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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

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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 Waldsiefersdorf (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.

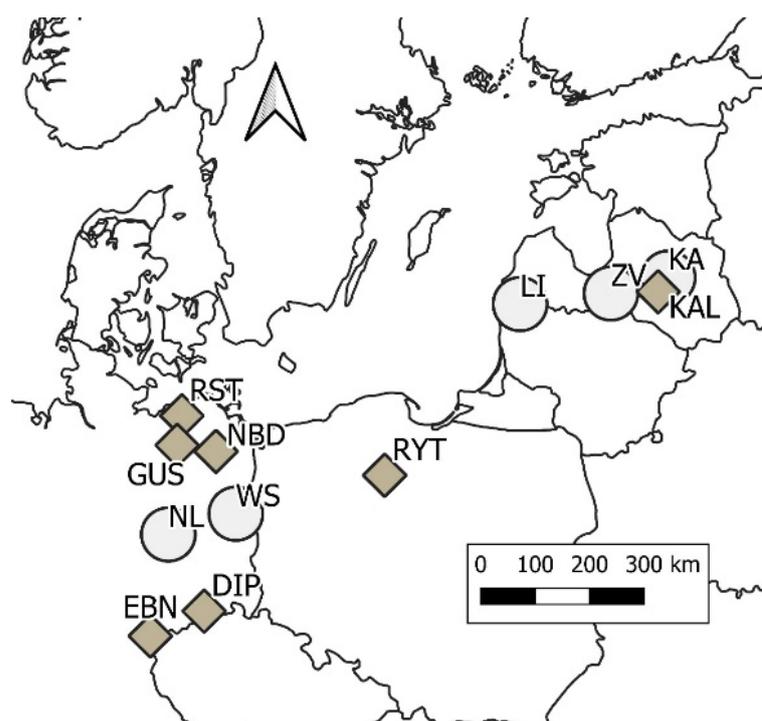


Figure 1. Location of the studied trials (circles) and origins of the studied provenances (squares) of the south-eastern Baltic Scots pine.

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 sub-regional 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 \pm 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 \pm 0.6	7.2 \pm 0.7	6.4 \pm 0.7	9.8 \pm 0.7	10.1 \pm 0.7
Mean May–September temperature, °C	15.0 \pm 0.7	15.2 \pm 0.8	14.8 \pm 0.8	16.9 \pm 0.7	16.9 \pm 0.7
Mean January temperature, °C	−1.9 \pm 2.4	−3.0 \pm 2.6	−4.2 \pm 2.7	0.5 \pm 2.5	1.3 \pm 2.4
Mean July temperature, °C	17.8 \pm 1.6	18.2 \pm 1.6	17.9 \pm 1.6	19.4 \pm 1.6	19.3 \pm 1.7
Mean annual precipitation sum, mm	789 \pm 91	659 \pm 75	689 \pm 81	568 \pm 80	542 \pm 73
May–September precipitation sum, mm	353 \pm 71	333 \pm 63	349 \pm 66	290 \pm 66	274 \pm 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 \pm 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 \pm 0.5	5.9 \pm 0.7	5.5 \pm 0.8	8.5 \pm 0.7	8.6 \pm 0.7	8.5 \pm 0.7	8.0 \pm 0.7
Mean May–September temperature, °C	13.6 \pm 0.7	12.6 \pm 0.8	14.4 \pm 0.8	15.4 \pm 0.7	15.2 \pm 0.7	15.2 \pm 0.8	15.4 \pm 0.7
Mean January temperature, °C	−2.6 \pm 2.4	−3.0 \pm 2.3	−6.5 \pm 3.7	−0.3 \pm 2.3	0.2 \pm 2.1	−0.1 \pm 2.3	−2.3 \pm 2.6
Mean July temperature, °C	15.3 \pm 1.2	14.7 \pm 1.3	17.0 \pm 1.2	17.7 \pm 1.3	17.3 \pm 1.2	17.3 \pm 1.3	17.7 \pm 1.3
Mean annual precipitation sum	804 \pm 68	994 \pm 101	624 \pm 77	577 \pm 75	570 \pm 81	599 \pm 79	546 \pm 73
May–September precipitation sum	402 \pm 32	499 \pm 60	328 \pm 66	290 \pm 48	284 \pm 51	300 \pm 50	310 \pm 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:

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

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:

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

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:

$$PCV = \frac{\sqrt{\sigma_p^2}}{\bar{y}} \quad (3)$$

where σ_p —variance component of provenance and \bar{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% ($\geq 86\%$ 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, \bar{r} —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
\bar{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.

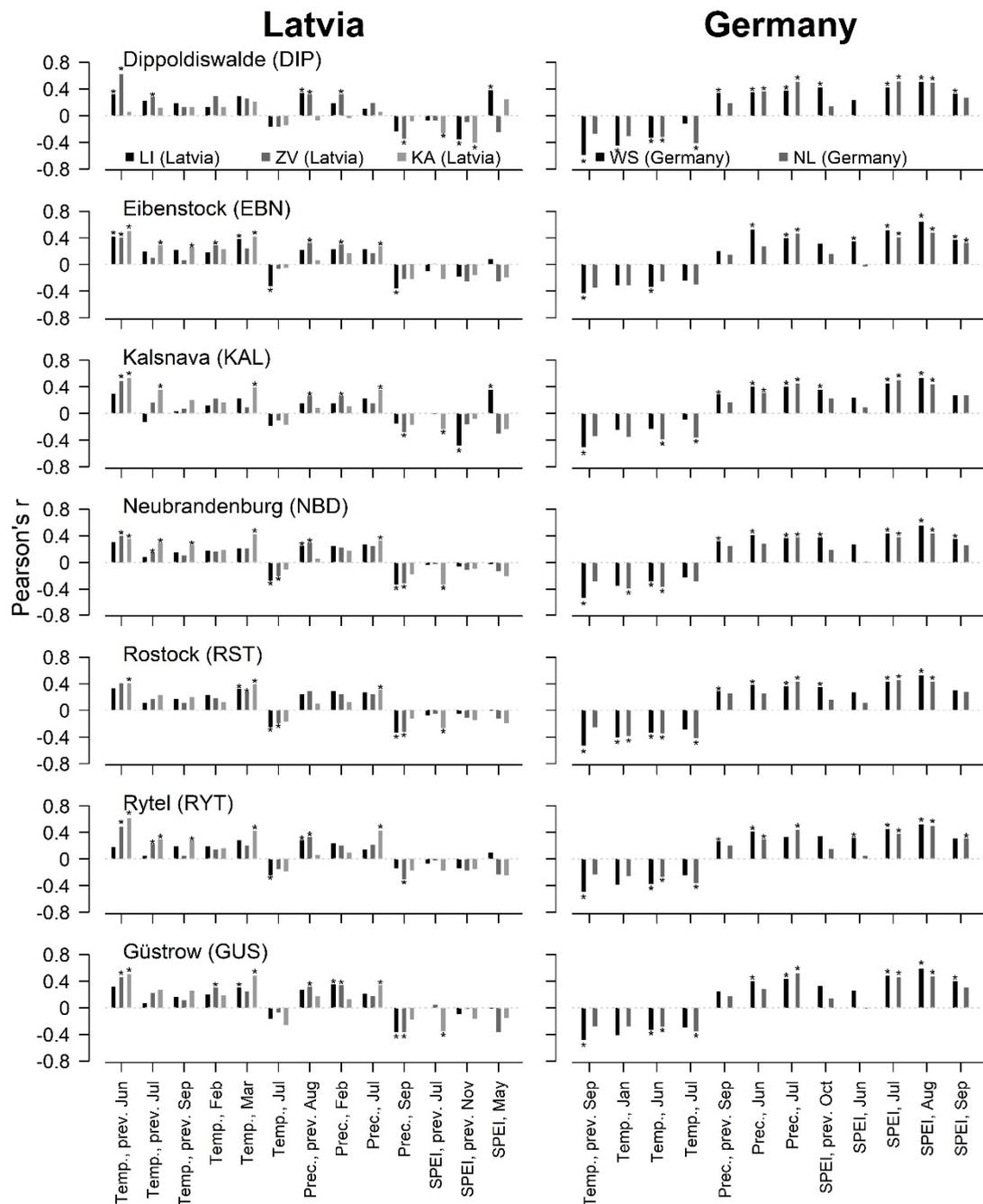


Figure 2. Bootstrapped Pearson correlation coefficients between the chronologies (prewhitened time series of the biweight robust mean) of basal area increment of the studied provenances of Scots pine and individual meteorological variables for the period 1985–2017 by trials (local weather data tested). 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 ($H^2 \pm$ 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 methylation 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 (\pm 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 (\pm 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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