural disturbances (e.g., wind) via ecological plasticity (interchangeability) of its elements (Bonnesoeur et al., 2016; Lebourgeois et al., 2014). The NSC are crucial for plasticity and resilience of trees after stresses, yet their formation is a complex process (Tomasella et al., 2020; Fonti et al., 2015; Plavcova and Jansen, 2015).

Alterations in size and initiation rates of WR, which extend beyond tree-ring borders (Spicer, 2014), have been identified as the main mechanism allowing adjustments in quantity of xylem parenchyma to meet the demands set by weather conditions throughout the season (Morris and Jansen, 2016; Olano et al., 2013). Nevertheless, the quantity and dimensions of WRs are restricted to ensure functional integrity of wood (Fonti et al., 2015), hence only small differences in WR proxies were observed among the trees with different canopy status (Fig. 1; Table 2). For Scots pine, WRs are mostly formed by a single row of cells and WR width is directly affected by cell size (von Arx et al., 2017; Martin et al., 2010). Wood cell size, in turn, depends on the timing of formation (Kilpeläinen et al., 2007) ensuring different functions under shifting ecological demand (Cuny et al., 2019; Fichot et al., 2009). Accordingly, pronounced differences in WR width occurred between the parts of tree-ring (Fig. 1), suggesting that formation of WR shows similar pattern to xylem, ensuring functional integrity of tree-ring and stem (Tomasella et al., 2020; Fonti et al., 2015). This also implies adjustments to meet the shifting water deficit during the vegetation period as observed for xylem tracheids (Cuny et al., 2019; Martin et al., 2010). The size of cells, though, is physiologically constrained (Cuny et al., 2019; Martin et al., 2010).

Parenchyma cells are mostly regular (von Arx et al., 2017; Fonti et al., 2015), hence the disproportional differences of WR height and width among the EW and LW (Fig. 1 A, B) suggest intra-annual variability in the number and size of parenchyma cells in a WR. Ray initiation rates (Olano et al., 2013; Gartner et al., 2000), however, appeared independent of canopy status and part of tree-ring (Table 2), supporting constant emergence of WR to ensure the integrity of wood as a stem grows (Fonti et al., 2015). Height of WR, which is primary depending on the number of cells (von Arx et al., 2015; Olano et al., 2013), differed according to canopy status and part of tree-ring (Fig. 1), suggesting that cell division has been the main mechanism for the adjustments of ray dimensions and storage capacity (Guerin et al., 2020; Morris and Jansen, 2016; Plavcova and Jansen, 2015). The WRs also tended to have a few tracheids at the top and bottom sides, which might have introduced some bias (underestimation) in their height, area and relative area (Fonti et al., 2015). Nevertheless, the area of WR was unaffected by the part of tree-ring (Fig. 1), suggesting height and width of WR to be mutually compensatory.

The relative ray area, which has been used as the main measure of ray quantity (von Arx et al., 2017; Fonti et al., 2015), appeared similar according to canopy status (Fig. 1), though it tended to be slightly higher for the intermediate trees as hinted by the significant interaction (Table 2). Higher relative ray area was estimated in EW, particularly for the intermediate trees, which might be related to the differences in WR width. More vigorous trees can form higher relative quantity of WRs (Gartner et al., 2000), yet for Scots pine under hemiboreal conditions, the amount of WRs likely is indicative of the potential storage capacity (von Arx et al., 2017). The studied WR proxies showed no relationship to increment (Table 2), which contradicts the observations of von Arx et al. (2017), probably as the studied trees were growing under milder, hence more favourable climate (Reid et al., 2004). This suggests that both the dominant and intermediate trees maintained good vigour and similar potential for growth and productions of defence mechanisms under extreme conditions (Sala et al., 2012), ensuring resilience of survival after extremes (Bonnesoeur et al., 2016; Spicer, 2014). More vigorous trees invest more assimilates to growth rather than storage (Reid et al., 2004), while increasing the NSC to simultaneously warrant short- and long-term fitness and competitiveness (von Arx et al., 2017). This also suggests that differences in tree size were likely caused by competition for space causing stress when the canopies started to close, thought trees have had time to adapt to it (Fonti et al., 2015), explaining weak effects of canopy status on WR.

4.2. *Inter-annual variation and climatic forcing*

The studied WR proxies displayed high individuality and the estimated inter-annual variation was low (Table 2), similarly to other studies (von Arx et al., 2017; Fonti et al., 2015). The low inter-annual variability (Table 2) could be explained by the physiological constrains of WR formation, maintaining their size and quantity around the optimum level to ensure functional integrity of stemwood (Fonti et al., 2015), also in the long-term. Accordingly, WR display delayed, hence smoothened, reaction to environmental fluctuations explaining autocorrelation and legacy effects in growth (von Arx et al., 2017). Nevertheless, common high-frequency signals were extracted (averaged) (Figs. 2,3, S2), despite the noise caused by the individuality (Olano et al., 2013), as in case of other wood anatomical proxies (Fonti and Jansen, 2012; Matisons et al., 2012).

Growing conditions and tree vigour can influence inter-annual variability of WR proxies and its sensitivity to meteorological conditions (von Arx et al., 2017; Olano et al., 2013), supporting the differences in high-frequency variation between the dominant and intermediate trees (Figs. 2,3). The range of loadings, particularly of the first PCs (Fig. 2 B) suggested the dominant trees to be more plastic in adjustments of WR to ensure integrity of wood under fluctuating meteorological conditions (Cuny et al., 2019; Fonti et al., 2015). As suggested by linkage of PC scores with meteorological variables, such plasticity can be related to contrasting reaction of WRs in EW and LW to conditions in the preceding vegetation season and dormant period, implying an intra-seasonal autocorrelation (von Arx et al., 2017). This also conforms to the higher activity of the youngest parts of WR hence timely adjustments of environmental demand (Spicer, 2014; Carbone et al., 2013; Richardson et al., 2013) and active control of carbon fluxes within trees from bark to pith (von Arx et al., 2017). The older parts of sapwood and also heartwood act as long-term reservoirs of assimilates, while the outer sapwood is deployed for short-time storage and transfer used for rapid growth at the beginning of the season (Carbone et al., 2013; Richardson et al., 2013). The second PC, which was related to the conditions in the year of growth, distinguished WR proxy variation between parts of tree-ring for the intermediate trees (Fig. 2) suggesting shifting responses during the growing season.

Climatic and meteorological conditions are the main drivers of tree growth (Nabuurs et al., 2018; Aitken and Bemmels, 2016), accordingly inter-annual variation of WR proxies contained climatic signals (Fig. 3), similarly to other wood anatomical proxies (de Micco et al., 2019; Fonti and Jansen, 2012; Matisons et al., 2012). Still, the estimated correlations were intermediate likely due to location of the studied trees in the mid-part of specie's distribution area (Hytteborn et al., 2005) and physiological constrains of WR formation (Fonti et al., 2015). The observed relationships between WR proxies and meteorological variables (Fig. 3) were comparable to these observed in Spain (Olano et al., 2013), supporting presence of general mechanisms determining formation of WR (Fonti et al., 2015). Though some specifics, e.g. contrasts in the effect of summer temperature, were present due to the regional climatic differences (Matias et al., 2017).

Formation of WR is related to meteorological conditions before and during their formation, hence the differences in timing of periods of responsiveness imply diverse mechanisms of regulation (Olano et al., 2013) to ensure multiple functions (Spicer, 2014). Under hemiboreal conditions, water deficit and temperature limitations can simultaneously affect carbon budget (Fonti et al., 2015; Olano et al., 2013), explaining the complexity of the observed relationships between WR proxies and meteorological conditions (Fig. 3). The effects of temperature and the precipitation in the late summer of the previous year (Fig. 3) might be explained by the increased formation of assimilate reserves in response to warm and sunny weather as growth starts to cease (Castagneri et al., 2019; Medlyn et al., 2002). Still, this was particular for LW of the intermediate trees. Nevertheless, the occurrence of rainy days hence reduced solar radiation had a negative effect on cross-section area of WR of the dominant trees likely due to reduced assimilation (Medlyn et al., 2002). Ray density in LW was affected by meteorological conditions (Fig. 3) suggesting that number of active WR initials can be adjusted intra-seasonally according to environmental requirements (Morris and Jansen, 2016; Spicer, 2014; Olano et al., 2013). This, however, was evident only for the intermediate trees, which are considered to be more dependent on assimilate reserves (Fonti et al., 2015; Reid et al., 2004), yet due to smaller size had stronger constraints of carbohydrate storage capacity (von Arx et al., 2017; Gartner et al., 2000).

The negative effect of previous October temperature might be related to the reallocation of assimilates to lignification of cell walls (Olano et al., 2013; Gindl et al., 2000) implying lower requirements for storage space of NSC (von Arx et al., 2017; Plavcova and Jansen, 2015). This correlation, however, was observed only for LW of the dominant trees (Fig. 3), suggesting modulation of the timing of carryover effect of meteorological conditions by tree vigour (Fonti et al., 2015). Precipitation in May, which ensures high stem water potential facilitating expansion of WR cells (Olano et al., 2013) showed a positive effect on size and quantity of WR (Fig. 3), suggesting that the dominant trees were able to assimilate reserves already at the beginning of the season (von Arx et al., 2017). Alternatively, this might be related to faster growth and formation of larger wood cells if water is abundant (Spicer, 2014; Gartner et al., 2000), thus providing larger storage space (von Arx et al., 2017). Xylem parenchyma has also been related to the ability to refill embolized vessels (Spicer, 2014), thus affecting susceptibility to water deficit, explaining carryover effects of meteorological fluctuation (Zweifel et al., 2020; Castagneri et al., 2019).

The observed differences in timing of the responsiveness of WR formation to environmental factors among trees with different canopy status, as indicated by the correlations (Fig. 3), suggested trade-offs in physiological processes aiming to reduce the asynchrony in assimilation and utilization of nutrients (Guerin et al., 2020; Bohn and Huth, 2017; Carbone et al., 2013; Richardson et al., 2013). The differences in timing of the significant meteorological variables according to parts of tree-ring, which also differ by the timing of formations (Fig. 3), suggested that reserves are stored for specific aims, i.e., deployment for growth at certain periods of season, highlighting the complexity of functioning of secondary xylem parenchyma (Spicer, 2014; Richardson et al., 2013).

5. Conclusions

Quantity and size of WRs of Scots pine growing in the mid-part of species range was little affected by canopy status of trees, indicating similar capacity for NSC, thus suggesting high resilience of trees to extremes irrespectively of canopy status. Particularly the dominant trees were more plastic to adjust the formation pathways of NSC storage capacity by altering the size of WRs in EW and LW. The formations of WRs appeared physiologically constrained (with highly individual baseline) to ensure integrity of wood, showing weak inter-annual variation. Nevertheless, high individuality of WR quantity among trees, as well as the trade-offs in sensitivity of WRs to meteorological conditions indicated within-species diversity of carbon allocation patterns. Structural and functional diversity of trees has been related to the sustainability of stands, thus suggesting high adaptability potential of Eastern Baltic Scots pine population. The variance of WRs indicated inter- and intra-annual autocorrelation of reserves, highlighting legacy effects of meteorological conditions, hence susceptibility of trees to cumulative effects of meteorological extremes.

Declaration of Competing Interest

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

Acknowledgements

The study was conducted under the framework of the post-doctoral studies in Latvia (‘Plasticity of development and xylogenesis of the native and introduced tree species under changing climate’, project No.: 1.1.1.2.VIAA/1/16/108) financed by the European Regional Development Fund.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.dendro.2021.125822.

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Climatic Sensitivity of the Top-Performing Provenances of Scots Pine in Latvia

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Matisons, R., Adamovičs, A., Jansone, D., Bigača, Z. and Jansons, Ā. 2018. Climatic Sensitivity of the Top-Performing Provenances of Scots Pine in Latvia. *Baltic Forestry* 24(2): 228-233.

Abstract

Provenance experiments are established to assess growth of diverse population in novel environmental conditions. Productivity has been the main trait for quantification of sufficiency of the provenances under current conditions. Information on climate-growth relationships can provide deeper insight regarding growth potential, especially considering climatic change. In this study, sensitivity of tree-ring width of two top-performing provenances of Scots pine originating from Northern Germany rowing in two trials differing by continentality in Latvia was assessed. Tree-ring width of both provenances was affected by climatic factors, yet the sets of significant factors differed between stands and provenances. Under milder climate, both provenances were sensitive to temperature in December and temperature in July, suggesting effect of cold damage and water deficit. The less productive provenance (Rostock) was additionally sensitive to conditions in winter. The specific climate growth relationships suggested that the more productive provenance (Neubrandenburg) was able to benefit from longer vegetation season. Under harsher climate, both provenances showed similar growth patterns and were sensitive to conditions in spring and preceding summer, which affect nutrient reserves. The provenance-specific responses were less pronounced. Rostock provenance was additionally sensitive to temperature in April, while Neubrandenburg provenance benefited from warmer summers. Considering the observed climate-growth relationships, the Neubrandenburg provenance appeared more suitable for wider application.

Keywords: provenance trial, *Pinus sylvestris*, tree-rings, dendroclimatology, tree growth, transfer

Introduction

Under warming climate, Scots pine (*Pinus sylvestris* L.), which is one of the main forestry species in Northern Europe, has been projected to decrease growth and survival due to competition and influence of herbivores and/or pests in a large part of its current distribution area (Reich and Oleksyn 2008, Hickler et al. 2012). Sensitivity to unfavourable weather conditions (e.g. water deficit, late frosts, etc.), which decrease vigour, and hence resilience of trees, has been considered as an important factor affecting growth and survival (Bolte et al. 2009, Martķnez-Vilalta et al. 2012, Taeger et al. 2013). Accordingly, reaction of trees to meteorological factors has been among the most studied issues in forest science during the past decades (Lindner et al. 2010), aiming for reduction of potential losses due to climatic changes (Bolte et al. 2009, Hanewinkel et al. 2012).

The sensitivity of Scots pine to weather conditions differs among regions and populations due to evolutionary adaptation of trees to specific conditions (Rehfeldt et al. 2002, Taeger et al. 2013). However, recent climatic changes are occurring faster than tree populations could adjust naturally, hence management appears necessary for maintaining forest productivity (Lindner et al. 2010). Application of the reproductive material from populations (provenances) better suited for future climates have been advised as one of the means for minimization of the negative effects of changing climate (Ledig and Kitzmiller 1992, Bolte et al. 2009, Huang et al. 2010). Already at present, results from provenance trials indicate that north-transferred (to harsher climate) forest reproductive material has improved productivity, compared to local material (Gunderson et al. 2012, Schreiber et al. 2013). Still, such transfer can result in increased risk of frost damages (Rehfeldt et al. 2003, Schreiber et al. 2013, Aarrestad et al. 2014). The effect of transfer also features regional specifics (Aarrestad et al. 2014).

Selection of the reproductive material (species, provenances, etc.) is mainly based on growth performance (Burton 2012), which summarizes compatibility of tree genetics and environmental conditions (Channel 1989, Ledig and Kitzmiller 1992). Due to changing climate, such compatibility is dynamic (Huang et al. 2010), and growth of trees can change notably (Wilmking et al. 2004). Considering the long-term nature of forestry decisions, information about the sensitivity of trees to meteorological conditions and their extremes (Taeger et al. 2013) can provide better insight in potential growth in future (Fritts 2001), aiding for application of the most suitable reproductive material, hence sustainability of stands (Burton 2012). In this regard, retrospective analysis of tree-ring width (TRW) can provide detailed information about the sensitivity of tree growth to climatic factors (Fritts 2001). The aim of this study was to assess sensitivity of TRW of two top-performing provenance of Scots pine originating from northern Germany in provenance trials differing by continentality in Latvia (hemiboreal zone). We hypothesized that the north-transferred provenances were sensitive to conditions in winter, and such relationships were stronger in sites with harsher climate.

Material and Methods

Studied trials and provenances

Two IUFRO 1975 trials of Scots pine provenances originating from Central and Eastern Europe (Jansons and Baumanis 2005) were studied. The studied trials were located near Liepāja (56.26°N, 21.12°E; coastal conditions) and near Kalsnava (56.79°N, 25.88°E; inland conditions). The sites differed by climate. In Liepāja site, climate was milder; the mean annual temperature (± confidence interval) during 1986–2015 was 7.8 ± 0.7° C; the mean monthly temperature ranged from 1.4 ± 1.3 to 17.8 ± 0.6° C in February and July, respectively. The annual sum of precipitation was 745 ± 37 mm; the mean monthly precipitation sums were the highest in summer months (ranging from 56 ± 8 to 81 ± 16 mm in June and August, respectively). In the Kalsnava site, climate was harsher and drier. The mean annual temperature was 6.3 ± 0.9° C and the mean monthly temperature ranged from 4.3 ± 1.3 to 18.0 ± 0.61° C in January and July, respectively. The mean annual precipitation sum was 655 ± 28 mm; the mean monthly precipitation sum during the summer months (June–August) was 68 ± 14 mm.

Both trials were located on a flat topography with oligotrophic well drained sandy soils (podzols). The trials were established by one-year-old bare-rooted seedlings, cultivated in local nurseries from seeds acquired from open-pollinated stands. The seedlings were planted in 2 × 1 m grid in 7 × 5 tree blocks. Blocks were randomly distributed in six replications. One thinning, leaving ca. 1/3 of the initially planted trees, was performed at the age of 21 years.

Provenance had significant and consistent effect on survival and growth of the studied trees (Jansons and Baumanis 2005). The inventory conducted at the age of 28 years (in 2003) showed that provenances from northern Germany were among the top-performing, yet their superiority compared to the mean of the plantations was more pronounced under milder climate in Liepāja trial. Based on the repeated inventory (in 2017, age: 42 years), Neubrandenburg (53.50° N, 13.25° E) and Rostock (54.15°N, 12.16° E) provenances were selected for sampling. In Liepāja trial, both provenances were among the top-ten according to their yield, yet stem diameter of the sampled trees was higher for Neubrandenburg provenance (Table 1). Under harsher climate in Kalsnava trial, trees were smaller, yet stem diameter of the sampled trees was practically similar for both provenances. Neubrandenburg provenance was among the top-five performers, while the performance of Rostock provenance was lower due to higher mortality, on average ranking 12. Still, performance of both provenances was above the mean value of the trials.

Sampling and measurements

The selected provenances were sampled in 2017 at the age of 42 years. In each trial, 18 dominant trees (three per replication) of each provenance were sampled. Two increment cores from opposite sides of stem at 1.3 m height above the base were collected form each tree with a 5-mm increment borer. Leaned trees were not sampled to avoid reaction wood.

In the laboratory, samples were glued into fixation planks and their surface was gradually grinded with sandpaper of three roughness grits (120, 240, and 400). Tree-ring widths were measured manually under a microscope, using LINTAB 5 (RinnTech, Heidelberg, Germany) measuring device. The accuracy of measurements was 0.01 mm.

Table 1. Mean diameter at breast height of the sampled trees and statistics of tree-ring width chronologies

	Liepāja trial		Kalsnava trial	
	Neubrandenburg	Rostock	Neubrandenburg	Rostock
Mean stem diameter at breast height (± conf. int.), cm	25.02±1.91	22.41±2.09	17.48±1.43	17.41±0.95
Mean TRW (± conf. int.), mm	3.54±0.14	3.20 ± 0.14	2.41±0.10	2.42±0.10
Number of trees	18	17	16	17
First order autocorrelation	0.82	0.83	0.79	0.77
Mean interseries correlation (*r*-bar)	0.41	0.40	0.34	0.42
Gleichläufigkeit	0.63	0.71	0.65	0.67
Expressed population signal	0.92	0.91	0.88	0.92
Signal-to-noise ratio	10.85	9.63	7.2	10.87

Data analysis

Time-series of TRW of each sample were crossdated by graphical inspection (Fritts 2001) and statistically, using program COFECHA (Grissino-Mayer 2001). The crossdated time-series were averaged for trees. To assess high-frequency variation, residual chronologies of TRW were produced. Time-series were detrended by modified negative exponential curve and then by cubic spline with the wavelength of 20 years, preserving 50% of variance. Autocorrelation was removed by autoregressive modelling ("AR"). Chronologies were built by averaging the detrended time-series of trees, using the biweight robust mean. Mean interseries correlation (*r*-bar), first order autocorrelation (AC), Gleichläufigkeit (GLK), expressed population signal (EPS; Wigley et al. 1984), and signal-to-noise ratio (SNR) were calculated for description of the chronologies.

The effect of climatic factors on high-frequency variation of TRW was assessed by bootstrapped (Johnson 2001) Pearson correlation analysis (10^4 iterations). The tested climatic factors were minimum, mean, and maximum monthly temperature, monthly precipitation sum, and standardized precipitation evapotranspiration index (SPEI) (Vicente-Serrano et al. 2010), calculated with the respect for previous three months. Climatic data were obtained from the gridded dataset provided by the Climatic Research Unit of University of East Anglia (Harris et al. 2014) for the stations located at < 20 km distance from the trials. Climatic window from July in the year preceding formation of tree-ring to September in year of tree-ring formation was used. Collinearity of climatic factors was assessed, and only non-collinear factors were presented.

Results

Most of the time-series of trees (≥ 16 per provenance; Table 1) were crossdated and passed quality checking. In both trials, mean time-series (variation) of TRW of the studied provenances (Figure 1) were highly similar (*r* ≥ 0.97). Nevertheless, in Liepāja trial, TRW of Neubrandenburg provenance consequently exceed Rostock one (except first three years). In Kalsnava trial, the TRW of the dominant trees of both provenances was practically the same (Figure 1, Table 1). The trials differed by growth trends. In the Liepāja trial, where trees were larger (Table 1), TRW followed negative exponential curve (Figure 1), while almost linear decrease was observed in the Kalsnava trial. All time-series of TRW contained high autocorrelation (AC ≥0.75) indicting effect of preceding growth.

High-frequency variation of TRW was similar among trees of each provenance/trial, as indicated by high *r* bar and GLK values (≥ 0.34 and ≥ 0.63, respectively; Table 1). Accordingly, the produced chronologies of TRW (Figure 1) contained common environmental signal (SNR e" 7.20) and EPS exceeded 0.85 (cf. Wigley et al. 1984). The developed chronologies (Figure 1) were significantly correlated indicating presence of common environmental signals (Table 2). The highest correlation (*r* ≥ 0.86) was observed between the chronologies from the same trial, similarly to mean times-series of TRW. The correlation between chronologies from different stands was considerably weaker, irrespectively of provenance (*r* = ~0.50), indicating regional specifics in environmental forcing of TRW. Nevertheless, common decrease in TRW was observed in all chronologies in 1997, 1999, and 2013 (Figure 1), when springs had extreme temperature contrasts (warm weather followed by cold spells). Common increase of TRW occurred in 1983, 1996, and 2016, when May was warmer than usual, yet early summer were cool.

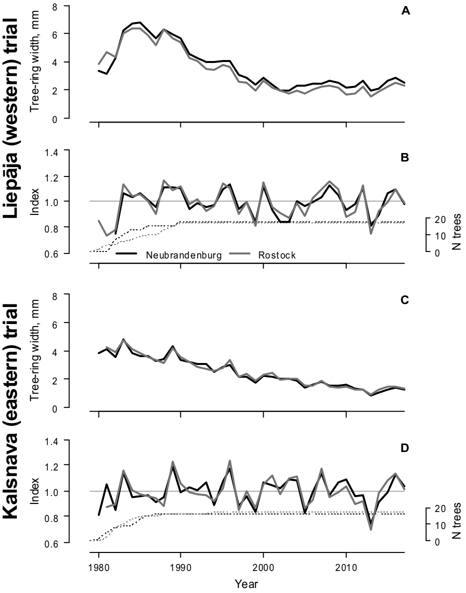

Figure 1. Mean time-series (A and C) and residual chronologies of tree-ring width (B and D) of the Neubrandenburg and Rostock provenances of Scots pine in the Liepāja (western) and Kalsnava (eastern) trials in Latvia for the period of 1980–2017. In B and D, fine dotted lines indicate sample depth (number of crossdated trees)

The developed residual chronologies of TRW significantly correlated with 10 of the tested climatic factors, yet the sets of significant factors differed by trials and provenances (particularly in Liepāja trial) (Figure 2). In Liepāja trial, where climate was milder, both provenances were sensitive to maximum temperature in December and July. Rostock provenance was specifically sensitive to mean temperature in March and April and to minimum temperature in January. Neubrandenburg provenance showed specific sensitivity to September temperature and drought index (SPEI) in May. Under harsher climate in Kalsnava trial, both provenances were sensitive to temperature in March and preceding September, and to SPEI in preceding July. Rostock provenance was specifically sensitive to temperature in April, while Neubrandenburg provenance to temperature in preceding July. In contrast to Liepāja one, in Kalsnava trial, temperature in July had a positive effect on TRW.

Discussion and Conclusions

Both north-transferred provenances were productive (Figure 1), as observed by Jansons and Baumanis (2005) and other studies (cf. Gunderson et al. 2012, Schreiber et al. 2013). In Liepāja trial, dominant trees differed by radial increment (Figure 1), implying that individuality of the provenances was expressed in the climatic conditions that were more similar to Northern Germany. Although in Kalsnava trail rankings of the studied provenances differed (Jansons and Baumanis 2005), patterns of TRW of the dominant trees were similar (Figure 1), indicating common environmental limitation of growth. The differences in productivity observed by Jansons and Baumanis (2005), apparently, were caused by trees of lower canopy status. The differences in growth curves might be related to growing conditions (Figure 1), as in harsher conditions radial increment is lower, yet culminates faster (Donis and Šņepsts 2015).

Presence of clear environmental signals in TRW (SNR > 7.20; Table 1) showed that the radial increment of the studied provenances has been sensitive to the meteorological conditions (Fritts 2001), similarly to trees from local populations (cf. Jansons et al. 2016). The high AC in TRW (Table 1) implied the radial increment has been affected by previous growth (Fritts 2001), likely via assimilation of nutrient reserves (Pallardy 2008). The correlations among the chronologies (Table 2) highlighted local patterns in the variation of TRW, which are common for species in the non-marginal parts of their range (Fritts 2001, Jansons and Baumanis 2005).

Although in both trials, the provenances showed common sensitivity to certain factors, provenance-specific sensitivity was more pronounced under milder climate in the Liepāja trial (Figure 2). Apparently, milder

		Liepāja trial		Kalsnava trial	
		Neubrandenburg	Rostock	Neubrandenburg	Rostock
Liepāja trial	Neubrandenburg		0.93	0.52	0.47
	Rostock	<0.001		0.53	0.53
Kalsnava trial	Neubrandenburg	0.001	0.001		0.86
	Rostock	0.004	0.001	<0.001	

Table 2. Pearson correlation coefficients (upper diagonal part) and their *p*-values (lower diagonals part) between residual chronologies of tree-ring width of the studied provenances/trials

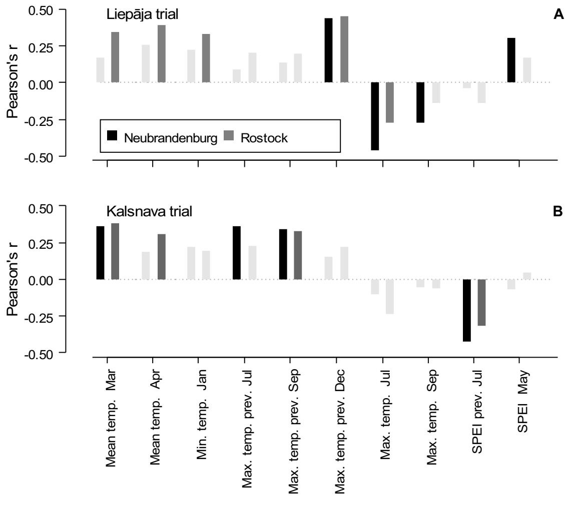

Figure 2. Pearson correlation coefficients between residual chronologies of tree-ring width of Neubrandenburg and Rostock provenances of Scots pine and local climatic factors in Liepāja (A) and Kalsnava (B) trials in Latvia for the period of 1985–2015. Significant correlations are shown by the intensive shades. The significance of the correlations (at α = 0.05) was determined by bootstrapping. Only the factors showing significant correlations are plotted

climate allowed clearer expression of genetically determined adaptation to specific micro-conditions at the areas of their origin (Rehfeldt et al. 2003, Taeger et al. 2013). The common sensitivity of both provenances to temperature in December (Figure 2) might be related with cold damage (Repo et al. 1994, Pearce 2001), particularly considering frequently shifting weather conditions in winter (frequent thaws) in the western part of Latvia (Harris et al. 2014). The correlation of TRW with temperature in July (Figure 2) might be related to physiological water deficit conditions in response to increased transpiration under raised temperature (Pallardy 2008).

The specific response of Rostock provenance, which originated from coastal region with milder climate, to winter and spring temperature in Liepāja trial (Figure 2) indicated increased susceptibility to conditions in the dormant period (Pearce 2001), due to northern transfer of the material (Schreiber et al. 2013). Alternatively, such connection (Figure 2) might be related to alterations in root dynamics (Jalkanen 1993), hence affected water relations in the following season (Pallardy 2008). The additional sensitivity to winter-spring conditions (Figure 2), which are often unstable, might explain lower productivity of Rostock provenance (Figure 1, Table 1). Neubrandenburg provenance was specifically sensitive to factors related to water availability at the beginning and at the end of vegetation season (Figure 2), suggesting non-sufficient water supply. Considering higher increments (Figure 1) and sensitivity to conditions in May and September (Figure 2), under milder climate, this provenance, apparently, was able to benefit from longer vegetation season.

Under harsher climate in Kalsnava trial, limitation of TRW by meteorological conditions, apparently, was stronger (Fritts 2001), suppressing specific responses of the provenances (Figure 2). Both provenances were sensitive to temperature in March (Figure 2), suggesting effect of cold damage (Pearce 2001) and/or affected root dynamics (Jalkanen 1993). The positive correlation with temperate in September in the year preceding formation of tree-ring (Figure 2) might be explained by additional nutrient assimilation (Oleksyn et al. 2000) due to extended vegetation season (Menzel and Fabian 1999). The negative correlation with drought index in May (Figure 2) is difficult to explain. Probably, such correlation might be related to decreased radiation in years with precipitation-rich springs. Rostock provenance appeared additionally sensitive to temperature in April, similarly as in Liepāja trial (Figure 2). The positive correlation with temperature in July of the year preceding growth (Figure 2), suggested that in cooler climate, Neubrandenburg provenance, benefited from warmer summers (cf. Helama et al. 2005).

As hypothesised, TRW of both north-transferred provenances showed sensitivity to weather conditions in winter, and climatic factors, apparently, had stronger effect in trial with harsher climate. Although both provenances were among the most productive, the sets of climatic factors significant for TRW were diverse, implying different climatic sensitivity. Considering the observed climate-growth relationships, Neubrandenburg provenance appeared more suitable for conditions in Latvia, as it was less sensitive to conditions in winter and was able to benefit from increasing length of vegetation season. Neubrandenburg provenance was more productive compared to Rostock one in Liepāja trial; accordingly, its superiority might be expected in the western part of Latvia, where climate is milder.

Acknowledgements

The study was conducted under the framework of post-doctoral studies in Latvia ("Plasticity of development and xylogenesis of the native and introduced tree species under changing climate", project No.: 1.1.1.2.VIAA/1/16/108) financed by the European Regional Development Fund

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Article

Weather–Growth Responses Show Differing Adaptability of Scots Pine Provenances in the South-Eastern Parts of Baltic Sea Region

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Abstract: Local adaptation and plasticity of growth play important roles in the adaptability of trees to changing conditions. Under accelerating climatic changes, the adaptive capacity of metapopulations can be exceeded, implying a necessity for assisted gene flow to sustain the productivity of forests. Such management is knowledge intensive, and information on the responsiveness of metapopulations (provenances) across the climatic gradient can aid more comprehensive projections of their performance. The plasticity of growth responses to weather conditions of five provenances of Scots pine with differing field performance across the climatic gradient of the south-eastern Baltic Sea region was assessed using dendrochronological methods and generalized additive models. Weather conditions related to water availability in summer, as well as during dormancy, were the main regional drivers of an increment in the provenances. The provenances differed by the plasticity of responses according to field performance, indicating adaptation in terms of growth sensitivity and uneven adaptability. The weather–growth responses of the top-performing provenances to summer weather were more plastic, providing advantages under a changing climate. Accordingly, regional sensitivity and plasticity of growth responses could be used for the screening of genotypes best suited for the projected climates. In addition, the estimated growth responses encourage supplementation of the local breeding populations with the top-performing provenances originating from sites with the projected climates.

Keywords: *Pinus sylvestris*; local adaptation; provenance trial; tree-ring width; nonlinear weather–growth relationships; climatic gradient

Citation: Matisons, R.; Jansone, D.; Bāders, E.; Dubra, S.; Zeltiņš, P.; Schneck, V.; Jansons, Ā. Weather–Growth Responses Show Differing Adaptability of Scots Pine Provenances in the South-Eastern Parts of Baltic Sea Region. *Forests* **2021**, *12*, 1641. https://doi.org/10.3390/f12121641

Academic Editor: Sparkle Malone

Received: 14 October 2021
Accepted: 24 November 2021
Published: 26 November 2021

1. Introduction

Substantial changes in forest composition are projected in Eastern and Northern Europe by the end of the 21st century [1,2] due to warming, the increasing heterogeneity of the precipitation regime [3–5], and other weather extremes [2]. This highlights the necessity for adaptive management to mitigate ecological and economic consequences [6–8]. Assisted migration/gene flow in combination with breeding have been identified as highly effective for the coupling of ecological demands of forest reproductive material with the projected climates [7,9–12]. Such an approach requires comprehensive information on biotic and abiotic factors influencing tree growth [6–8,13]. The ongoing changes in tree growth in Eastern and Northern Europe [1,2,14], though, are exemplifying differences in the adaptability of genotypes [10,15,16].

To cope with a wide spectrum of environmental conditions [10,17–19], trees have evolved considerable phenotypical plasticity [15,16,20,21]. Nevertheless, metapopulations of wide-distribution species adapt to local/regional conditions restricting plasticity to optimize performance/survival [15,16,18,22–24]. For traits of survival/reproductive significance, genetic adaptation occurs, resulting in the heritability of phenotypes [16,20,22,25]. Furthermore, genetic adaptations can persist under intensive gene flow [15,20], which might also cause natural adaptation to lag behind the accelerating environmental changes [10], implying provenance–specific environmental optima and plasticity [11,20,24,26,27]. Accordingly, phenotypical plasticity and genetic adaptation indicate the adaptability of genotypes [15,16,21].

Provenance trials have been historically established to screen the performance of genotypes under common conditions [17,24,28], and parallel traits are sufficient for the evaluation of assisted gene transfer/migration [11,15,28,29]. Provenance trials are revisited for assessment of the adaptability of metapopulations [17,24,28,30], screening performance, and the sensitivity of genotypes under extended ecological gradient(s) [15,17,28,29]. Such information is crucial for breeding programs [7,13], aiding the development of more tolerant genotypes [10,28].

A retrospective analysis of increment is efficient for the assessment of the sensitivity of genotypes to weather fluctuations [11,19,31,32] and their conformity with climates [18,25,33]. Under shifting environments, such an approach appears more informative than a comparison of allometric variables, which represent cumulative responses to past conditions [7,28,31]. Tree-ring width (TRW) and its derivatives (e.g., relative additional increment, etc.) are widely used for such an analysis due to their convenience of sampling and measurements [19,26,32,34]. Accordingly, sensitivity of growth (TRW) has been related to the productivity of genotypes [19,27,31,35,36], although xylogenesis is a continuous process [37,38], and TRW represents the effects of conditions during and prior to growth [26,34].

Ecological responses across environmental gradients are usually bell-shaped [39,40]. Close-to-linear responses can be observed under a limited part of a gradient [26,41–43], often implying their biasness [39]. Trees experience a wide spectrum of environmental (e.g., meteorological) conditions, which can have disproportional effects [26,40,42,44]. Accordingly, assessments of nonlinear responses across spatiotemporal climatic gradient(s) are essential for growth projections under a shifting climate [18,23,34,42]. This allows screening of the main regional climatic drivers of growth [14,18,23], which, though, might be moderated by local adaptation(s) [15,16,25,26].

Scots pine (*Pinus sylvestris* L.) is a stress-tolerant [45], wide-distributed and economically important species [46]; hence, efforts are made to improve its sustainability [11,47]. The species is genetically diverse [48], yet its populations show varying degrees of local adaptation [16,24,34,49]. Scots pine is ecologically plastic [46] and can be considered more resilient to climatic changes than other temperate conifers [1,3]. However, it is also sensitive to water shortages [3,26,34,50], and its abundance is projected to decrease in the eastern Baltic region [1,2] due to increasing water stress [3–5] and competition [21,51]. Regional (eastern Baltic) responses of Scots pine to water-deficit-related conditions are nonlinear [26], implying disproportional effects of climatic changes [43]. Nevertheless, there is high potential for assisted gene flow to anticipate the shifts in climatic gradient [10–12,15,29] and improve the tolerance of trees [8,9,52]. Genetic adaptations in terms of weather–growth sensitivity has been suggested for the south-eastern Baltic metapopulations [27,35], supporting the potential for breeding for climatic tolerance [25,47,53].

The aim of the study was to assess the plasticity of responses of provenances of Scots pine originating from the south-eastern Baltic Sea region differing by productivity to weather fluctuations under the regional climatic gradient. Provenances with differing productivity were selected to screen relationships between their climatic sensitivity and field performance. We hypothesized growth responses to be nonlinear and their shape to differ by field performance of the provenances. We also assumed more productive provenances to have responses with wider optimum intervals, hence, to be more tolerant to weather fluctuations, suggesting higher sustainability under a shifting climate.

2. Materials and Methods

2.1. Trials, Provenances, and Measurements

An international provenance experiment established under the collaboration of the German Democratic Republic and the USSR in 1975 for assessment of performance of Scots pine metapopulations from Eastern Europe and the USSR [54] was studied. The seed material for the experiment was collected in 36 open-pollinated stands (20–25 plus trees per stand) distributed in 50–57° N and 11–27° E (Baltics, Ukraine, Belarus, Poland, and Germany) [54,55]. Such region currently comprises climates projected for the Baltic States (Latvia) by the end of the 21st century [1,56]. Five parallel trials (Figure 1) growing under lowland ($\leq$220 m above sea level) conditions near Liepaja (LI), Zvirgzde (ZV), Kalsnava (KA), Waldsieversdorf (WS), and Nedlitz (NL) on freely drained oligotrophic mineral (sandy or silty) podzols (LI, ZV, and KA) or mesotrophic sandy brown soil (WS and NL) with a flat topography (Table 1) were sampled. Thus, the trials represented regional climatic gradient and projected amplitude of its shift by the end of the 21st century [1,56].

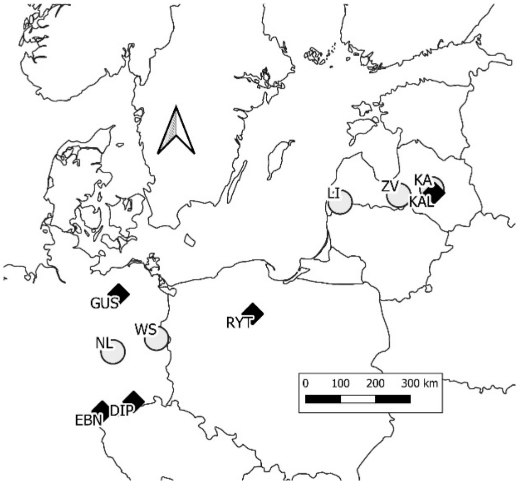

Figure 1. Location of the studied trials (circles) and origins of the studied provenances (squares) of Scots pine.

Table 1. Location (in decimal degrees) and general climatic description (mean temperature and precipitation sums for the period 1988–2017) of the studied parallel provenance trials of Scots pine.

	LI	ZV	KA	WS	NL
Vicinity	Liepaja (Latvia)	Zvirgzde (Latvia)	Kalsnava (Latvia)	Waldsieversdorf (Germany)	Nedlitz (Germany)
Latitude, °N	56.45	56.65	56.8	52.53	52.02
Longitude, °E	21.63	24.37	25.93	14.05	12.33
Elevation, m a.s.l.	15	50	220	60	115
Annual temperature	7.5 ± 0.6	7.2 ± 0.7	6.4 ± 0.7	9.2 ± 0.7	9.6 ± 0.6
May–September temperature	15.0 ± 0.7	15.2 ± 0.8	14.8 ± 0.8	16.2 ± 0.7	16.6 ± 0.07
January temperature	−1.9 ± 2.4	−3 ± 2.6	−4.2 ± 2.7	0.1 ± 2.5	0.4 ± 2.4
July temperature	17.8 ± 1.6	18.2 ± 1.6	17.9 ± 1.6	18.7 ± 1.6	19.3 ± 1.7
Annual precipitation sum	789 ± 91	659 ± 75	689 ± 81	568 ± 80	662 ± 73
May–September precipitation sum	353 ± 71	333 ± 63	349 ± 66	290 ± 66	294 ± 59

The climate at the trials can be characterized as temperate moist continental (Dfb; [57]), yet with explicit coastal features, as preconditioned by the dominating westerlies and proximity of the Baltic and North Seas. The trials differed by continentality due to varying distance from sea. During the period 1988–2017, January and July were the coldest and the warmest months, respectively (Table 1; Supplementary Material, Figure S1). In the trials in Latvia, the mean annual temperature ranged 6.4–7.5 °C, decreasing with growing distance from the sea; mean summer (May–September) temperature was higher in ZV trial. The annual precipitation sum was higher in the coastal (LI) compared to ZV and KA trials. Summer precipitation, which comprised approximately half of the annual, was similar among the trials.

In northern Germany, the mean annual temperature was higher, yet the difference among the trials was smaller compared to Latvia (Figure S1, Table 1). The annual precipitations sums were approximately 20% lower compared to trials in Latvia; the highest monthly precipitation occurred in the summer months. The vegetation period, when the mean diurnal temperature > 5 °C, was approximately 3–4 weeks longer compared to Latvia. The climatic changes are expressed as warming during the dormancy period, extension of vegetation period (by approximately 10 days during the past 50 years), and increasing heterogeneity of summer precipitation regime [56,58]. In Germany, a negative trend for summer precipitation has been estimated [56].

The trials were established by planting one-year-old bare-rooted seedlings raised in local nurseries on forest land. The studied trails contained common set of provenances. In trials in Latvia, provenances were represented by six to eight randomly distributed blocks of 5 × 7 trees planted with 1 × 2 m spacing (5000 trees ha^{-1}). At the age of 21 years, the trials were systematically thinned (from bottom) removing two thirds of the trees, resulting in stand density of ca. 1800 trees ha^{-1} [55]. In each trial in Germany, provenances were represented by four randomly distributed blocks of 100 (5 × 20) trees planted with the initial spacing of 0.5 × 2 m (10,000 trees ha^{-1}). The WS trial has undergone three thinnings (last in the winter of 2013/2014), reducing stand density to ca. 1400 trees ha^{-1}. The NL trial was thinned once directly prior to sampling, reducing stand density from ca. 4200 to ca. 1300 trees ha^{-1}.

To assess effect of local (genetic) adaptation on plasticity of metapopulations of Scots pine in terms of growth responses to regional weather drivers and productivity [14,15,20,26,27,35], five provenances were selected based on their field performance (two top-, two low-performing provenances, and one with intermediate performance). The selection was based on field performance of provenances (according to tree height and survival) in trials in Latvia according to an inventory conducted in 2016. Metapopulations Güstrow (GUS) and Rytel (RYT), which originated from lowland sites (Figure 1) with warmer and drier climate compared to trials in Latvia (Table 2; Supplementary Material, Figures S1 and S2), were selected for representation of the top-performing provenances (Supplementary Material, Table S1). Metapopulations Eibenstock (EBN) and Dippoldiswalde (DIP), which originated from the Orr mountains (Table 2) where mean annual temperature was similar but precipitation higher compared to Latvia (Table 1; Supplementary Material, Figures S1 and S2), were selected as the low-performing provenances (Supplementary Material, Table S1). Such selection represents provenances subjected to decreasing ecological transfer differences [7,11,12] in the Baltics (Latvia). To assess adaptability of native metapopulations [52,59] (from Latvia's perspective), Kalsnava (KAL) provenance representing lowland conditions in Latvia (Table 2), which showed intermediate field performance (Supplementary Material, Table S1) but superior stem quality [55], was selected. The performance of the provenances was consistent across the trials in Latvia [55], although coastal LI trial was more productive (Supplementary Material, Table S1). The selected provenances showed comparable rankings also in the trials in Germany [52,54].

Table 2. Location (in decimal degrees) and general climatic description (mean temperature and precipitation sums for the period 1946–1975) of the origin of the studied provenances (from southern Poland, Northern Germany, and Latvia) of Scots pine.

	Dippoldiswalde (DIP)	**Eibenstock (EBN)**	**Kalsnava (KAL)**	**Güstrow (GUS)**	**Rytel (RYT)**
Latitude, °N	50.82	50.45	56.7	53.75	53.67
Longitude, °E	13.87	12.43	25.9	12.25	18.02
Elevation, m a.s.l.	590	710	190	25	130
Annual temperature, °C	6.6	6.0	6.3	8	7.9
Temperature May–September, °C	13.1	12.5	14.6	14.8	15
Temperature Jan, °C	−2.5	−3.1	−4.3	−0.9	−1.4
Temperature Jul, °C	15.3	14.8	18.0	16.8	17.2
Annual precipitation, mm	809	993	650	586	597
Precipitation May–September, mm	405	501	340	303	301

In each trial, 9–16 trees per provenance were sampled (Supplementary Material, Table S2). One to three visually healthy non-leaning (to avoid reaction wood) dominant trees per block were cored at the breast height using a 5 mm increment corer. Two increment cores from randomly oriented opposite sides of stem were extracted. Samples were collected in the autumn of 2017 (Latvia) and spring of 2021 (Germany). In a laboratory, cores were fixed on wooden mounts, and their surface was levelled using the WSL core microtome [60]. A LINTAB6 measurement table (RinnTech, Heidelberg, Germany) was used to manually measure TRW. All measurements were carried out by the same person; the accuracy of measurements was 0.01 mm.

2.2. Data Analysis

The quality of TRW measurements was ensured by graphical and statistical cross-dating [61]. The high-frequency variation of TRW datasets was described by the mean interseries correlation (r-bar), first order autocorrelation (AC1), mean sensitivity (SENS), signal-to-noise ratio (SNR), and the expressed population signal (EPS; [62]). These metrics were calculated based on detrended (by a cubic spline with the wavelength of 25 years and 50% cut-off frequency) time series of trees. To assess local weather–growth relationships, a residual chronology of TRW was developed for each provenance within each trial. The time series of trees were double detrended by the modified negative exponential curve and by a flexible cubic spline with the wavelength of 25 years and 50% cut-off frequency, prewhitened by the first order autoregressive model (′ar1′), and averaged by the biweight robust mean [63,64]. Such detrending was performed to minimize effects of local conditions.

Considering that each trial represents limited part of the regional climatic gradient [18,23,26,39], bootstrapped Pearson correlation analysis (nonparametric percentile interval bootstrapping with 1000 iterations; [65]) was used to assess local linear relationships between the residual chronologies and meteorological variables during the common period of 1985–2017. Such common period was selected to reduce noise associated with juvenile wood and to ensure sufficient replication of measurements (sample depth). Mean monthly temperature, precipitation sums, and standardized precipitation-evapotranspiration indices calculated with the respect to preceding three months (SPEI; [66]), arranged into the time windows from June of the year preceding growth (previous June) to October in the year of tree-ring formation, were used as the meteorological variables. Gridded climatic data (CRU TS) were obtained [67].

Generalized additive mixed models [68] were used to assess plasticity of growth responses of the provenances across the regional (south-eastern Baltic) spatiotemporal climatic gradient represented by the trials (Table 1, Figure S1). Such models are proven efficient for the analysis of spatiotemporally heterogeneric ecological data representing environmental gradient(s) [18,26,41,42]. A model was constructed for each provenance for the common period. The models were based on the detrended and prewhitened TRW time series of individual trees, as produced for calculation of the residual chronologies (before averaging). For cross-verification (ensuring absence of overfit) of the refined models, ca. 10% of trees per provenance/trial were randomly excluded from calibration. The index values of the detrended series, which represent the annual relative additional increment, were used as the response variable.

Arbitrary combinations of weather variables (based on correlation analyses and presuming conformity with the biological realism) were tested as predictors; model selection was based on the Akaike Information Criterion. The predictors were tested as a complex, i.e., commonly for the studied provenances. Collinear predictors were omitted according to the variance inflation factor. To account for the influence of local conditions and temporal dependencies of responses, year and tree nested within repetition and trial were used as the random effects [69,70], and general first order autocorrelation term was included. The models were fit using the restricted maximum likelihood approach. Smoothening parameters were estimated by the generalized cross-validation procedure, which avoids overfit. Regression spline with shrinkage was used to smooth the results. Due to limited regional climatic gradient, the basis dimension for smoothing splines was restricted to three, implying responses with up to two inflection points to avoid overfit. Model residuals were checked for normality and homogeneity by diagnostic plots. Data analysis was conducted in R v. 4.1.1 [71] using libraries "dplR" [64], "car" [72], and "mgcv" [68].

3. Results

3.1. Local Linear Weather–Growth Relationships

Most of the measured time series of TRW (9–16 trees per provenance per trial; ≥86% of the measured) showed good agreement, were successfully crossdated, and ensured sufficient replication during the common period (Supplementary Material, Figure S3). Wider TRW was measured in the coastal LI trial compared to others, implying generally comparable productivity. The studied datasets (provenances/trial) contained a common environmental signal, as EPS exceeded 0.85 (cf. [62]; Table 3). The strength of the common environmental forcing of the increment did not show explicit geographic tendencies; the mean r-bar ranged from 0.35 to 0.49 in NL and WS trials, while SNR ranged from ca. 8.55 to 16.21 in LI and WS trials, respectively. Nevertheless, AC1 and GINI were higher in trials in Latvia compared to Germany (ca. 0.77 vs. 0.51 and ca. 0.26 vs. 0.22, respectively) and SENS showed the opposite. Across the studied trials, the provenances showed comparable r-bar and AC1 (ca. 0.40 and 0.67, respectively; Table 3). Nevertheless, the low-performing DIP and EBN provenances appeared more sensitive to environmental fluctuations, showing higher GINI and SENS, though lower SNR.

Table 3. Statistics of the crossdated datasets of tree-ring width time series of the studied south-eastern Baltic provenances of Scots pine (from southern Poland, Northern Germany, and Latvia) by the trials for the period 1985–2017. N—number of crossdated trees, TRW—mean tree-ring width (±standard deviation), r-bar—mean interseries correlation, GINI—Gini coefficients, AC1—first order autocorrelation, SENS –mean sensitivity, SNR—signal-to-noise ratio, and EPS—expressed population signal.

Trial	Provenance	N	TRW	r-bar	GINI	AC1	SENS	SNR	EPS
LI	DIP	12	2.58 ± 1.57	0.44	0.34	0.79	0.24	11.36	0.92
LI	EBN	11	2.87 ± 1.32	0.36	0.25	0.80	0.20	7.69	0.88
LI	GUS	11	3.30 ± 1.62	0.36	0.27	0.78	0.19	7.65	0.88
LI	KAL	12	3.07 ± 1.45	0.33	0.25	0.78	0.19	7.28	0.88
LI	RYT	12	3.38 ± 1.74	0.37	0.27	0.82	0.19	8.78	0.90
ZV	DIP	9	2.00 ± 1.06	0.43	0.30	0.77	0.23	9.04	0.90
ZV	EBN	9	2.11 ± 1.19	0.41	0.31	0.79	0.23	8.39	0.89
ZV	GUS	10	2.45 ± 1.11	0.41	0.24	0.80	0.19	8.58	0.90
ZV	KAL	10	2.25 ± 1.01	0.41	0.25	0.77	0.21	9.14	0.90
ZV	RYT	10	2.86 ± 1.25	0.38	0.23	0.68	0.22	7.84	0.89
KA	DIP	10	2.02 ± 0.94	0.34	0.27	0.77	0.23	6.76	0.87

Table 3. *Cont.*

Trial	Provenance	N	TRW	r-bar	GINI	AC1	SENS	SNR	EPS
KA	EBN	13	2.02 ± 1.02	0.39	0.28	0.78	0.24	10.26	0.91
KA	GUS	12	2.37 ± 0.97	0.42	0.23	0.74	0.22	10.88	0.92
KA	KAL	14	2.36 ± 0.90	0.37	0.22	0.70	0.21	9.87	0.91
KA	RYT	12	2.77 ± 1.00	0.44	0.20	0.75	0.19	11.50	0.92
NL	DIP	12	2.21 ± 0.98	0.30	0.23	0.58	0.26	6.19	0.86
NL	EBN	13	2.09 ± 0.84	0.35	0.21	0.60	0.24	8.48	0.90
NL	GUS	13	2.33 ± 0.89	0.37	0.20	0.59	0.25	9.24	0.90
NL	KAL	13	2.07 ± 0.74	0.37	0.19	0.46	0.27	9.55	0.90
NL	RYT	15	2.55 ± 0.75	0.37	0.16	0.45	0.23	10.60	0.91
WS	DIP	13	2.18 ± 1.22	0.46	0.27	0.52	0.30	13.43	0.93
WS	EBN	12	2.22 ± 1.10	0.44	0.25	0.48	0.31	11.53	0.92
WS	GUS	15	2.35 ± 1.04	0.55	0.22	0.52	0.27	21.88	0.96
WS	KAL	12	2.27 ± 1.04	0.53	0.24	0.49	0.30	16.76	0.94
WS	RYT	16	2.36 ± 0.91	0.48	0.20	0.45	0.26	17.45	0.95

The developed chronologies (Figure 2) showed regional and local specifics and the similarity in growth patterns decreased with distance. Nevertheless, within each trial, provenance-specific variations, particularly differences in index values (rather than synchrony of chronologies), indicated differing sensitivity to the principal drivers of growth. A higher correlation among the chronologies was observed within compared with between the trials ($0.71 \leq r \leq 0.86$ vs. $0.16 \leq r \leq 0.23$, respectively). The chronologies correlated significantly with 27 (eight common) of the 54 meteorological variables tested; meteorological variables significant in Latvia and Germany were generally comparable (Figure 3). These variables were related to the thermal and moisture regime in late summer and the dormant period preceding the growth, as well as in the current vegetation period. The strength of the correlations was generally similar, ranging from −0.52 to 0.60 and from −0.44 to 0.60 (absolute means of 0.35 and 0.36) in trials in Latvia and Germany, respectively, indicating intermediate local individual effects of meteorological variables. However, the strength of correlations differed by trials, implying local specifics in growth sensitivity.

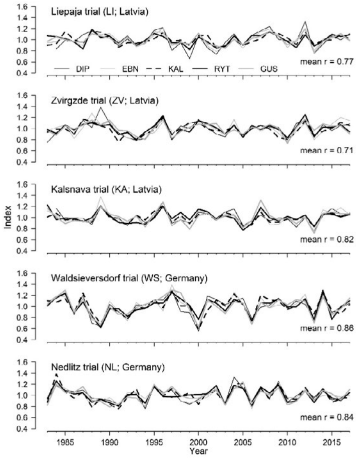

Figure 2. Residual chronologies of tree-ring width of the studied provenances of Scots pine according to trial. The mean interseries correlation between the chronologies by trial are indicated in the panels (mean r).

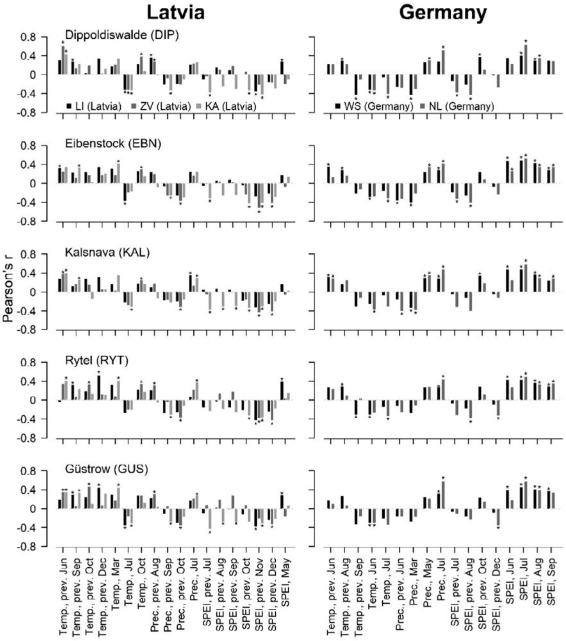

Figure 3. Bootstrapped Pearson correlation coefficients between the time series of annual relative radial additional increment (represented by the residual chronologies) of the studied south-eastern Baltic provenance of Scots pine and local (by trial) meteorological variables: mean monthly temperature (Temp.), precipitation (Prec.), and standardized precipitation-evapotranspiration index (SPEI) for the period 1985–2017. Only the variables showing significant correlations with increment (at $\alpha = 0.05$) are shown; the significant correlations are highlighted by asterisks. The results are summarized by country for clarity. Prev. indicates conditions in the year preceding formation of tree-ring.

Among the meteorological variables showing common correlations with chronologies in Latvia and Germany, July precipitation and temperature in the previous June showed positive effects, while temperature in July and SPEI in the previous July, August, and December showed negative effects (Figure 3). The correlations with temperature in the previous September were contrasting. Correlations with temperature during the dormancy period (December and March) and precipitation in the previous vegetation period (August–October), as well as SPEI in May were specific to trials in Latvia. In Germany, provenances showed correlations with precipitation in March and May, June–September's SPEI, and temperatures in June and the previous August.

The strength of correlations with most of the significant meteorological variables differed by provenance, indicating local adaptations (Figure 3). In the trials in Latvia, the differences among the provenances were related to temperatures in the December and March, to which the top-performing provenances were more sensitive, particularly in LI and KA trials. The low-performing provenances (DIP and EBN), as well as RYT, appeared less sensitive to summer precipitation both in the current and preceding years. Correlation with SPEI in May was significant for DIP, RYT, and GUS under coastal conditions (LI trial). Stronger (and significant) correlations with SPEI in the previous November and December were observed for EBN, KAL, and RYT.

Under the drier and warmer climate in trials in Germany (Table 1), July precipitation and SPEI showed the strongest correlations with TRW, particularly for the low-performing provenances (Figure 3). The top-performing provenances showed non-significant correlations with precipitation in March and May but were sensitive to SPEI in the previous December (in NL trial). In turn, the low-performing provenances, specifically, showed correlations with SPEI in the previous July and August. Correlations with temperature in July and the previous August differed among the provenances, irrespective of their productivity (significant for DIP, EBN, and RYT). In turn, DIP and GUS showed weaker correlations with September's temperature and SPEI.

3.2. Regional Nonlinear Responses

The plasticity of responses to the main regional weather drivers of relative radial additional increments in the studied provenances were estimated by the generalized mixed additive models. The responses estimated across the regional spatiotemporal gradient (timespan of 33 years and length of the geographic gradient of 900 km; Figure 1) indicated climate-dependent sensitivity of TRW to weather conditions (Figure 4). The refined models were strictly significant (p-value < 0.001) and indicated a complex of nine meteorological variables as the main regional drivers of radial increment (Table 4). In most cases, the meteorological variables included in the refined models were significant (p-value < 0.01); however, their effects differed by provenances considerably ($1.69 \leq F$-value ≤ 38.78), indicating specific sensitivity. The estimated effective degree of freedom reached 1.96, implying response curves with up to one inflection point (linear or quadratic).

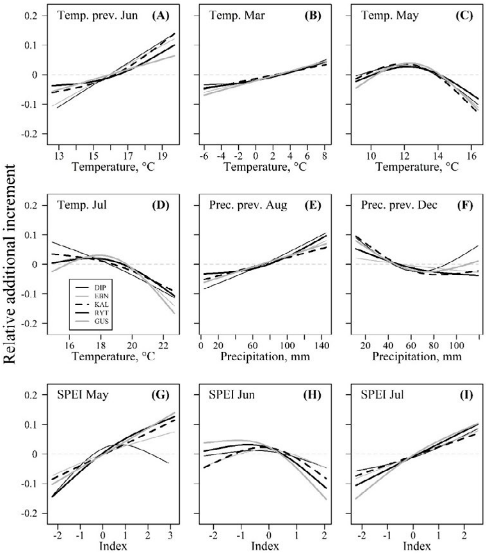

Figure 4. Estimated response splines of relative annual additional radial increment (represented by the residual chronologies) of the studied south-eastern Baltic provenance of Scots pine to meteorological variables: monthly mean temperature (Temp.), precipitation (Prec.), and standardized precipitation-evapotranspiration index (SPEI) for the year of tree-ring formation as well as previous (prev.) year across the south-eastern Baltic climatic gradient during the period 1985–2017. Confidence intervals of the response splines omitted for clarity. The legend corresponds to all panels. For provenance codes see Table 2.

Table 4. The effective degrees of freedom, strength (F-values shown in brackets) and significance of the fixed effects (meteorological variables), variances of random effects, and overall statistics of models of weather–growth relationships for the studied south-eastern Baltic provenance of Scots pine. The presented meteorological variables are monthly mean temperature (Temp.), precipitation (Prec.), and standardized precipitation-evapotranspiration index (SPEI) for the year of tree-ring formation as well as previous (prev.) year for the period 1985–2017. Significance codes, *p*-values: * < 0.05, ** < 0.01, *** < 0.001. For provenance codes see Table 2.

	DIP	**EBN**	**KAL**	**RYT**	**GUS**
Fixed effects, effective degree of freedom and *F*-value					
Temp. prev. June	$1.00_{(30.6)}^{***}$	$1.00_{(31.2)}^{***}$	$1.76_{(10.46)}^{***}$	$1.78_{(7.5)}^{***}$	$1.00_{(10.45)}^{**}$
Temp. March	$1.57_{(3.1)}$	$1.00_{(5.06)}^{*}$	$1.00_{(3.57)}$	$1.47_{(4.78)}^{*}$	$1.00_{(7.28)}^{**}$
Temp. May	$1.89_{(9.29)}^{**}$	$1.94_{(14.28)}^{***}$	$1.94_{(17.44)}^{***}$	$1.93_{(11.23)}^{***}$	$1.96_{(20.94)}^{***}$
Temp. July	$1.35_{(10.02)}^{***}$	$1.91_{(8.34)}^{***}$	$1.62_{(5.30)}^{**}$	$1.89_{(10.03)}^{**}$	$1.96_{(16.08)}^{***}$
Prec. prev. August	$1.27_{(20.56)}^{***}$	$1.63_{(8.45)}^{**}$	$1.00_{(10.41)}^{**}$	$1.80_{(13.59)}^{***}$	$1.00_{(18.89)}^{***}$
Prec. prev. December	$1.92_{(7.34)}^{**}$	$1.11_{(1.32)}$	$1.85_{(9.49)}^{**}$	$1.62_{(6.37)}^{*}$	$1.89_{(8.02)}^{**}$
SPEI. May	$1.90_{(12.64)}^{***}$	$1.28_{(9.36)}^{**}$	$1.00_{(15.16)}^{***}$	$1.66_{(38.78)}^{***}$	$1.00_{(29.02)}^{***}$
SPEI. June	$1.69_{(1.69)}$	$1.87_{(3.38)}$	$1.92_{(6.99)}^{**}$	$1.93_{(12.99)}^{***}$	$1.94_{(19.08)}^{***}$
SPEI. July	$1.51_{(8.09)}^{*}$	$1.00_{(13.5)}^{***}$	$1.00_{(10.39)}^{**}$	$1.00_{(31.23)}^{***}$	$1.66_{(21.33)}^{***}$
Random effects, variance					
Year	2.03×10^{-3}	1.00×10^{-6}	3.24×10^{-4}	1.21×10^{-4}	6.25×10^{-4}
Trial	7.94×10^{-3}	1.02×10^{-2}	$8. \times 10 \times 10^{-3}$	7.06×10^{-3}	7.92×10^{-3}
Replication	1.00×10^{-6}	1.00×10^{-6}	1.00×10^{-6}	1.00×10^{-6}	1.00×10^{-6}
Tree	3.39×10^{-2}	2.92×10^{-2}	3.88×10^{-2}	2.13×10^{-2}	2.31×10^{-2}
Residual	3.60×10^{-5}	1.21×10^{-4}	2.50×10^{-5}	4.90×10^{-5}	4.00×10^{-6}
Model performance					
Adjusted R^2	0.28	0.24	0.21	0.28	0.30
RMSE	0.21	0.19	0.21	0.17	0.18
RMSE (verification)	0.19	0.18	0.18	0.17	0.18

Among the random effects, tree and trial were estimated with the most random variance (Table 4), indicating individual and local growth specifics. The variance of repetition was low, implying homogeneous growing conditions within a trial. Variance related to the year of tree-ring formation indicated slightly higher temporal instability of responses for DIP and GUS. The adjusted marginal R^2 values of the models were intermediate (cf. [18]) ranging from 0.21 to 0.30 for KAL and GUS, respectively, and indicated the lack of overfit; while conditional R^2 exceeded 0.85. The cross-validation of the models based on data excluded from calibration confirmed the lack of overfit, showing comparable errors.

The estimated regional drivers of radial increment (Table 4) were similar to meteorological variables identified by the local weather–growth relationships (Figure 3). Regarding the top-performing provenance (RYT and GUS), the strongest effects (highest *F*-values) were estimated for SPEI in May and July (Table 4). Temperature and SPEI in May had the strongest effect on KAL. The low-performing provenances were most affected by temperature in the previous June, as well as precipitation in the previous August (DIP), and May's temperature (EBN). The majority of the response curves were nonlinear (quadratic; Figure 4), confirming the dependence of weather–growth relationships on the intensity of variables.

The studied provenances differed by plasticity of weather–growth responses, as shown by the flatness of response curves (Figure 4). The most explicit differences among the provenances were observed for responses to variables determining the moisture regime, particularly temperature in July and the previous June, as well as SPEI in May, June, and July. The response curves to July's temperature (Figure 4D) showed a clear negative effect, particularly on the low-performing DIP across the gradient. For other provenances, particularly GUS, the negative effect was caused by July's temperature exceeding ca. 19 °C. All but DIP showed a generally positive response to May's SPEI across its gradient, though a flatter curve (at SPEI > 0.5) was estimated for EBN and RYT (Figure 4G); DIP showed an optimum ($-0.5 < \text{SPEI} < 2.0$), which gained a positive increment.

The responses to June's SPEI differed according to the productivity of provenances (Figure 4H). The top-performing RYT and GUS were irresponsive to SPEI < 0 while producing a positive additional increment; however, excessive moisture (SPEI > 0.5) resulted in a negative additional increment. The response of KAL indicated a short interval of optimum with no negative additional increment; the low-performing provenances were irresponsive (Table 4). The responses to July's SPEI highlighted differences in the provenances' sensitivity to water shortage (SPEI < −0.5; Figure 4I). The sensitivity to July's SPEI was proportional to field performance with more productive provenances being more sensitive, thus contrasting with the hypothesis.

The low-performing provenances were particularly sensitive to legacy effects of temperature in the previous June, showing steep linear responses across the gradient (Figure 4A). The responses of the top-performing provenances were flatter, but intensified when temperature exceeded ca. 16 °C, particularly for KAL. The responses to precipitation in the previous December showed a generally negative tendency when monthly precipitation ranged from 10 to 60 mm/month (Figure 4F); DIP showed a local minimum at ca. 50–90 mm/month, while EBN was irresponsive (Table 4). Although the response curves to March's temperature were practically identical (Figure 4B), the effect was not significant for DIP and KAL (Table 4), implying differing sensitivity. Precipitation in the previous August (particularly its abundance) had a positive effect on the additional increment, especially for DIP (Figure 4E). The studied provenances were similarly sensitive to May's temperature with responses indicating an optimum of ca. 11–14 °C, although warmer temperatures reduced growth (Figure 4C).

4. Discussion

4.1. Plasticity of Growth Responses

The geographic differences in correlations (Figure 3) and the regional response curves of the studied provenances (Figure 4) highlighted the plasticity of weather–growth responses [18,41,42], as observed for native populations within the region [14,26]. Such responses imply a modulating effect of climate on growth sensitivity [23,34,73,74], projecting disproportional effects of climatic changes [40,42,44]. This subjects trees to novel conditions [10,23,74] amplifying the effects of local adaptation [15,25,73] and challenging the adaptability of metapopulations. The nonlinearity of growth responses also relate to spatiotemporal non-stationarity of the local linear weather–growth relationships [39,41,75], as local climates shift along the regional gradient [26,40,44,56]. Hence, the estimated response curves (Figure 4) indicate the presence of stationary, yet nonlinear regional weather–growth relationships [26,39], revealing varying adaptability of metapopulations [11,24,27,52,59]. Accordingly, the assessment of weather–growth relationships at a regional scale aids more reliable growth projections [14,18,23,32,39].

The differences in growth sensitivity (Figures 3 and 4) suggest genetic adaptation of metapopulations to local climates, indicating uneven phenotypic plasticity [11,17,24,27,35] and adaptability to environmental changes [20,30]. The genetic adaptation of traits crucial for survival and reproduction can persist under high gene flow [15,20], supporting the evolutionary relevance of weather–growth relationships [19,32,51]. Accordingly, Scots pine provenances are shown to differ by their tolerance to meteorological conditions and their extremes [11,24,27,35,44]. This suggests the potential for improvements via targeted supplementation of breeding populations [25,47,52,53]. The estimated local adaptation might also be linked to the relatively high genetic diversity of populations of Scots pine [48,49]. However, the regional within-population genetic diversity [48], has likely resulted in the individuality of growth (indicated by the prevailing random variance of trees; Table 4).

The genotype–environment (provenance-by-trial) interaction was characterized by the second highest variance component related to the trial (Table 4), indicating the adaptability of genotypes [13,25] and explaining local specifics of weather–growth responses [20,31]. Such effects might also be related to specific interactions of meteorological, as well as edaphic conditions [27,76]. Accordingly, genotype–environment interactions can moderate the effects of meteorological conditions [18,23], explaining the intermediate performance of models (Table 4). The year of tree-ring formation was, though, estimated with low variance (Table 4), implying temporally stationary weather–growth relationships [39,42]. Still, a somewhat higher variance of year indicated a higher complexity of weather–growth relationships [69] for the low-performing DIP (Table 4), suggesting a stronger influence of micro-site conditions [18,23]. Considering the south-eastern Baltic (southern Poland and Northern Germany) origin for most of the provenances' (Figure 1; Table 2) higher diversity of weather–growth correlations (Figure 3), this might imply the "marginality" of conditions for the north-transferred genotypes in Latvia.

The regional weather–growth responses generally differed according to the field performance of the provenances (Figure 4), supporting the linkage between sensitivity and productivity [11,19,27,31,35,44,52]. Although the differences in responses among provenances were mostly small (Figure 4), they can result in substantial ecological effects in the long-term [43,51,77,78]. In contrast to the hypothesis, the top-performing provenances were more sensitive to some of the regional weather drivers of growth (Figure 4). This suggests the ability to rapidly adjust growth-tolerance trade-offs to be highly advantageous under a rapidly changing climate [35,77,79,80], facilitating resilience to ascending stresses [52,59,81,82]. On the other hand, an increased allocation of resources to stress tolerance reduces growth [77,80] and competitiveness [21,51], supporting the projected northward retreat of conifers in the eastern Baltic region [1].

4.2. Regional Weather Drivers of Radial Growth

Meteorological conditions affecting increments in the studied provenances (Table 4, Figure 4) and native populations within the region [14,26] were similar. However, the provenances differed by the timing of their responsiveness (Figures 3 and 4) due to local adaptation [11,15,17,20,21,29,38]. The provenances were prevailingly sensitive to the summer moisture regime (Figures 3 and 4), supporting the intensification of drought effects on nemoral and hemiboreal forests [4,5,14,34,73]. This raises the management of the moisture regime as an issue for adaptive, climate-smart management within the region [4,8,69]. The identified regional weather drivers, though, had a weaker effect on KAL (lower R^2; Table 4), probably due to the differing climatype [14,49].

The estimated weather–growth responses (Figures 3 and 4) indicated direct and legacy effects of meteorological conditions [26,34,37], highlighting the complex climatic influence on the control of increments [14,26,34]. The responses to temperature in May and July, as well as May–July's SPEI (Figure 4C,D,G–I) indicated the direct effect of thermal and moisture conditions on xylogenesis [37,38,83,84]. The generally positive responses to May and July's SPEI (Figure 4G,I) portrayed the limiting effect of water shortage [3–5,38,84], to which the top-performing provenances were more sensitive, likely due to the higher plasticity of xylogenesis [27,52] and lower wood density [24,33,35].

Under a temperate climate, June is the time when most of the earlywood is formed [38] based on current assimilates [83,85,86]. Accordingly, decreased assimilation under rainy conditions might explain the negative responses to June's SPEI > 0.5 (Figure 4H), although the low-performing provenances (DIP and EBN) were less sensitive to June and July's SPEI (Table 4, Figure 4H,I), likely due to their higher wood density [24,33,35,38] and/or more conservative survival strategy common for slower growing genotypes [24,77,79,80,83]. The responses to May's SPEI were steeper under drought conditions (SPEI < 0.0; [66]), indicating the sensitivity of xylogenesis to early drought [38,79,85,87]. Still, the DIP responded negatively to May's SPEI > 1.0, probably due to decreased assimilation on rainy days [88].

The responses to summer temperature shaped an arc (Figure 4C,D), suggesting a trade-off between the rate of assimilation and water deficiency [75,84]. These arcs, however, were asymmetric, implying the disproportional negative effects of increasing temperature [40–42]. The responses to July's temperature differed by provenance (Figure 4D), indicating varying temperature preferences [10,37,52,59]. The low-performing DIP, which originated from a higher elevation (Table 2), appeared particularly sensitive;

the top-performing RYT showed a flatter response, suggesting better adaptation to heat stress [4,36]. The studied provenances showed similar responses to May's temperature (Figure 4C), implying the common limitation of early growth [38,84].

Conditions during the dormancy period and previous summer showed significant legacy effects (Table 4, Figures 3 and 4B,E), as observed for native populations [14,26]. The positive responses to temperature in the previous June (Figure 4A) might be explained by the formation of additional nutrient reserves [89] under warmer and drier conditions [88], which facilitate growth in the following season [69,86,89]. Such an effect was stronger for the low-performing provenances (Table 4), implying a greater dependence on nutrient reserves due to their more conservative growth strategy [9,11,24,79]. The top-performing provenances were less sensitive (showed flatter slopes) to conditions in the previous June (Figure 4A,H), likely due to their higher plasticity of growth [27,35,77].

Conditions at the end of the growing season, when terminal buds are formed, affect the ratio between vegetative and generative growth initials [90]; hence, the growth–reproduction trade-offs [91]. Considering sensitivity to water shortage (Figures 3 and 4), the positive responses to precipitation in the previous August (Figure 4E) might be related to formation of the vegetative initials and, hence, facilitated growth [91]. This effect was stronger for the low-performing DIP, probably due to their more conservative growth strategy [24,35]. Considering their origin from a higher elevation with a harsher climate (Table 2), the low-performing provenances were less sensitive to conditions during the dormancy period (Table 4). The positive effect of March's temperature (Figure 4; Table 4) might be explained by soil freeze and its impact on root dynamics and water relations in the following growing season [92], to which fast-growing provenances are more sensitive [24,33]. The negative responses to December's precipitation (Table 4, Figure 4F), might be explained by soil moisture excess, which could have negative legacy effects on xylogenesis [35,93] or on fine root dynamics, hence, water relations in the following spring [92].

Under accelerating climate change and intensifying droughts [4,5], the observed responses of the provenances to regional weather drivers (Table 4, Figure 4) support the genetic adaptation of metapopulations to local climates [15,17,29]. This implies the possibility of improving the ecological plasticity of forest reproductive material in terms of growth sensitivity by targeted supplementation of breeding populations [7,25,47] to improve the climatic tolerance of northern genotypes [3] with the application of a semi-conservative management strategy.

5. Conclusions

The studied south-eastern Baltic provenances of Scots pine differed by their plasticity of responses to regional weather drivers of increment, implying the specific sensitivity of growth. The observed responses indicate the uneven adaptive significance of sensitivity to metrological conditions throughout the year, with the conditions related to water availability during the formation of the tree-ring playing the main role under a temperate climate, although, the top-performing provenances showed higher sensitivity to these conditions, implying the advantages of more plastic growth regulation under a rapidly changing climate. Accordingly, the sensitivity and plasticity of increment can be a valuable trait facilitating the selection and breeding of trees better adapted to the future climates. Moreover, the obtained results encourage supplementation of the local breeding populations with the top-performing provenances originating from regions with projected climatic conditions.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/f12121641/s1, Figure S1: Mean monthly temperature (line) and precipitation sums (bars) at the studied trials during 1997–2017; Figure S2: Mean monthly temperature (lines) and precipitation sums (bars) at the origin of the studied provenances during 1931–1960; Figure S3: Sample depth (replication) of the crossdated datasets of tree-ring width of the studied provenance of Scots pine according to trial; Table S1: Number of surviving trees, overall survival, mean tree height (H), stem diameter at breast height (DBH), standing volume (M), and ranking (according to tree height) of the studied provenances of Scots pine in three trials in hemiboreal zone in Latvia; Table S2: Number of Scots pine trees cored according to provenances and trials.

Author Contributions: Conceptualization, R.M. and Ā.J.; methodology, R.M. and V.S.; software, E.B. and P.Z.; validation, R.M., E.B. and V.S.; formal analysis, D.J. and S.D.; investigation, D.J., S.D. and P.Z.; resources, Ā.J.; data curation, D.J.; writing—original draft preparation, R.M. and P.Z.; writing—review and editing, Ā.J., V.S. and E.B.; visualization, R.M. and P.Z.; supervision, R.M. and Ā.J.; project administration, R.M.; funding acquisition, R.M. and Ā.J. All authors have read and agreed to the published version of the manuscript.

Funding: The study was funded by the Latvian Council of Science (grant number: lzp-2020/2-0416). Sampling and measurements were partially supported by the framework of post-doc studies in Latvia funded by the European Regional Development Fund (project number: 1.1.1.2.VIAA/1/16/108).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Data sharing not applicable.

Acknowledgments: We would like to acknowledge the technical staff who helped with sampling and lab-work. We also thank Renāte Saleniece, who proofread the manuscript.

Conflicts of Interest: The authors declare no conflict of interests.

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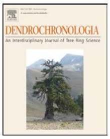

Plasticity of response of tree-ring width of Scots pine provenances to weather extremes in Latvia

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ARTICLE INFO

Keywords:
Pinus sylvestris
Transfer experiment
Climate-growth relationships
Provenance trial
Adaptation
Forestry

ABSTRACT

Climatic changes and weather extremes are causing shifts in distribution of tree species, affecting productivity of forests. With the northwards advance of deciduous species in Northern Europe, Scots pine (*Pinus sylvestris* L.) is predicted to decrease survival and productivity. Nevertheless, Scots pine have adapted to diverse environments, hence selection among its populations could be applied to sustain productivity of stands under changing climate. In this study, sensitivity of tree-ring width of Eastern European provenances of Scots pine differing by field performance (Dippoldiswalde, Eibenstock, Rytel, Gustrow, and Kalsnava) to weather extremes in three trials in Latvia (hemiboreal zone) was assessed via pointer year and tolerance analyses. The studied provenances were sensitive to winter temperature regime; the effects of water deficit and vegetation period's length were also observed, likely due to warming. The sensitivity of tree-ring width to weather extremes, which differed among the provenances indicating plasticity of growth, correlated with field performance. Although transferred north, the top-performing provenances (Gustrow and Rytel) were able to promptly recover after cold spells as well as dry summers and were able to benefit from warm winters and precipitation-rich summers. The bottom-performing provenances (Dippoldiswalde and Eibenstock) were sensitive to cold spells and summer water deficit, yet were unable to benefit from warm winters, nor moist summers. Considering sensitivity and resilience of growth, the studied top-performing provenances, particularly Rytel, showed commercial potential in the hemiboreal region under warming climate.

1. Introduction

Climate is one of the main factors determining distribution and productivity of forest ecosystems (Reich and Oleksyn, 2008; Hickler et al., 2012). Climatic models predict increase of mean temperature and extension of vegetation period (IPCC, 2013), which are expected to have mainly positive effect on productivity of forests in Northern Europe (Menzel and Fabian, 1999; Lindner et al., 2010), and to alter forest composition (Hickler et al., 2012). The frequency and magnitude of meteorological extremes, which have considerable impact on forest growth and survival of trees (Fuhrer et al., 2006; Schlyter et al., 2006; Lindner et al., 2010), are also projected to increase (Beniston, 2004; Avotniece et al., 2012), thus adding challenges to forest management. Frequency and duration of thaws, which influence water relations of trees and nutrient reserves affecting the following increment, are increasing in Northern Europe (Ögren, 1997; Mayr et al., 2003). The extension of vegetation period, which causes earlier onset and later cessation of growth (Menzel and Fabian, 1999), subjects trees to increasing risk of frost damage (Gu et al., 2008; Zeps et al., 2017). Lengthening and intensification of drought events, which are substantial forestry risk in the Central and Southern Europe (Beniston, 2004), are emerging in forest ecosystem, previously not considered as water-limited (Schlyter et al., 2006; Allen et al., 2010). Increasing temperature during vegetation period, particularly in combination with water deficit, causes heat stress, resulting in explicit reduction of increment (Allen et al., 2010).

The rate of climatic changes apparently exceeds the rate of natural adaptation of local tree populations; hence, forest management has been highlighted for sustaining productivity of stands (Bolte et al., 2009; Lindner et al., 2010). To cope with the upcoming ecologic and economic risks (Hanewinkel et al., 2012), diverse adjustments in management strategies have been proposed (Lindner et al., 2010),

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https://doi.org/10.1016/j.dendro.2019.01.002
Received 17 August 2018; Received in revised form 10 January 2019; Accepted 11 January 2019

among which application of the most resilient reproductive material has been considered highly efficient (Bolte et al., 2009). Scots pine (*Pinus sylvestris* L.), which is economically important in Northern Europe, has been predicted to decrease its survival and alter productivity due to warming (Reich and Oleksyn, 2008; Hickler et al., 2012). Nevertheless, the species has extensive distribution range, where its populations have adapted to diverse environments (Martinez-Vilalta et al., 2009); hence, an educated choice of reproductive material could minimize the negative effects of shifting climate (Bolte et al., 2009; Taeger et al., 2013, 2015) via utilizing species' genetic diversity (Kohlstock and Schneck, 1992).

Provenance trials are established to assess performance of diverse populations under certain environments (Kohlstock and Schneck, 1992). The performance of provenances is mainly evaluated based on their yield and stem quality, which summarize suitability of growing conditions over the entire life cycle of trees (Burton, 2011), which is a rather long period. During the life of trees, their sensitivity to environmental factors shifts due to ageing (Thomas and Winner, 2002; Zang et al., 2012), as well as changing climate (Buntgen et al., 2006; Carrer and Urbinati, 2006), hence information about the plasticity of growth response is essential for the assessment of growth potential in the future.

Sensitivity and plasticity of tree growth can be efficiently assessed via retrospective analysis of tree-ring width (TRW), which is a widely applied proxy of increment (Speer, 2010; Burton, 2011). The effect of climatic factors on radial increment has been often assessed via correlation analysis of standardized series of TRW and meteorological variables (e.g., Oberhuber et al., 1998; Linderholm, 2001; Buntgen et al., 2006; Jansons et al., 2016). Considering the relevance of climatic extremes (Fuhrer et al., 2006), specific standardization methods, e.g., pointer year (PY) analysis, have been developed to identify the occurrence of abrupt changes in increment and to relate them with environmental events (Speer, 2010; Neuwirth et al., 2004; Bigler et al., 2006; Eilmann and Rigling, 2012; Taeger et al., 2013). The effect of climatic extremes can be lasting, as certain period might be needed for trees to restore previous growth levels after a disturbance (Bigler et al., 2006; Eilmann and Rigling, 2012; Zang et al., 2012; Merlin et al., 2015). Accordingly, patterns of recovery can be considered as indicators of plasticity, hence sustainability of tree growth (Eilmann and Rigling, 2012; Taeger et al., 2013). The tolerance analysis, which accounts for resistance and recovery of growth, has been developed for quantification of tree response to environmental extremes (Lloret et al., 2011).

In the hemiboreal zone in Latvia, considerable shifts in stand composition and tree growth are projected already during the 21st century (Reich and Oleksyn, 2008; Lindner et al., 2010; Hickler et al., 2012). The results from the international provenance experiment (Kohlstock and Schneck, 1992) have shown that the Scots pine provenances from Poland and Northern Germany have been highly productive in Latvia (Jansons and Baumanis, 2005), implying early response to warming (Rehfeldt et al., 2003). Radial increment of native Scots pine growing on dry oligotrophic and mesotrophic soils have mostly been sensitive to temperature regime in winter and early spring, though some stands have also been affected by water availability in summer (Jansons et al., 2016). The PYs in TRW have been related to winter-spring temperature, as well as June precipitation extremes, implying water deficit in summer (Elferts, 2007), likely due to climatic changes (Avotniece et al., 2012).

The aim of this study was to assess climatic drivers of PYs (extremes) in TRW and to evaluate plasticity of growth of Scots pine provenances differing by yield across the continentality gradient in Latvia. We hypothesized that the extent of growth extremes was stronger for the more productive provenances, particularly in sites with more continental climate, yet they also were able to recover more efficiently. We also assumed that north-transferred provenances were less sensitive to water deficit due to better adaptation to drought conditions, hence might be applied to improve sustainability of commercial stands in the future.

Table 1

Location, elevation, soils, and climate (annual and monthly mean temperature, and precipitation sums (± confidence interval) of the studied trials. Climatic data refers to 1987–2017.

	Liepāja (LPJ)	Bauska (BSK)	Kalsnava (KLN)
Latitude, N	56°29′	56°32′	56°49′
Longitude, E	21°05′	24°13′	26°07′
Elevation, m a.s.l.	15	50	220
Relief	Flat	Flat	Flat
Soil type	Podsols	Podsols	Podsols
Site type	*Vacciniosa*	*Vacciniosa*	*Vacciniosa*
Mean annual temperature, °C	7.8 ± 0.7	7.2 ± 0.8	6.3 ± 0.9
Mean January temperature, °C	1.4 ± 1.3	2.9 ± 1.3	4.3 ± 1.3
Mean July temperature, °C	17.8 ± 0.6	18.4 ± 0.7	18.0 ± 0.6
Mean annual precipitation, mm	745 ± 37	647 ± 26	656 ± 28
Mean monthly precipitation May–September, mm	65 ± 6	67 ± 5	67 ± 6

2. Material and methods

2.1. Studied trial and provenances

Three international provenance trials of Scots pine in Latvia, established in 1975 under the collaboration between the German Democratic Republic and the USSR (Kohlstock and Schneck, 1992; Jansons and Baumanis, 2005), were studied. The trials were growing in lowland conditions on dry well-drained (sandy) oligotrophic soils near Liepaja (LPJ), Bauska (BSK), and Kalsnava (KLN) (Table 1), thus covering local climatic gradient from slightly maritime to continental (LPJ, BSK, and KLN, respectively). Climate in the studied trials was temperate; summers were warmer in BSK (Table 1). January and July were the coldest and warmest months, respectively. Vegetation period, when the mean diurnal temperature exceeded 5 °C, extended from mid-April to October (180–201 days); it was ca. two weeks longer in BSK. The highest monthly precipitation occurred in the summer months (May–-September; Table 1). The mean annual precipitation was higher in LPJ. Climatic changes were expressed as warming, particularly during the December-April period, hence as more frequent thawing in winter and extending vegetation period (by 13–19 days during the past 50 years). Although summer precipitation lacked explicit trend, duration of the warm precipitation-free periods was increasing (Avotniece et al., 2012). During the period 1987–2017, several meteorological extremes, particularly related to temperature during the dormant period (November–March), as well as water availability in the summer months (June–September), occurred (Table 2).

The trials were established to assess performance of Scots pine from 36 open-pollinated stands growing on well-drained oligotrophic soils, located between 50 and 56 °N, and 11 and 27 °E (Poland and Germany; Table 3), thus representing projected near future climate in Latvia (IPCC, 2013). For each provenance, seed material originated from 20 to 25 dominant trees (plus-trees). The trials were established by planting one-year-old bare rooted seedlings (raised in local nurseries), and contained identical set of provenances. In each trial, each provenance was represented by six randomized plots of 35 (7 × 5) trees; the spacing of trees was 2 × 1 m (stand density was 5000 trees ha^{-1}). All trials were thinned at the age of 21 years (January 1996); ca. 35% of the initially planted trees per plot were left (ca. 1800 trees ha^{-1}).

Previous studies showed that provenance have had considerable effect on yield and stem quality of trees (Jansons and Baumanis, 2005). To assess climatic sensitivity of TRW and its relationships with productivity, two top- and two bottom- performing provenances (above 80th and below 20th percentile, respectively) were selected based on their yield ranking according to the trial inventory conducted in 2016.

Table 2
Extremes in the mean monthly temperature (T), precipitation sums (P), and SPEI during 1987–2017 in Latvia. The numbers in brackets show scaled difference (z-score) from the 30-year mean. Only the extremes with |Z-score| > 1.50 are shown. Pos – positive, Neg – negative pointer years.

Year	Description	Pointe year/Trial
1987	Jan T (-3.31), Mar-Apr T (-2.76), Aug T (-1.67), Mai P (1.97)	Neg (BSK)
1988	Jan-Feb P (-1.57)	–
1989	Jan-Feb T (1.83), Jan-Feb P (-1.78)	Neg (KLN)
1990	Jan-Feb T (1.64), Apr P (-1.70)	–
1991	May T (-1.94), Jul P (-1.59), Sep P (2.13)	Neg (LPJ, BSK)
1992	Oct T (-2.2), Sep-Oct P (1.56)	Neg (all)
1993	May T (1.99), Jun-Aug T (-1.98), Sep-Oct T (-2.99), Jul P (1.55)	Neg (LPJ, BSK)
1994	Feb T (-1.66), Jun T (-1.62), Jul P (-1.67)	Neg (all)
1995	Dec T (-1.57), Mar-Apr P (1.59)	–
1996	Jan-Feb T (-1.73), Mar T(-1.51), Jul T (-1.57), Aug P (-1.68)	Thinning
1997	Mar-Apr T (-1.65), May T(-1.55), Aug T (1.88)	Neg (all)
1998	Aug T (-1.88), Sep-Oct T (-1.92), Feb P (1.71)	Neg (LPJ, KLN)
1999	Jun T (2.38), Jan-Feb P (2.28), Jun-Aug P (-1.95)	Neg (LPJ, KLN)
2000	Apr T (2.41), Oct T (1.69), Mar P(1.86), Jul P (1.66)	Neg (LPJ)
2001	Jul T (1.56), Dec T (-1.54), Apr P (1.52), Jun-Aug P (1.58)	Neg (LPJ)
2002	May T (1.73), Aug T (2.02), Oct T (-2.33), Aug P (-1.97)	Neg (LPJ, BSK)
2003	Apr T (-1.61), Mar P (-1.58)	Neg (LPJ, BSK)
2004	–	–
2005	Mar T (-1.78), May P (-1.51), Jun P (2.13), Jun-Aug P (2.13)	Neg (KLN)
2006	Mar T (-1.77), Dec T (1.90), Sep-Oct T (1.71), Jul P (-1.67)	Neg (KLN)
2007	Mar T (1.65), Oct P (1.81)	Pos (LPJ, KLN)
2008	Mar P (2.32),	Pos (LPJ), Neg(KLN)
2009	Mar-Apr P (-1.97), May P (-1.74)	—
2010	Jan T (-2.16), Jun-Aug T (1.94), Jul P (1.60)	Neg (BSK)
2011	Jun-Aug T (1.67), Sep-Oct P (-1.87)	–
2012	–	–
2013	Mar T (-1.82), May T (2.38), Jun T (2.12), Sep P (1.63)	Neg (all)
2014	Aug P (2.32)	–
2015	Jan P (1.89), Oct P (1.86), Jun-Aug P (-1.58)	Pos (LPJ)
2016	Feb T (2.31), Mar T (1.78)	Pos (LPJ)
2017	Aug P (2.65)	–

The rankings of the provenances were consistent among the trials. Güstrow (GUS) and Rytel (RYT), which originated form lowland region with warmer and drier climate (Table 3), were selected as the top-performing provenances. Dippoldiswalde (DIP) and Eibenstock (EBN), which originated from the Orr Mountains, where climate was cooler and more humid, were selected as the bottom-performing provenances. Additionally, Kalsnava (KAL) provenance, which showed above-average performance, was selected for assessment of plasticity of the local population (Taeger et al., 2013).

2.2. Sampling and measurements

One to three vigorous undamaged dominant trees per plot for each provenance (9–18 tree per provenance per trial) were sampled (198 trees in total). Two cores at breast height from the opposite sides of stem avoiding reaction wood were extracted with a 5-mm Pressler increment corer (Speer, 2010). Considering that the trials were ongoing and have been thinned, the number of sampled trees was restricted. The sampling was done in November 2017, when trees were 43 years old.

In the laboratory, cores were mounted and grinded, gradually decreasing grit of sand paper from 150 to 400 grains per inch. The measurements of TRW were done manually, using a LINTAB 5 measuring table, equipped with a microscope and the TSAP software (Rinntech Inc., Heidelberg, Germany). The accuracy of measurements was 0.01 mm.

2.3. Data analysis

The quality of measured series of TRW was checked by a graphical and statistical crossdating, using COFECHA program (Grissino-Mayer, 2001). Series of TRW from 167 trees, representing 15 provenances by trials (9–14 trees per dataset), passed quality checking and were used for the analysis. Mean sensitivity (MS), interseries correlation (r-bar), first order autocorrelation (AC), signal-to-noise ratio (SNR), and expressed population signal (EPS) (Wigley et al., 1984) were calculated for description of the datasets (based on series detrended by a flexible cubic spline with the wavelength of 20 years).

To assess occurrence of extremes in TRW, PY values were calculated based on a modified skeleton plot method (Neuwirth et al., 2004). The relative difference of each TRW in respect to the preceding five was calculated as:

$$\Delta x_i = \frac{x_i - \bar{x}_{i-5..i-1}}{\bar{x}_{i-5..i-1}} \qquad (1)$$

where x_i –TRW in the i-th year. The Δx_i was then expressed as scores ranging from 5 to 5 (except 0) with 20% (0.2) steps (−5 corresponding to $\Delta x_i <$ -80%, and 5 to a $\Delta x_i >$ 80%, respectively). For each provenance in each trial for the period represented by ≥ 5 trees, PY values were calculated as:

$$I = \frac{100}{kn}\sum_{j=1}^{k} h_j s_j \qquad (2)$$

where k – number of possible score values (10 here), n – total number of trees, h_j – number of trees with score (event), and s_j – score of event year. The PYs exceeding an arbitrarily threshold $|I| > 25$ were considered as remarkable (cf. Elferts, 2007).

The main patterns in PY variation among the provenances and trials during the common period (1987–2017) were assessed by principal component (PC) analysis. Years and provenances (by trial) were considered as variables and samples, respectively. The significance of the PCs was determined by Monte Carlo test (10^4 permutations).

Climatic drivers of PY values, as well as their first two PCs (loadings

Table 3
Location and climatic description of origin of the studied provenances of Scots pine.

	Güstrow (GUS)	Rytel (RYT)	Dippoldis-walde (DIP)	Eibenstock (EBN)	Kalsnava (KAL)
Latitude, N	53°45'	53°40'	50°49'	50°27'	56°42'
Longitude, E	12°15'	18°01'	13°52'	12°26'	25°54'
Elevation, m a.s.l.	25	130	590	710	190
Mean annual temperature, °C	8.0	7.9	6.6	5.9	6.3
Mean temperature May-Sep., °C	14.8	15.0	13.2	12.6	14.7
Mean temperature Jan, °C	−0.8	−1.4	−2.6	−3.0	−4.3
Mean temperature Jul, °C	16.8	17.2	15.3	14.7	18.0
Mean annual precipitation, mm	585	590	804	994	656
Mean precipitation May-Sep., mm	297	306	402	499	337

of years), were identified by bootstrapped Pearson correlation analysis (10^4 iterations). The tested climatic factors were monthly mean temperature, precipitation sums, and standardized precipitation-evapotranspiration indices (SPEI, calculated with the respect of preceding three months; Vicente-Serrano et al., 2010). Time window from the previous July (preceding formation of tree-ring) to October in the year of tree-ring formation was used. The significant factors were checked for collinearity. The CRU TS3.10 climatic data (Harris et al., 2014) for stations located $\leq$ 12 km from the trials were used.

Tolerance analysis (Lloret et al., 2011; Taeger et al., 2013) was used to assess the plasticity of radial growth regarding the identified remarkable (both positive and negative) PYs. As all trees were at the same age and grew in similar density, the analysis was based on individual TRW series. Tolerance indices were calculated for comparison of TRW in a PY (TRW_p) with mean three-year increment before and after it (TRW_{Pre} and TRW_{Post}, respectively). Growth resistance was calculated as the ratio of TRW in and before a PY (TRW_p/TRW_{Pre}). Recovery was calculated as the ratio of TRW after and in a PY (TRW_{Post}/TRW_p), and resilience as the ratio of TRW after and before a PY (TRW_{Post}/TRW_{Pre}). Additionally, relative resilience, accounting for severity of growth changes in a PY, was calculated as (TRW_{Post}-TRW_p)/TRW_{Pre}. Considering that TRW was used, tolerance indices might be slightly biased by the age trend (Taeger et al., 2013), which, for the studied trees was practically linear. The effects of provenance, trial, type of weather extreme (i.e., cold or warm winter, dry or moist summer), and their interaction (fixed effects) on the tolerance indices regarding the remarkable PYs were assessed by a mixed model (Bates et al., 2015). Plot, tree, and year were used as random effects. Separate models were built for the positive and the negative PYs. Considering local specifics in PY, marginal means of the provenances across the trials and years were estimated from the mixed models using the 'emmeans' function, and they were compared using Tukey's post-hoc test. Data analysis was conducted in R v. 3.5.1 (R Core Team, 2018), using packages 'DplR' (Bunn, 2008), 'emmeans' (Lenth, 2018), and 'lme4' (Bates et al., 2015).

3. Results

3.1. Radial growth parameters and pointer years

The mean TRW was higher in LPJ compared to BSK and KLN trials (Table 4). Most of the datasets contained representative environmental signals, as r-bar > 0.30 and EPS > 0.85 (cf. Wigley et al., 1984); though, signal was weaker for the bottom-performing DIP in KLN trial (Table 4). For all datasets, MS was intermediate (ranging 0.16–0.26; cf. Speer, 2010); AC was high ($\geq$ 0.69; cf. Speer, 2010), indicating considerable effect of previous growth on current increment.

Table 4
Descriptive statistics of the studied datasets of tree-ring width for the common period from 1987 to 2017. SD– standard deviation, AC – first order autocorrelation, EPS – expressed population signal, SNR – signal-to-noise ratio, MS – mean sensitivity.

	Tree-ring width, mm				N, trees	r-bar		EPS	SNR	MS
	Min.	Max.	Mean	SD			AC			
Liepaja (LPJ) trial										
DIP	0.19	8.17	2.66	1.78	12	0.40	0.83	0.90	6.70	0.26
EBN	0.47	9.01	2.95	1.50	11	0.35	0.80	0.87	5.18	0.20
GUS	0.57	8.54	3.43	1.83	11	0.34	0.81	0.86	4.79	0.18
KAL	0.92	9.32	3.21	1.64	12	0.30	0.84	0.85	4.61	0.18
RYT	0.80	10.32	3.47	1.93	12	0.31	0.81	0.86	4.68	0.19
Bauska (BSK) trial										
DIP	0.22	5.57	2.07	1.22	9	0.39	0.80	0.86	4.93	0.23
EBN	0.30	7.06	2.26	1.36	9	0.36	0.82	0.86	4.79	0.25
GUS	0.25	6.35	2.54	1.21	10	0.35	0.82	0.86	4.75	0.18
KAL	0.17	5.61	2.35	1.15	10	0.34	0.78	0.85	4.51	0.20
RYT	0.98	8.16	2.94	1.41	10	0.34	0.69	0.85	4.52	0.20
Kalsnava (KLN) trial										
DIP	0.22	5.7	2.13	1.18	10	0.24	0.77	0.75	2.61	0.22
EBN	0.13	6.60	2.12	1.17	13	0.33	0.78	0.88	5.39	0.22
GUS	0.36	8.12	2.54	1.23	12	0.41	0.74	0.91	7.10	0.19
KAL	0.34	5.99	2.47	1.07	14	0.33	0.70	0.89	6.05	0.20
RYT	0.40	7.74	2.88	1.20	12	0.38	0.75	0.90	6.31	0.16

The PY values (Fig. 1) were intermediate (cf. Neuwirth et al., 2004); their range was similar among the trials, yet it was slightly higher for DIP and lower for RYT. The r-bar between the provenances within a trial was higher (ranging 0.87–0.68 in LPJ and BSK, respectively) than among the trials (0.51). During 1987–2017, the number of remarkable PYs ranged from 9 to 13 for KAL and DIP, respectively; the remarkable PYs were more frequent in the coastal LPJ trial compared to others. Most of the remarkable PYs were negative, indicating more frequent growth suppressions than releases.

The strength of PYs differed among the trials and provenances (Fig. 1), indicating plasticity of growth. In the coastal LPJ trial, remarkable negative PYs, which might be associated with winter and summer temperature extremes (Table 2), occurred during most of the period 1991–2005 (Fig. 1), and were stronger for DIP and EBN. In 1999, DIP showed explicit reduction of TRW (Fig. 1) responding to a hot and dry summer (Table 2), and in 2013, due to a cold spring followed by a hot summer. The positive PYs (2007 for DIP and EBN, and 2016 for GUS and RYT; Fig. 1) occurred after warm February/March (Table 2). Under warmer climate in BSK trial, the remarkable negative PYs (Fig. 1) particularly for KAL, EBN, and DIP occurred in response to cold spells in the January-March period (Table 2). The top-performing GUS and RYT provenances showed remarkable negative PY in 1997 (Fig. 1), when spring was cold and summer hot (Table 2). Under continental climate in KLN trial, negative PYs (Fig. 1) occurred when February/March was cold and summers were dry or hot (1994, 1999, 2005, 2006, 2011, 2013; Table 2); the positive PYs occurred after warm winters (1989 and 2007, Table 2). The GUS and RYT showed negative PY in 2007, yet growth reduction of 2013 was stronger for DIP. In BSK and KLN trials, all provenances, particularly DIP and RYT, showed explicit response to thinning.

3.2. Climatic signals in pointer years

The first two PCs of PY series were significant (p-values < 0.01) and explained ca. 63% of variance (Fig. 2A). The grouping of series (Fig. 2B) illustrated the site-specific variation; still, the within-group ranges of scores indicated provenance-specific variation of PYs. The first PC distinguished LPJ trial from others (Fig. 2), and was related to extremes of winter and spring temperature (e.g., 1989, 2000, 2005, and 2006; Table 2). The second PC distinguished BSK trial (Fig. 2) and was related to extremes in summer temperature and precipitation (e.g. 1991, 1993, 1999, and 2015; Table 2). The loadings of the first PC were significantly (at $\alpha = 0.05$) correlated with temperature in September ($r = 0.45$) and in the previous December ($r = 0.44$); the second PC was correlated with temperature in March ($r = 0.46$), June ($r = -0.47$), and October ($r = -0.34$).

The series of PYs significantly (at $\alpha = 0.05$) correlated with eight of the 48 climatic factors tested (Fig. 3). In LPJ trial, all provenances, particularly the top-performing GUS and RYT, showed correlation with temperature in the previous December. Additionally, GUS and RYT were sensitive to temperature in the previous October and precipitation in the previous August, respectively. The local KAL showed correlation with precipitation in July and temperature in the previous October. In the BSK trial, all provenances were sensitive to temperature in October; GUS and RYT were additionally sensitive to temperature and precipitation in the previous October. All except DIP showed negative correlation with precipitation in September; the strength of the correlation increased with the field performance of provenances. Correlation with precipitation in the previous August was significant for EBN, GUS and RYT. In KLN trial, EBN, GUS, and KAL showed correlation with temperature in March. All except RYT were also sensitive to

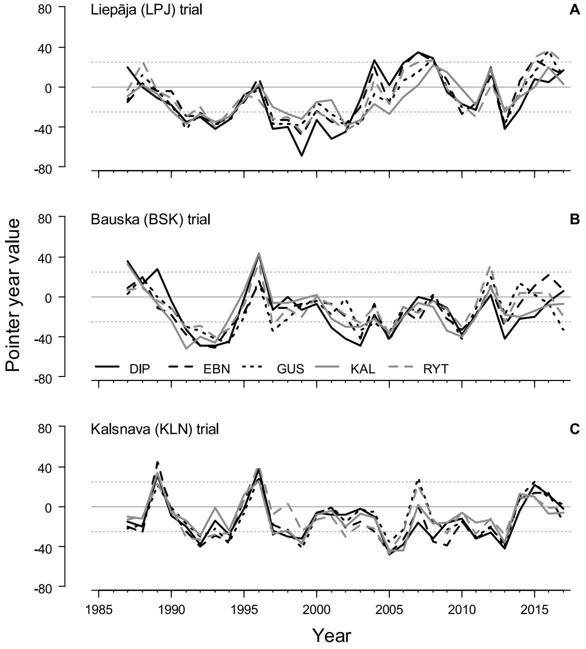

Fig. 1. Pointer year values of tree-ring width of the studied provenance of Scots pine in three trials for the common period 1987–2017.

precipitation in July. The negative correlation with precipitation in the previous October was apparent for EBN and KAL.

3.3. Tolerance analysis

Tolerance analysis was conducted for three positive and seven negative PYs (Fig. 4). Regarding the negative years, the mean resistance and resilience indices (Fig. 4) were intermediate (means were 0.81 and 0.86, respectively); the recovery and relative resilience were rather low (1.10 and 0.05, respectively; cf. Taeger et al., 2013), suggesting some suppression of TRW after disturbances. Regarding the positive years, mean resistance (improvement) and recovery (growth release) were 1.10 and 0.80, respectively (Fig. 4), suggesting weaker reaction of TRW compared to the negative years. Higher resilience (showing duration of release) and relative resilience (0.90 and -0.25, respectively) suggested that TRW more promptly returned to pre-release level.

Tolerance indices showed significant (p-values < 0.01) trial by weather extreme interaction (Table 5), implying trial-specific responses of TRW. The non-interacted effect of provenance was observed for resistance and resilience to the negative PYs, and relative resilience (duration of release) to the positive years (Table 5). These tolerance indices followed the field performance of provenances (Fig. 4). The differences in resistance and resilience to the negative PYs among provenances were significant only for the strongest contrasts (DIP and RYT; Fig. 4). Differences in relative resilience to the positive PY lacked statistical significance among the provenances (Fig. 4), likely due to the adjustments of p-values of multiple pairwise comparisons (Lenth, 2018).

The provenance by weather extreme interaction was significant (p-value < 0.01) for relative resilience to the negative years (Table 5). The highest indices were observed for EBN and RYT (means were 0.21 and 0.22, respectively) after cold winter (e.g., in 2005), while the lowest for KAL (0.02) and DIP (0.06) in years with cold winter and hot and dry summer (e.g., in 1997, 2010, and 2013; Table 2). The provenance by trial interaction was significant (p-values < 0.05) for the recovery (release) after the positive PYs (Table 5). The lowest indices were observed for DIP and KAL in BSK trial (0.69 and 0.78, respectively), suggesting some growth release after mild winters. The highest indices were estimated for the top-performing RYT under maritime climate in LPJ trial (0.95), indicating prompt return of growth to previous level.

4. Discussion

The studied trials differed by productivity (Table 4) which, besides the edaphic conditions, could be related to climate (Jansons and Baumanis, 2005) and environmental transfer distance of seed material (Rehfeldt et al., 2003; Schlyter et al., 2006). Temperature has been considered as the main factor limiting growth of the north-transferred trees (Schlyter et al., 2006); accordingly, milder climate in LPJ trial (Table 1) was favourable for the provenances from regions with a warmer and dryer climate (Taeger et al., 2013), particularly GUS and RYT (Table 3). Nevertheless, moisture regime also affected growth of studied provenances, particularly EBN and DIP, which originated from more humid climate (Table 3). Although longer vegetation period (as in BSK trial) is considered favourable for north-transferred provenances (Repo et al., 2000; Rehfeldt et al., 2003), it apparently could not compensate for drier summers there (Table 1), hence TRW was similar to the more continental KLN trial (Table 1). Additionally, the explicit reaction to thinning (1996) in BSK and KLN trials (Fig. 1), where summers were hotter and drier, suggested release from competition for

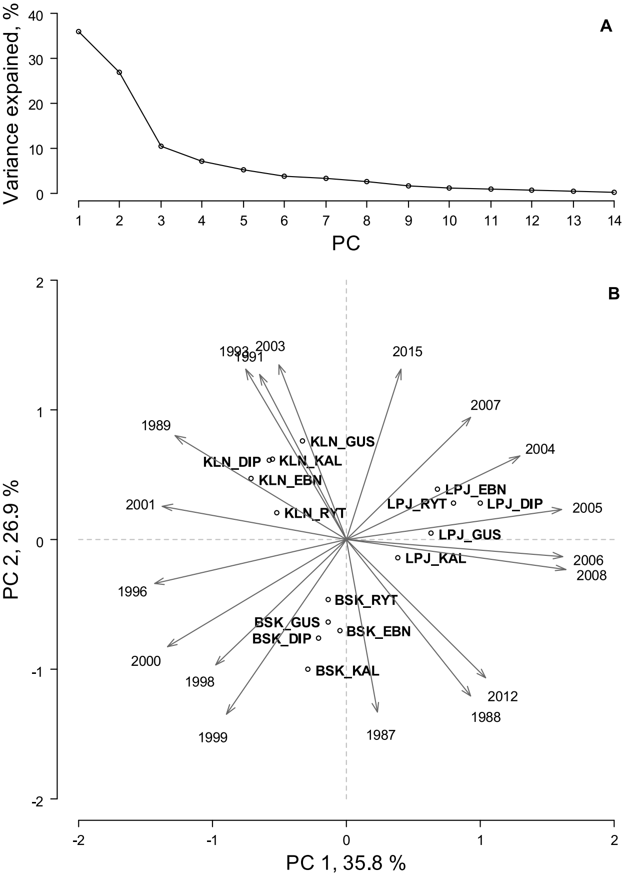

Fig. 2. Variance of pointer year values explained by principal components (PC; A), and the first two principal components of pointer year values of tree-ring width of the studied provenance of Scots pine for the common period 1987–2017 (B). In B, dots indicate samples (series) and arrows indicate variables (years). Number of axis indicate variance explained by each component. Coordinates of points are rescaled for clarity. Names of points consist of abbreviation for trial and provenance.

soil water in summer (Merlin et al., 2015; Zang et al., 2012).

The performance of the studied provenances was related to their sensitivity to environmental fluctuation, as indicated by the negative relationships (Fig. 1; Table 4) between TRW, as well as range of PY values, and MS, which has been previously shown by Zang et al. (2012) and Taeger et al. (2013). Alternatively, such relationships might be related to allocation of carbon to root growth in provenances from harsher sites (Nikolova et al., 2011), or to differing control of stomatal conductance, hence reaction to water availability (Hartmann, 2011). Nevertheless, PY values, their statistics, climate-growth correlations, and tolerance indices (Figs. 1, 3, 4; Table 4) were intermediate, suggesting moderate influence of weather fluctuations, as expected in the mid-part of specie's distribution range (Martinez-Vilalta et al., 2009; Speer, 2010; Taeger et al., 2013).

The PC analysis (Fig. 2) highlighted temperature in the dormant period and moisture availability in summer, which is determined by temperature and precipitation regime (Trajkovic, 2005), as the main determinants of the inter-annual variation of PY values of the studied provenances. The synergy of these factors caused the remarkable PYs (Table 2); common PYs occurred in e.g., 1994, 1997, and 2005 (Fig. 1), when cold winters were followed by warm/dry summers (Table 2), indicated susceptibility of the studied provenances to repeated stress (Marshall et al., 2000). Such effects are consistent with the regional signals in growth of Scots pine (Elferts, 2007; Jansons et al., 2016; Hordo et al., 2009).

The effect of temperature in the dormant period was trial-specific (Figs. 2,3), implying diverse mechanisms of response (Hansen and Beck, 1994; Weih and Karlsson, 2002) in the mid-part of specie's range (Friedrichs et al., 2009). In LPJ trial, the effect of temperature in previous December (Fig. 3) could be related to cold damage (Weih and Karlsson, 2002). Under coastal climate, winter accession is slower (Harris et al., 2014) delaying cold hardening (Repo et al., 2000; Beck

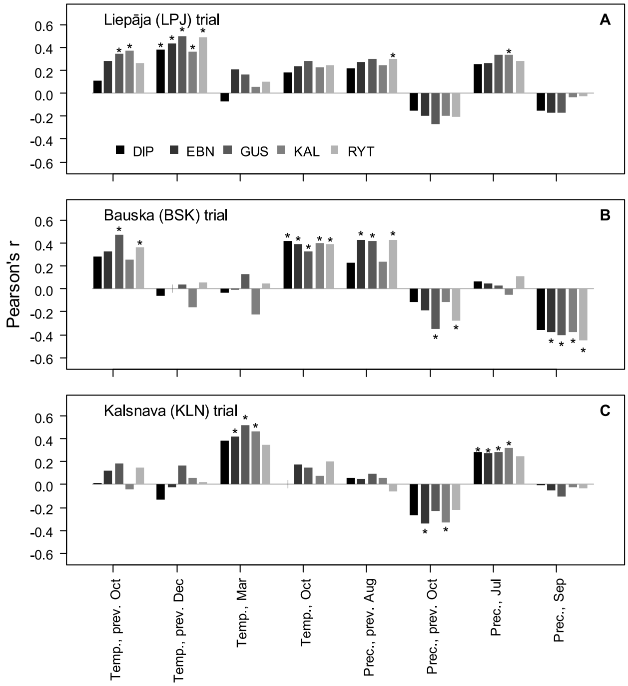

Fig. 3. Correlations between the pointer year values of studied provenances of Scots pine and climatic factors (monthly mean temperature and precipitation sums) for the common period 1987–2017. Asterisks indicate correlations significant at α = 0.05. Only the climatic factors showing significant correlations are plotted.

et al., 2004), thus increasing susceptibility of trees to sudden temperature drops (Avotniece et al., 2012). Although the top-performing provenances showed higher correlations (Fig. 3), the PY values (Fig. 1; Table 2) suggested that they mostly benefited from warm Decembers. In contrast, the bottom-performing provenances showed stronger negative PY after cold winters, probably due to lesser nutrient reserves, hence affected cold hardening (Hansen and Beck, 1994; Ögren, 1997). In KLN trial, the effect of temperature in March/April (Fig. 3) might be related to soil freeze and root growth (Tierney et al., 2001), which occur at that time (Hansen and Beck, 1994), and affect water relations of trees in the following season (Kramer and Boyer, 1995). The top-performing GUS provenance showed higher correlation with this factor (Fig. 3C), still the PYs (e.g., in 2005, 2006, and 2007; Fig. 1; Table 2) showed that trees were able to benefit from warm years and show lesser growth reduction in cold years.

The effect of summer moisture regime was stronger under drier climate in BSK and KLN trials (Fig. 3). In KLN trial, direct effect of water deficit on growth (Eilmann and Rigling, 2012) was indicated by the positive correlations with precipitation in July (Fig. 3). In BSK trial, the correlations with precipitation in previous August suggested effect of water deficit on formation of nutrient reserves, which affect overwintering (Ögren, 1997; Tierney et al., 2001; Weih and Karlsson, 2002) and growth in the next spring (Hansen and Beck, 1994; Barbaroux and Breda, 2002; Mayr et al., 2003). Considering intensifying summer water deficit (Avotniece et al., 2012), most of the PYs related to dry years were negative (Table 2). Still, the top-performing provenances, particularly RYT, were able to benefit from moist years and show weaker reduction of TRW in response to dry summers (Fig. 1; Table 2), suggesting better adaptation to future climate in Latvia.

The ability of the north-transferred provenances to utilize longer vegetation period increases increment, as well as the risk of frost damage (Repo et al., 2000; Rehfeldt et al., 2003; Bolte et al., 2009; Schreiber et al., 2013). The correlation with October temperature (Fig. 3) suggested formation of some additional increment in warm autumns (Oberhuber et al., 1998). The effect of previous October implied additional assimilation (Barbaroux and Breda, 2002), hence improved overwintering (Hansen and Beck, 1994), particularly for the top-performing provenances. The correlations with September precipitation (Fig. 3) suggested influence of decreased radiation on assimilation in cloudy days (Strand et al., 2006). These effects have likely been slight (no PY related; Table 2); still, the observed correlations implied potential gains from extending vegetation period (Walther et al., 2002; Bolte et al., 2009; Lindner et al., 2010; Schreiber et al., 2013).

The tolerance of the studied trees to weather extremes (Fig. 4) was generally similar to that observed in Germany (cf. Taeger et al., 2013), suggesting comparable reaction of radial increment to sudden environmental fluctuations. Still, the relative resilience (Fig. 4) was lower, indicating higher plasticity of growth (Taeger et al., 2013). The significant and consistent effect of provenance on resistance and resilience in the negative PYs (Table 5) implied that selection by provenance might be applied for reduction of forestry risks related to weather extremes (Repo et al., 2000; Taeger et al., 2013, 2015) across the continentality gradient in Latvia. Accordingly, GUS and RYT provenances

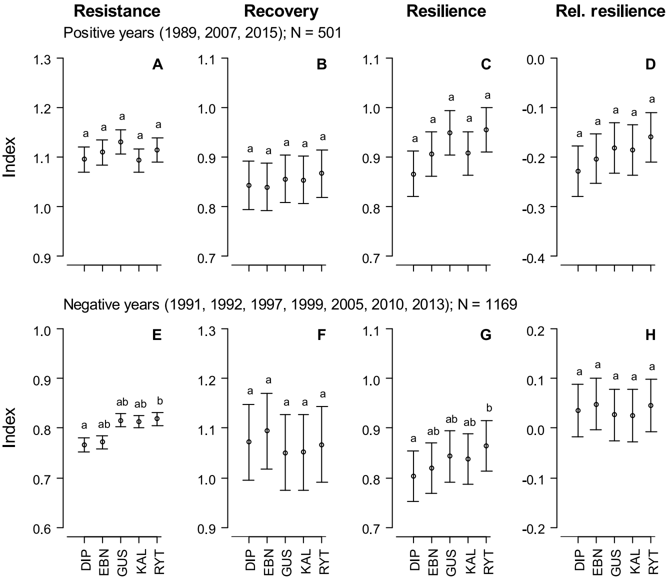

Fig. 4. The estimated marginal means of the tolerance indices (resistance, recovery, resilience and relative resilience) of TRW of the studied provenances of Scots pine in the positive (A–D) and negative (E–H) pointer years across the trials and years. Similar letters indicate lack of significant differences among the provenances, as determined by Tukey's HSD post-hoc test. Note that the axes differ. N – number of observations.

Table 5

The *F*-values of fixed effects (provenance, trial, type of weather extremes (cold or warm winter, cool or warm and dry summer) and their interactions) and variance of random effects (tree and year) of tolerance indices of radial growth (tree-ring width) of Scots pine in the identified positive and negative pointer years. Significance codes, *p*-values: * < 0.05, ** < 0.01, *** < 0.001; df – degree of freedom.

	Resistance	Recovery	Resilience	Relative resilience
Positive pointer years (1989, 2007, and 2015)				
Fixed effects, F-value				
Provenance	$0.39_{(df=4,\ 464)}$	$0.31_{(df=4,\ 464)}$	$2.21_{(df=4,\ 464)}$	$2.38_{(df=4,\ 464)}^{*}$
Trial	$3.82_{(df=}2{,}464_{)}^{*}$	$1.76_{(df=2,\ 464)}$	$1.88_{(df=}2{,}464_{)}$	$5.01_{(df=2,\ 464)}^{**}$
Extreme	$2.88_{(df=1,\ 464)}$	$0.21_{(df=1,\ 464)}$	$0.79_{(df=1,\ 464)}$	$0.11_{(df=1,\ 464)}$
Provenance × trial	$1.61_{(df=8,\ 464)}$	$2.24_{(df=8,\ 464)}^{*}$	$0.92_{(df=8,\ 464)}$	$1.83_{(df=8,\ 464)}$
Provenance × extreme	$0.63_{(df=4,\ 464)}$	$0.43_{(df=4,\ 464)}$	$1.65_{(df=4,\ 464)}$	$0.39_{(df=}4{,}464_{)}$
Trial × extreme	$43.64_{(df=2,\ 464)}^{***}$	$37.67_{(df=2,\ 464)}^{***}$	$4.85_{(df=2,\ 464)}^{**}$	$52.89_{(df=2,\ 464)}^{***}$
Provenance × trial × extreme	$1.23_{(df=8,\ 464)}$	$1.32_{(df=8,\ 464)}$	$0.41_{(df=8,\ 464)}$	$1.27_{(df=8,\ 464)}$
Variance of random effects				
Plot (as intercept)	$1.6{\cdot}10^{-6}$	$1.1{\cdot}10^{-7}$	$7.7{\cdot}10^{-8}$	$4.4{\cdot}10^{-9}$
Tree (as intercept)	$2.1{\cdot}10^{-5}$	$6.5{\cdot}10^{-5}$	$5.6{\cdot}10^{-6}$	$8.5{\cdot}10^{-7}$
Year (as intercept)	$9.4{\cdot}10^{-4}$	$5.2{\cdot}10^{-3}$	$4.1{\cdot}10^{-3}$	$5.6{\cdot}10^{-3}$
Residual	0.054	0.031	0.043	0.038
Negative pointer years (1991, 1992, 1997, 1999, 2005, 2010, and 2013)				
Fixed effects, F-value				
Provenance	$3.85_{(df=4,\ 1102)}^{**}$	$0.70_{(df=4,\ 1102)}$	$3.09_{(df=4,\ 1102)}^{*}$	$0.62_{(df=4,\ 1102)}$
Trial	$15.51_{(df=2,\ 1102)}^{***}$	$4.99_{(df=2,\ 1102)}^{**}$	$12.64_{(df=2,\ 1102)}^{***}$	$3.47_{(df=2,\ 1102)}^{*}$
Extreme	$1.85_{(df=3,\ 1102)}$	$0.51_{(df=3,\ 1102)}$	$1.25_{(df=3,\ 1102)}$	$0.67_{(df=3,\ 1102)}$
Provenance × trial	$0.16_{(df=8,\ 1102)}$	$0.53_{(df=8,\ 1102)}$	$0.81_{(df=8,\ 1102)}$	$1.06_{(df=8,\ 1102)}$
Provenance × extreme	$1.35_{(df=12,\ 1102)}$	$1.57_{(df=12,\ 1102)}$	$1.49_{(df=12,\ 1102)}$	$4.82_{(df=12,\ 1102)}^{**}$
Trial × Extreme	$17.65_{(df=6,\ 1102)}^{***}$	$5.86_{(df=6,\ 1102)}^{***}$	$29.74_{(df=6,\ 1102)}^{***}$	$12.97_{(df=6,\ 1102)}^{***}$
Provenance × trial × extreme	$1.23_{(df=24,\ 1102)}$	$0.59_{(df=24,\ 1102)}$	$1.40_{(df=24,\ 1102)}$	$0.72_{(df=24,\ 1102)}$
Variance of random effects				
Plot (as intercept)	$1.7{\cdot}10^{-6}$	$2.4{\cdot}10^{-5}$	$6.6{\cdot}10^{-9}$	$2.6{\cdot}10^{-6}$
Tree (as intercept)	$6.3{\cdot}10^{-9}$	$3.9{\cdot}10^{-6}$	$2.7{\cdot}10^{-10}$	$4.3{\cdot}10^{-5}$
Year (as intercept)	$1.1{\cdot}10^{-3}$	0.030	0.014	0.015
Residual	0.032	0.087	0.039	0.035

showed the highest tolerance, hence could be recommend for wider application. Lower resilience of EBN and DIP (Fig. 4) indicated growth depressions (Lloret et al., 2011), particularly in response to multiple stressors (Fig. 1; Table 2). The interactions in tolerance indices involving provenance (Table 5) were generally related to local specifics in susceptibility of the bottom-performing provenances to repeated stress (not shown).

5. Conclusions

Considering location of the trials in hemiboreal zone, PYs of the studied Scots pine provenances were prevailingly caused by winter temperature regime. The effects of climatic factors related to water deficit and vegetation period's length were apparent, likely due to warming of climate and seed transfer, respectively. Growth response to weather fluctuations and weather extremes highlighted linkage between climatic sensitivity and productivity of the studied provenances; while, the diversity of responses indicated plasticity of Scots pine from different populations, suggesting that selection by provenance might be sufficient for improvement of sustainability of stands. As expected, the top-performing provenances (GUS and particularly RYT) showed lower sensitivity of growth to weather conditions and were more resilient to unfavourable weather extremes, likely due to the ability to utilize longer vegetation period and assimilate greater nutrient reserves. Although transferred north, the top-performing provenances were able to benefit from warm winters and showed lesser growth reduction in cold winters, yet were more tolerant to water deficiency, indicating increasing commercial potential. Considering that provenance had consistent effect of growth tolerance, indicating genetic control, the top-performing provenances might be applied in commercial forestry and/or included in breeding program to amplify positive effects of the transfer.

Acknowledgements

The study was conducted under the framework of post-doctoral studies in Latvia ("Plasticity of development and xylogenesis of the native and introduced tree species under changing climate", project No.: 1.1.1.2.VIAA/1/16/108) financed by the European Regional Development Fund.

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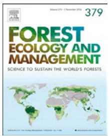
Forest Ecology and Management 452 (2019) 117568

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Plasticity and climatic sensitivity of wood anatomy contribute to performance of eastern Baltic provenances of Scots pine

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ARTICLE INFO

Keywords:
Common garden
Pinus sylvestris
Seed transfer
Dendroclimatology
Baltic Sea region
Tracheid parameters
Hemiboreal zone

ABSTRACT

The efficiency of water use and transport are among the main factors affecting competitiveness, growth, and distribution of trees under warming climate. The phenotypical and genetic plasticity of tree populations is considered as an indicator of their adaptive capacity under changing environment. Climatic changes are expected to affect growth of Scots pine (*Pinus sylvestris* L.), and selection of reproductive material among the populations suitable for future climates has been advised for sustaining productivity of stands. In this regard, provenance trials can serve as source of comprehensive information about growth plasticity and climate-growth interactions of diverse populations. Quantitative wood anatomy can provide detailed information about xylogenesis and factors affecting it, which are crucial for long-term predictions. Wood anatomy of two top- (Gustrow and Rytel), two low-performing (Eibenstock and Dippoldiswalde), and one local (Kalsnava) provenances of Scots pine from the eastern Baltic region growing in three provenance trials in Latvia was studied using mixed models, accounting for the experimental design, as well as using the time-series approach. Provenance had a significant effect on the studied wood anatomical proxies, indicating genetic adaptation of xylogenesis. The top-performing provenances, which originated from warmer and drier conditions, had tracheids with larger lumens and thinner walls, thus indicating adaptation to water deficit. The top-performing Rytel provenance showed the highest phenotypical plasticity of lumen cross-section area and cell wall thickness of stemwood tracheids. The studied low-performing provenances, which originated from the Orr Mountains, had tracheids with thicker wall and smaller lumens, likely to ensure mechanical durability. The local provenance showed intermediate values of the studied wood anatomical proxies. The effect of provenance on wood anatomical proxies showed some variations among the trials, which differed by continentality, likely due to ecological transfer distance. The studied anatomical proxies were affected by weather conditions prior and during formation of a tree ring, yet these relationships differed by trial and provenance. In general, wood anatomy of earlywood was affected by temperature in the dormant period and beginning of summer, as well as precipitation in the end of the previous vegetation period. Proxies of latewood showed correlation with temperature (negative) and precipitation (positive) in summer, suggesting response to the availability of water. Considering the observed relationships, the top-performing provenances, particularly Rytel, have a high potential to sustain productivity of stands within the region in the future.

1. Introduction

Scots pine (*Pinus sylvestris* L.) is predicted to decrease growth and survival in a large part of its distribution range (Buras and Menzel, 2019) due to increasing heat stress and water deficit (Martinez-Vilalta et al., 2009; Martin et al., 2010; Allen et al., 2015), causing severe economic consequences (Hanewinkel et al., 2013; Nabuurs et al., 2018). Hence, the observed and predicted extension and intensification of periods of water deficit (IPCC, 2013) are raising new challenges in forest management across vast regions in Europe (Allen et al., 2015; Yousefpour et al., 2017; Nabuurs et al., 2018). Consequences of water shortage, such as increment reduction (Anderegg et al., 2015; Popkova et al., 2018; De Micco et al., 2019) and pest outbreaks (Martini et al., 2017), are considered as a major threat counteracting growth improvements due to extended vegetation periods (Yousefpour et al., 2017; Nabuurs et al., 2018). Under a warming climate, the effect of

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https://doi.org/10.1016/j.foreco.2019.117568
Received 5 May 2019; Received in revised form 20 August 2019; Accepted 21 August 2019

water deficit emerges also in ecosystems not considered as water-limited, such as boreal and hemiboreal forests (Savva et al., 2002; Lloyd et al., 2011; Vicente-Serrano et al., 2014; Yousefpour et al., 2017). The influence of climatic changes on tree growth can differ at fine geographic scale due to the micro-site and historical factors (Eckert et al., 2015; Fei et al., 2017; Moran et al., 2017), thus adding complexity to the assessment of the future growth potential.

Water conductivity of wood, embolization, and ability to refill embolized tracheids/vessels have been among the main factors determining sensitivity of trees to water deficit and their ability to efficiently utilize available water resources throughout the vegetation period (Fonti and Jansen, 2012; Mayr et al., 2014; Allen et al., 2015; Moran et al., 2017; Choat et al., 2018; Chauvin et al., 2019). These issues are linked to the hydraulic architecture of wood, hence to wood anatomy (Tyree and Zimmermann, 2002; Fonti and Jansen, 2012; Anderegg et al., 2015; Carrer et al., 2015; Popkova et al., 2018). Wood of conifers is mostly consists of tracheids (Cuny et al., 2014). Size, cell wall properties, and lumen area are among the main parameters, which determine functioning of tracheids under stress conditions (Martin et al., 2010; Rathgeber et al., 2016; Arzac et al., 2018; De Micco et al., 2019). The cross-section area of cell lumen (LCA), particularly in earlywood (EW) determines conductivity of water and probability of embolism under water shortage (Eilmann et al., 2009; Martin et al., 2010; Bryukhanova and Fonti, 2013). Cell wall thickness (CWT), particularly in latewood (LW) influence mechanical properties (De Micco et al., 2019), yet drought sensitivity as well (Anderegg et al., 2015; Nabais et al., 2018). Also, CWT can be considered as an indirect proxy of assimilation (Fonti et al., 2013; Arzac et al., 2018; Nabais et al., 2018) and carbon reserves (Mayr et al., 2003, 2014).

The dimensions of tracheids are affected by the timing and duration of their formation (Anfodillo et al., 2013; Cuny et al., 2014; Rathgeber et al., 2016; Butto et al., 2019), which are influenced by weather conditions (Castagneri et al., 2017; Cuny et al., 2019), genetic (Savva et al., 2002, Martinez-Vilalta et al., 2009; Housset et al., 2018; Nabais et al., 2018), and legacy (response to preceding conditions) factors (Fonti et al., 2013; Anderegg et al., 2015; Sass-Klaassen et al., 2016; Cuny et al., 2019). Both, cell expansion and cell wall deposition (which decreases lumen area) is directly affected by temperature, while the first is also highly sensitive the availability of water (Bryukhanova and Fonti, 2013; Cuny et al., 2014; Rathgeber et al., 2016; Butto et al., 2019). The direct and indirect (via vigour, assimilation, hormone concentrations, etc.) effects of these factors also influence the rate of cell division and the number of wood cells formed in each year, hence tree-ring width and increment (Butto et al., 2019; De Micco et al., 2019). Wood formation is a continuous process, and the trade-offs in tracheid development (hence intra-annual variation of their dimensions) allow trees to plastically adjust xylem according to the hydraulic demands being set by meteorological conditions (Bryukhanova and Fonti, 2013; Dalla-Salda et al., 2014; Arzac et al., 2018; Cuny et al., 2019).

Trees, as long living organisms, are subjected to a wide spectrum of fluctuating environmental conditions, hence they have developed mechanisms allowing high phenotypical plasticity, including that of xylogenesis, to survive various environmental conditions (Bryukhanova and Fonti, 2013; Dalla-Salda et al., 2014; Aitken and Bemmels, 2016; Cuny et al., 2019; Klisz et al., 2019). Being of adaptive significance, traits related to hydraulic architecture, hence susceptibility to water deficit, are often genetically controlled (Savva et al., 2002; Li et al., 2018; Nabais et al., 2018). Populations of trees with wide distribution range have evolutionary adapted to local conditions, restricting variability of traits and physiological reactions to environment, even under high gene flow (Li et al., 2018; Moran et al., 2017; Chauvin et al., 2019). Scots pine from drier sites form tracheids with larger lumen to improve conductivity with minimal investment in carbon (Eilmann et al., 2009, Martin et al., 2010), while trees from windy sites have thicker cell walls to improve mechanical strength (Savva et al., 2002; Martinez-Vilalta et al., 2009; Martin et al., 2010). However, considering the increasing rate of climatic changes, evolutionary adaptation of local populations might be lagging behind, hence assisted migration appears necessary (Aitken and Bemmels, 2016). High phenotypic plasticity in combination with genetic adaptation, including the ability to maintain optimum conduit size (Bryukhanova and Fonti, 2013; Arzac et al., 2018), therefore are crucial for the adaptation to novel conditions (Aitken and Bemmels, 2016; Moran et al., 2017; Housset et al., 2018).

Provenance trials, which historically have been established for screening of the most productive populations (Leites et al., 2012; Nabais et al., 2018), provide an opportunity for assessment of genetic (between provenances) aspects of local adaptation, as well as the phenotypical plasticity of trees (Aitken and Bemmels, 2016; de Villemereuil et al., 2016; Moran et al., 2017; Nabais et al., 2018). They also provide the possibility to evaluate reactions of tree populations to the potential future climates, providing a deeper insight in sensitivity of genotypes, thus aiding for more comprehensive assessment of growth potential (Taeger et al., 2013; Nabuurs et al., 2018; Matisons et al., 2019). Klisz et al. (2019) demonstrated efficiency of provenance trials regarding these issues, particularly under non-marginal conditions. Information about the genetic control of growth sensitivity is crucial for the adaptive management, including tree breeding, to cope with the changing climate (de Villemereuil et al., 2016; Nabuurs et al., 2018).

The aim of this study was to assess plasticity of LCA and CWT of the eastern Baltic provenances of Scots pine differing by filed performance under hemiboreal conditions. The objectives were (i) to assess phenotypic and genetic (between-provenance) plasticity of wood anatomical proxies, and (ii) to assess their sensitivity to climatic factors. We hypothesized, that the top-performing provenances showed higher phenotypic plasticity of wood anatomy compared to the low-performing ones, which affected sensitivity to climatic factors. We also assumed, that the top-performing provenances formed tracheids with larger lumens and thicker walls, hence more efficient water transport, allowing faster growth, and that these differences were genetically controlled.

2. Material and methods

2.1. Studied trials and provenances

Three international Scots pine provenance trials, which were established in 1975 under the collaboration between the USSR and the German Democratic Republic (Kohlstock and Schneck, 1992; Jansons and Baumanis, 2005) in the hemiboreal zone in Latvia near Liepāja (LI), Zvirgzde (ZV), and Kalsnava (KA) were studied (Table 1, Fig. 1) to account for the local variability of growth (Jansons and Baumanis, 2005; Eckert et al., 2015). The trials are situated on well-drained (sandy or slightly loamy) dry oligotrophic podsols with flat topography at low

Table 1
Location, elevation, soils, and climate (annual and monthly mean temperature, and precipitation sums (± 95% confidence interval) of the studied trials. Climatic data refers to 1997–2017.

	Liepāja (LI)	Zvirgzde (ZV)	Kalsnava (KA)
Latitude, N	56°29′N	56°32′N	56°49′N
Longitude, E	21°05′E	24°13′E	26°7′E
Elevation, m a.s.l.	15	50	220
Relief	Flat	Flat	Flat
Soil type	Podsols	Podsols	Podsols
Site type	*Vacciniosa*	*Vacciniosa*	*Vacciniosa*
Mean annual temperature, °C	7.8 ± 0.7	7.2 ± 0.8	6.3 ± 0.9
Mean temperature May-Sep., °C	15.0 ± 0.3	15.3 ± 0.3	14.8 ± 0.4
Mean temperature Jan., °C	−1.4 ± 1.3	−2.9 ± 1.3	−4.3 ± 1.3
Mean temperature Jul., °C	17.8 ± 0.6	18.4 ± 0.7	18.0 ± 0.6
Mean annual precipitation, mm	745 ± 37	647 ± 26	656 ± 28
Mean precipitation May–Sep., mm	65 ± 6	67 ± 5	67 ± 6

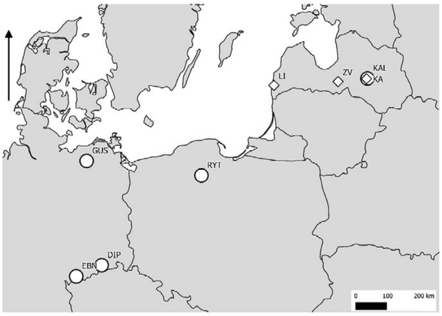

Fig. 1. Location of origin of the studied provenances (circles and three letter codes) and provenance trials (squares and two letter codes). The arrow indicates geographic (true) north.

elevation (≤220 m above sea level). The trials represent the spatial climatic gradient from coastal (in LI) to continental (in KA). January and July were the coldest and the warmest months, respectively (Supplementary material, Fig. S1). The mean annual temperature was higher in ZV and LI trials (Table 1). Vegetation period (mean daily temperature > 5 °C) extended from mid-April to October. In ZV, it was about two weeks longer compared to LI and KA. Annual precipitation was higher in LI. The highest monthly precipitation mostly occurred in the summer months (May–September; Fig. S1). Climatic changes were expressed as warming in the dormant period and spring (more frequent and intensive thaws), and as extension of vegetation period (ca. by two weeks during the past 50 years; IPCC, 2013), as well as increasing variability of precipitation regime (increasing frequency and extension of the dry periods) in summer (Avotniece et al., 2012).

The trials were established by planting one-year-old bare-rooted seedlings raised in local nurseries. The seeds were collected in 36 open-pollinated stands (20–25 trees) distributed within 50–56°N, and 11–27°E (Poland and Northern Germany) (Kohlstock and Schneck, 1992). Such region represents the projected climatic conditions for Latvia in the near future (IPCC, 2013). In each trial, each provenance was planted in six randomly distributed plots of 7 × 5 trees with 1 × 2 m spacing (5000 trees ha^{-1}). All trials contained identical set of provenances. At the age of 21 years, the trials were thinned; about two thirds of the initially planted trees (per plot) were harvested (the post-thinning stand density was ca. 1800 trees ha^{-1}) (Jansons and Baumanis, 2005).

Provenance had a consistent effect on field performance and stem quality of Scots pine in the studied trials (Jansons and Baumanis, 2005). Based on the trial inventory conducted in 2016 (stem diameter at breast height and tree height measured), two of the top- and two of the low-performing provenances according to their field performance (dimensions of trees and survival; Supplementary material, Table S1) were selected for sampling. Such a selection was done to assess the linkage between productivity and plasticity of wood anatomy (Martin et al., 2010; Fonti et al., 2013; Arzac et al., 2018). Consequently, Güstrow (GUS) and Rytel (RYT), which originated from lowland sites with dryer and warmer climate (Fig. 1; Table 2; Supplementary material, Fig. S2), where selected as the top-performing provenances. Dippoldiswalde (DIP) and Eibenstock (EBN), which originated from the Orr Mountains (Fig. 1), where climate was cooler and more humid (Table 2), were selected for the representation of the low-performing provenances. Considering a northward transfer of the provenances, higher field performance of the provenances was observed under milder climate in the coastal LI trial (Jansons and Baumanis, 2005). Additionally, the local Kalsnava (KAL) provenance, which showed intermediate field performance (Supplementary material, Table S1), was selected for the representation of plasticity, hence adaptability of the native population (Taeger et al., 2013; Aitken and Bemmels, 2016).

2.2. Sample collection and preparation

For each provenance within each trial, one to three undamaged dominant trees from each of the six plots (9–16 trees per provenance per trial in total; Supplementary material, Table S2) were sampled in November 2017. Considering that the trials were planned to be ongoing, the number of sampled trees was restricted. Two 5-mm increment cores from the opposite randomly oriented sides of the stem at 1.3 m height were collected. To avoid the occurrence of reaction wood, tilted trees were not sampled.

In the laboratory, cores were glued on wooden mounts using a water-based PVA glue. In case of twisted samples, they were steamed (steam jet) and straightened (as far as possible) before fixing (Speer, 2010). Samples for microscopy were prepared according to the guidelines described by Gärtner et al. (2015). From each core, a thin section (thickness 14–18 µm) was cut with the WSL core microtome (Gärtner and Nievergelt, 2010) equipped with the Leica Surgipath DB80 LX blades. It was ensured that the prepared thin sections contained ≥ 21 outermost tree-rings. A mixture of glycerine and rice starch was applied before the final cut to stabilize the sample and to avoid cell wall rupture (Schneider and Gärtner, 2013). Transparent water-dissolving tape was used to transfer cut thin sections onto glass slides. The samples were covered with 50% water-glycerine solution to avoid drying-out before dyeing with Astrablue and Safranin, following the protocol described by Gärtner and Schweingruber (2013). The dyed thin sections were dehydrated using ethanol and xylol, and sealed in Canada balm as permanent samples.

2.3. Measurements

Tree-ring width from the permanent samples was measured manually, using a Lintab 5 measuring table, equipped with an object table with a white background, and TSAP software (RinnTech Inc., Heidelberg, Germany). To measure wood anatomical proxies, high resolution (ca. 0.9 pixels µm^{-1}) overlapping distortion free microscopic images were acquired at 40× optical magnification using a light microscope (Gärtner et al., 2015) and a digital camera with an 18 Mpx cropped matrix. The images were stitched using the PTGui software (New House Internet Services B.V., Rotterdam).

Wood anatomical proxies – LCA and CWT in EW and LW (LCA_{EW}, LCA_{LW}; and $CWT_{EW,}$ CWT_{LW}, respectively), which determine conductivity, risk of dysfunction, and mechanical properties of wood (Tyree and Zimmermann, 2002; Martin et al., 2010; Carrer et al., 2015; Cuny et al., 2019), were measured using the WinCELL 2007a (Regent Instrument, Inc.) software. Considering the limitations due to the version of the software, areas of typical EW and LW tracheids, containing > 120 cells in > 18 radial files, were distinguished arbitrarily and cut from image of each tree ring (Supplementary material, Fig. S3A) formed during 1997–2017 (the outermost 21 rings), and used for measurements. To warrant correct measurements of cells, it was ensured that the tangential axis of wood in each of the cut images was horizontal (± 5°). Images, in which axial direction of tracheids was not perpendicular to the cutting plane due to improper orientation of samples (or its parts) or anatomical anomalies of wood (as e.g., frost rings, reaction wood, etc.), were discarded (Supplementary material, Fig. S3B, C), resulting in interrupted time series of measurements. Some images were also discarded due to the issues related to naturally varying orientation of tracheids within wood (Schweingruber et al., 2012). Number of images for each provenance/trial/year is shown in Supplementary material, Fig. S4. In WinCELL, pixel classification based on colour was used, applying the "H and V" mode of cell measurements. The batch function was applied for automated image processing. Size

Table 2
Location and climatic description of origin of the studied provenances of Scots pine. Climatic data refers to 1997–2017.

	Güstrow (GUS)	Rytel (RYT)	Dippoldis-walde (DIP)	Eibenstock (EBN)	Kalsnava (KAL)
Latitude, N	53°45′	53°40′	50°49′	50°27′	56°42′
Longitude, E	12°15′	18°01′	13°52′	12°26′	25°54′
Elevation, m a.s.l.	25	130	590	710	190
Mean annual temperature, °C	8.0	7.9	6.6	5.9	6.3
Mean temperature May-Sep., °C	14.8	15.0	13.2	12.6	14.7
Mean temperature Jan, °C	−0.8	−1.4	−2.6	−3.0	−4.3
Mean temperature Jul, °C	16.8	17.2	15.3	14.7	18.0
Mean annual precipitation, mm	585	590	804	994	656
Mean precipitation May-Sep., mm	297	306	402	499	337

filters were applied to exclude any erroneously detected objects. Individual cell data was stored for the analysis.

2.4. Data analysis

To ensure correct dating of each tree-ring (wood images), cross-dating based on tree-ring widths was performed by graphical inspection and using the COFECHA program (Grissino-Mayer, 2001). The dating of measurements was adjusted if necessary. The effect of provenance on the studied wood anatomical proxies was assessed using linear mixed models (Bates et al., 2015) to account for the unbalancedness in the data. The individual cell was considered as an observation and wood image was considered as a statistical unit. Since tree age and meteorological conditions affect wood anatomy (Eilmann et al., 2009; Anfodillo et al., 2013, Castagneri et al., 2017), the year of tree-ring formation, core (side of stem), tree, and plot were used as random factors to account for the dependencies in the data. Tree-ring width was included in the models as a numeric covariate to account for the effect of growth rate.

Bootstrapped Pearson correlation analysis (Zang and Biondi, 2013) was used to assess the relationships of the inter-annual variation of LCA and CWT with climatic factors, accounting for missing data. Considering that some time proxies showed a linear age trend (age/size related increase of LCA and CWT; Eilmann et al., 2009; Anfodillo et al., 2013), time series were detrended using a simple linear model and prewhitened before the pooling by the biweight robust mean (Bunn, 2008). The tested climatic factors were the mean monthly temperature, monthly precipitation sum, and monthly water deficit, represented by the standardized precipitation evapotranspiration index (SPEI; Vicente-Serrano et al., 2010). The tested climatic factors were arranged according to the time windows from June in the year preceding tree-ring formation (previous June) to June in the year of tree-ring formation, and from previous June to September of tree-ring formation for EW and LW, respectively. The significant factors were checked for collinearity. The interpolated climatic data (CRU TS3.10) were obtained from the online repository (Harris et al., 2014) for the stations located at ≤12 km distance from the trials. Pearson correlation was calculated to assess the relationships between the time series of LCA and CWT across the trials and provenances. Data analysis was conducted in R, v. 3.5.1 (R Core team, 2019), using packages “lme4” (Bates et al., 2015), “dplR” (Bunn, 2008), “emmeans” (Lenth, 2018), and “bootRes” (Zang and Biondi, 2013).

3. Results

3.1. Differences among provenances and trials

The mean LCA$_{\mathrm{EW}}$ and LCA$_{\mathrm{LW}}$ of the studied provenances of Scots pine ranged 761–867 and 101–178 μm^2, respectively; the mean CWT$_{\mathrm{EW}}$ and CWT$_{\mathrm{LW}}$ ranged 2.6–4.4 and 5.1–10.7 µm, respectively (Fig. 2). The studied wood anatomical proxies showed varying within-provenance variation (Table 3), indicating intermediate (cf. Chauvin et al., 2019) phenotypical plasticity of xylogenesis. The highest within-provenance variation was observed for LCA$_{\mathrm{LW}}$, while the lowest for CWT$_{\mathrm{EW}}$. Among the provenances, the top-performing RYT overall showed the highest phenotypical plasticity of the studied proxies, followed EBN, KAL, GUS, and DIP provenances, implying limited linkage between phenotypical plasticity and field performance.

The origin of Scots pine significantly affected both LCA and CWT ($10.08 \leq F$-value ≤ 26.77; p-value < 0.001; Table 4), indicating local genetic adaptation of xylogenesis. The provenance-by-trial interactions were significant ($6.96 \leq F$-value ≤ 27.49, p-value < 0.001), particularly for CWT, highlighting local specifics in responses of xylogenesis to environment. The individual effect of trial was significant for CWT (F-value ≥ 22.52) and LCA$_{\mathrm{EW}}$. Tree-ring width had a significant (p-value < 0.01) positive effect on LCA, yet a negative effect on CWT$_{\mathrm{EW}}$, indicating a linkage between increment and wood anatomy. Among the random effects, core (side of stem) showed the highest variance, indicating within-tree variability in wood anatomy. The year of tree-ring formation was also associated with a certain variance indicating inter-annual (phenotypical) variation. Plot was estimated with the lowest variance, suggesting similar reaction within a trial, although the variance of trees indicated some micro-site effects, particularly for CWT.

The analysed proxies highlighted the relation between field performance and wood anatomy of the studied provenances of Scots pine. The top-performing provenances, particularly RYT, had the largest LCA$_{\mathrm{EW}}$ and LCA$_{\mathrm{LW}}$ (Fig. 2). In contrast, the low-performing provenances, particularly DIP, showed the lowest LCA$_{\mathrm{EW}}$ and LCA$_{\mathrm{LW}}$, (Fig. 2). The effect of trial on lumen size was inconsistent, particularly for LCA$_{\mathrm{EW}}$, as indicated by the significant interactions (Table 4). The DIP, EBN, and GUS provenances showed the highest LCA$_{\mathrm{EW}}$ under harsher climate at KA trial (Table 1), and the lowest LCA$_{\mathrm{EW}}$ under warmer climate at ZV trial (Fig. 2); KAL provenance showed the highest LCA$_{\mathrm{EW}}$ at ZV trial. The DIP and GUS provenances also showed the highest and lowest LCA$_{\mathrm{LW}}$ in KA and ZV trials, respectively. For KAL and RYT provenances, LCA$_{\mathrm{LW}}$ decreased with increasing continentality of the trials (Table 1).

The CWT$_{\mathrm{EW}}$ showed weak negative relationship with the field performance of the provenances (Fig. 2), suggesting prevailingly phenotypic variation. The significant effect of trial (Table 4) indicated a similar response to regional factors; for most of the provenances, particularly DIP and RYT; CWT$_{\mathrm{EW}}$ decreased with increasing continentality of the trails. The opposite, however, was observed for the top-performing GUS provenance (Fig. 2). The CWT$_{\mathrm{LW}}$ was also affected by provenance; however, this proxy appeared non-related to the field performance of the trees. The highest CWT$_{\mathrm{LW}}$ was observed for DIP and KAL provenances, and the lowest – for EBN and RYT (Fig. 2), which showed contrasting field performance. A similar trial effect (Table 4) was observed for GUS, DIP, and particularly KAL provenances, for which CWT$_{\mathrm{LW}}$ decreased with increasing continentality of the trials (Fig. 2). In ZV trial, the top-performing RYT provenance had highest CWT$_{\mathrm{LW}}$, while the low-performing EBN provenance showed the opposite.

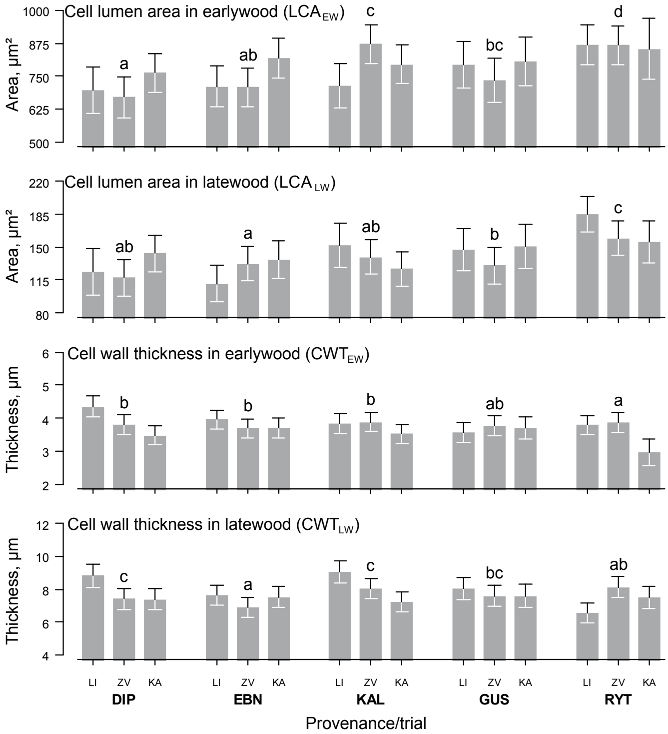

Fig. 2. Mean lumen cross section area and cell wall thickness of tracheids in earlywood and latewood of the studied provenances of Scots pine in three trials in hemiboreal zone in Latvia. Conditional means and their 95% confidence intervals (whiskers) calculated for the period 1997–2017 are shown. Different letters above the bars indicate significant (p-value ≤ 0.05) differences among the provenances, as determined by the Tukey's post-hoc test. Note that the scales between earlywood and latewood differ.

Table 3
Coefficient of variation for lumen cross-section area and cell wall thickness of tracheids in earlywood and latewood of the studied provenances of Scots pine in three studied trials.

	Lumen cross section area		Cell wall thickness	
	Earlywood	Latewood	Earlywood	Latewood
Dippoldiswalde (DIP)	0.182	0.271	0.162	0.140
Eibenstock (EBN)	0.180	0.367	0.184	0.147
Kalsnava (KAL)	0.212	0.325	0.142	0.175
Gustrow (GUS)	0.155	0.362	0.128	0.114
Rytel (RYT)	0.261	0.368	0.150	0.218

3.2. Inter-annual variation and climatic signals

The analysed proxies showed inter-annual variation (Supplementary material, Fig. S5), as highlighted by the variance component of random effect of year (Table 4). During the period 1997–2017, the time series of the proxies contained a linear or non-significant trend. The correlation between the time series of the same proxy among provenances within a trial was generally weak (Table 5), indicating provenance-specific variation, hence genetically determined sensitivity to environmental fluctuation. Still, some common tendencies were indicated by stronger correlations for LCA_{EW} and CWT_{LW} in KA and ZV trials, suggesting influence of common limiting factors. The correlations between time-series of the same proxy/provenance among the trials was generally weak (Supplementary material, Table S3) indicating mostly local variation. Nevertheless, some common sensitivity was observed for RYT and EBN provenances, for which correlation was higher. The correlation between the proxies varied across the trials and provenances, ranging from −0.63 to 0.64 and from −0.80 to 0.30 for EW and LW, respectively. The varying correlations between LCA and CWT in EW suggested high plasticity of trade-offs in cell expansion and cell wall deposition according to local environment and provenances. Still, the local KAL provenances showed positive correlation between LCA and CWT in all three tails. Regarding LW, LCA and CWT were prevailingly negatively correlated, and the pattern was stronger under warmer summers in ZV trial, implying the linkage between cell expansion and cell wall deposition later in the vegetation period.

The time series of the studied wood anatomical proxies of EW and LW significantly (at $\alpha = 0.05$) correlated with five and three of the studied climatic factors, respectively (Fig. 3). The EW proxies showed generally stronger correlations with the climatic factors compared to LW. Both EW and LW proxies correlated with the climatic factors before

Table 4
The *F*-values of fixed effects of provenance, trial, tree-ring width, and provenance-by-trial interaction and variance of the random effects in lumen cross-section area and cell wall thickness in earlywood and latewood of studied provenances of Scots pine in three trials in hemiboreal zone in Latvia for the period 1997–2017. Numbers in brackets show degrees of freedom. Significance codes, *p*-values: * < 0.05, ** < 0.01, *** < 0.001.

	Lumen cross section area		Cell wall thickness	
	Earlywood	Latewood	Earlywood	Latewood
Fixed effects				
Provenance, F-value	$10.08_{(4,\ 1015)}^{***}$	$21.71_{(4,\ 1015)}^{***}$	$12.62_{(4,\ 1015)}^{***}$	$26.77_{(4,\ 1015)}^{***}$
Trial, F-value	$5.14_{(2,1011)}^{**}$	$1.99_{(2,\ 1011)}$	$29.67_{(2,\ 1011)}^{***}$	$22.52_{(2,\ 1011)}^{***}$
Provenance-by-trial interaction, F-value	$8.69_{(8,\ 1012)}^{***}$	$6.96_{(8,\ 1012)}^{***}$	$11.37_{(8,\ 1012)}^{***}$	$27.49_{(8,\ 1012)}^{***}$
Tree-ring width, F-value	$9.78_{(1,\ 965)}^{**}$	$56.75_{(1,\ 965)}^{***}$	$9.78_{(1,\ 965)}^{**}$	$0.04_{(1,\ 965)}$
Coefficient of the covariate (tree-ring width; ± st. err.)	0.21 ± 0.07	0.14 ± 0.01	−0.0006 ± 0.0002	−0.0004 ± 0.0020
Random effects, variance				
Year	9026.2	169.3	1.9	14.0
Core	14,360	401.4	19.4	27.8
Tree	559.5	5.3	3.1	42.2
Plot	0.5	144.2	0.1	0.1
Residual	18,440	1500.0	19.9	98.8
Conditional pseudo-R^2	0.62	0.49	0.57	0.54

and during tree-ring formation, yet the correlations were mostly provenance-specific. The top-performing provenances showed correlations with March precipitation in LI and ZV trials (LCA_{EW} and CWT_{EW}), while the low-performing provenances showed correlation with this factor in KA trial (LCA_{EW}). Some correlations between the wood anatomical proxies of EW and SPEI in the previous August were observed. Significant correlations with February temperature were observed for LCA_{EW} of the low-performing provenances and for CWT_{EW} in ZV trial (Fig. 3). The correlations with April temperature were significant for LCA_{EW} of the top-performing provenances in LI trial, for the top- and low-performing provenances in ZV, and for the low-performing provenances in KA. A similar pattern among the provenances/trials was observed for the correlation between June temperature and CWT_{EW}, though LCA_{EW} of the top-performing provenances showed sensitivity to this factor in ZV trial.

Wood anatomical proxies of LW in ZV and KA trials correlated with temperature in June, as observed also for EW (Fig. 3). August precipitation showed a positive effect on LCA_{LW}, and a negative effect on CWT_{LW}; August SPEI showed even stronger correlations with LCA_{LW}. Mostly, these factors were significant for the top-performing provenances in LI trial and for the low-performing provenances in ZV and KA trials.

4. Discussion

4.1. Genetic and phenotypic plasticity

The differences in phenotypic plasticity of wood anatomy among the eastern Baltic provenances of Scots pine (Table 3) indicated varying adaptability of hydraulic architecture of wood, hence tolerance to environmental fluctuations and extremes (Bryukhanova and Fonti, 2013; Anderegg et al., 2015; Sass-Klaassen et al., 2016). The top-performing RYT and the low-performing DIP provenances showed the highest and the lowest plasticity of wood anatomy, respectively (Table 3), explaining the contrasting field performance (Supplementary material, Table S1; Jansons and Baumanis, 2005) and resilience of radial increment (Matisons et al., 2019). Nonetheless, the inconsistency between phenotypical plasticity and field performance of other provenances (Table 3) suggested effect of genetic factors, hence restricted responses to environment (Martin et al., 2010; Chauvin et al., 2019). Accordingly, explicit genetic adaptation of wood anatomy (Moran et al., 2017; Nabais et al., 2018) was indicated by the significant effect of provenance (Table 4), as observed previously (Savva et al., 2002; Martinez-Vilalta et al., 2009; Martin et al., 2010). This implied local specialization even under high gene flow (Moran et al., 2017; Housset et al., 2018), demonstrating the importance of phenotype-by-genotype plasticity for survival and growth (Aitken and Bemmels, 2016; Housset et al., 2018), as highlighted by the provenance-by-trial interactions (Table 4).

The top-performing provenances, particularly RYT, formed cells with the largest lumens (Fig. 2), implying more efficient water transport (Fonti et al., 2013; Dalla-Salda et al., 2014), allowing trees to better compensate transpiration (Eilmann et al., 2009; Martin et al., 2010), thus promoting assimilation and growth (Fonti et al., 2013; Arzac et al., 2018). This was supported by the positive linkage between LCA and tree-ring width (Table 4), which also indicating intra-annual adjustments of wood anatomy to meteorological conditions (Cuny et al., 2019). More humid (ameliorated) conditions in the studied trials compared to the origins of the top-performing provenances (Tables 1 and 2), apparently, contributed to their growth (Supplementary material, Table S1), hence competitiveness. Wider lumens and thinner cell walls (Fig. 2) also imply minimal investments of carbon into vascular system (Eilmann et al., 2009; Martin et al., 2010), allowing allocation of more resources to stress-tolerance and/or growth (Herms and Mattson, 1992; Bryukhanova and Fonti, 2013; Mayr et al., 2014), contributing to resilience and competitiveness (Matisons et al., 2019), hence sustainability. However, such conformation of wood, might increase the risk of embolism and fatal xylem dysfunction under extreme

Table 5
The mean correlation among the mean time series of tracheid lumen cross-section area and cell wall thickness of provenances of Scots pine within each of the studied trials. The numbers in square brackets indicate the range of correlations.

Trial	Lumen cross section area		Cell wall thickness	
	Earlywood	Latewood	Earlywood	Latewood
Liepāja (LI)	−0.09[−0.60.0.0.61]	0.09[−0.22.0.0.83]	−0.07[−0.42.0.0.32]	0.01[−0.67.0.0.36]
Zvirgzde (ZV)	0.37[0.35.0.0.77]	0.11[−0.41.0.0.47]	0.05[−0.47.0.0.77]	0.04[−0.19.0.0.81]
Kalsnava (KA)	0.25[−0.36.0.0.77]	0.13[−0.49.0.0.59]	0.33[−0.12.0.0.76]	0.31[−0.38.0.0.66]

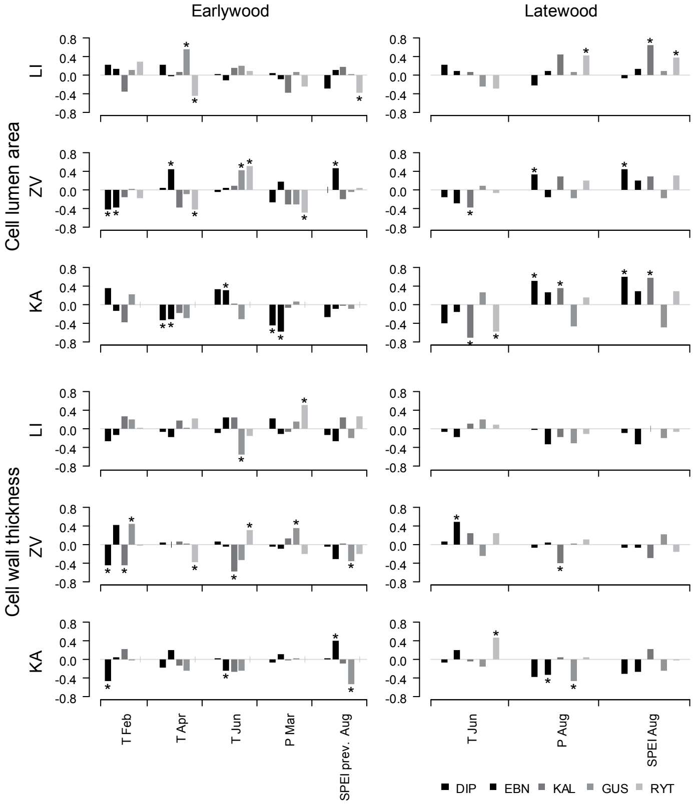

Fig. 3. Bootstrapped Pearson correlation coefficients between studied climatic factors (mean monthly temperature, precipitation, and standardized precipitation evapotranspiration indices–SPEI) and chronologies of lumen cross-section area and cell wall thickness of tracheids in earlywood and latewood for the studied provenances of Scots pine for the period 1997–2017. Asterisks denote the statistical significance of correlations at α = 0.05. Collinear factors are not shown.

water deficit (Eilmann et al., 2009; Popkova et al., 2018), which can cause large-scale die-offs (Allen et al., 2015; Choat et al., 2018).

Smaller lumens and thicker tracheid walls of the low-performing provenances (DIP and EBN; Fig. 2; Table 4) can be explained by their origin in mountain areas (Table 2), where trees form denser wood in response to higher mechanical loads (e.g., wind and snow; Martin et al., 2010; Fonti et al., 2013; Nabais et al., 2018). Smaller lumen is also an adaptation to the winter embolism in response to freeze-thaw cycles under unstable mountain weather (Pittermann and Sperry, 2003). Accordingly, enhanced allocation of resources to stress-tolerance reduced growth (Herms and Mattson, 1992; Mayr et al., 2014) decreasing competitiveness of the trees. Cooler temperatures and higher precipitation at the origin of the low-performing provenances (Table 2) imply lower transpiration, hence sufficiency of smaller lumen (Castagneri et al., 2017; Popkova et al., 2018). Under transfer to direr and warmer conditions (Tables 1 and 2), such strategy, however, appeared unsuccessful, resulting in low field performance (Supplementary material, Table S1). Considering the improving growth of deciduous trees (Buras and Menzel, 2019), competitiveness appears vital for the light-demanding Scots pine, projecting negative perspectives for the slow-growing trees (Loehle, 1998; Reich and Oleksyn, 2008).

The explicit provenance-by-trial interactions (Table 4) implied plasticity of the strategies of xylogenesis to cope with local conditions (de Villemereuil et al., 2016; Moran et al., 2017; Li et al., 2018, Nabais et al., 2018), hence adaptability of Scots pine. The top-performing RYT provenance showed high LCA_{EW} in all trials (Fig. 2), responding to transfer to more humid, hence ameliorated conditions (Tables 1 and 2), suggesting fit to the regional moisture regime. Under warmer climate in ZV trial (Table 1), the local KAL provenance formed EW tracheids with wider lumens (Fig. 2), likely to compensate increased transpiration (Bryukhanova and Fonti, 2013). The opposite was observed for the transferred top-performing GUS, which showed the lowest plasticity of EW anatomy (Table 3), hence had to form smaller tracheids likely to minimize the risks of their dysfunction (Tyree and Zimmermann, 2002; Mayr et al., 2003). The low-performing provenances formed wider lumens in EW under harsher climate (Fig. 2), to maintain conductivity under suppressed growth (Eilmann et al., 2009). Similar patterns were observed for LCA_{LW}, which might act as a backup water transport likely under extreme conditions (Leal et al., 2007), though in *Pseudotsuga menziesii* latewood embolized first (Dalla-Salda et al., 2014). The CWT mostly decreased with the increasing distance from the Baltic Sea (Fig. 1), which might be explained by the decreasing wind loads (Salmen and Burgert, 2009; Martin et al., 2010). Nevertheless at LI trial, RYT provenance formed the thinnest LW cell walls, likely in response to delayed vegetation period and increased late-summer precipitation (Supplementary material Fig. S1), thus producing of low-density wood (Arzac et al., 2018).

4.2. Climatic forcing

The provenance-specific inter-annual variation of LCA and CWT (Table 5) implied genetically determined sensitivity to weather fluctuation (Housset et al., 2018; De Micco et al., 2019). The intermediate (cf. Matisons et al., 2019), yet contrasting correlations of the studied wood anatomical proxies with the climatic factors (Fig. 3), as well as the correlations among the mean time series (Supplementary material, Table S3) implied a spectrum of responses resulting from the genotype-environment interactions (Eckert et al., 2015; Moran et al., 2017; Housset et al., 2018). Such diversity of responses also illustrated the plasticity and adaptability of trees to environmental fluctuations (Aitken and Bemmels, 2016; de Villemereuil et al., 2016; Chauvin et al., 2019). Nevertheless, the common signatures (as also indicated by positive correlation) implied impact of weather extremes suppressing individuality of responses (Lange et al., 2018; Matisons et al., 2019) also in the mid-part of the species' range, and such effects are intensifying under the changing climate (Sass-Klaassen et al., 2016; Klisz et al., 2019).

The EW and LW proxies showed significant inter-annual correlations with climatic factors (Fig. 3), implying the effect of weather conditions on tracheid formation (Carrer et al., 2015; Castagneri et al., 2017; Popkova et al., 2018; De Micco et al., 2019). Cuny et al. (2019) demonstrated explicit intra-annual buffering capacity of growth sensitivity via kinetics of xylogenesis regarding the environmental fluctuations, thus suggesting indirect effects of climatic factors. The EW proxies exhibited the effect of climatic factors before xylogenesis, implying cumulative influence of environmental fluctuation likely via nutrient reserves (Anderegg et al., 2015; Sass-Klaassen et al., 2016; De Micco et al., 2019), biological signals (Rathgeber et al., 2016), or overwintering (Ögren, 1997; Mayr et al., 2003, 2014), as observed for tree-ring width (Matisons et al., 2019). Such relationships also imply that EW anatomy is partially predetermined, decreasing the plasticity (Table 3) of responses during a growing period.

The negative correlation between February temperature and $\mathrm{LCA}_{\mathrm{EW}}$ in ZV trial (Fig. 3), where thaws are frequent (Harris et al., 2014), might be explained by the adaptation to winter embolism (Pittermann and Sperry, 2003). February temperature also affected $\mathrm{CWT}_{\mathrm{EW}}$ (Fig. 3), which is depending on the nutrient reserves (Fonti et al., 2013; Nabais et al., 2018), indicating linkage between the thermal regime and respiratory loss of nutrient reserves (Ögren, 1997; Mayr et al., 2014). These relations were apparent for DIP and KAL provenances (Fig. 3), suggesting a decrease in conductivity (Bryukhanova and Fonti, 2013; Popkova et al., 2018) of wood, hence slower assimilation and growth (Carrer et al., 2015) as a consequence of warming winters. In contrast, $\mathrm{CWT}_{\mathrm{EW}}$ of the top-performing GUS correlated positively with February temperature (Fig. 3), suggesting improved overwintering under warmer conditions.

The correlations of EW proxies with April temperature (Fig. 3) might be related to the development of roots, which occur at that time and is facilitated by temperature, thus affecting water absorption (Hansen and Beck, 1994; Hardy et al., 2001). The contrasting correlations indicated diverse responses of the genotypes. The top-performing RYT decreased $\mathrm{LCA}_{\mathrm{EW}}$ in response to warm Aprils, hence improved water supply (Hardy et al., 2001), implying lesser necessity for adjustments of wood structure (Martin et al., 2010; Popkova et al., 2018). This also appeared the case of the low-performing provenances under harsher climate in KA trial. However, under milder climate, EBN and GUS provenances showed positive correlations, implying that warm spring might increase the susceptibility to embolization later in the season (Fonti et al., 2013; Arzac et al., 2018). The correlations with precipitation in March, which is often in the form of snow, can be explained by the insulating effect of show layer on root growth (Hardy et al., 2001).

June temperature apparently affected both EW and LW, likely due to the inter-annual differences in phenology of xylogenesis (Castagneri et al., 2017). Such correlations might be explained by a direct effect of temperature on xylogenesis (e.g., cell expansion and cell wall deposition; Rathgeber et al., 2016) and/or via response to intensifying transpiration (Martin et al., 2010; Popkova et al., 2018). Accordingly, LCA showed positive and CWT showed negative correlations (Fig. 3), thus indicating adjustments of conductivity of wood according to evapotranspiration (Cuny et al., 2019). However, in ZV trial, the top-performing RYT provenance, which had the largest tracheids (Fig. 2), increased cell wall deposition in response to raised temperature (Fig. 3), likely to improve the resilience to increased evapotranspiration and water deficit (Cuny et al., 2014; Nabais et al., 2018; Butto et al., 2019). This might also explain the reactions of wood anatomy in LW to June temperature under the harsher climate of KA trial (Table 1). The correlations of LW anatomy with precipitation and SPEI in August (Fig. 3) indicate the effect of water availability on cell expansion and cell wall deposition also at the cessation of growing period (Anfodillo et al., 2013; Cuny et al., 2019). Considering the predicted warming and extension of the precipitation free periods in the eastern Baltic region (Avotniece et al., 2012; IPCC, 2013), temperature related increase of cell lumen suggests increasing risk of xylem dysfunction under the intensifying water deficit (Allen et al., 2015; Choat et al., 2018).

5. Conclusions

The differences in wood anatomy highlighted phenotypic plasticity and genetic (local) adaptations of xylogenesis of the studied provenances of Scots pine in the hemiboreal zone, hence high potential to sustain growth under changing climate, counteracting the predicted decrease in abundance. As hypothesized, explicit genetic adaptation was observed, implying possibility to improve hydraulic architecture of wood, hence drought resistance of trees by breeding. As expected, the top-performing provenances, particularly RYT, formed larger tracheids with thinner walls, as well as expressed the highest phenotypical plasticity of wood anatomy, which have been advantageous under warming climate, aiding for improved competiveness and sustainability of the stands. Such wood structure, however, implies lower mechanical durability of wood, as well as higher risk of dysfunction under extreme conditions. The low-performing provenances formed smaller tracheids with thicker walls, implying higher stress-tolerance, yet by the costs of competitiveness (growth), which had limited advantages in a managed stand; under transfer to warmer and drier conditions, such strategy, appeared unsuccessful, as shown by low field performance. The determined relationships between the analysed wood proxies and climatic factors suggest integrative weather-related regulatory mechanisms of xylogenesis, which appear genetically controlled. These relationships also suggest that the studied top-performing provenances, particularly RYT, would be able to better adapt their conductive properties to the projected warming and extension of precipitation free periods in the eastern Baltic region, likely decreasing wood (timber) density. The obtained results suggest, that the information about wood structure is complimentary to that of field performance, aiding for more precise selection of the best adapted provenances.

Acknowledgements

The study was conducted under the framework of post-doctoral studies in Latvia ("Plasticity of development and xylogenesis of the native and introduced tree species under changing climate", project

No.: 1.1.1.2.VIAA/1/16/108) financed by the European Regional Development Fund. We acknowledge the anonymous reviewers, whose comments much helped to improve the quality of the manuscript.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.117568.

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Forest Ecology and Management 457 (2020) 117729

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Occurrence of ‘blue’ and ‘frost’ rings reveal frost sensitivity of eastern Baltic provenances of Scots pine

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ARTICLE INFO

Keywords:
Assisted gene flow
Frost damage
Pinus sylvestris
Climate extremes
Experimental forestry
Quantitative wood anatomy

ABSTRACT

Assisted gene flow is advised as one of the most effective means to sustain the productivity of forests under warming climate via application of the provenances (genotypes) capable to utilize longer vegetation season. Nevertheless in the temperate and boreal zones, the extension of vegetation period also subjects trees to effects of frosts, which can have severe economic impact under warming climate. In this study, wood anatomical anomalies related to late frosts in spring (‘frost’ rings) and early frosts in late summer (‘blue’ rings) for the eastern Baltic provenances of Scots pine (*Pinus sylvestris* L.) with a contrasting field performance were analysed retrospectively. Three trials with the age of 40 year in Latvia were sampled. The frost-related wood anomalies were identified using microscopy methods. Generalized mixed effects models were used to assess the effect of provenance on the probability of frost damage, accounting for the design of the trials, as well as for the inter-annual variability. The overall mean probability of frost-related wood anomalies was low (ca. 0.025), yet it increased with continentality of the trials, showing limited relation to the inter-annual variability of minimum temperatures. The probability of anomalies decreased with age. Provenance had a significant effect on the occurrence of ‘frost’ and ‘blue’ rings, implying genetically determined frost sensitivity, while the genotype (provenance) by environment (trial) interaction indicated high phenotypic plasticity of the trees. The probability of anomalies appeared related to the field performance of the provenances. The low-performing provenances (Dippoldiswalde and Eibenstock, which originated from the Orr Mountains) were most sensitive to frost, while the top-performing ones (Rytel and, particularly, Güstrow, which originated from coastal areas) showed only a few anomalies, indicating the linkage between frost sensitivity and growth. The local provenance, which showed an average field performance, also showed intermediate sensitivity to early frosts, thus supporting a necessity for the assisted gene flow in the eastern Baltic region.

1. Introduction

In Europe, the abundance of Scots pine (*Pinus sylvestris* L) is predicted to decrease due to warming (Buras and Menzel, 2019), causing ecologic and economic impact (Hanewinkel et al., 2012; Yousefpour et al., 2017). Nonetheless, under cold climates, the observed and predicted extension of vegetation period (Menzel, 2000) might improve the productivity of Scots pine stands (Lloyd et al., 2011; Fei et al., 2017), compensating predicted changes in the abundance of the species, particularly in the regions where water is non-limiting (Dumroese et al., 2015; Nabuurs et al., 2018). Regarding local tree populations, such improvements, however, appear limited, as trees have evolutionary adapted to a certain length of vegetation periods, restricting the formation of additional increment (Hänninen, 2006; Rossi et al., 2006; Kolari et al., 2007; Berlin et al., 2016; Zohner et al., 2016). Accordingly, assisted gene flow (migration) has been advised to facilitate adaptability and to sustain the productivity of forests under accelerating climate changes (Park and Talbot, 2012; Dumroese et al., 2015; Aitken and Bemmels, 2016; Nabuurs et al., 2018).

Under a warming climate in the nemoral, hemiboreal, and boreal vegetation zones, the north-transferred trees often show improved productivity, as they can utilize longer vegetation periods (Bolte et al., 2009; Schreiber et al., 2013; Chakraborty et al., 2015; Berlin et al., 2016), as well as they are better adapted to water deficit (Taeger et al.,

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https://doi.org/10.1016/j.foreco.2019.117729
Received 3 September 2019; Received in revised form 24 October 2019; Accepted 26 October 2019

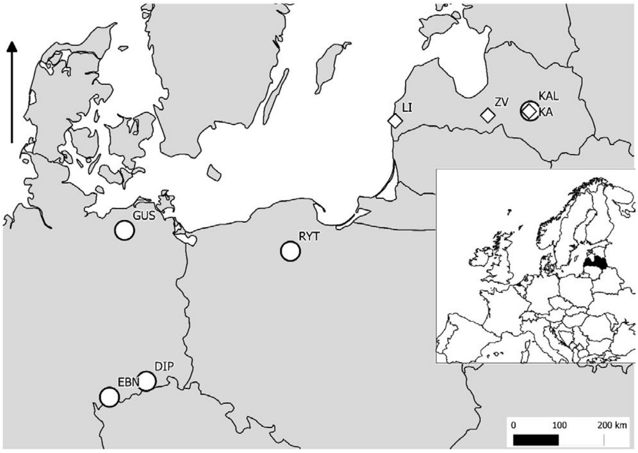

Fig. 1. Location of the studied trials (squares; two letter codes) and origins of the studied provenances of Scots pine (circles; three letter codes). Trial codes: LI – Liepāja, ZV – Zvirgzde, and KA – Kalsnava. Provenance codes: top-performing RYT – Rytel and GUS – Güstrow; low-performing Dip – Dippoldiswalde and EBN – Eibenstock; local KAL – Kalsnava).

2013; Matisons et al., 2019). Nonetheless, the ability to utilize longer vegetation period, which results from altered cold/frost hardening/dehardening also subjects trees to late/early frosts (Repo et al., 2000; Beck et al., 2004; Kreyling et al., 2012). Accordingly, the intensification of frosts due to climate change and can have strong effects on growth and survival of trees (Gu et al., 2008; Augspurger, 2009; Schreiber et al., 2013; Montwe et al., 2018). The frost-hardiness of trees is affected by nutrient reserves, hence their vigour (Ögren, 1997; Beck et al., 2004; Repo et al., 2006), suggesting a feedback loop between growth and tolerance to cold events.

Trees as sessile long-lived organisms have developed mechanisms allowing high phenotypical plasticity to cope with the wide environmental fluctuations during their life (Aitken and Bemmels, 2016; Klisz et al., 2019). The traits crucial for survival and competitiveness are genetically controlled (Leites et al., 2012; Schreiber et al., 2013; Nabais et al., 2018), thus express restricted variation. Accordingly, the genetic adaptation in combination with the phenotypical plasticity can be considered as a measure of adaptiveness to changing (novel) conditions (Chakraborty et al., 2015; Aitken and Bemmels, 2016; Housset et al., 2018).

Retrospective tree-ring analysis is efficient for the assessment of the genetic and phenotypic aspects of tree growth (Heer et al., 2018; Housset et al., 2018). Tree-rings also can serve as a source of highly informative proxies regarding growth sensitivity to the year-to-year environmental fluctuation, as well as their extremes (Speer, 2010; Taeger et al., 2013; Hänninen et al., 2013; Wang et al., 2013; Matisons et al., 2019). In this sense, the quantitative wood anatomy can provide additional specific information about the xylogenesis throughout the season, including the stresses suffered by trees (Fonti and Jansen, 2012; Gärtner et al., 2015; Piermattei et al., 2015).

The effects of late frosts in spring/summer, which disturb xylogenesis and damage cambium and expanding xylem cells, can be detected in wood as 'frost' rings (FR; Payette et al., 2010; Panayotov et al., 2013). In case of early autumn frosts, abrupt temperature reduction, or water deficit in late summer, xylogenesis can be terminated prematurely and the lignification of the cells formed last can be incomplete, thus resulting in a 'blue' ring (BR; Piermattei et al., 2015; Montwe et al., 2018). This name has been adopted from the double-stained (with Safranin and Astra blue) wood samples, where cell wall or its part is blue, indicating disrupted lignification (Gärtner and Schweingruber, 2013; Gärtner et al., 2015; Piermattei et al., 2015). A BR can be followed by FR if cambium has been damaged (Montwe et al., 2018). Consequently, the occurrence of frost-related wood anatomical anomalies can be considered as indicators of the conformity of genotypes to local climate and its extremes (Kolari et al., 2007; Stoffel et al., 2010; Montwe et al., 2018). Both anatomical anomalies affect the mechanical strength of timber, causing weak spots due to insufficiently lignified layers of xylem (Beery et al., 1983; Lee et al., 2007; Gärtner et al., 2015), thus affecting the value of timber. Nonetheless, the occurrence of wood anomalies, particularly FR, decrease with increasing cambial age due to thickening bark, which acts as insulator, and shifts in phenology of xylogenesis, hence such effects might not be visible in older trees (Payette et al., 2010).

Frost resistance of trees (cambium) from cold climates is multifactorial, depending on genetics, age, and vigour of trees, season, as well as on the nature of temperature drops (Repo et al., 2000; Beck et al., 2004; Payette et al., 2010; Rixen et al., 2012; Hänninen et al., 2013; Charrier et al., 2015; Lehtinen and Pulkkinen, 2017), resulting in varying ecological plasticity. In this regard, provenance trials, which have been established for the selection of the best performing populations, can provide information about the genetic and phenotypic plasticity, as well as environmental sensitivity of trees under a variety of environmental conditions (Leites et al., 2012; de Villemereuil et al., 2016; Housset et al., 2018; Nabais et al., 2018). Considering the long-term nature of decisions in forestry, such information is crucial for sustainability and climate-smart management (Taeger et al., 2013; Wang et al., 2013; Nabuurs et al., 2018).

The aim of this study was to assess the occurrence of FR and BR in wood of eastern Baltic provenances of Scots pine differing by field performance. We hypothesized that the north-transferred provenances had a higher occurrence of BR and FR, as well as their occurrence was related to the field performance (dimensions and survival) of trees. We assumed that the top-performing provenances showed lower occurrence of BR and FR due to better vigour than the low-performing ones.

2. Material and methods

2.1. Trials and provenances

Three international provenance trials (Fig. 1), established in 1975 in Latvia for the evaluation of the eastern Baltic provenances of Scots pine originating between 50 and 56° N, and 11–27° E (Kohlstock and

Table 1
Location and climatic description of the studied provenance trials of Scots pine. The 95% confidence intervals are shown.

	Liepāja (LI)	Zvirgzde (ZV)	Kalsnava (KA)
Latitude	59°29′ N	56°32′ N	56°49′ N
Longitude	21°05′ E	24°13′ E	26°7′ E
Elevation, m a.s.l.	15	50	220
Topography	Flat	Flat	Flat
Site type	*Vacciniosa*	*Vacciniosa*	*Vacciniosa*
Soil type	Podsols	Podsols	Podsols
Mean January temperature, °C	−1.4 ± 1.3	−2.9 ± 1.3	−4.3 ± 1.3
Mean July temperature, °C	17.8 ± 0.6	18.4 ± 0.7	18.0 ± 0.6
Mean annual temperature, °C	7.8 ± 0.7	7.2 ± 0.8	6.3 ± 0.9
Mean annual precipitation, mm	745 ± 37	647 ± 26	656 ± 28
Mean precipitation May–September, mm	325 ± 31	335 ± 28	331 ± 36

Schneck, 1992; Jansons and Baumanis, 2005), were studied to assess the regional variability (Leites et al., 2012) in frost tolerance of Scots pine. The trials were situated in lowland conditions (elevation was ≤220 m above sea level) with a flat topography near Liepāja (LI), Zvirgzde (ZV), and Kalsnava (KA) on dry sandy oligotrophic soils (Table 1). The climate was temperate. The trials represent local climatic gradient with increasing continetality in the eastern direction (from LI to KA trial). Accordingly the mean annual temperature decreases eastwards (Table 1, Supplementary material, Fig. S1). Although the climatic gradient was not large, it has differentiated growth of the local populations of Scots pine (Jansons and Baumanis, 2005), highlighting the importance of local and micro-site conditions. July and January were the warmest and the coldest months, respectively. The vegetation period (diurnal temperature > 5 °C), lasting from mid-April to mid-October, was approximately two weeks longer in ZV compared to LI and KA trials. In all trials, precipitation mostly exceeded evapotranspiration; the highest monthly precipitation generally occurred during the summer months. The highest annual precipitation occurred in LI trial. Climatic changes were expressed as an increase of the mean temperature during the period from November to April (thus extending vegetation period), and as an extension and intensification of thaws in winter, as well as precipitation-free periods in summer (Avotniece et al., 2012).

The trials were established by planting one-year old seedlings raised in local nurseries; the seed material has been collected from 20 to 25 open-pollinated plus-trees within each provenance (Kohlstock and Schneck, 1992; Jansons and Baumanis, 2005). The trials had a complete randomised block design (Jansons and Baumanis, 2005). All trials contained identical set of provenances. In each trial, each provenance was represented by six randomly distributed plots of 7 × 5 trees. Trees were planted with 1 × 2 m spacing (5000 trees ha^{-1}). One thinning was performed at the age of 21 years (1996) reducing the plots to about one third of the initially planted trees (post-thinning density ca. 1800 trees ha^{-1}).

To assess the effects of seed transfer on the occurrence of FR and BR and its connection with the field performance of trees (Montwe et al., 2018), two of the top- and two of the low-performing provenances (according to dimensions and survival, Supplementary material, Table S1) were selected for sampling according to the trial inventory conducted in 2016. The selected provenances showed consistent ranking according to their field performance among the trials. The selected top-performing provenances were Güstrow (GUS) and Rytel (RYT), which originated from lowland conditions in the Northern Germany and Southern Poland, hence areas with a warmer and drier climate compared to the trials (Fig. 1, Table 2, Supplementary material, Fig. S2). Dippoldiswalde (DIP) and Eibenstock (EBN), which originated from the Orr Mountains, where climate was cooler and more humid, compared to the studied trials, were selected for the representation of the low-performing provenances. Additionally, local Kalsnava (KAL) provenance, which has adapted to the local climate and showed intermediate field performance, yet superior stem quality (Jansons and Baumanis, 2005), was selected to assess the ecological plasticity (adaptability) and frost resistance of the native Scots pine population under changing climate (Taeger et al., 2013).

2.2. Sample collection, preparation, and measurements

For each provenance from each of the six plots within a trail, one to three dominant trees were sampled in November 2017; in total, 9–16 tree per provenance/trial were sampled (Supplementary material, Table S2). Considering that the trials were ongoing, the number of sampled trees was restricted. Two increment cores from opposite sides of the stem were extracted at breast height (ca. 1.3 m) using a 5-mm increment borer. Damaged or leaning trees were not sampled to avoid callous tissue, traumatic resin ducts or reaction wood.

In the laboratory, thin (15–20 µm) cross-sections of the increment cores were cut using a WSL core microtome (Gärtner and Nievergelt, 2010), following the protocol described in Gärtner et al. (2015). It was ensured that each cross-section contained at least 20–25 of the outermost tree-rings. The cut sections were then stained in Safranin and Astra Blue to enhance the contrast between the lignified and non-lignified xylem cells, following the protocol described in Gärtner and Schweingruber (2013). Dyed cross-sections were then dehydrated using ethanol, rinsed with xylol and sealed in Canada balsam as permanent samples (Gärtner and Schweingruber, 2013). The years (tree-rings) with of BR (Piermattei et al., 2015) and FR (Payette et al., 2010) were recorded for each cross-section during a visual inspection of samples (Supplementary material, Fig. S3) under a transmitted light microscope using 40× magnification. Additionally, tree-ring widths were measured for each cross-section for cross-dating purposes using a Lintab 5 measurement table (Rinntech Inc., Heidelberg, Germany).

2.3. Data analysis

Graphical and statistical crossdating based on the measured time series of tree-ring width was performed to verify exact dating of each tree-ring (Speer, 2010); corrections in the dating were made if necessary (ca. 3% of the series due to a lost outermost ring). The replication of the crossdated datasets is shown in the supplementary material, Fig. S4. The occurrence of FR and BR in the samples was pooled (year was considered positive if an anomaly has been recorded at least by one core), producing time series for each tree. Based on the tree data, probability of FR and BR (proportion of trees showing anomaly) in each year was calculated for each provenance/trial resulting in the mean time series. The effects of provenances and trial on the probability of FR and BR based on the mean time series was assessed using a linear mixed model (Bates et al., 2015):

$$y = \mu + P_{ij} + Ti_{j} + P_{ij} \times T_{ij} + (Y_k) + (Z_{ij}) + \varepsilon_{ijk},$$

where P_i – the effect of provenance, T_{ij} – the effect of trial, $P_{ij} \times T_{ij}$ – the effect of provenance-by-trial interaction, (Y_k) the random effect (intercept) of year, and (Z_{jl}) the random effect (intercept) of a plot nested within a trial. Only the years with wood anomalies in any of the provenance/trial were included in the analysis (non-recording were omitted). The restricted maximum likelihood approach using the χ^2 criterion was used to assess the statistical significance of the fixed effects. The levels of significant factors were compared using the Tukey's Honest Significant Differences post-hoc test.

Considering temperature anomalies as the prevailing driver of FR and BR (Payette et al., 2010; Panayotov et al., 2013; Piermattei et al., 2015; Montwe et al., 2018), the mean time series of probabilities were compared (visually superposed) with the hourly absolute minimum temperature at the beginning (May–June; FR) and cessation (July–-September when latewood is formed; BR) of the vegetation period. The minimum temperature between the years with and without wood

Table 2
Location and climatic description of origin of the studied provenances of Scots pine. The 95% confidence intervals are shown.

	Güstrow (GUS)	Rytel (RYT)	Dippoldis-walde (DIP)	Eibenstock (EBN)	Kalsnava (KAL)
Latitude, N	53°45′	53°40′	50°49′	50°27′	56°42′
Longitude, E	12°15′	18°01′	13°52′	12°26′	25°54′
Elevation, m a.s.l.	25	130	590	710	190
Mean temperature Jan, °C	−0.8	−1.4	−2.6	−3	−4.3
Mean temperature Jul, °C	16.8	17.2	15.3	14.7	18
Mean annual temperature, °C	8	7.9	6.6	5.9	6.3
Mean temperature May-Sep., °C	14.8	15	13.2	12.6	14.7
Mean annual precipitation, mm	585	590	804	994	656
Mean precipitation May-Sep., mm	297	306	402	499	337

anomalies for each provenance/trial was compared by the one-sided t-test. Such a simplified approach was chosen due to the overall low probability of wood anomalies (abundant zero values), which did not allow the application of time series (dendrochronological) analysis (Speer, 2010) nor logistic binomial regression. The climatic data for the stations located at < 20 km distance from the studied trials were obtained from Latvian Environment, Geology, and Meteorology Agency. Data analysis was conducted in R, v. 3.5.2 (R Core Team, 2019), using the package "lme4" for mixed modelling (Bates et al., 2015).

3. Results

3.1. Provenance effects

During the visual inspection of ca. 4634 tree-rings representing the period 1985–2017, 126 BR and 97 FR were observed, hence their overall mean probability was 0.027 and 0.021, respectively. In five cases, both wood anomalies co-occurred in a single tree-ring. All BR occurred in latewood, yet the majority of FR were in the mid-part of earlywood, indicating the effect of late frosts. The mean probability of both wood anomalies was significantly (p-value < 0.001) affected by provenance and trial, as well as their interaction, indicating genetic adaptation and differing phenotypic plasticity, which was stronger in case of BR (Table 3). The differences in probability of the wood anomalies among the trials (ranging from < 0.01 to ≥ 0.07 in LI and KA, respectively; Fig. 2), apparently followed the local temperature regime (Table 1), indicating that moderate differences in climate could have notable effect on frost damage.

Table 3
The fixed effect (χ^2 values) of provenance, trial, and their interaction on the probability of "blue" and 'frost' rings in wood of Scots pine during 1985–2017 and variance of random effect of year of tree-ring formation. The significance of the fixed effects was determined using restricted maximum likelihood approach.

	χ^2	Degree of freedom	p-value
'Blue' rings			
Fixed effects			
Provenance	37.69	4	< 0.001
Trial	47.41	2	< 0.001
Provenance by trial interaction	117.02	8	< 0.001
Random effects, variance			
Year	0.12		
Plot	0.07		
Residual	4.61		
'Frost' rings			
Fixed effects			
Provenance	21.31	4	< 0.001
Trial	38.78	2	< 0.001
Provenance by trial interaction	26.93	8	< 0.001
Random effects, variance			
Year	0.21		
Plot	0.06		
Residual	4.19		

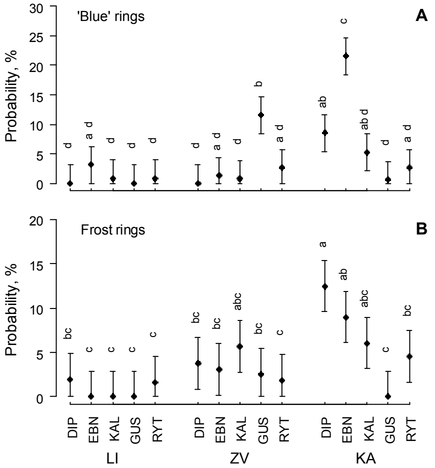

Fig. 2. Probability of 'blue' (A) and 'frost' (B) rings in xylem of the studied provenances of Scots pine in three trials in Latvia during 1985–2017. Estimated marginal means are shown. The whiskers indicate 95% confidence intervals. Similar lower-case letters above the points indicate lack of significant differences (p-value > 0.05) in the mean probability of anomalies among the groups (similar means) as determined by the Tukey's post-hoc test. The trials are denoted by the two letter codes (LI – Liepāja, ZV – Zvirgzde, and KA – Kalsnava) and provenances are indicated by the three letter codes (top-performing RYT – Rytel and GUS – Güstrow; low-performing Dip – Dippoldiswalde and EBN – Eibenstock; local KAL – Kalsnava). Note that the scales differ.

The differences in mean probability of BR among the provenances were inconsistent among the trials, as indicated by the significant interaction term (Table 3). Under a milder climate in LI trial (Table 1), the differences among the provenances were non-significant (Fig. 2), although a few wood anomalies were observed for all, except GUS provenance. In contrast in ZV trial, where vegetation period was longer (Table 1), the top-performing GUS provenances showed significantly (p-value < 0.05) higher probability of BR compared to the others (Fig. 2). Under more continental climate in KA trial (Table 1), where vegetation period was the shortest, the low-performing provenances, particularly EBN, showed increased probability of BR, while the top-performing ones practically lacked BR (Fig. 2). The local KAL provenance, which originated from the vicinity of KA trial (Fig. 1), had intermediate probability of BR.

The mean probability of FR showed a similar pattern to BR (Fig. 2). Under milder coastal climate in LI trial (Table 1), only a few FR were

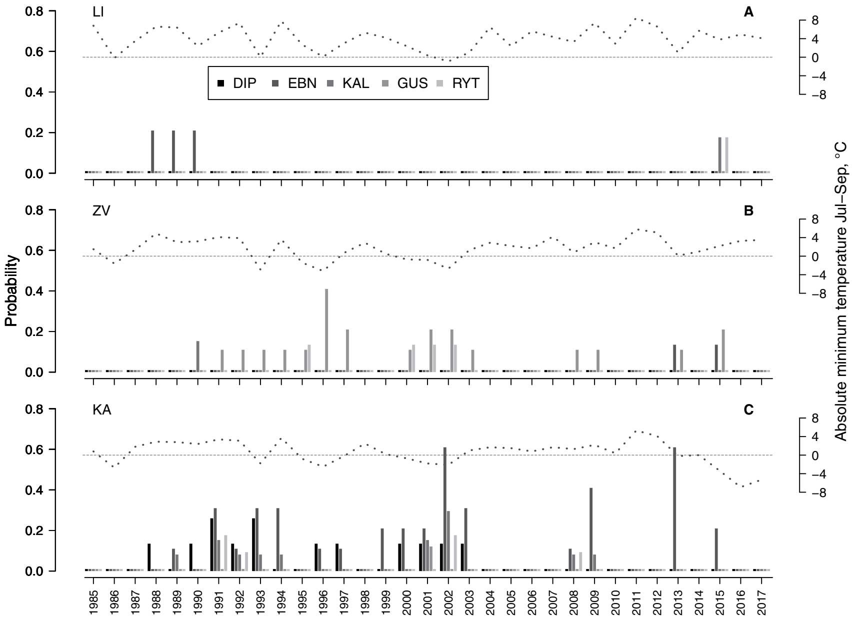

Fig. 3. Annual variation in the occurrence of 'blue' rings among the studied provenances of Scots pine in three trials differing by continentality (ranged ascendingly). Broken line shows the absolute minimum temperature during the July–September period.

observed for the north-transferred DIP and RYT provenances, yet the differences among the provenances were not significant (Fig. 2). In ZV trial, the probabilities were slightly higher, particularly for the native KAL provenance, yet mostly the differences between the provenances were non-significant. Under harsher climate in KA trial (Table 1), the low-performing provenances, particularly DIP, showed significantly higher probability of FR compared to the top-performing ones (Fig. 2), while the probability was intermediate for the native KAL.

3.2. Inter-annual dynamics

The occurrence of BR and FR was periodic and showed interannual variation, yet its pattern differed among the trials (Figs. 3 and 4). Most of the wood anomalies, particularly FRs, occurred, when the trees were young (their probability decreased as trees reached ca. 25–30 years), indicating age-dependent sensitivity to cold events. Nevertheless, low probability of anomalies was observed also when the trees were younger than 10 years, although the replication of the datasets was lower during that period (Supplementary material, Fig. S4). The linkage between the anomalies and fluctuation of the minimum temperature appeared limited (Table 4). In LI trial, the few BR occurred for EBN provenance during 1988–1990, yet for KAL and RYT provenances in 2015 (Fig. 3), irrespectively of the minimum temperature in late summer (Table 4). In the ZV trial, BR were observed for GUS and RYT provenances during 1990–1997, 2000–2003, and 2008–2009 (Fig. 3), particularly when the minimum temperature was decreased (Table 4) indicating linkage with cold events. Under harsher climate in KA trial, BR rings with varying probability were observed for all of the studied provenances (Fig. 3), yet their occurrence appeared not related to the fluctuation in the minimum late summer temperature (Table 4). Nevertheless, the highest occurrences of BR was observed for EBN provenance in response to a drop of temperature (frosts) in 2002 and 2013 (Fig. 3).

As LI trial was located in the coastal zone, where the cooling effect of Baltic Sea on the temperature regime in spring is explicit (Fig. 1; Supplementary material, Fig. S1), only a few FRs were observed (Fig. 4); nevertheless for the top-performing RYT provenance, their occurrence appeared related to the minimum temperature (Table 4). In the ZV trial, FR with intermediate probabilities occurred during most of the period 1990–1999 (Fig. 4). The low-performing DIP was the only provenance showing linkage between FR and temperature under warmer summers in ZV trial (Table 4). In the more continental KA trial, FRs with varying probabilities occurred in most years of the period 1987–2011, particularly for the low-performing DIP and EBN provenances. A statistically significant linkage between FR and the minimal temperature at the beginning of vegetation period was estimated for the native KAL provenance (Table 4), while the transferred provenances likely appeared sensitive to lower temperature irrespectively of its fluctuations.

4. Discussion

The occurrence of BR and FR in wood of the transferred, as well as the native population (Fig. 2) indicated susceptibility of Scots pine to cold events in the mid-part of species range (Hytteborn et al., 2005), despite the presumed optimal growing conditions (Speer, 2010). The BR occurred more frequently than FR (Fig. 2), indicating higher susceptibility to unfavourable conditions (e.g., decreased temperature, frosts) in autumn, rather than at the beginning of summer (Montwe et al., 2018), likely due to the extension of vegetation period (Menzel,

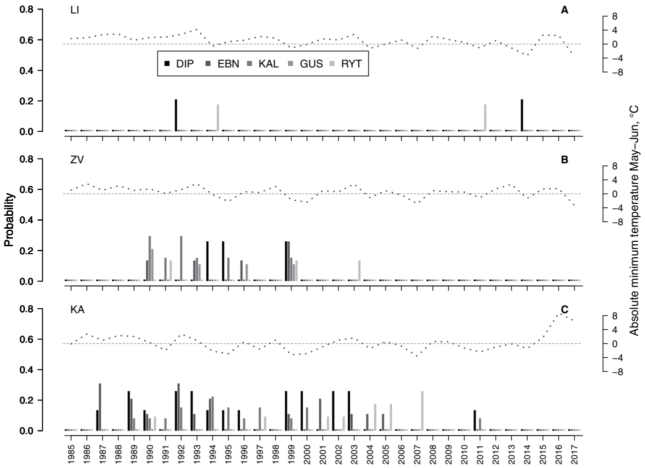

Fig. 4. Annual variation in the occurrence of 'frost' rings among the studied provenances of Scots pine in three trials differing by continentality (ranged ascendingly). Broken line shows the absolute minimum temperature during the July–September period.

2000; Repo et al., 2000; Hänninen et al., 2013; Zohner et al., 2016). Apparently, damage by decreased temperature and, subsequently, its effects on growth and competitiveness (Hänninen, 2006; Charrier et al., 2015) are contributing to the projected decrease in abundance of Scots pine in Europe (Buras and Menzel, 2019). However, the overall mean probability of BR and FR of the studied provenances of Scots pine (≤ 0.027) was considerably lower compared to the studies of Piermattei et al. (2015) and Montwe et al. (2018), likely due to milder climate under lowland conditions and/or shorter transfer of provenances. Similarly to those studies, most of the anomalies, particularly FRs, occurred when the trees were young (Figs. 3 and 4), which has been related to lower height and weaker heat absorption of smaller trees (Kidd et al., 2014), as well as to thinner bark, which provide less insulation to cambium (Payette et al., 2010; Montwe et al., 2018). During the first ten years of tree life, the probability of frost-related wood anomalies at breast height was also low (Figs. 3 and 4), possibly due to altered phenology of secondary growth (Payette et al., 2010). Considering that the wood anomalies occurred prevailingly in the juvenile wood, their overall effect on the mechanical properties and the value of timber, however, appeared limited.

The observed differences in the probability of wood anomalies among the trials (Table 3, Fig. 2) followed the differences in mean temperatures (Table 1), highlighting the relation of BR and FR with the thermal regime (Hänninen, 2006; Piermattei et al., 2015). The sensitivity of wood anomalies to the inter-annual fluctuations in minimum temperature, however, was limited (Table 4), which might be related to ecological transfer distance (Montwe et al., 2018). Under milder coastal conditions in LI trial, the occurrence of wood anomalies was low (Figs. 3 and 4), indicating non-limiting effect of temperature (Table 4). Considering the buffering effect of the Baltic Sea on the coastal climate (Meier, 2006), the thermal regulation of the active period (Zohner et al., 2016), apparently, ensured the timing of xylogenesis to frost-free periods. Still, FR in the top-performing RYT provenance appeared related to temperature, suggesting an extended growing period of the trees.

In ZV trial, where the vegetation period was longer and temperature higher, yet climate more continental (Table 1), the effect of temperature was most likely cleared due to delayed frost hardening (Beck et al., 2004), as suggested by the formation of BR in the top-performing provenances in response to cold events (Table 4, Fig. 4). The limited sensitivity of the low-performing provenances, which originated from cooler and more humid climate (Table 2), might be also related to modulating effects of other factors, such as water deficit (Camarero et al., 2010; Kreyling et al., 2012; Taeger et al., 2013). Nevertheless these relationships suggest increasing occurrence of damage by tow temperature/frosts to cambium under the warming climate (Gu et al., 2008; Augspurger, 2009; Montwe et al., 2018). Under harsher climate in KA trial (Figs. 3 and 4), lower minimum temperatures resulted in wood damage of the north transferred provenances (Figs. 3 and 4), indicating susceptibility of the transferred Scots pine at young age (Klisz et al., 2019).

Moderate differences in climate (Table 1, Supplementary material,

Table 4

The *p*-values of differences in the minimum absolute temperature (July–September and May–June for 'blue' and 'frost' rings, respectively) between years with and without 'blue' and 'frost' rings during 1985–2017 for the studied provenances/trials, as determined by one-tailed t-test. NA – evaluation of differences was not available due to the lack of anomalies.

Provenance\Trial	'Blue' rings			'Frost' rings		
	Liepāja (LI)	Zvirgzde (ZV)	Kalsnava (KA)	Liepāja (LI)	Zvirgzde (ZV)	Kalsnava (KA)
Dippoldiswalde (DIP)	NA	NA	0.42	0.38	0.03	0.18
Eibenstock (EBN)	0.77	0.34	0.38	NA	0.64	0.43
Kalsnava (KAL)	NA	NA	0.84	NA	0.41	0.02
Güstrow (GUS)	NA	0.01	NA	NA	0.64	NA
Rytel (RYT)	NA	< 0.001	0.74	< 0.001	0.48	0.06

Fig. S1) caused explicit differences in the probability of wood anomalies (Fig. 2), highlighting local diversification of tree responses (Eckert et al., 2015; Montwe et al., 2018), which also adds uncertainty to the projections of forest growth (Pellizzari et al., 2017; Nabuurs et al., 2018). Under such conditions, the importance of genetic adaptation and phenotypic plasticity, hence the adaptability of tree populations is increasing (Aitken et al., 2008; Aitken and Bemmels, 2016), supporting the necessity for adaptive management (Bolte et al., 2009; Yousefpour et al., 2017). The significant effect of provenance on the probability of BR and FR (Table 3) indicated genetic determination of timing of growth hence susceptibility to cold events (Repo et al., 2000; Montwe et al., 2018). This also suggests opportunities for improvements via adaptive management, e.g., tree breeding (Bolte et al., 2009; Yousefpour et al., 2017). The explicit provenance-by-trial interaction (Table 3), however, indicated phenotypic plasticity of the mechanisms preventing frost damage to cambium (Andersson and Fedorkov, 2004), thus indicating unequal adaptability of the genotypes (Aitken et al., 2008; Aitken and Bemmels, 2016).

The hypothesis of the study was proven only partially, as among the north-transferred provenances, only the low-performing ones showed higher probability of BR and FR (Figs. 2–4; Table 3), thus indicating higher susceptibility to cold events under harsher climate (Augspurger, 2009; Hewitt et al., 2011; Montwe et al., 2018). The increased probability of wood anomalies (Fig. 2) also suggested lower ecological plasticity of the low-performing provenances. In addition, the low-performing provenances originated from the mountain areas, where the vegetation period is shorter (Table 2), hence under lowland conditions these trees start active period earlier subjecting xylogenesis to potential frosts (Montwe et al., 2018). In contrast to what we expected, native KAL provenance, which has evolutionary adapted to local conditions, showed an intermediate sensitivity particularly to cold events in late spring (Figs. 2 and 4; Table 4), likely due to the negative effects of warming and increasing variability of weather conditions (Gu et al., 2008; Augspurger, 2009; Montwe et al., 2018). The intermediate probability of anomalies observed in the local population also supported the necessity for assisted gene flow and adaptive management for the sustainability of forests (Aitken and Bemmels, 2016; Yousefpour et al., 2017).

The top-performing provenances showed a low probability of BR and FR, also under harsher climate (Fig. 2), highlighting the relationship between the field performance and frost hardiness of trees (Ögren, 1997; Rikala and Repo, 1997; Repo et al., 2006; Charrier et al., 2015). Under more continental conditions in KA trial, GUS provenance showed negligible probability of the wood anomalies (Fig. 2), likely due to earlier frost hardening (Repo et al., 2000; Beck et al., 2004), indicating higher plasticity and better adaptability to a cooler climate compared to the others. Nevertheless in ZV trial, GUS provenance showed an increased probability of BR (Fig. 2), which was linked to the occurrence of cold events in early autumn (Fig. 3, Table 4), suggesting some maladaptation to warming under milder climate (Charrier et al., 2015; Zohner et al., 2016). The other top-performing provenance RYT showed low probability of BR and FR similarly in all trials (Fig. 2), implying superior plasticity and adaptability to the expected climatic changes (Dumroese et al., 2015; Nabuurs et al., 2018). Better frost hardiness of the top-performing provenances (Fig. 2) likely has contributed to a higher plasticity of growth and more efficient recovery after unfavourable weather extremes (Matisons et al., 2019), projecting promising perspectives for a wider application of the provenances in commercial practice in the Eastern Baltic region under warming climate. Still, considering the local variability in susceptibility to cold events of the studied provinces (Fig. 2), seed transfer should be conservative (Montwe et al., 2018).

5. Conclusions

Maladaptation of the north-transferred reproductive material to an increasing variability of weather conditions and the likelihood of frost occurrence is a major concern in forestry; however, the occurrence of frost damages (BR and FR) in the local provenance, especially at its origin, supported the necessity for a limited-range assisted gene flow in the future. In juvenile wood, incomplete lignification of latewood (BRs) was observed more frequently than FR, suggesting some limited negative effect of the extending growing period on the quality of timber. The studied north-transferred provenances of Scots pine differed in susceptibility to cold events in spring and autumn due to genetically determined specifics of frost resistance, as well as transfer distance. Nevertheless, the probability of the damages was related to field performance of the studied provenances indicating a feedback loop between environmental sensitivity and growth. Accordingly, selection of the potential forest reproductive material by its field performance appears sufficient also for minimizing frost damages under changing climate. Nevertheless, the susceptibility to cold events showed local specifics, hence more detailed spatial analysis appears necessary before the implementation of assisted gene flow on a wider scale. Based on field performance and probability of BR and FR among the studied provenances, RYT could be suggested for a wider commercial application, as well as for breeding programs in the eastern Baltic region (Baltic States) to minimize potential negative effects of changing climate.

Declaration of Competing Interest

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

Acknowledgements

The study was conducted under the framework of post-doctoral studies in Latvia ("Plasticity of development and xylogenesis of the native and introduced tree species under changing climate", project No.: 1.1.1.2.VIAA/1/16/108) financed by the European Regional Development Fund. We acknowledge Latvia Environment, Meteorology, and Geology Centre for the meteorological data.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.117729.

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South-Eastern Baltic Provenances of Scots Pine Show Heritable Weather-Growth Relationships

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Abstract: The productivity of forests has been linked to the sensitivity of tree growth to meteorological conditions and their fluctuations, hence moderation of tree sensitivity is one of the goals for climate-smart forest management. For this, tree breeding is among the most effective means, particularly if breeding populations are supplemented with genotypes (provenances) adapted to the expected climates. Nonetheless, heritability of traits is essential for their improvement by breeding. In this study, heritability of growth sensitivity of south-eastern Baltic provenances of Scots pine differing by field performance to meteorological conditions was assessed combining methods of quantitative genetics and dendrochronology. Five parallel provenance trials within the south-eastern Baltic region were investigated. The effects of regional weather drivers of growth (moisture regime in summer, temperature regime in preceding summer and in the dormancy period) were estimated, yet their strengths differed among the provenances, indicating local specialization of metapopulations of Scots pine. The heritability of growth sensitivity to these factors ranged from low to moderate, similarly as observed for the morphometric traits within the region; however, the provenance (genetic) variation appeared to be higher. The differences in heritability of responses, however, indicated uneven adaptive significance of weather conditions. Although the estimates were based on a limited set of genotypes implying caution in the extrapolation of results, the weather-growth relationships and their heritability indicate that sensitivity of growth is a complementary trait aiding breeding of forest reproductive material best suited for future climates. Heritable weather-growth relationships also imply a high potential for forest breeding to moderate the sensitivity of the trees.

Keywords: parallel trials; quantitative genetics; *Pinus sylvestris*; growth sensitivity; local specialization

Citation: Matisons, R.; Schneck, V.; Jansone, D.; Bāders, E.; Dubra, S.; Zeltiņš, P.; Jansons, Ā. South-Eastern Baltic Provenances of Scots Pine Show Heritable Weather-Growth Relationships. *Forests* **2021**, *12*, 1101. https://doi.org/10.3390/f12081101

Academic Editor: Giovanbattista de Dato

Received: 27 July 2021
Accepted: 16 August 2021
Published: 18 August 2021

1. Introduction

Changes in composition and productivity of forests in Northern and Eastern Europe [1] imply substantial economic and ecologic consequences already during the 21st century [2]. The pace of climatic changes apparently exceeds the natural rate of adaptability of local tree populations [3], hence proactive adaptive management is crucial to sustain the productivity of forests [4,5]. For this, tree breeding and assisted gene flow have been highlighted as the most efficient practices [3,6,7], while the synergy of both, i.e., supplementation of breeding populations, which mostly consist of local genotypes, with the best-performing provenances (transferred genotypes), appears particularly promising [8–12]. However, the efficiency of breeding depends on the strength of the genetic control, hence the heritability of the traits providing adaptive advantages [6,10,13–15]. Propitiously, traits with adaptive significance or affecting reproductive success are often genetically controlled [16–18], although the strength of the control can differ [13,19–23].

Provenance trials, which have been established for the assessment of performance of genotypes from diverse origins, are being revisited as the source of information on the adaptability of tree populations in the longer term [11,23,24], which is crucial for climate-smart forestry [4,5]. The adaptability of trees depends on genetic specialization and phenotypic plasticity, which have evolved to maximize survival and competitiveness of genotypes under certain conditions [14,16,18]. For the evaluation of both, the parallel provenance trials are particularly informative due to the extension of ecological gradients, revealing the genotype–environment interactions and adaptability [8–10,14,23,25]. Furthermore, provenance trials can act as source of tested genetic material for supplementation of local breeding populations, thus contributing to growth potential of forest reproductive material [12,26].

In most breeding programmes, the selection of genotypes is based on multiple traits, which are consolidated into selection indices, although the set of traits can differ [27–29]. Usually, selection indices contain traits related to productivity under certain environments, such as size of trees (tree height and stem diameter) [21,22,25,29]. However, considering the acceleration rate of climatic changes [3], such traits represent cumulative performance of genotypes under the past climates, which might be already outdated [8,10]. In this regard, information about the environmental sensitivity of genotypes is more universal, as it represents the plasticity of tree performance under a temporal spectrum of environmental conditions [10,14,30]. Considering climate as one of the main drivers of tree growth [1,31,32], the sensitivity of growth to meteorological conditions can be considered as a trait indicative for conformity of genotypes with environments [10,14,23,25]. Accordingly, such information can facilitate breeding of genotypes better suited for the future conditions.

Sensitivity of trees to weather conditions can be assessed in detail via retrospective analysis of tree-ring width and its derivatives, which act as an archive of radial increment [30,31,33]. Variation of tree-ring width contains several components, which can be separated by dendrochronological (time series decomposition) methods [34–36]. An inter-annual (high frequency) growth variation component, as represented by the relative additional increment, is commonly used for the assessment of weather-growth relationships [34,36]. Considering that genotypes (trees) in provenance trials are subjected to a limited part of the climatic gradient, linear weather–growth responses are expected [37,38]. Although extrapolation of such responses is limited [39,40], they are still sufficient and straightforward for the comparison of genotypes under common conditions [11,20,38].

Scots pine (*Pinus sylvestris* L.), which is a widespread and stress-tolerant species [41], is expected to decrease its abundance in Eastern and Northern Europe during the 21st century [1,42], and such changes are expected to be apparent in the eastern Baltic region [1]. Changes in the abundance of Scots pine appear to be caused by the trade-offs in growth and competitiveness with other tree species [42,43], which are modulated by climate [44–46]. Due to the high economic and ecological importance of Scots pine within the region [41], efforts are made to maintain species performance by national breeding programmes [7,22,26]. At the regional level, productivity of metapopulations of Scots pine has been linked to weather growth sensitivity [22,47,48], and the regional weather drivers of growth (both temperature in winter and moisture regime in summer) suggest genetic specialization of local metapopulations [32,37,47]. Accordingly, weather growth sensitivity appears as a promising trait aiding selection and breeding of the most sustainable genotypes. The aim of this study was to assess the strength of genetic specialization and heritability of weather-growth relationships for south-eastern Baltic population(s) of Scots pine based on provenance trials. Considering that the studied region is situated in the mid-part of species range [41], where specialization of growth sensitivity to common factors can be explicit [49], we expected intermediate heritability of growth sensitivity to weather fluctuations.

2. Materials and Methods

2.1. Trials and Provenances

Five international parallel provenance trials of Scots pine in Latvia near Liepaja (LI), Zvirgzde (ZV), and Kalsnava (KA) and in the northern Germany near Waldsieversdorf (WS) and Nedlitz (NL) were studied (Figure 1). The trials were established under the collaboration of the USSR and the German Democratic Republic in 1975 to assess the performance of provenances from the eastern block and the USSR [50,51]. The studied trials contained a common set of 36 Scots pine provenances originating from the region ranging 46–60° N and 11–30° E. For each provenance, seed material has been collected from 20–25 plus-trees growing in managed open-pollinated forest stands. One-year-old seedlings were raised in local nurseries and planted with the initial spacing of 2 × 1 and 2 × 0.5 m in the trials in Latvia and northern Germany, respectively. The design of the trials was complete randomized blocks; four 100-tree blocks per provenance were established in each trial in Germany, and six 35-tree blocks in the trials in Latvia. The trials in Latvia were thinned from below at the age of 21 years (in January 1996), resulting in the mean stand density of ca. 1800 trees ha^{-1}. In the northern Germany, the NL trial was thinned from below once directly prior to sampling, while the WS trial was gradually thinned from below three times (last in winter 2013/2014). Nevertheless, in both trials, thinning resulted in stand density of approximately 900–1200 trees ha^{-1}.

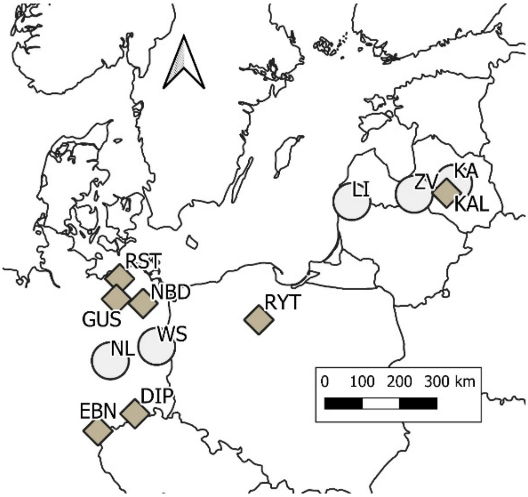

Figure 1. Location of the studied trials (circles) and origins of the studied provenances (squares) of the south-eastern Baltic Scots pine.

The trials were growing on well-drained oligotrophic (in Latvia) or mesotrophic (in Northern Germany) sandy or silty soils on flat topography under lowland conditions (Table 1). The climate of the trials can be described as temperate moist continental (Dfb [52]), although a coastal-inland gradient was evident due to increasing distance from the Baltic Sea, particularly in Latvia (Supplementary material, Figure S1). The trials represented subregional climatic gradient, length of which corresponds to the predicted shift in climatic gradient during the 21st century from Latvia's perspective [53]. In Latvia, the mean annual temperature and precipitation sum was higher in the coastal LI trial, while ZV and KA were the driest and coldest trials, respectively (Table 1, Figure S1). In northern Germany, climate was warmer, yet the differences in temperature between the trials were smaller. In all trials, July and January were the warmest and the coldest months, respectively. The highest monthly precipitation fell during the vegetation period and comprised approximately half of the annual. Still, annual and summer precipitation was by approximately 22% higher in the trials in Latvia. Climatic changes were mainly expressed as warming during the November–April period and concomitant increase in heterogeneity of summer precipitation regime [53]. However, summer precipitation showed a decreasing trend in northern Germany, while a slight increase in precipitation in the dormant period was occurring in Latvia [53,54].

Table 1. Location and general climatic description (means ± standard deviation for the period 1988–2017) of the studied trials of Scots pine.

	LI	ZV	KA	WS	NL
Latitude, °	56.45	56.65	56.80	52.53	52.02
Longitude, °	21.63	24.37	25.93	14.05	12.33
Elevation, m	15	50	220	60	125
Soil	Oligotrophic sandy (podzol)	Oligotrophic sandy (podzol)	Oligotrophic silty (podzol)	Mesotrophic brown sandy	Mesotrophic brown sandy
Mean annual temperature, °C	7.5 ± 0.6	7.2 ± 0.7	6.4 ± 0.7	9.8 ± 0.7	10.1 ± 0.7
Mean May–September temperature, °C	15.0 ± 0.7	15.2 ± 0.8	14.8 ± 0.8	16.9 ± 0.7	16.9 ± 0.7
Mean January temperature, °C	−1.9 ± 2.4	−3.0 ± 2.6	−4.2 ± 2.7	0.5 ± 2.5	1.3 ± 2.4
Mean July temperature, °C	17.8 ± 1.6	18.2 ± 1.6	17.9 ± 1.6	19.4 ± 1.6	19.3 ± 1.7
Mean annual precipitation sum, mm	789 ± 91	659 ± 75	689 ± 81	568 ± 80	542 ± 73
May–September precipitation sum, mm	353 ± 71	333 ± 63	349 ± 66	290 ± 66	274 ± 59

To assess the strength of genetic control over sensitivity of growth to weather conditions and its relationships with the field performance of trees, four of the top-performing and two of the low-performing provenances were selected for sampling. The selection was based on consolidated rankings of dimensions and survival in the trials in Latvia measured during the inventory in 2016. The selected provenances showed consistent effect of field performance of trees ([50]; Supplementary material, Table S1). Provenances Rytel (RYT), Güstrow (GUS), Rostock (RST), and Neubrandenburg (NBD), which originated from lowland coastal areas in northern Germany and Poland (Table 2, Figure 1 and Figure S2) were selected for representation of the top-performing genotypes. Dippoldiswalde (DIP) and Eibenstock (EBN), which originated from upland areas of the Orr mountains, were selected for the representation of the low-performing genotypes. Compared to conditions in Latvia (Table 1), the top-performing provenances originated from sites with warmer and drier climate, while the low-performing provenances originated from more humid climates (Table 2). Due to climatic changes [53], these differences show decreasing tendencies, implying reduction of ecological transfer distance [55]. Such selection was made accounting for the projected shifts in vegetation zones in the south-eastern Baltic region [1,42], presuming advantages from the northwards transfer of genotypes [55,56]. Additionally, Kalsnava provenance, which originates from the central part of Latvia and shows above-average field performance and superior stem quality [50,57], was selected for the representation of local genotypes (from Latvia's perspective). Seven provenances were selected in total.

Table 2. Location and general climatic description (means ± standard deviation for the period 1945–1974) of the studied provenances of Scots pine.

	DIP	EBN	KAL	NBD	RST	GUS	RYT
Latitude, °	50.54	50.30	56.47	53.52	54.15	53.51	53.44
Longitude, °	13.58	12.29	25.60	13.26	12.16	12.16	18.01
Elevation, m	590	710	190	40	15	25	130
Field performance in trials in Latvia	Low	Low	Moderate (local)	High	High	High	High
Mean annual temperature, °C	6.6 ± 0.5	5.9 ± 0.7	5.5 ± 0.8	8.5 ± 0.7	8.6 ± 0.7	8.5 ± 0.7	8.0 ± 0.7
Mean May-September temperature, °C	13.6 ± 0.7	12.6 ± 0.8	14.4 ± 0.8	15.4 ± 0.7	15.2 ± 0.7	15.2 ± 0.8	15.4 ± 0.7
Mean January temperature, °C	−2.6 ± 2.4	−3.0 ± 2.3	−6.5 ± 3.7	−0.3 ± 2.3	0.2 ± 2.1	−0.1 ± 2.3	−2.3 ± 2.6
Mean July temperature, °C	15.3 ± 1.2	14.7 ± 1.3	17.0 ± 1.2	17.7 ± 1.3	17.3 ± 1.2	17.3 ± 1.3	17.7 ± 1.3
Mean annual precipitation sum	804 ± 68	994 ± 101	624 ± 77	577 ± 75	570 ± 81	599 ± 79	546 ± 73
May-September precipitation sum	402 ± 32	499 ± 60	328 ± 66	290 ± 48	284 ± 51	300 ± 50	310 ± 48

2.2. Sampling and Measurements

Increment cores from 9 to 18 dominant visually healthy trees per provenance in each of the five trials (one to four trees per block) were collected; 459 trees were sampled in total. Two increment cores per tree from opposite randomly oriented sides of stem were taken at breast height using a 5 mm increment corer. Tilted trees were not sampled to avoid reaction wood. In a laboratory, increment cores were fixed into individual wooden mounts and their surface was prepared for measurements using the WSL core microtome [58]. The measurements of tree-ring width were taken manually using the LINTAB6 measurement table (RinnTech, Heidelberg, Germany). The accuracy of the measurements was 0.01 mm; all measurements were taken by the same person.

2.3. Data Analysis

Exact dating of increment (tree-ring widths) is essential for the assessment of weather-growth relationships of trees [34] and, accordingly, the quality of measurement time series (particularly their dating) was ensured during visual and statistical crossdating [59]. Time series showing poor agreement with others (Pearson's r < 0.4) were omitted from the analysis, or their dating was adjusted if reasonable. The sufficiency of the datasets to capture common environmental effects on radial growth of trees was described by the mean sensitivity, expressed population signal and signal-to-noise ratio. These indices were calculated for detrended (by a cubic spline) datasets. The presence of a weather-related component in the variation of tree-ring width was estimated via dendroclimatic analysis. For this, a residual chronology representing the relative additional radial increment for each provenance within each trial was calculated. Mean time series of tree-ring width for trees were calculated and converted to time series of basal area increment (BAI) to minimize the trend related to ageing. The individual time series of BAI were detrended by a flexible cubic spline with the wavelength of 20 years and 50% cut-off frequency to remove the effects of ageing and thinning, and prewhitened using an autoregressive model ('ar1') to eliminate the effect of previous growth. Individual detrended time series of BAI were then averaged into residual chronologies using the biweight robust mean [60]. The presence of local linear weather growth relationships was assessed by a bootstrapped (non-parametric percentile bootstrapping) Pearson correlation analysis (non-parametric percentile interval bootstrapping, 1000 iterations [61]) between residual chronologies of BAI and meteorological variables. The tested meteorological variables were mean monthly temperatures, precipitation sums, and standardized precipitation evapotranspiration indices (SPEI) arranged into climatic window from June in the year preceding growth (previous June) to September. The analysis was conducted for the common period of 1985–2017. Gridded climatic data (CRU TS [62]) from the closest observation grid entry were used.

To assess the strength of genetic control over the sensitivity of the increment to weather fluctuations arising from local adaptation across the studied trials [16,18,63,64], the broad-sense heritability and the provenance coefficient of variation were estimated [64,65]. The calculation was based on responses of individual trees. Considering that each trial represents a limited part of the regional climatic gradient, linear responses of individual trees (detrended and prewhitened BAI series) to each of the meteorological variables were estimated by the mean value of bootstrapped (non-parametric bootstrapping with repetition, 1000 iterations) slope coefficients of linear regression within the 10–90 percentile interval. The variance components of genetic and environmental effects of the responses of trees (slope coefficients) were extracted using mixed effects (random intercept) models:

$$y_{ijk} = \mu + t_i + b_{(j)i} + (p_k) + (p_k : t_i) + \left(p_k : b_{j(i)}\right) + \varepsilon \tag{1}$$

where t_i—fixed effect of trial, $b_{j(i)}$—fixed effect of block nested within trial, (p_k)—random effect of provenance, $(p_k{:}t_i)$ random interaction of provenance and trial, $(p_k{:}b_{j(i)})$—random effect of interaction of provenance and block (repetition) nested within trial. The models were fitted using the maximum likelihood approach. Broad-sense heritability (H^2) was calculated as:

$$H^2 = \frac{\sigma_p^2}{\sigma_p^2 + \sigma_{p:t}^2 + \sigma_{p:b}^2 + \sigma_\varepsilon^2} \tag{2}$$

where σ_p^2—variance component of provenance, $\sigma_{p:t}^2$—variance component of provenance by trial interaction, $\sigma_{p:b}^2$—variance component of provenance by block interaction, and σ_ε^2—variance. Standard error for H^2 was estimated using the Dickerson's approximation [66]. The provenance coefficient of variation (PCV; [64]) was calculated as:

$$PCV = \frac{\sqrt{\sigma_p^2}}{\overline{y}} \tag{3}$$

where σ_p—variance component of provenance and $\overline{y}$ is the phenotypical mean of the response variable (mean bootstrapped slope coefficient). Data analysis was conducted in R v. 4.1.0 [67] using the libraries 'lme4' [68] and 'dplR' [60].

3. Results

3.1. Datasets

The cross-dated datasets contained 9–18 trees per provenance per stand, and 93% (≥86% per provenance per trial) of the measured time series of tree-ring width (from 427 trees) with verified dating were used for the analysis (Table 3). The mean tree-ring width was similar among the studied five trials irrespective of differing growing conditions, yet it differed among the provenances according to their field performance. For all of the datasets, EPS values exceeded 0.85 (cf. [69]) indicating their sufficiency to capture a common variation of increment represented by the datasets. The mean interseries correlation of the datasets (r-bar) ranged 0.27–0.53, although it tended to be higher for NBD and RST provenances, implying higher agreement among trees.

The strength of the environmental signal captured by tree-rings varied by provenance and trial ranging 4.22–15.41, although it tended to be higher in Germany than in Latvia (9.18 and 7.44, respectively), particularly for NBD and RST provenances. The mean sensitivity of time series was intermediate, yet it also tended to be higher in trials in Germany than in Latvia (0.26 and 0.19, respectively). The first order autocorrelation, however, was higher in Latvia than in Germany (0.78 and 0.63, respectively), indicating differences in the effect of previous growth on increment. The mean sensitivity and first order autocorrelation, however, were comparable among the provenances.

Table 3. General statistics of the cross-dated datasets of tree-ring width of the studied south-eastern Baltic provenances of Scots pine. Ranges of the values across the studied trials are shown. AR1—first order autocorrelation, r-bar—mean interseries correlation, gini—gini coefficient, SENS—mean sensitivity, EPS—expressed population signal, and SNR—signal to noise ratio.

	DIP	**EBN**	**KAL**	**NBD**	**RST**	**GUS**	**RYT**
Number of cross-dated trees	9–13	9–13	10–14	14–18	14–17	10–15	10–16
Mean series length, years	33.1–34.6	34.0–35.0	34.4–34.8	34.5–35.0	34.2–34.9	33.6–34.9	34.1–35.0
Mean tree-ring width, mm	2.06–2.65	2.10–2.94	2.20–3.20	2.35–3.53	2.34–3.16	2.44–3.42	2.51–3.50
St. dev. tree-ring width, mm	1.00–1.61	0.96–1.36	0.95–1.54	0.99–1.71	0.89–1.64	1.01–1.73	0.86–1.82
r-bar	0.27–0.41	0.32–0.39	0.31–0.44	0.33–0.51	0.37–0.53	0.33–0.48	0.32–0.42
gini	0.25–0.34	0.23–0.32	0.22–0.26	0.21–0.26	0.20–0.28	0.22–0.28	0.18–0.28
AR1	0.67–0.82	0.66–0.83	0.60–0.83	0.57–0.82	0.58–0.83	0.63–0.82	0.55–0.83
SENS	0.22–0.28	0.19–0.30	0.16–0.29	0.16–0.30	0.18–0.28	0.17–0.26	0.16–0.26
EPS	0.85–0.89	0.85–0.88	0.86–0.90	0.88–0.94	0.90–0.94	0.85–0.93	0.87–0.92
SNR	4.22–8.38	4.68–7.64	5.33–9.39	7.32–14.76	8.63–15.41	5.52–13.86	4.63–11.68

3.2. Linear Weather-Growth Relationships

The developed chronologies (mean time series) showed that formation of relative additional BAI was synchronous (mean $r \geq 0.74$), yet the strength of the inter-annual variation differed among the provenances within a trial (Supplementary material, Figure S3) implying varying sensitivity. The synchrony among the trials, which differed by climate (Table 1), was lower (mean $r = 0.45$), implying specific limitation of radial growth by meteorological conditions. Accordingly, the sets of weather variables showing significant correlation with the chronologies of relative additional BAI, as well as the strength of the correlations, differed by provenance, particularly in the trials in Latvia (Figure 2). Under hemiboreal conditions in Latvia, meteorological variables related to both conditions in the dormant period and in summer showed significant correlations with the chronologies of BAI of the studied provenances. The sets of the significant variables, however, differed between the coastal and inland trials.

Temperature in the previous June showed the strongest correlations, particularly for the top-performing provenances under more continental conditions (KA trial, Figure 2). Temperature in the previous July and September, as well as in March, were significant for most of the provenances there, although the correlations were weaker. Precipitation in July and SPEI in the previous July were positively correlated with BAI, and the correlations were stronger for the top-performing provenances. Under milder climate in the LI and ZV trials, the correlations of BAI with temperature in July were mostly significant for the top-performing provenances. Precipitation in previous August showed significant correlations for most provenances, although the correlations were stronger for NBD, GUS and, DIP, despite differences in their field performance. Precipitation in late summer (September) showed negative correlations in the LI and ZV trials, where vegetation period was longer. The moisture balance represented by SPEI in May and in previous November had an effect on BAI of DIP and KAL provenances under the coastal climate in LI trial.

Under the nemoral conditions in Northern Germany, weather variables particularly related to summer moisture regime showed a correlation with BAI of the studied provenances (Figure 2). At each trial, the sets of the significant factors were generally similar, and the differences among the provenances were related in particular to the strength of the correlations. The limiting effects of summer water shortage were highlighted by the highest correlations estimated between BAI and SPEI in July and August, which were significant for all datasets, with only slight differences among the provenances. The correlations with SPEI in June, however, were significant for some provenances in the WS trial. The correlations with temperature (negative) and precipitation (positive) in June and July showed higher variation among the provenances and trials. Similarly, the provenances showed uneven sensitivity to SPEI in September. All of the provenances showed strong and significant correlations with temperature in the previous September in the WS trial.

Considering that climate in Northern Germany is temperate, January temperature was significant for DIP, NBD, and RST provenances, although the correlations were negative.

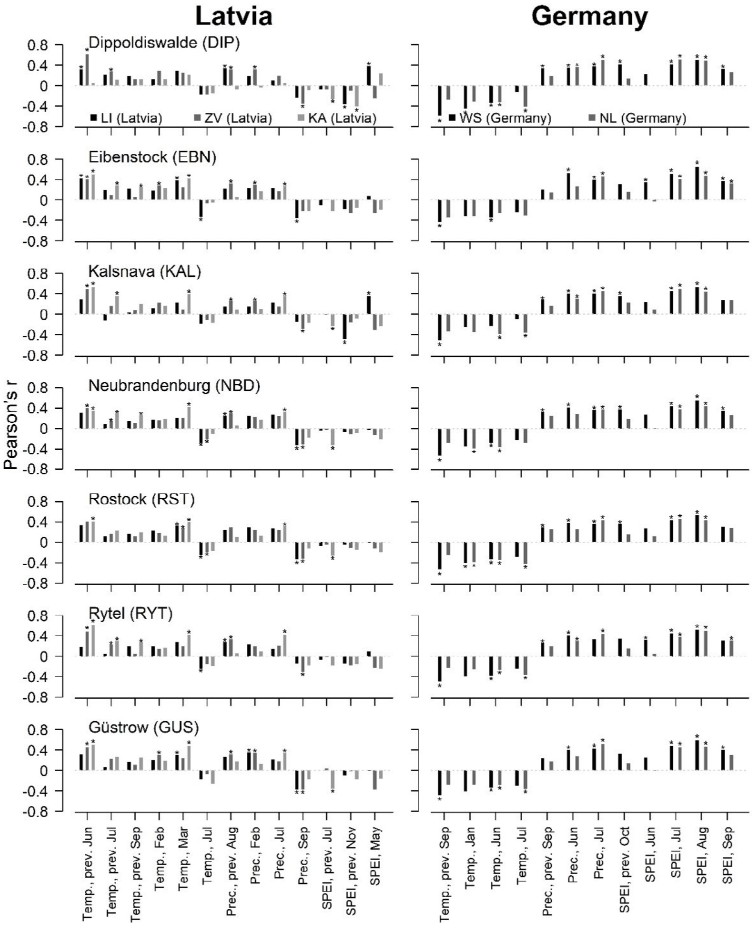

Figure 2. Bootstrapped Pearson correlation coefficients between the chronologies (prewhitened time series of the biweight robust mean) of basal area increment of the studied provenances of Scots pine and individual meteorological variables for the period 1985–2017 by trials (local weather data tested). The tested meteorological variables are monthly mean temperature (Temp.), precipitation sums (Prec.) and standardized precipitation evapotranspiration indices (SPEI). Asterisks (*) indicate significant correlations at $\alpha = 0.05$. Note that a separate legend is given for each column of the panels (Latvia and Germany). Prev.—previous year.

3.3. Genetic Parameters of Weather-Growth Responses

The individual responses of relative additional BAI to 13 of 51 meteorological variables analyzed were estimated with H^2 coefficient exceeding 0.15 (reaching 0.32; Table 4). Most of these variables were estimated with varying correlations with mean time series of relative additional BAI in the trials in northern Germany or Latvia, although heritability estimates did not show consecutive temporal patterns, indicating intra-seasonal fluctuation of genetic control of weather–growth interactions. Likewise, for these responses the provenance variation fluctuated, PCV of these responses ranged considerably (from 0.18 to 0.65) indicating differing genetic plasticity.

Table 4. Coefficients or broad-sense heritability (H^2 ± standard error) and provenance coefficient of variation (PCV) for the responses of relative additional basal area increment (BAI) to meteorological variables: monthly mean temperature, precipitation sums and precipitation evapotranspiration indices (SPEI). Only the variables showing heritability above 0.15 are shown.

	H^2	PCV
Temperature previous July	0.27 ± 0.17	0.60
Temperature previous September	0.25 ± 0.16	0.45
Temperature January	0.21 ± 0.11	0.65
Temperature June	0.29 ± 0.17	0.44
Precipitation previous June	0.32 ± 0.15	0.24
Precipitation March	0.23 ± 0.15	0.56
Precipitation July	0.26 ± 0.14	0.18
SPEI previous October	0.15 ± 0.10	0.58
SPEI previous November	0.25 ± 0.17	0.47
SPEI June	0.24 ± 0.18	0.54
SPEI July	0.17 ± 0.11	0.44
SPEI August	0.25 ± 0.17	0.50
SPEI September	0.27 ± 0.16	0.62

The highest H^2 was estimated for the response of BAI to precipitation in the previous June which did not show significant correlations with the chronologies (Figure 2). However, below average PCV indicated low variability of the response due to provenance. The lowest heritability (H^2) hence the strongest environmental control was estimated for the responses to SPEI in July and previous October, for which, the provenance variation was intermediate (Table 4). The responses to January temperature had the highest PCV, while the heritability was relatively low. Responses to SPEI in September had the second highest PCV and above average H^2. The responses to temperature in the current June, which showed significant correlation with BAI in northern Germany, were estimated with the second highest H^2 and intermediate PCV. The H^2 for the responses to SPEI in June, August and the previous November was lower, yet the PCV was above average. In contrast, the response to precipitation in July was estimated with the lowest PCV implying similar plasticity of the provenances to summer temperature. The response of BAI to temperature in previous July was estimated with above-average H^2 and relatively high PCV.

4. Discussion

4.1. Weather-Growth Relationships

The studied datasets of radial increment of Scots pine captured the main regional weather-growth relationships (climatic signals; Figure 2), which imply complex effects of conditions in dormancy and vegetation periods [37,70]. Considering intensifying summer water shortage across diverse forest ecosystems [31,71,72], significant positive individual effects of precipitation and SPEI in summer (Figure 2) indicated an effect of water deficit on the growth of Scots pine, particularly under warmer and drier climate in trials in Germany [57]. Likewise, the negative individual effects of temperature in summer (Figure 2), can be explained by intensification of evapotranspiration [73] and hence water deficit. The increment of the top-performing provenances tended to show higher correlations with moisture conditions in summer (Figure 2), which is likely caused by the explicit reaction to favorable conditions, while showing higher tolerance to the adverse conditions [47].

The second part of the growing season is the time when primordia of the increment of the consecutive year are formed [74] and weather conditions (temperature) determine the ratio of generative and vegetative primordia, thus affecting the growth–reproduction trade-off [75]. This explains the observed relationships of radial increment with the meteorological conditions in the previous July–September (Figure 2). The effects of conditions in the previous June, particularly under cooler climate in trials in Latvia (Figure 2) might be related to the restoration of nutrient reserves used for early growth [76,77] and their legacy effects [78].

The studied provenances originated and were tested in sites with temperate climate (Tables 1 and 2), hence conditions in the dormancy period had an effect on radial growth (Figure 2). Under cold/temperate climate, temperature and snow cover influence soil freezing, which affects roots and water relations of trees in the subsequent vegetation season [79], explaining positive relationships between increment and temperature and precipitation in winter, particularly for the north-transferred provenances in Latvia (Figure 2). Although under warmer climate, increased winter temperature can decrease the cold hardiness of trees and subject them to damage from cold spells [80], which explains the negative relationships between increment with winter temperature in trials in Germany (Figure 2).

4.2. Local Specialization and Provenance Variation of Growth Sensitivity

The sensitivity of growth and subsequently increment depends on genotype and regulation of gene expressions [30,81], hence weather-growth relationships can be considered as a cumulative proxy of the fitness of genotypes to certain environments and their fluctuations [10,14,25,30]. The strength of weather-growth relationship differed by provenance (Figure 2), indicating local genetic specialization of metapopulations [31,47,70,82,83]. The heritability estimates (Table 4) confirmed the presence of genetic control over the sensitivity of growth of the studied south-eastern Baltic provenances of Scots pine to meteorological conditions. Genetic specialization of metapopulations in terms of phenology is one of the main evolutionary adaptations allowing trees to avoid damage and maximize growth via coupling of the active period(s) with favorable meteorological conditions [56,63,83,84]. However, the inter-annual fluctuations of weather conditions mostly deviate from the optimal conditions, causing growth to be sensitive to certain deviations [34,81]. Weather sensitivity of genotypes has been linked with their growth [16,17,45,47,48,82], which in turn determine their competitiveness, distribution, and spread [5,42,43]. Accordingly, sensitivity of growth can be considered as a trait(s) of adaptive significance, confirming the presence of local genetic specialization of metapopulations (provenances) in terms of weather-growth relationships [13,16,18,24]. However, local specialization of metapopulations might also partially be due to the regulation of gene expression by metilation of DNA [85,86], which decreases heritability.

In the core regions of species distribution, trees can synchronize their local specialization to common large-scale factors thus maximizing growth [49]. However, the observed differences in regional weather-growth relationships (Figure 2) implied explicit local genetic specialization of metapopulations of Scots pine [18,32,70,83], confirming their heritability (Table 4). Similarly, explicit differences in wood anatomy have been observed both at the core and margin of distribution of Scots pine [23,82], highlighting local genetic specialization of xylogenesis [17,30,33,83]. Local specialization is apparently linked to the ecological plasticity and stress tolerance of Scots pine [87], which warrants its survival under diverse conditions of its vast range [41].

The differing heritability estimated for the responses of radial growth, indicated varying strength of genetic specialization (Table 4), hence uneven adaptive significance of meteorological conditions throughout the season [19,20,22,23,86]. As hypothesized, the estimated heritability of growth responses to monthly weather variables was low to intermediate (Table 4), as observed for the growth and quality traits of Scots pine within the region [22]. Low to moderate heritability might be explained by the multifactorial regulation of xylogenesis [37,70], which involves multiple genes [30,81,85]. Also, the time windows of sensitivity of xylogenesis to weather conditions can vary throughout the year [88,89] blurring their effect at the monthly scale (Table 4). In contrast, the preselection of provenances with differing field performance, most of which were top-performing (Supplementary material, Table S1), might have caused overestimation of PCV [65]. Nevertheless, multi-trial data used for the calculation of the genetic parameters reduces the overestimation, and hence improves the precision of the genetic control of growth [90].

Most of the meteorological factors with heritable ($H^2 \geq 0.15$) responses were related to moisture conditions during the vegetation period (Table 4), highlighting local specialization of Scots pine metapopulations to local moisture regimes [18,23,70,82] in the mid-part of the species distribution. Due to climatic changes, droughts emerge and intensify across diverse ecosystems including various hemiboreal and boreal forest [71,72], hence the observed heritability and, in particular, values of PCV of growth sensitivity (Table 4) highlight the potential of tree breeding to improve drought tolerance of trees [4,7,55,57]. Accordingly, sensitivity of growth to drought conditions appears as a promising trait for climate-smart tree breeding [4,30,57].

The heritability of responses to conditions in late summer of the preceding year (Table 4) could be related to the phenological differences of metapopulations [55,56,63,83,84]. Still, such genetic control over the responses to late summer conditions (Table 4) indicate the potential to alter the trade-offs between the reproductive effort and growth [75], thus maximizing growth potential under warming summers. Considering that the studied provenances originated from areas and were tested in trials with seasonal temperate climate (Tables 1 and 2), the responses to meteorological conditions in the dormancy period also appeared genetically controlled (Table 4). Considering warming of the dormancy period [53], this likely contributes to the complexity of genetic and environmental controls of the growth of metapopulations of trees [10,14,25,37,70].

The estimates of heritability of responses (Table 4) are based on a limited number of provenances (metapopulations), even though they are represented by the progenies from several plus-trees, thus implying cautious extrapolation of these results [22,65,90]. Nevertheless, local specialization and heritability of sensitivity of growth to meteorological conditions, as shown by the studied provenances (Figure 2; Table 4), supports assisted gene flow for improvement of breeding populations [3,6–11,28], thus enhancing the adaptability of forest reproductive material within the region [4,5,7,22]. Furthermore, most of the studied provenances originated from generally comparable climates (Table 2), yet differed in productivity (Supplementary material, Table S1), implying that information on growth sensitivity would be complementary to ecological transfer distance [8,55] when selecting genotypes for propagation of forest reproductive material [8–12]. The estimates of the genetic correlations between the traits might, however, be informative in terms of interactions between genes and traits that can be included in selection indices [20,91], hence analysis of an extended dataset would be needed [22,90].

5. Conclusions

The differences in sensitivity of radial growth of the studied south-eastern Baltic provenances of Scots pine to the main regional weather drivers highlighted genetic specialization of metapopulations to local climates in the mid-part of species distribution. The strength of genetic control over growth sensitivity, however, differed throughout the season, indicating varying adaptive significance of weather conditions. The highest heritability was estimated for the sensitivity of radial growth to weather conditions affecting the summer moisture regime, as well as to conditions in winter and late summer of the preceding year. Accordingly, growth sensitivity appears to be a promising and complementary trait for selection of the most suitable genotypes for propagation of forest reproductive material and would be facilitating the sustainability of pine forests within the region. Thus, the estimated heritability of growth responses supports the potential for moderation of the sensitivity of trees to intensifying climatic stresses.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/f12081101/s1, Figure S1. Climatic description of the studied trials of Scots pine for the period 1988–2017. Mean (±standard deviation) monthly temperature (lines) and precipitation (bars) are shown. Figure S2. Climatic description of the studied provenances of Scots pine for the period 1945–1974. Mean (±standard deviation) monthly temperature (lines) and precipitation (bars) are shown. The fine dotted line represents 0 °C temperature. Figure S3. Residual chronologies of basal area increment (prewhitened time series of the biweight robust mean of relative additional basal area increment) of the studied provenances by trials for the period 1985–2017. Table S1. General description of field performance of the studied provenances of Scots pine in three trials in the hemiboreal zone in Latvia. Number of surviving trees, overall survival, mean tree height (H), stem diameter at breast height (DBH), standing volume (M), and ranking (according to tree height) are shown.

Author Contributions: Conceptualization, R.M. and Ā.J.; methodology, R.M. and V.S.; software, E.B. and P.Z.; validation, R.M., E.B., V.S.; formal analysis, D.J. and S.D.; investigation, D.J., S.D., P.Z.; resources, Ā.J.; data curation, D.J.; writing—original draft preparation, R.M. and P.Z.; writing—review and editing, Ā.J., V.S., E.B.; visualization, R.M., P.Z.; supervision, R.M., Ā.J.; project administration, R.M.; funding acquisition, R.M., Ā.J. All authors have read and agreed to the published version of the manuscript.

Funding: The study was funded by the Latvian Council of Science (grant number: lzp-2020/2-0416). Sampling and measurements were partially supported by the framework of post-doc studies in Latvia funded by the European Regional Development Fund (project number: 1.1.1.2.VIAA/1/16/108).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Data sharing not applicable.

Acknowledgments: We acknowledge the technical staff who helped with sampling and measurements. We acknowledge Renate Saleniece for proofreading the paper.

Conflicts of Interest: The authors declare no conflict of interest.

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BALTIC FORESTRY

https://balticforestry.lammc.lt
ISSN 1392-1355
eISSN 2029-9230

Baltic Forestry 2024 30(1): id 719
Category: Research article
https://doi.org/10.46490/BF719

The genetic and environmental variance of radial increment in Scots pine of south-eastern Baltic provenances in response to weather extremes

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Abstract

Intensification of weather anomalies, particularly those related to temperature in warming winters and moisture availability, have been identified as the major emerging climatic threats to forest ecosystems in the hemiboreal zone. Considering the large-scale nature of the threats, assisted migration and tree breeding appear as the most promising means for mitigating the climatic risks. However, for successful implementation of such means, information on the genetic control over the weather sensitivity of trees is needed. Local genetic adaptations of populations occur to maximize competitiveness and survival, while the differences in phenotypic plasticity, implying varying genotype by environmental interactions, can be utilized for the acquisition of locally targeted reproductive material. To gain initial (rough) estimates of genetic control and phenotypic plasticity of growth responses to weather anomalies, a set of seven native eastern Baltic provenances differing by productivity in five trials in Latvia and northern Germany were studied. Tree-ring widths were measured for 10–15 trees per provenance per trial. Relative growth changes and pointer year values were calculated to link changes in increment with weather anomalies and to estimate heritability on an annual basis by the methods of quantitative genetics. During the analysed period (1987–2017), four to seven trial- and provenance-specific pointer years (common relative growth changes) were estimated, which were mainly triggered by co-occurring anomalies in moisture availability and winter thermal regime. This implied resilience of the studied trees to singular weather anomalies, suggesting their adaptability. Furthermore, the heritability estimates peaked one to two years after the pointer years, implying that growth recovery and hence resilience rather than resistance was genetically controlled. Still, local variability of pointer years and heritability estimates portrayed explicit phenotypic plasticity of responses, implying the potential for breeding to locally improve weather tolerance of growth.

Keywords: *Pinus sylvestris*; local adaptation; phenotypic plasticity; growth recovery; tree-ring width; pointer years

Matisons, R., Krišāns, O., Jansone, D., Jansons, Ā. and Zeltiņš, P. 2024. The genetic and environmental variance of radial increment in Scots pine of south-eastern Baltic provenances in response to weather extremes. *Baltic Forestry* 30(1): id 719; https://doi.org/10.46490/BF719.

Received 29 July 2023
Revised 13 January 2024
Accepted 28 January 2024

Introduction

In north-eastern Europe, the intensification of weather extremes, particularly regarding the summer moisture regime, has been identified as the major risks for forest productivity (Allen et al. 2015), which can have carry-over and legacy effects (Jetschke et al. 2019, Schwarz et al. 2020). Under extreme environmental conditions, genetic effects and genotype by environment (G × E) interactions are intensifying, largely determining the survival and/or success of recovery (Taeger et al. 2013, Moran et al. 2017, Chauvin et al. 2019). Due to the local genetic adaptation of populations of widespread tree species, the susceptibility of trees to weather anomalies and to the climatic changes amplifying them, is increasing (Taeger et al. 2013, Aitken and Bemmels 2016, Isaac-Renton et al. 2018, Klisz et al. 2023). Still, the genetic differences can diminish if the conditions are explicitly marginal (Klisz et al. 2019). Nevertheless, the presence of local genetic adaptation is a precondition for successful forest breeding (Jansson et al. 2017, Moran et al. 2017), which is crucial for climate-smart management (Aitken and Bemmels 2016, Nabuurs et al. 2018). Furthermore, the G × E interactions have been revisited as the indicator of adaptability, as they are the measure of the phenotypic and hence the ecological plasticity of tree populations (Li et al. 2017, Moran et al. 2017, Ansarifar et al. 2020, Chmura et al. 2021, de la Mata et al. 2022). In this regard, quantification of genetic control over the traits relevant for adaptability is necessary (Li et al. 2017, Arnold et al. 2019), for which parallel provenance trials testing genotypes across extended environmental gradients, are advantageous (Leites et al. 2012, Leites and Benito Garzon 2023).

Morphometric and physiological traits have been commonly used for the quantification of the genetic and environmental effects on growth, quality, and sustainability of trees under certain environments (Burdon and Klapste 2019). However, such proxies indicate the conformity of genotypes with the past conditions including climatic gradients, which are being out-dated by the accelerating environmental changes (Meier et al. 2022). This is particular for the populations, which are managed conservatively (Aitken and Bemmels 2016, Jansson et al. 2017), especially under cold climates, where local adaptations can be narrow (Isaac-Renton et al. 2018, Matisons et al. 2019, Klisz et al. 2023). Hence analysis of the time series of increment is highly informative of the environmental sensitivity, as well as the intrinsic (e.g. ageing) effects on growth (Housset et al. 2018), aiding projections under a shifting environment (Li et al. 2017, Pennacchi et al. 2021).

Under temperate climate, tree growth is seasonal, and increment stores information on the underlying conditions, thus providing natural archives of environmental fluctuations (Speer 2010). Accordingly, retrospective analysis of increment is a source of highly detailed information regarding tree growth (Speer 2010, McCullough et al. 2017, Housset et al. 2018). In this regard, tree-ring width (TRW) is a particularly informative and sufficient proxy of tree growth and productivity (McCullough et al. 2017, Xu et al. 2017) and the underlying genetic effects (Housset et al. 2018). The TRW, though, is a product of several environmental, genetic, and ageing effects, hence diverse standardization techniques have been developed to deconstruct and partition the variance captured by the time series (Speer 2010, Jetschke et al. 2019). Furthermore, specific techniques, such as event/pointer year (PY) and resilience analyses, have been deployed for estimation of growth responses to environmental extremes/anomalies (Jetschke et al. 2019), thus allowing more elaborate assessment of the adaptability of trees (Arnold et al. 2019, Schwarz et al. 2020, de la Mata et al. 2022).

In the eastern Baltic Sea region, Scots pine (*Pinus sylvestris*) is an economically important tree species, which is though predicted to decrease in abundance, raising uncertainty about the growth of local populations (Buras and Menzel 2019). Considering that the climate in the region is temperate, meteorological and climatic control over the radial increment (TRW) is complex with winter thermal regime and summer moisture availability identified as the principal drivers of growth (Matisons et al. 2019, 2021a, Harvey et al. 2020). Considering the regional climatic gradient, local populations appear quite flexible in terms of inter-annual variation of increment under non-extreme conditions (Henttonen et al. 2014, Matisons et al. 2021a, 2021b). Nevertheless, the local populations also show genetic adaptation, and their sensitivity can relate to productivity, particularly regarding summer moisture availability (Martin et al. 2010, Taeger et al. 2013, Harvey et al. 2020). Considering weather anomalies, provenance-related differences have been demonstrated (Matisons et al. 2019, 2021b), while the estimates of genetic and phenotypic variance necessary for decision making concerning breeding have not been reported yet.

The study aimed to estimate the effect of genetic and environmental variance of Scots pine TRW in response to weather anomalies (e.g. cold winters, dry summers, etc.) from the eastern Baltic Sea region. Considering location under temperate moist continental climate, we hypothesized genetic effects to be stronger in response to extremes/anomalies in summer moisture regime. We also hypothesized local populations to show explicit G × E interaction indicating high phenotypic plasticity.

Material and methods

Trials

A set of five parallel provenance trials near Liepāja (LI), Zvirgzde (ZV), and Kalsnava (KA) in Latvia, as well as near Waldsieversdorf (WS) and Nedlitz (NL) in Germany (Figure 1, Table 1) were studied to assess the genetic and environmental effects on the growth responses to meteorological extremes/anomalies. The trials were established in 1975 under the collaboration of the USSR and the German Democratic Republic (Kohlstock and Schneck 1992, Jansons and Baumanis 2005). The trials contained a set of 36 common provenances of Scots pine originating from the region spanning 46–60° N and 11–30° E. The seed material was collected from 20–25 plus-trees at each provenance, which were open-pollinated and mostly

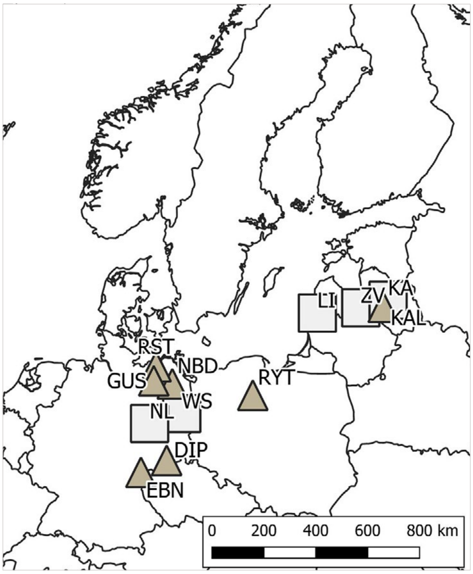

Figure 1. Location of the studied trials (squares; two letter notation) and origins of the provenances (triangles; three letter notation) of the south-eastern Baltic Scots pine

Table 1. Location and climatic description of the studied parallel provenance trials of eastern Baltic Scots pine established in 1975 under international collaboration

Code	LI	ZV	KA	WS	NL
Vicinity	Liepāja	Zvirgzde	Kalsnava/ Madona	Wald-sieversdorf	Nedlitz
Country	Latvia	Latvia	Latvia	Germany	Germany
Latitude, N	56°27'	56°39'	56°48'	52°32'	52°1'
Longitude, E	21°38'	24°22'	25°56'	14°3'	12°10'
Elevation, m a.s.l.	< 20	< 100	220	< 100	130
Soil type	Oligotrophic sandy podzol	Oligotrophic sandy podzol	Oligotrophic silty podzol	Mesotrophic brown	Mesotrophic brown
Mean annual temperature, °C	7.5	7.2	6.4	9.8	10.1
Mean temperature May–September, °C	15.0	15.2	14.8	16.9	17.0
Mean temperature January, °C	–1.9	–3.0	–4.2	0.5	1.3
Mean temperature July, °C	17.8	18.2	17.9	19.4	19.3
Mean annual precipitation sum, mm	789	659	689	568	542
Mean precipitation sum May–September, mm	353	333	349	290	274
Ewert's continentality index	42	46	48	42	39

managed stands, thus representing the local best performing genotypes. The provenances were planted according to a randomized block design, yet the size and number of the blocks differed between the countries. In the trials in Latvia, the provenances were represented by six blocks (replications) of 35 (5 × 7) trees, while in Germany by four blocks of 100 (10 × 10) trees.

The trials were situated on freely-draining oligotrophic sandy (Latvia) and mesotrophic silty podzolic (Germany) soils; the topography of all sites was flat, as typical for the lowland region. The trials were established by planting one-year-old containerized seedlings raised in local nurseries. The initial spacing of the planting was 2 × 1 and 2 × 0.5 m for the respective trials in Latvia and Germany. Initially, weed control of all trials was implemented if necessary, yet the thinning regimes differed. In Latvia, the trials have undergone a single thinning from below to 1800 trees ha^{-1} at the age of 21 years in 1996, while in Germany NL one year before sampling was thinned from below to 1100 trees ha^{-1}. In the WS trial, three thinnings have been implemented with the last one in the winter of 2013–2014, thus decreasing stand density to 900–1,200 trees ha^{-1}.

The studied trails represented subregional latitudinal and local continentality climatic gradients, thus subjecting the genotypes to an extended range of meteorological conditions (Arnold et al. 2019, de la Mata et al. 2022). The mean annual temperature ranged from 6.4°C in KA to 10.1°C in the NL trial (Table 1). In all sites, January and July have been the coldest and warmest months with the respective monthly temperatures ranging from –4.2 (in KA) to 1.3°C (in NL) and from 17.8 (in LI) to 19.4°C (in WS), respectively. The precipitation regime was comparable for all sites with the highest monthly precipitation falling during the summer (June–September) months, though the precipitation sums were higher (by ca. 22%) in the trials in Latvia compared to those in Germany. The climatic changes were mainly expressed as the warming related reduction of the dormancy period length and increasing heterogeneity of the summer precipitation regime resulting in the emergence and extension of drought conditions (Meier et al. 2022). From 1978 to 2017, several weather anomalies/extremes were recorded, which were generally comparable in Latvia and Germany (Table 2). In general, the weather anomalies were related to the inflow of warm/cold air masses during the dormancy period (November–April period), as well as to the conditions altering water availability during the vegetation period (May–September; Meier et al. 2022). Thought, the frequency of the anomalies tended to be higher in the first part of the reference period in Latvia, while in Germany, they were more evenly distributed, indicating ongoing marginalization of weather conditions.

Provenances, sampling, and measurements

To gain an insight into the genetic control and phenotypical plasticity of responses of increment to weather anomalies/extremes, a set of seven provenances (Figure 1), which were represented in the studied trials in Latvia and Germany, was selected based on inventory (in 2016). To account for the possible sensitivity-productivity relationships and to estimate conditions triggering plastic responses (Arnold et al. 2019, de la Mata et al. 2022), two low-performing, Dippoldiswalde (DIP) and Eibenstock (EBN), four high-performing, Güstrow (GUS), Rytel (RYT), Rostock (RST) and Neubrandenburg (NBD), and one local from Latvia, Kalsnava (KAL), provenances, which excelled in stem quality (Kohlstock and Schneck 1992, Jansons and Baumanis 2005), were selected (Table 3). The selection was based on the consolidated rankings of the field performance (Matisons et al. 2019). Considering the anticipated northward shift of vegetation zones (Buras and Menzel 2019), the selection was done from the perspective of the trials in Latvia; still, the rankings of the provenances were comparable across the trials (Matisons et al. 2021b). The low-per-

Table 2. Anomalies in monthly mean temperature (Temp.), precipitation sums (Prec.), and standardized precipitation evapotranspiration indices (SPEI) in Latvia and Germany for the period 1987–2017. The number in brackets shows the z-score of respective meteorological conditions. Anomalies for aggregate periods, mean values for winter (December–February), spring (March–April), summer (June–August), vegetation period (veg., May–September), as well as the climatic year from (ann., September–August) are also shown

Year	Latvia	Germany
1987	Temp. ann. (–3.0), Temp. Jan (–3.3), Prec. Oct (–1.8)	Temp. ann. (–2.5), Temp. veg. (–2.5), Temp. Jan (–2.8)
1988	-	Prec. Feb (2.3)
1989	-	SPEI ann. (–2.4), SPEI. veg. (–2.0)
1990	Prec. veg. (1.9), Prec. Sep (2.1)	Temp. Feb (1.8), Prec. Jun (2.0)
1991	Temp. May (–1.8)	Temp. May (–2.7), Temp. Jun (–1.8)
1992	SPEI summer (–2.1), Prec. Jun (–2.2), Temp. Oct (–2.2)	SPEI summer (–2.1), Prec. Mar (2.4), Temp. Oct (–1.9)
1993	Temp. summer (–2.1), Temp. May (2.3), Temp. Sep (–2.9), SPEI Jun (–1.8)	Temp. summer (–2.1), Temp. Nov (–2.6)
1994	Temp. Feb (–1.9), Prec. Jul (–2.1)	Prec. spring (2.5), Temp. prev. Nov (–2.6), Temp. Jul (2.0), Prec. prev. Dec (2.5)
1995	SPEI May (2.2), SPEI Jun (1.9)	-
1996	Temp. ann. (–1.8), SPEI ann. (–1.9), Temp. winter (–2.0), Prec. Aug (–2.0)	Temp. ann. (–2.4), Temp. winter (–2.2), Temp. veg. (–2.2), Prec. Jan (–1.9), Temp. Sep (–2.0)
1997	Temp. Apr (–1.9), SPEI Jun (1.8), Prec. Oct (2.0)	Temp. prev. Dec (–1.9), Temp. Apr (–2.2), Prec. Jan (–2.4)
1998	Prec. ann. (2.3), Temp. Aug (–1.9), Temp. Nov (–2.3)	Prec. Oct (2.7), Temp. Nov (–2.0)
1999	SPEI veg. (–2.0), Temp. Jun (2.0)	Temp. Sep (2.0)
2000	Temp. Apr (2.1), SPEI Oct (–2.1)	-
2001	-	Prec. Sep (3.0), Temp. Oct (1.8)
2002	Temp. veg. (2.0), Prec. Feb (1.9), Prec. Aug (–2.0), Temp. Oct (–2.2)	Prec. Feb (2.3), Prec. Oct (2.4)
2003	SPEI ann. (–2.3), Temp. prev. Dec (–2.0)	SPEI veg. (–1.9), Temp. Jun (1.9), Temp. Oct (–2.0)
2005	Temp. Mar (–1.8)	-
2006	SPEI ann. (–2.5)	Temp. Jul (2.0), Temp. Sep (2.1)
2007	Temp. prev. Dec (1.9), Prec. Jan (2.5)	Temp. ann. (2.4), Prec. veg. (2.5), Prec. Jan (2.4)
2008	-	Prec. Apr (3.1), SPEI Jul (–1.9)
2009	-	Temp. Apr (2.4), Prec. Oct (1.9)
2010	SPEI veg. (2.1), Temp. Jan (–2.1), Temp. Jul (1.9)	Temp. Jan. (–1.9), temp. May (-1.8), temp. Jul (1.8), Prec. Aug (3.4)
2011	Prec. prev. Dec (2.7), Prec. Nov (–1.8)	Temp. prev. Dec (–2.5), Temp. Apr (2.2), Prec. Jul (2.1), Prec. Nov (–2.1)
2012	-	Prec. Jul (1.8)
2013	Temp. Mar (–2.0), Temp. May (1.9)	Temp. Mar (–2.4)
2014	Prec. Nov (–1.8)	Temp. spring (1.8)
2015	Prec. Jun (–1.8), Prec. Oct (–2.1)	Temp. Aug (2.1)
2016	-	Prec. summer (2.7), Temp. prev. Dec (2.1), Temp. Sep (2.1)

forming provenances originated from the Ore mountains (DIP and EBN), where the climate was cooler and harsher compared to the trials in Latvia, and particularly in Germany. The high-performing provenances originated from the coastal lowland conditions of northern Poland and northern Germany (North European Plain), where the climate was mild with pronounced coastal features (Kottek et al. 2006).

In each trial, one to three visually healthy, undamaged and non-leaning dominant/co-dominant trees per provenance per block were selected. Accordingly, 10–15 trees per provenance per trial were selected in total. Block edge trees were omitted if possible. Using a Pressler borer, two opposite cores from each tree were collected at breast height from random opposite directions. In the laboratory, increment cores were mounted, their surface was prepared by cutting, and TRWs were measured manually using LinTab 6 (RinnTech, Heidelberg, Germany) measurement table. The measurements were done by the same person with an accuracy of 0.01 mm.

Data analysis

To ensure the quality of the measurements and hence the reliability of the dating, the time series were crossdated graphically and statistically using the computer program COFECHA (Holmes 1983). Agreement metrics, expressed population signal (EPS; Wigley et al. 1984), signal-to-noise ratio (SNR), mean interseries correlation (*r*-bar), synchrony index (GLK), mean sensitivity (MA), and gini coefficient were calculated to describe common environmental forcing of radial increment for each provenance by trial (Bunn 2008, Speer 2010). To quantify the responses of trees to meteorological anomalies/extremes, PY analysis according to the approach described by Jetschke et al. (2019) and Schwarz et al. (2020), which implies complex assessment, was used. To estimate the severity of growth changes in a particular year, TRW was relativized with respect to the preceding five years, as the trees were quite young showing modest growth variability. According to

Table 3. Location and climatic description of the origin of the studied provenances of eastern Baltic Scots pine differing by productivity in trials in the southeastern Baltic Sea region

Code	DIP	EBN	KAL	NBD	RST	GUS	RYT
Name	Dippoldiswalde	Eibenstock	Kalsnava	Neubrandenburg	Rostock	Güstrow	Rytel
Latitude, N	50°33'	50°18'	56°28'	53°31'	54°9'	53°31'	53°27'
Longitude, E	13°35'	12°17'	25°36'	13°16'	12°10'	12°10'	18°1'
Elevation, m	590	710	190	< 50	< 20	< 50	130
Mean annual temperature, °C	6.6	5.9	5.5	8.5	8.6	8.5	8.0
Mean May-September temperature, °C	13.6	12.6	14.4	15.4	15.2	15.2	15.4
Mean January temperature, °C	–2.6	–3.0	–6.5	–0.3	0.2	–0.1	–2.3
Mean July temperature, °C	15.3	14.7	17.0	17.7	17.3	17.3	17.7
Mean annual precipitation sum, mm	804	994	624	577	570	599	546
May–September precipitation sum, mm	402	499	328	290	284	300	310

the relativized TRW (relative growth change), tree-level event year time series were constructed. Considering the location of the studied trials under mild climates (Kottek et al. 2006), moderate relative growth change thresholds (40% for positive and 25% for negative changes) were used to determine "significance" of the individual tree event years (Jetschke et al. 2019, Schwarz et al. 2020). Due to the differences in climate, PYs were estimated for each trial in years when more than 50% of the series showed coherent (positive or negative) signatures. The PY values (proportion of trees with a signature year) were calculated for trials. To depict the differences in responses among the provenances, the mean relative growth deviation (van der Maaten-Theunissen et al. 2021) across the time series of relative growth change for each provenance was calculated.

To relate the changes in increment of the provenances with weather conditions across the stands, gridded climatic data were used (CRU TS4; Harris et al. 2020). The mean monthly temperature, precipitation and potential evapotranspiration datasets for the grid points closest to the trials (at < 0.25° distance) were extracted from the online repository. The standardized precipitation evapotranspiration index (SPEI; Vicente-Serrano et al. 2010) was calculated to characterize the drought conditions with the respect to three-month period. Ewert's thermal continentality index (Szymanowski et al. 2017) was calculated for the description of the climate of the trials. For the period 1987–2017, *z*-scores were calculated for the weather variables to evaluate their deviance from the "norm", hence the anomaly. The anomaly/extreme was considered if the absolute *z*-score of the variables exceeded 2.0.

For the description of genetic control over the responses of increment in the case of years with weather anomalies/extremes, as well as in the "ordinary" years, broad sense heritability (H^2) and provenance coefficient of variation (*CVP*) were calculated based on variance components of the relative growth change for each year. H^2 was calculated as the ratio of the provenance variance from the total random (provenance and residual) variance (Falconer and Mackay 1996, Loha et al. 2006, de la Mata et al. 2022). The *CVP* was calculated as the ratio of provenance standard deviation (square root of variance) and the phenotypical mean of the relative growth change (Loha et al. 2006). Considering that the effects of meteorological conditions on growth responses of provenances might differ due to local genetic adaptations, variance components were extracted on an annual basis. For this, simple mixed effects models were used for each trial with provenance used as a random (genetic) effect and the replication (within a trial) used as the fixed (environmental) effect. To generalise genetic and environmental control over growth changes across the entire reference period, more elaborate mixed models were used for the extraction of variance components:

$$y = \mu + y_i + r_j + y_i\!:\!r_j + t_{k[j]} + (P_l) + (P_l\!:\!y_i) + (P_l\!:\!r_j) + \varepsilon\,, \quad (1)$$

where y_i is the fixed effect of year, r_j is the fixed effect of replication (within a trial), $y_i : r_j$ is the fixed effect of the year by replication interaction, $t_{k[j]}$ is the fixed effect of a tree, (P_l) is the random effect of provenance, $(P_l : y_i)$ is the random effect of provenance by year interaction, and $(P_l : r_j)$ is the random effect of provenance by replication interaction.

The data analysis was conducted in R, version 4.2.2 (R Core Team 2022) using the packages "dplR" (Bunn 2008), "pointRes" (van der Maaten-Theunissen et al. 2021), and "lme4" (Bates et al. 2015).

Results

Representability of the dataset

The crossdated datasets contained a time series of 427 trees (9–18 trees per provenance per trial), which were 93% of those initially measured (≥ 86% per provenance per trial; Table 4). The mean TRW matched the field performance of the provenances, though the medians were smaller, implying a skewed distribution. Such skewness was apparently related to the age trend of the time series (Figure 2), which differed among the trials. The age trend in TRW was explicit in the LI and ZV trials (Latvia), while in the trials in Germany, age-related decrease in TRW was rapid, after which increment stabilized, yet was generally slower.

Table 4. General description (mean values and the range of the metrics across the trials) of the crossdated datasets of tree-ring width time series. r-bar – mean interseries correlation, EPS – expressed population signal, SNR – signal to noise ratio, ar1 – first-order autocorrelation, gini – the gini coefficient, MS – mean sensitivity of the series, and GLK – mean synchronicity index. The signal metrics represent spline-detrended series

	DIP	EBN	GUS	KAL	NBD	RST	RYT
Mean tree-ring width, mm	2.07 (1.90–2.43)	2.14 (1.93–2.73)	2.44 (2.21–3.11)	2.29 (1.97–3.11)	2.47 (2.15–3.20)	2.35 (2.08–2.86)	2.67 (2.23–3.18)
Median tree-ring width, mm	1.79 (1.58–1.88)	1.94 (1.77–2.35)	2.20 (2.05–2.65)	2.10 (1.88–2.65)	2.26 (1.95–2.71)	2.14 (1.95–2.38)	2.43 (2.14–2.60)
St. dev. tree-ring width, mm	1.02 (0.84–1.45)	0.96 (0.71–1.19)	1.00 (0.79–1.44)	0.90 (0.60–1.44)	0.95 (0.66–1.39)	0.94 (0.67–1.38)	1.02 (0.68–1.58)
Crossdated trees	11 (9–13)	11 (9–13)	12 (10–15)	12 (10–15)	15 (14–18)	15 (14–17)	13 (10–16)
r-bar	0.33 (0.22–0.45)	0.33 (0.25–0.41)	0.35 (0.25–0.43)	0.34 (0.31–0.43)	0.39 (0.30–0.47)	0.42 (0.32–0.48)	0.36 (0.30–0.47)
EPS	0.86 (0.84–0.91)	0.85 (0.84–0.88)	0.87 (0.85–0.92)	0.86 (0.85–0.92)	0.91 (0.86–0.94)	0.91 (0.87–0.94)	0.88 (0.85–0.91)
SNR	5.49 (3.08–9.67)	5.65 (3.83–7.49)	6.55 (4.37–11.26)	6.23 (5.24–11.26)	10.58 (6.33–15.99)	11.56 (6.46–15.6)	7.41 (4.25–10.54)
ar1	0.29 (0.20–0.36)	0.28 (0.12–0.44)	0.28 (0.20–0.35)	0.24 (0.14–0.35)	0.25 (0.09–0.44)	0.29 (0.25–0.38)	0.28 (0.14–0.40)
gini	0.15 (0.13–0.17)	0.14 (0.13–0.15)	0.12 (0.10–0.15)	0.13 (0.10–0.15)	0.13 (0.11–0.15)	0.14 (0.12–0.16)	0.12 (0.10–0.15)
MS	0.25 (0.23–0.30)	0.24 (0.2–0.31)	0.22 (0.19–0.27)	0.24 (0.19–0.27)	0.24 (0.19–0.30)	0.23 (0.19–0.28)	0.22 (0.19–0.26)
GLK	0.67 (0.63–0.70)	0.69 (0.65–0.76)	0.70 (0.68–0.71)	0.68 (0.65–0.71)	0.68 (0.66–0.73)	0.72 (0.69–0.75)	0.70 (0.67–0.72)

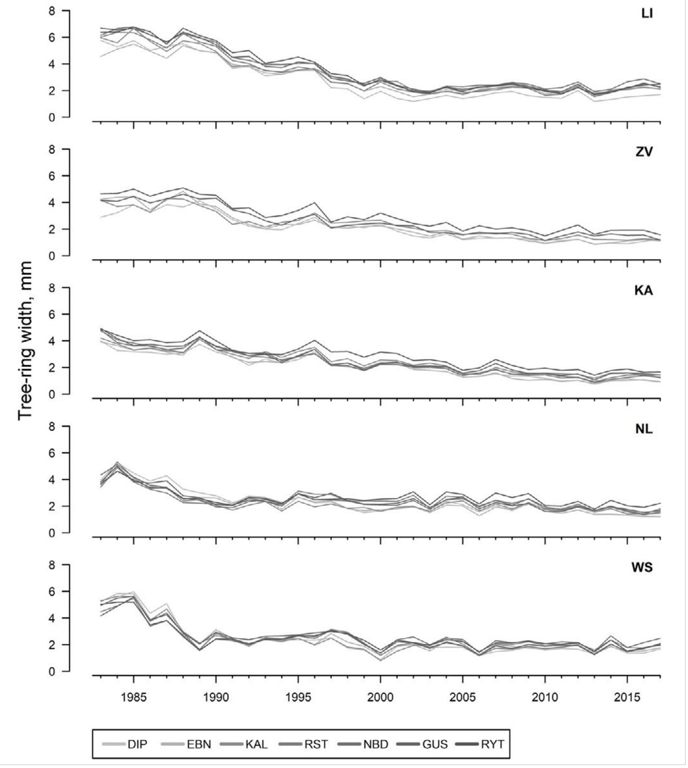

Figure 2. Mean time series of tree-ring width for the studied provenances of Scots pine in trials in Latvia and Northern Germany for the period 1983–2017

The TRW of the studied provenances showed responsiveness to environmental fluctuations, as indicated by the inter-annual variation (standard deviations) and moderate MS, though the variation was limited, hence as the gini coefficient was low (Table 4). Nevertheless, the EPS of the crossdated datasets tended to be higher for the more productive provenances; the growth patterns of trees of the less productive provenances were more individual showing lower agreement metrics. Generally, the *r*-bar was moderate irrespectively of a trial, yet EPS exceeded or approached the arbitrary threshold of 0.85, highlighting the representativeness of the datasets. The synchrony of the datasets was similar as GLK were high and varied slightly. The strength of the environmental signal, as shown by the SNR, was generally low to moderate, although the NBD and RST showed nearly two times higher values, indicating clearer environmental forcing. The autocorrelation was low (ar1 < 0.31) indicating weak buffering effect of the preceding growth on increment.

Meteorological forcing of increment

During the analysed period of 1988–2017, 16 PYs were "significant" at the trial level, and all of them were negative though mild, considering the low thresholds set for the calculations (Figure 3). The number of the "significant" PYs ranged from three to seven in KA and WS trials, respectively. Occurred PYs were largely trial-specific, indicating local growth patterns, though half of the PYs were the same in two or three trials, indicating some regional signatures. The temporal distribution of the "significant" PYs differed between the trials; in LI and particularly NL the PYs occurred at the beginning of the analysed period, when trees were juvenile, while throughout the period in the others. In most of the "significant" PYs, the provenances generally showed coherent changes in growth responses, as indicated by the mean growth deviations. Still, in the WS trial, the mean growth deviations tended to follow productivity of the provenance (in 1992, 2000, 2006 and 2013), hinting at some sensitivity-productivity relationships. The plasticity of increment of the more productive provenances was also indicated by the regular occurrence of "significant" deviations.

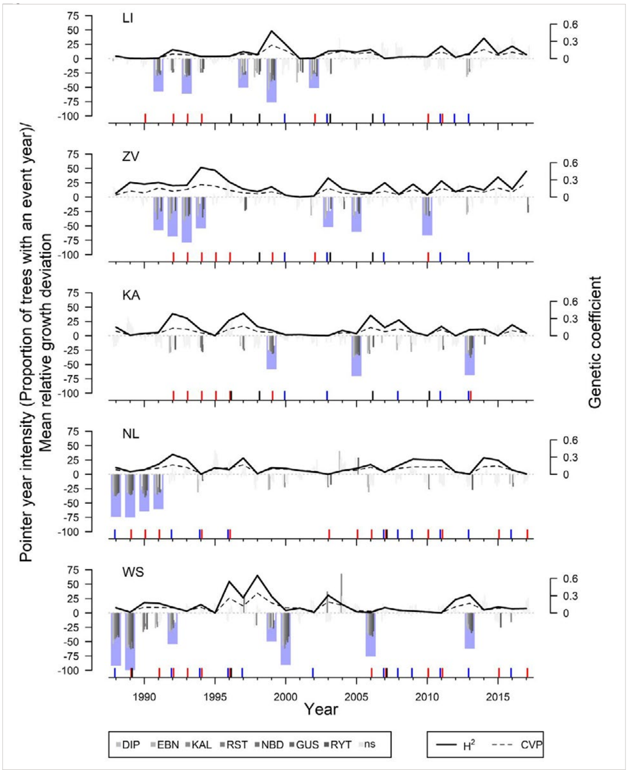

Figure 3. Estimated pointer year values (proportion of trees showing "significant relative growth changes") for trials (wider blue bars) and mean growth deviation for the studied provenances (narrow bars), as well as the broad sense heritability (H^2; solid line, secondary axis) and provenance coefficient of variation (*CVP*; dashed line, secondary axis). ns – non "significant". The red, blue, and black inside ticks on the horizontal axis indicate years with weather anomalies ($|z\text{-score}| \geq 2.0$) in temperature and precipitation in summer (May–August), winter (December–March), as well as at the annual scale (previous September to August)

The relationships between the meteorological anomalies/extremes and the responses of radial increment were complex in their character (Figure 3). The timing of the PYs indicated both immediate and delayed responses to weather anomalies, which varied depending on the underlying meteorological conditions, as well as the provenances. In the LI trial (Latvia), the PYs were associated with cold or dry springs and summers in the years of growth or the preceding years (Table 2). In the ZV trial, low-temperature anomalies were related to the PYs, especially if they were preceded by dry spells in the previous summer. Cold spells during the dormancy periods were primarily associated with the PYs in the more frigid climate of the KA trial, with moisture deficit affecting local and low-performing provenances. In the warmer climate of the NL trial (Germany), the PYs at a juvenile stage coincided with extreme cold years followed by dry years. Individual provenances also showed some responsiveness to summer heat. In the WS trial, the strongest PYs occurred in response to dry and hot summers, while spring temperature coincided with the PYs during the later part of the analysed period. However, the decline in growth in 2000 was not related to a weather anomaly on the monthly scale.

Genetic controls over growth responses

As shown by the heritability coefficients (H^2 and *CVP*), the genetic control of growth changes were largely related to tree recovery, as its expression was delayed and occurred with a one- or two-year lag after a weather anomaly (Figure 3). Hence, during the PYs, the heritability coefficients were generally low. Furthermore, the manifestation of the genetic control differed by years and trials/sites, while being stronger after the years with several weather anomalies, especially, the mixture of cold and dry conditions. During the analysed period, the H^2 ranged from low to high, yet the *CVP* was lower and reached only moderate values, indicating limited genetic variability. In the LI trial, the genetic coefficients peaked in 1999, which coincided with the strongest PY, which was preceded by the years with cold anomalies (Table 2). Weaker peaks in genetic coefficients occurred also in 1992, 2011, 2014, and 2016 which were preceded by low-temperature or moisture availability anomalies. In the ZV trial, H^2 and *CVP* were overall higher and fluctuated annually. Nevertheless, the coefficients peaked in 1994, 1995, 2003, and 2017, as the trees were recovering from colder and/or dryer summers than usual. In the KA trial, cold conditions in spring/summer and dry summers preceded and co-occurred with the peaks in 1992, 1993, 1997, and 2006. The peak in 1997, however, might be related to response to thinning.

Although German trials occurred in the similar climates (Table 1), genetic control over the increment varied locally, as the peak genetic coefficients explicitly differed between the WS and NL trials (Figure 3). In the NL trial, the genetic indices peaked in 1992, 1997, 2009–2011, and 2014, generally following co-occurring cold and moisture regime anomalies (Table 2). Four explicit peaks in the genetic coefficients were estimated in the WS trial in 1996, 1998, 2003, and 2012–2013. The earlier two ones could explicitly be related to the responses and recovery after the cold years (1996 and 1997). The peak in 2003 indicated direct response to drought conditions, which were aggravated by heat. Complex effect of cold spells and water availability was associated with the later peak.

The variance components when generalized over the studied period showed only a slight effect of provenance on increment (Table 5), as the residual variance, which arose from the uncontrolled conditions, was excessive. Nevertheless, the variance components highlighted the plasticity of the genotypes in terms of growth changes as the variance of G × E interactions exceeded that of provenance up to several times. The interaction variances, however, were generally comparable among the trials indicating coherent plasticity of the genotypes (provenances), although the provenance by trial (G × E) interaction was higher in the ZV trial. Hence, this supported the local specifics in responses of radial increment to weather anomalies.

Discussion

Controls of increment

The crossdated datasets of TRW were representative of environmental effects (EPS > 0.85; Table 4), allowing assessment of interannual weather-growth relationships (Wigley et al. 1984). This was supported by the intermediate MS, although the interannual variation was limited as shown by the gini coefficient (Speer 2010). The strength of the environmental signals (SNR) was moderate, suggesting the effects of local conditions on growth (Wigley et al. 1984). Still, the TRW series within the trials were synchronous (moderately high GLK), indicating the magnitude of fluctuations to be sensitive to the environment. The autocorrelation in the detrended TRW for the region (cf. Matisons et al. 2021a) was lower than estimated, suggesting plastic growth responses (Speer 2010). Apart the edaphic conditions and stand density, the differences in the age trends in TRW among the trials (Figure 2) might be related to the decrease in productivity with a warmer and drier climate (Table 1). Nevertheless, the provenance-related differences in environmental signal strength (Table 4) suggested genotypes to differ by growth strategy (Martin et al. 2010, Breed et al. 2013). The high-performing genotypes likely maximized growth via plasticity in terms of synchronizing responses to common weather drivers (Cavin and Jump 2017), while the low-performing ones appeared more sensitive to micro-site conditions (Martin et al. 2010, Matisons et al. 2019).

The trials were situated in sites with temperate, yet generally mild climate and the conditions have been optimized for tree growth (Table 1), hence the PYs (Figure 3) were moderate, considering the low thresholds used in the calculation (Jetschke et al. 2019, Schwarz et al. 2020). Such PY values suggested tolerance of the trees to current weather anomalies, which largely correspond to the on-going climatic changes (Taeger et al. 2013, Klisz et al. 2019, Meier et al. 2022). The identified PYs were negative and tended to be consistent for the provenances (Figure 3), implying the effects of weather anomalies acting as stacking stresses (Harvey et al. 2020, Matisons et al. 2021a). The occurrence of PYs (Figure 3) indicated modulating effects of local and genetic effects on growth (G × E interaction), suggesting adaptability of the genotypes (Moran et al. 2017, Ansarifar et al. 2020, de la Mata et al. 2022). Still, the presence of PYs, which were common for some trials (Figure 3) presumed large-scale limiting weather effects (Henttonen et al. 2014, Harvey et al. 2020, Schwarz et al. 2020).

The provenance-specific growth releases occurred following anomalies (Figure 3) suggesting the ability of the more productive genotypes (e.g. RYT, GUS) to utilise ecological opportunities (Matisons et al. 2019) and likely increase competitiveness (Loehle 1998). Furthermore, the presence of the provenance specific changes in growth rate (Figure 3), both positive and negative, implied effects of local adaptation (Loha et al. 2006, Moran et al. 2017, Chauvin et al. 2019), which differed by trial, revealing complex interactions with local conditions (Li et al. 2017, Chmura et al. 2021, Matisons et al. 2021a), especially in the harsher climate (KA trial; Table 1). Still, the consistent responses of the provenances in the PYs in the WS trial (Figure 3) suggested that in a warmer and dryer climate (Table 1), relationships between the sensitivity to anomalies and productivity can intensify (Cavin and Jump 2017, Tei et al. 2017, Xu et al. 2017).

In the eastern Baltic Sea region, the weather-growth relationships are complex, as the effects of winter and late summer thermal regimes interact with moisture availability during the growing period (Taeger et al. 2013, Henttonen et al. 2014, Harvey et al. 2020, Matisons et al. 2021a). Accordingly, anomalies in these weather conditions were estimated as the underlying conditions for the PYs (Figure 3, Table 2). The complexity of weather drivers of the PYs implies varying limitation of increment, as the conditions divert from the optimum, resulting in disproportional effects (Way and Oren 2010, Tei et al. 2017, Wilmking et al. 2020), and hence inconsistencies in correspondence of the PYs and weather anomalies (Figure 3). Though, most of the PYs were related to multiple anomalies (Figure 3), suggesting cumulative effects and robustness of TRW regarding single/short-time events. Weather conditions can have carryover effects on increment (Way and Oren 2010), thus explaining the delayed occurrences of PYs (Figure 3), as assimilates might be allocated to recovery rather than invested in growth (Brunner et al. 2015).

Although droughts are globally emerging threats to tree growth (Allen et al. 2015, Isaac-Renton et al. 2018), in the trials in Latvia and Germany, the anomalies in winter thermal regime still were the strongest triggers of the genetic effects (Figure 3, Table 2). The influence of anomalies in winter temperature was persistent despite the explicit warming during the dormancy period (Harvey et al. 2020), confirming intensifying cold damage in warming climate (Gu et al. 2008). Warmer conditions can affect tree dormancy and reduce cold hardening, thus increasing susceptibility to cold spells, as well as increase in respiratory nutrient loss (Ögren 1997, Beck et al. 2004). Still, drought and the underlying conditions were related to the abrupt changes in TRW (Figure 3, Table 2) with their effects tending to increase as suggested by the most recent peaks in heritability in the trials in Germany (Figure 3). This supports the necessity for proactive climate-smart management (Nabuurs et al. 2018). Though, the sensitivity of trees to weather conditions and their anomalies often increase with age, hence the moderate pointer-year intensity (Figure 3) might be related to higher tolerance of younger trees (Carrer and Urbinati 2004). On the other hand, the sensitivity of trees to frost/cold is higher at younger age (Klisz et al. 2022), which might be related to the PYs in response to temperature in spring (Table 2).

Adaptability of native genotypes

Local genetic adaptation (i.e. genetic variance, H^2) and phenotypic plasticity (i.e. G × E interaction variance), which determine adaptability (Arnold et al. 2019, Pennacchi et al. 2021), appeared unbalanced (Table 5), supporting the increase in local variability of growth patterns and disproportional effects of accelerating environmental changes (Ansarifar et al. 2020, de la Mata et al. 2022). The locally specific peaks in heritability estimates (Figure 3), as well as the variance partitioning (Table 5) revealed explicit phenotypic plasticity of the genotypes across the studied gradient, suggesting some adaptive potential (Moran et al. 2017, Chauvin et al. 2019). The phenotypic plasticity of radial increment has been related to the productivity and resilience of genotypes due to the efficient redistribution of resources between growth and defence (e.g. hydraulic security) (Corcuera et al. 2011, de la Mata et al. 2022). When the entire period was considered, the genetic (provenance) variance was low likely due to the G × E interaction (Table 5), as well as the excessive random variance indicating explicit effects of micro-site conditions (Ansarifar

Table 5. The share of the genetic (provenance-related) variance components from the total random variance for relative growth changes of eastern Baltic Scots pine provenances was generalised over the analysed period of 1988–2017

	LI	ZV	KA	NL	WS
Provenance by year interaction	0.030	0.059	0.036	0.027	0.046
Provenance by replication interaction	0.009	0.031	0.014	0.006	0.013
Provenance	0.003	0.003	0.004	0.004	0.003
Residual	0.958	0.907	0.947	0.963	0.938

et al. 2020, Chmura et al. 2021). Nevertheless, moderate to high heritability was estimated on an annual basis indicating specific genetic adaptation (Figure 3).

The lagged peaks in the heritability estimates after the PYs (Figure 3) implied that the growth recovery potential has been subjected to the local genetic adaptation (Moran et al. 2017); though, tolerance analysis was not performed due to inconsistency of the lags (Schwarz et al. 2020). The synergic effect of weather anomalies on the heritability estimates (Figure 3) complied with the multifactorial regulation of the growth plasticity and recovery (efficiency and period) (Pennacchi et al. 2021, Vuosku et al. 2022). Accordingly, local genetic adaptation can be related to cumulative weather effects and hence the ability to cope with multiple stresses (Ansarifar et al. 2020, Chmura et al. 2021), which have likely contributed to productivity (Way and Oren 2010) and are increasingly important under the anticipated climatic changes (Li et al. 2017). The multifactorial genetic controls under optimal growing conditions (de la Mata et al. 2022, Vuosku et al. 2022) have likely caused the estimates of H^2 and *CVP* to be intermediate and low, respectively. The low heritability estimated at the PYs (Figure 3) implied uniform resistance of increment of the local populations to growth changes, supporting the regional synchronization of sensitivity (Cavin and Jump 2017). Nevertheless, the sensitivity to non-extreme fluctuations in moisture availability on an annual basis has been shown to be subjected to local adaptation (Matisons et al. 2021b), supporting the current estimates.

The estimation of genetic control overgrowth recovery (Figure 3), which is a major determinant of resilience and productivity of stands (Schwarz et al. 2020, Leites and Benito Garzon 2023) supported the potential of tree breeding to improve sustainability of forests regarding intensifying weather anomalies (Jansson et al. 2017, Nabuurs et al. 2018, Burdon and Klapste 2019). The local effects (Figure 3, Table 5) implied the limited breeding efficiency to alter tolerance to meteorological anomalies at a wider scale (Loha et al. 2006, Li et al. 2017, de la Mata et al. 2022). Still, the explicit phenotypic plasticity (G × E interaction) indicated the potential of targeted breeding for local improvements by applying semiconservative (intra-regional) assisted migration (Corcuera et al. 2011, Breed et al. 2013, Aitken and Bemmels 2016, Li et al. 2017, Chmura et al. 2021). However, the selection of the provenances, which generally showed above-average performance, might have introduced some bias in variance partitioning and hence the heritability estimates at the trial level (Falconer and Mackay 1996, Leites et al. 2012). As the study was based on a limited set of genotypes, the upscaling of the results; however, should be precautious (Loha et al. 2006, Arnold et al. 2019, Chmura et al. 2021).

Conclusions

Considering that genotypes from the mid-part of the distribution of the species growing under comparable conditions were analysed, radial growth lacked explicit sudden changes evidencing the conformity of the genotypes with the environments, hence their adaptability. Furthermore, multiple weather anomalies were needed to cause a growth decline, which implied a high tolerance for growth. Nevertheless, the co-occurrence of weather anomalies triggered the expression of genetic differences, especially regarding the recovery of growth, which, however, strongly interacted with environmental conditions. Due to explicit phenotypic plasticity arising from the G × E interactions, targeted breeding might improve tolerance of reproductive material regarding weather anomalies locally. Although, the limited set of the genotypes analysed implies that the estimates might be biased. Still, the current estimates suggest that more detailed analysis based on progeny data, as well as under-projected future climates, appears advantageous for more accurate evaluation.

Acknowledgements

The study was funded by JSC 'Latvia's State Forests' within the framework of research project 'Effect of climate change on forestry and associated risks' (grant No. 5-5.9.1_007p_101_21_78). The preparation of the manuscript was supported by the European Social Fund project 'LUA's transition to the new doctoral funding model' (grant No. 8.2.2.0/20/I/001).

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