

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

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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 ($G \times E$) 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 $G \times E$ 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, Ansarifard 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 var-

iance 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 $G \times E$ 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 Waldsiefersdorf (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

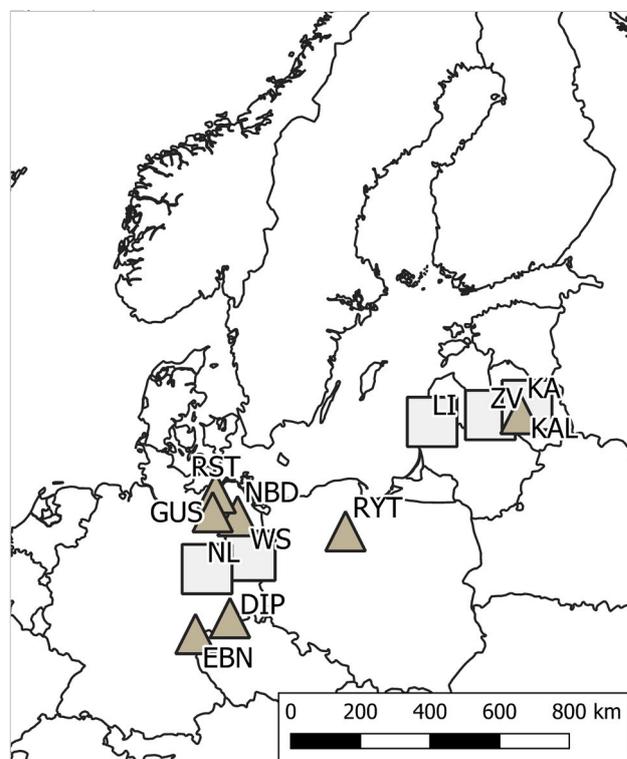


Figure 1. Location of the studied trials (squares; two letter notation) and origins of the provenances (triangles; three letter notation) of the south-eastern Baltic Scots pine

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 chang-

es 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 ($\geq 86\%$ 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) |
| <i>r</i> -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) |

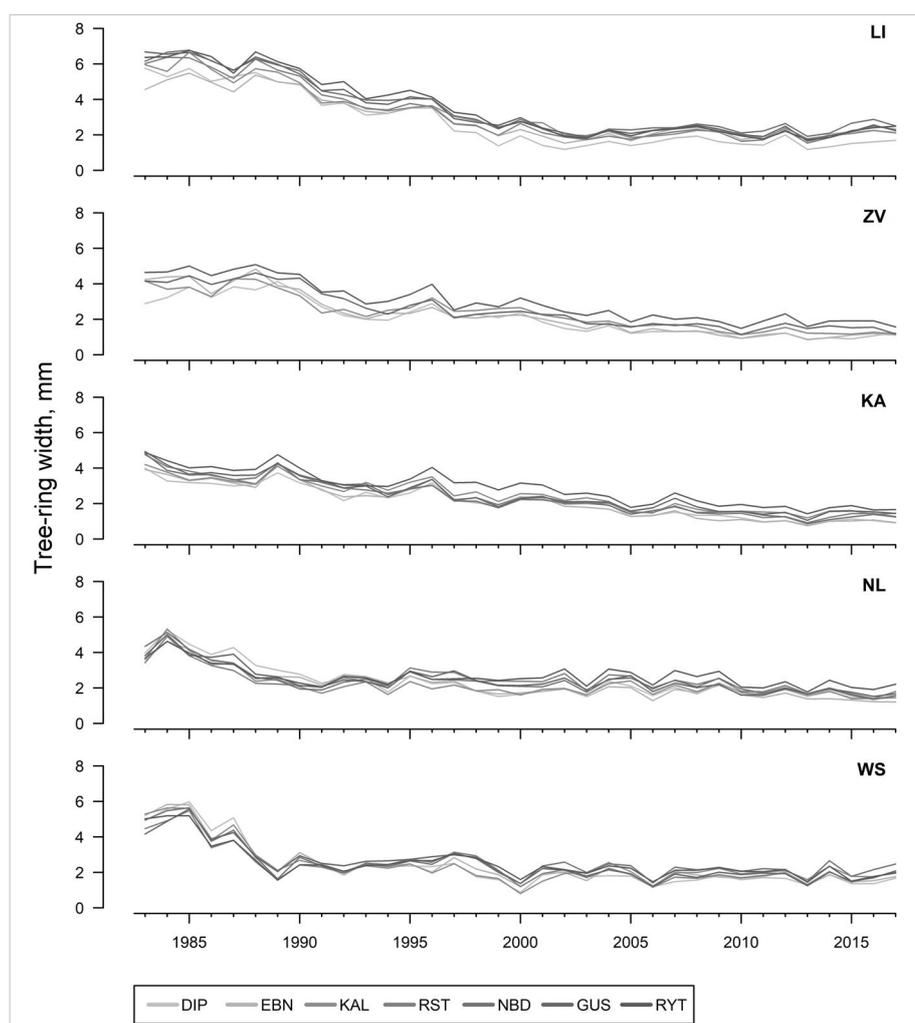


Figure 2. Mean time series of tree-ring width for the studied provenances of Scots pine in trials in Latvia and Northern Germany for the period 1983–2017

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.

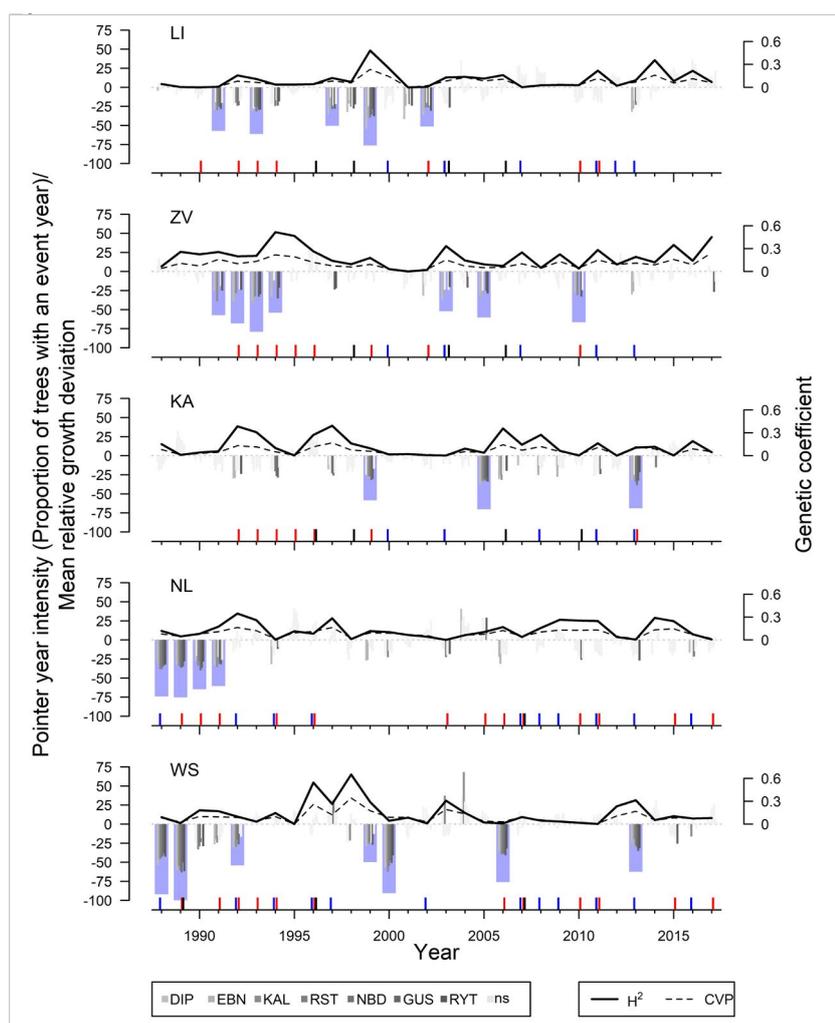


Figure 3. Estimated pointer year values (proportion of trees showing “significant relative growth changes”) for trials (wider blue bars) and mean growth deviation for the studied provenances (narrow bars), as well as the broad sense heritability (H^2 ; solid line, secondary axis) and provenance coefficient 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 $G \times E$ 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 ($G \times E$) 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 ($G \times E$ 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 win-

ter 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. $G \times E$ 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 $G \times E$ 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 ($G \times E$ 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 precautionary (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 $G \times E$ 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.

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