



Genetic insights into drought responses of boreal Scots pine

Alper Tuna Kavlak¹ · Harri Mäkinen¹ · Olli-Pekka Tikkasalo¹ · Hanni Kärkkäinen^{3,4} · Matti Haapanen¹ · Katri Kärkkäinen² · Sonja Tuulia Kujala²

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Abstract

Climate change is increasing the frequency and severity of drought in boreal forests, raising concern about the resilience of key tree species such as Scots pine (*Pinus sylvestris* L.). Understanding tree-level drought responses and their genetic basis is essential for climate-adaptive breeding and management strategies. We assessed drought responses and heritability of drought-response traits in 1,443 Scots pine trees from three progeny trials in southern and central Finland using basal area increment data. Two early-summer droughts in 2019 and 2021 were identified using the Standardized Precipitation–Evapotranspiration Index (SPEI). We quantified resistance, recovery and resilience using a growth-based framework and introduced a novel deviation-from-boundary metric describing departure from the theoretical full resilience in the resistance–recovery plane. Most trees failed to return to pre-drought growth within one year, indicating incomplete short-term recovery. Phenotypic correlations between drought-response and growth traits were weak in magnitude (up to 0.24), indicating limited overlap between these trait groups. Genetic-correlation estimates ranged from -0.72 to 0.63 and were associated with substantial standard errors. Genomic best linear unbiased prediction (GBLUP) models revealed drought-response trait heritabilities of 0.03 – 0.16 in Tuusula and 0.13 – 0.29 in Hankasalmi. The deviation-from-boundary metric also showed heritable variation, with heritability estimates of 0.03 – 0.09 in Tuusula and 0.26 in Hankasalmi. Cross-event phenotypic and genetic correlations were weak or imprecise, indicating limited stability across drought events. However, the overlapping 2020 event windows warrant caution. Further validation across independent drought events and sites is needed before these resilience metrics can be considered for operational tree breeding.

Keywords Resilience · Genetic variation · Tree breeding · Tree rings · Climate adaptation

Introduction

Climate change is unfolding more severely than earlier projections indicated, coinciding with an increased frequency and intensity of extreme weather events (Abrams et al. 1998; Allen et al. 2010; Bose et al. 2024; Knutzen et al. 2025). Droughts coinciding with heatwaves (“hotter droughts”), late spring frosts and windstorms are major causes of growth decline and mortality (Allen et al. 2015; Anderegg et al. 2019; Hammond et al. 2022; Knutzen et al. 2025). Northern boreal regions are warming faster than other forest ecosystems (IPCC 2023), and declining forest growth and increased mortality have been reported (Laudon et al. 2024; Korhonen et al. 2024; Knutzen et al. 2025; Sánchez-Pinillos et al. 2022). These trends emphasize the need to understand natural variation in the resilience of forest trees to drought and other climate-related stresses (DeSoto et al. 2020; Bose et al. 2024). Understanding such variation

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✉ Alper Tuna Kavlak
alper.kavlak@luke.fi

¹ Natural Resources Institute Finland (Luke),
Latokartanonkaari 9, 00790 Helsinki, Finland

² Natural Resources Institute Finland (Luke), Paavo Havaksentie 3, 90570 Oulu, Finland

³ Natural Resources Institute Finland (Luke), 31600 Jokioinen, Finland

⁴ Boreal Kasvinjalostus Oy, Myllytie 10, 31600 Jokioinen, Finland

is also important for forest management and tree breeding, helping to maintain forest health and productivity under increasing climatic variability (Bolte et al. 2009; Gil-Muñoz et al. 2025). This requires a transparent, comparable method of quantifying individual tree performance before, during, and after extreme events (Bolte et al. 2009; Ingrisich and Bahn 2018; Schwarz et al. 2020).

The impacts of drought vary between different forest types and tree species (Pardos et al. 2021). There are indications that drought is reducing the growth of Scots pine (*Pinus sylvestris* L.) in northern Finland, an area that is expected to be resilient to climate warming (Mäkinen et al. 2022). Furthermore, drought effects can persist for several years, and a second drought can therefore affect trees differently than the first (Bose et al. 2020; Sánchez-Pinillos et al. 2022). This highlights the need to examine multiple drought events within and across sites. However, there is no universally accepted definition of a ‘drought event year’, pre-event and post-event reference periods vary, and background climatic change is rarely explicitly considered (Carnwath and Nelson 2017). The Standardized Precipitation–Evapotranspiration Index (SPEI) is a climate-based water-balance index that integrates precipitation and atmospheric demand via potential evapotranspiration (PET), and it can be computed at multiple accumulation windows (e.g., 1, 3, 6, or 12 months) (Vicente-Serrano et al. 2010; Lloret et al. 2011; Schwarz et al. 2020). SPEI accumulation windows represent the period over which the climatic water balance is aggregated, thereby capturing drought conditions operating over different temporal scales (Vicente-Serrano et al. 2010). For example, June SPEI-1 represents the climatic

water balance for June, whereas June SPEI-12 represents the accumulated climatic water balance from July of the preceding year through June of the current year (Vicente-Serrano et al. 2010; Pasho et al. 2011). June SPEI-1 has been identified as an important driver of Scots pine radial growth in northern environments, indicating that even a short, month-specific accumulation window can be informative (Merlin et al. 2024).

To quantify tree-level responses to disturbances, multiple resilience concepts have been proposed (Ingrisich and Bahn 2018). However, translating resilience into operational forest metrics (e.g., for forest tree breeding) is challenging because observations over several years are needed for a large number of individual trees (Housset et al. 2018; Björklund et al. 2019). Dendroecology offers a practical solution in the form of ring-width series measured from increment cores, which record the growth of trees before, during, and after stressful periods (Lloret et al. 2011; Housset et al. 2018; Schwarz et al. 2020).

In the dendroecological framework, drought responses are commonly characterized by two complementary indices - resistance (R_t) and recovery (R_c) - together with resilience (R_s) and relative resilience (RR_s) (Lloret et al. 2011; Hodgson et al. 2015; Schwarz et al. 2020; Fig. 1). This provides a standardized way to compare tree responses to disturbance events, and was formalized by Lloret et al. (2011), although the concept was founded in earlier work (Abrams et al. 1998). Resistance and recovery often trade off, such that high growth maintenance during stress can be associated with weaker post-stress rebound, and vice versa (Hoffmann et al. 2018). To address this trade-off, Schwarz et al. (2020) proposed interpreting responses jointly in the R_c – R_t plane relative to a theoretical full-resilience boundary ($R_c = 1/R_t$), which distinguishes complete recovery, overcompensation, and incomplete recovery. This framework is being increasingly adopted to compare resilience responses across individuals, sites, and disturbance events (Bose et al. 2020; Pardos et al. 2021).

Beyond their use in characterizing short-term growth responses, growth-based resilience metrics are also ecologically relevant, as low resilience to drought has been associated with an increased risk of tree mortality (DeSoto et al. 2020; Bose et al. 2024). Moreover, increasing drought stress may overwhelm compensatory mechanisms in trees, further elevating mortality risk under climate change (Anderegg et al. 2019; Bose et al. 2024). Previous studies suggest that vulnerability to drought is not restricted to trees growing at the dry margins of a species’ distribution (Aakala and Kuuluvainen 2011). In mesic environments, Scots pine often achieves rapid growth and higher above-ground biomass under favorable conditions, but these same structural and physiological traits may increase vulnerability during

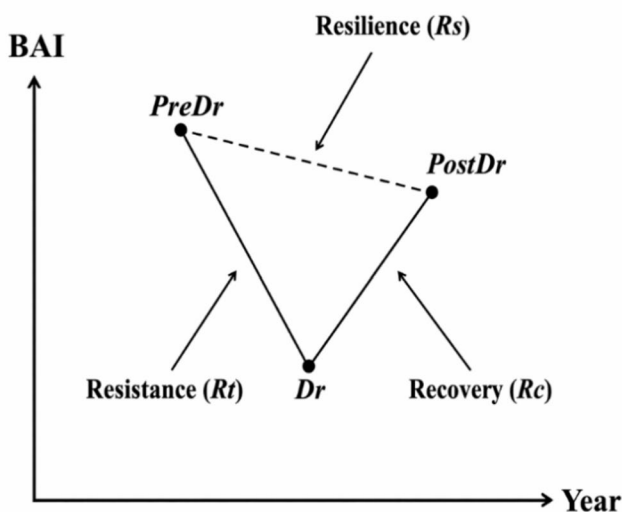


Fig. 1 Defining drought-resilience indices from ring-based basal area increment (BAI). The annual BAI series for an individual tree is partitioned into pre-drought (PreDr), drought (Dr), and post-drought (PostDr) years. The index definitions follow Lloret et al. (2011)

periods of extreme drought (Rigling et al. 2002; Timofeeva et al. 2017; Bose et al. 2024). This implies that productive stands within the core distribution area of Scots pine may also face elevated drought-related risk under future climates (Camarero et al. 2011; Sánchez-Salguero et al. 2015; Bose et al. 2024).

Drought-response traits may also be relevant for forest tree breeding (Marguerit et al. 2014). In breeding programs, traits are useful if they show heritable variation and provide information beyond conventional selection traits such as height and diameter. Estimating the heritability of drought-response metrics and their correlations with conventional traits is therefore an important step in evaluating whether they could complement existing breeding criteria in Scots pine. Previous provenance studies in the Baltic region have identified provenance-related differences in tree-ring-based resistance and resilience of Scots pine to weather extremes, consistent with a genetic component underlying these responses (Matisons et al. 2019). Recent work has demonstrated genetic variation and low-to-moderate genomic heritability for tree-ring-derived resistance, recovery, and resilience traits in Scots pine and evaluated their potential for genomic selection (Chaudhary et al. 2026). However, the consistency of these genetic responses across distinct drought events remains poorly understood in Scots pine. Studies in other conifers have shown that drought-response stability itself may vary among genetic origins and across repeated drought events (George et al. 2017).

This study focuses on the resilience of Scots pine, a key forestry species in Finland that accounts for approximately half of the national growing stock volume (Korhonen et al. 2024). In this study, our aims were to (i) quantify tree-level responses of Scots pine to two recent drought events using the growth-based indices of resistance, recovery, resilience, and relative resilience, together with a novel deviation-from-boundary metric developed here; (ii) estimate the heritability of these drought-response traits using genomic best linear unbiased prediction (GBLUP) models; and (iii) evaluate the consistency of tree responses across drought events and their relationships with conventional growth traits.

Materials and methods

Study material

We analyzed 1443 Scots pine trees from three progeny trials at two locations in southern and central Finland: one trial in Tuusula (60°21'N, 25°01'E) and two adjacent trials in Hankasalmi (62°23'N, 26°42'E). The Tuusula trial represented the southern Finnish breeding population, whereas the two Hankasalmi trials represented the central Finnish

breeding population. The trials mainly comprised full-sib families generated through controlled crosses among plus-tree parents from the respective regional breeding populations (Haapanen and Mikola 2008). The parents were selected in natural stands for their superior growth and external quality (e.g., stem straightness and branching).

The Tuusula trial (217901; T1) was established with 80 test entries planted in 5-by-5-tree square plots across two randomized complete blocks in spring 2006. The 768 trees used in this study were selected from 64 full-sib families, consisting of six trees sampled from each of the two plots per family (a total of 12 trees per family).

The Hankasalmi progeny trial (215804; H1) was established in spring 2005, with 102 test entries planted in five-tree row plots with replicates in eight complete blocks. For this study, we selected 27 full-sib families from those available for sampling in the trial and sampled five trees from each of three blocks per family (15 trees per family). The sampled plots represented all eight blocks, although the specific blocks differed among families. The Hankasalmi H2 trial (218702; adjacent to H1) was established with 80 test entries in spring 2007. The entries were planted randomly within three complete blocks comprising 4-by-4-tree square plots. From this trial we subsampled five trees per plot in all three blocks from 22 families, for a total of 15 sample trees per family. The sampled full-sib families were unique to each Hankasalmi trial, although some parents were represented in both trials. Since the two Hankasalmi trials consisted of material from the same breeding population, included some shared parents, and were located next to each other, their data were combined for the analyses.

The two trial locations represent different environmental conditions, with Tuusula characterized as a mesic site and Hankasalmi as a sub-xeric site. Site-specific climatic conditions and drought severity were evaluated separately for the two locations using the climate data and SPEI analyses described below.

Annual and overall growth data

To measure annual radial increments, one core per tree was extracted at breast height (1.3 m) in May 2023. The trees in Tuusula (T1) were thus cored 17 years and the trees in Hankasalmi 16 (H2) or 18 (H1) years after the trial establishment. The annual radial increments of the increment cores were measured using the QTRS-01X microdensitometer (Quintec Measurement Systems, Knoxville, USA). The system comprises an X-ray source and a detector connected to a computer for data acquisition. To measure ring widths, 1.6 mm thick strips were sawn from the air-dried increment cores and scanned at a resolution of 0.02 mm. The measurements were cross-dated and visually quality-checked.

Ring widths (R , mm) were converted to basal area increment (BAI, cm^2) using the `bai.out` function in the R package `dplR` (Biondi and Qeadan 2008; Bunn et al. 2025). The transformation

$$BAI_t = \pi (R_t^2 - R_{t-1}^2)$$

expresses growth as an increase in stem cross-sectional area. To ensure a common calendar period across the three trials and to reduce the influence of the earliest, rapidly growing juvenile rings, we restricted the analyses to 2016–2022. Because the trials were established between 2005 and 2007, this period represented slightly different tree ages among trials. Differences between the two Hankasalmi trials were accounted for in the statistical model.

Height and diameter at breast height (DBH) were used as conventional traits for comparison with the drought-response metrics. We used the most recent complete inventory available for each trial: T1 was measured in 2018 at age 12, H1 in 2020 at age 15, and H2 in 2021 at age 14. These measurements were interpreted as indicators of cumulative growth performance rather than as measurements contemporaneous with the drought events.

Drought identification

Drought severity at the trial sites was assessed using the Standardized Precipitation–Evapotranspiration Index (SPEI) (Vicente-Serrano et al. 2010). Meteorological data were obtained from the Finnish Meteorological Institute (FMI) gridded monthly dataset (1980–2022) at a spatial resolution of $10 \text{ km} \times 10 \text{ km}$. Potential evapotranspiration (PET) was estimated using the Spatial Forest Hydrology model (SpaFHy; Launiainen et al. 2019). In the SpaFHy simulations, we set the forest LAI (Leaf Area Index) to 3 m^2 (leaf) m^{-2} (ground) for both experimental sites and the site type to mesic for Tuusula and sub-xeric for Hankasalmi. The site type was used to derive soil properties such as porosity, wilting point and the van Genuchten model parameters according to Launiainen et al. (2022). SpaFHy calculates PET following the Penman-Monteith equation (Monteith 1965). Effective precipitation was estimated by subtracting changes in snow water equivalent (simulated with SpaFHy) from the precipitation obtained from the gridded weather dataset. Finally, both PET and effective precipitation were used to calculate SPEI with the `climate_indices` package in Python (Adams 2017).

Correlations between SPEI and BAI were calculated across May–September and the available SPEI accumulation scales of 1, 2, 3, 4, 6, 12, and 24 months. Multiple regression was not fitted because only seven annual observations were available per site, which would have resulted

in an overparameterized and unstable model. Because BAI may retain an age- or time-related trend, correlations with SPEI were calculated using both raw and linearly detrended annual mean BAI. For each site, a linear trend was fitted against calendar year, and the residuals were used as the detrended BAI series. Linear detrending was selected because the common series comprised only seven annual observations, precluding reliable estimation of more flexible detrending functions. To evaluate the robustness of the relationship between annual mean BAI and SPEI, the analyses were conducted separately for each site. Pearson and Spearman correlation coefficients were calculated, and uncertainty was evaluated using 2000 nonparametric bootstrap resamples. Sensitivity to individual years was examined using leave-one-year-out analyses.

Finally, June SPEI-1 was retained as the focal event indicator because it showed the strongest positive raw Pearson association with annual mean BAI at both sites among the tested SPEI windows and represents a biologically relevant early-summer moisture indicator (Merlin et al. 2024). Given the short seven-year time series, this selection was treated as exploratory rather than as evidence that June SPEI-1 was uniquely superior to the other tested windows. A year was classified as a drought year when the site-specific June SPEI-1 was ≤ -1.0 , corresponding to moderate or more severe drought conditions according to the commonly used classification of standardized drought indices (McKee et al. 1993). The same fixed threshold was applied consistently across sites and years.

Resilience indices

We used tree-ring-based growth data to quantify drought responses from pre-drought, drought, and post-drought basal area increments. Quantifying resilience means assessing how a disturbance affects performance relative to a reference state (Lloret et al. 2011). We derived four metrics using the fixed pre-, during-, and post-drought years as illustrated in Fig. 1:

- (1) *Resistance* (R_t): growth maintained during the drought relative to the pre-event level, $R_t = \frac{Dr}{PreDr}$.
- (2) *Recovery* (R_c): rebound after the drought relative to the minimum during the drought, $R_c = \frac{PostDr}{Dr}$.
- (3) *Resilience* (R_s): return toward the pre-drought level, $R_s = \frac{PostDr}{PreDr}$.
- (4) *Relative resilience* (RR_s): the fraction achieved of the full recovery, $RR_s = \left(\frac{PostDr - Dr}{PreDr - Dr} \right) \left(1 - \frac{Dr}{PreDr} \right)$.

The periods 2018–2020 ($PreDr=2018$, $Dr=2019$, and $PostDr=2020$) and 2020–2022 ($PreDr=2020$, $Dr=2021$,

and PostDr=2022) were examined as two separate drought events. Thus, 2020 served as the post-drought year for the 2019 drought and as the pre-drought year for the 2021 drought. Due to the short time series available and the proximity of the two drought events, the pre-drought and post-drought years consisted of a single year only.

The above components are linked by $R_s = \frac{\text{PostDr}}{\text{PreDr}} = \left(\frac{\text{PostDr}}{\text{Dr}}\right)\left(\frac{\text{Dr}}{\text{PreDr}}\right) = R_c \times R_t$. It has been suggested that R_t and R_c should be interpreted jointly rather than in isolation. An exact return to the pre-drought level occurs when $R_s = 1$, which defines the full-resilience boundary $R_c = 1/R_t$ (Schwarz et al. 2020). Points on this line indicate a complete return within the post-drought year, while points above the line indicate over-recovery/compensation ($R_s > 1$), and points below the line indicate incomplete recovery ($R_s < 1$). For each drought event, each tree was represented by its observed R_t and R_c values as a point in the resistance–recovery plane (Fig. 3), with R_t on the x-axis and R_c on the y-axis, and its position was evaluated relative to the full-resilience boundary $R_c = 1/R_t$.

To quantify how far each tree lies from the full-resilience boundary, we defined the signed vertical deviation as, D , as shown in Eq. (1).

$$D = R_c - \frac{1}{R_t} = \frac{R_s - 1}{R_t} \quad (1)$$

using the identity $R_s = R_t \times R_c$. We computed separate deviation traits for the two drought events (D_1 for 2019; D_2 for 2021). The deviation metric was set to missing when $R_t = 0$, because the term $1/R_t$ is undefined, and when $R_t < 0$, because negative resistance values are not biologically interpretable for a ratio derived from non-negative BAI values. Records with missing components were also set to missing. All retained event records had positive R_t values; thus, the R_t rule served only as a computational safeguard. Because the index window spanned ± 1 year around each event, D summarizes within-one-year departure from the full-resilience boundary. To test whether the site-level mean deviation from the full-resilience boundary differed from zero while accounting for the block and trial structure, linear mixed models were fitted separately for each site and drought event. The site-specific models were specified as Eqs. (2a) and (2b) for Tuusula and Hankasalmi, respectively:

$$D \sim \text{Block} + (1|\text{Family}), \text{ Tuusula} \quad (2a)$$

and

$$D \sim \text{Trial} : \text{Block} + (1|\text{Trial} : \text{Family}), \text{ Hankasalmi} \quad (2b)$$

Because the sampled full-sib families were unique to each Hankasalmi trial, the Trial: Family term represents family nested within trial rather than a trial-by-family interaction across common families. The model-adjusted mean of D was tested against zero, which represents an exact return to the pre-drought growth level. Negative and positive adjusted means indicate incomplete return and post-drought growth exceeding the pre-drought level, respectively.

To visualize the relationship between resistance (R_t) and recovery (R_c), we applied locally estimated scatterplot smoothing (LOESS; Cleveland and Devlin 1988) to the R_c – R_t scatterplots, separately for each site and drought year. LOESS smoothing was used solely for descriptive visualization of overall trends and was not intended for formal statistical inference.

Genotyping

We used single nucleotide polymorphism (SNP) genotypes of the 1,443 trees to estimate genomic relatedness among individuals, which was subsequently used to estimate heritability. All genotyping was performed using the Axiom PiSy50k SNP array for Scots pine (Thermo Fisher Scientific) at the University of Bristol Genomics Facility, UK. The genotype data for the Hankasalmi trees were produced previously by Kastally et al. (2022), and the procedures for DNA isolation, genotyping, and genotype calling for those trees are described there. The Tuusula trees were genotyped in this study. DNA from the Tuusula trees was isolated from needles using the DNeasy Plant Pro Kit (Qiagen).

For the Hankasalmi trees, 40,405 SNP markers were successfully converted during the PiSy50k SNP array performance testing reported by Kastally et al. (2022). For the Tuusula genotypes, starting from the same set of 40,405 markers, we further removed markers with a call rate below 95%, markers with $\text{BestandRecommended} = 0$, markers showing plate effects, markers that were heterozygous in haploid control megagametophyte samples, markers showing genotype-call differences between Kastally et al. (2022) and the present genotyping round in at least two shared trees, markers showing significant deviation from Hardy–Weinberg equilibrium (tested using the parent population only), and markers with 50 or more Mendel errors. Finally, we retained the SNP markers that passed quality control in both Hankasalmi and Tuusula. The final filtered genotype matrix, comprising 31,329 SNPs for 1443 trees, was used to construct the genomic relationship matrix applied in the subsequent GBLUP analyses.

Heritability estimation

The data sets from Tuusula and Hankasalmi were analyzed separately because the test materials represent different regional breeding populations (southern and central Finland). Each trait was analyzed independently using a genomic best linear unbiased prediction (GBLUP) mixed model. A genomic relationship matrix G was constructed using VanRaden's (2008) Method 1, based on genotypes centered by allele frequencies and scaled by their expected variance. The phenotypic traits analyzed included annual BAI for 2016–2022, mean BAI across 2016–2022, DBH, height, and Rt, Rc, Rs, RR_s, and D for each of the two drought events. For each site-by-trait analysis, we used data from trees with both genotype data and records for the relevant phenotypic trait (Tuusula, $n=713$; Hankasalmi, $n=730$, after quality control). For Tuusula, block was included as a fixed effect. For Hankasalmi, trial and block nested within trial were included as fixed effects to account for the two adjacent trials. The general single-tree GBLUP formulation is given in Eq. (3), while additional implementation details are provided in Supplementary Methods S1.

For each site and trait, observations at the single-tree level were modeled using the GBLUP model in Eq. (3):

$$y_{ijk} = \mu + trial_i + block_{j(i)} + u_k + \epsilon_{ijk} \quad (3)$$

where y_{ijk} is the phenotypic observation of tree k in block j of trial i ; μ is the overall mean; $trial_i$ and $block_{j(i)}$ are the fixed effects; u_k is the random additive genetic effect of tree k ; and ϵ_{ijk} is the residual.

The random additive genetic effects and residuals were assumed to follow the distributions given in Eq. (4):

$$u \sim N(0, G\sigma_A^2), \epsilon \sim N(0, I\sigma_E^2) \quad (4)$$

where G is the genomic relationship matrix among genotyped trees (VanRaden 2008), σ_A^2 and σ_E^2 denote the additive genetic and residual variances, respectively, and I is an identity matrix of appropriate dimension.

The additive genetic ($\hat{\sigma}_A^2$) and residual ($\hat{\sigma}_E^2$) variance components were estimated using restricted maximum likelihood (REML; Patterson and Thompson 1971). Narrow-sense heritability was calculated using Eq. (5):

$$h^2 = \frac{\sigma_A^2}{\sigma_A^2 + \sigma_E^2} \quad (5)$$

The standard errors (SEs) of heritability were obtained using the delta method (Weisberg 2014) based on the variance-covariance matrix of $\hat{\sigma}_A^2$ and $\hat{\sigma}_E^2$.

The mixed models were fitted in R (v3.6.2) using the package sommer (function mmer). Selected analyses were repeated using rrBLUP to verify the consistency of the results (R Core Team 2019; Covarrubias-Pazaran 2016; Endelman 2011).

Phenotypic and genetic correlation analyses

Phenotypic correlations (r_p) between the drought-response traits (Rt, Rc, Rs, RR_s, and the deviation-from-boundary traits D1 and D2) and the conventional growth traits (DBH and height) were calculated separately for each site using Pearson correlation coefficients to evaluate the relationship between the drought response and overall tree size.

Genetic correlations (r_g) between the drought-response traits and the conventional growth traits DBH and height were estimated using bivariate GBLUP models, separately for each site and drought event. The bivariate models used the same fixed-effect structure and genomic relationship matrix as the corresponding univariate GBLUP models and jointly estimated the additive-genetic variances of the two traits and their additive-genetic covariance. Genetic correlations were calculated using Eq. (6):

$$r_g = \frac{\sigma_{A,xy}}{\sqrt{\sigma_{A,x}^2 \sigma_{A,y}^2}} \quad (6)$$

where $\sigma_{A,xy}$ is the additive-genetic covariance between traits x and y , and $\sigma_{A,x}^2$ and $\sigma_{A,y}^2$ are their respective additive-genetic variances.

Phenotypic event-to-event stability was evaluated for Rt, Rc, Rs, RR_s, and D using Pearson product-moment correlations (r_p) and Spearman rank correlations (ρ) at both the individual-tree and family/test-entry mean levels. Standard errors were estimated from 2000 nonparametric bootstrap resamples. Corresponding event-to-event genetic correlations between the 2019 and 2021 drought-response traits were estimated using the same bivariate GBLUP framework described above.

Unless otherwise stated, statistical analyses and graphical outputs were conducted in R version 3.6.2.

Results

Average annual basal area increment and its association with June drought

During 2016–2022, annual mean BAI ranged from 5.05 to 7.01 cm² in Hankasalmi and from 5.86 to 9.99 cm² in Tuusula. Applying the June SPEI-1 threshold defined above,

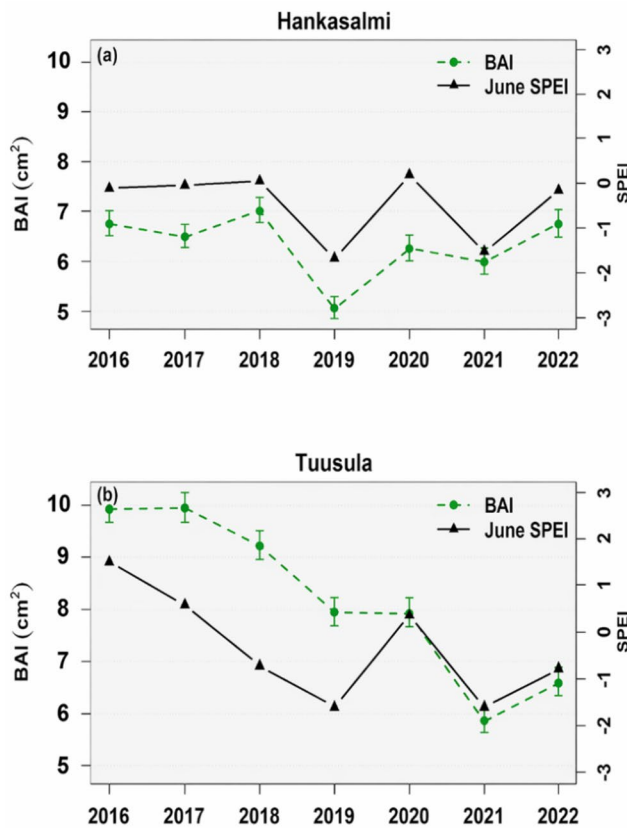


Fig. 2 Raw annual basal area increment (BAI) and June SPEI-1 values from 2016 to 2022 for **a** Hankasalmi and **b** Tuusula. Green dashed lines with circles show mean raw BAI with 95% confidence intervals, and black solid lines with triangles show June SPEI-1

2019 and 2021 were identified as drought years. The association between annual mean BAI and June SPEI-1 was positive at both sites. The raw Pearson correlations were 0.74 in Tuusula and 0.83 in Hankasalmi, and the corresponding correlations after linear detrending were 0.31 and 0.78, respectively. Bootstrap confidence intervals indicated substantial uncertainty associated with the short seven-year time series, and leave-one-year-out analyses were used to assess sensitivity to individual years. June SPEI-1 was retained as the focal early-summer drought indicator because its raw Pearson correlation with annual mean BAI was 0.74 in Tuusula and 0.83 in Hankasalmi and because it has biologically relevant timing; however, given the short time series, we do not infer that it is uniquely superior to the other tested SPEI windows (Table S1). In Hankasalmi, mean annual BAI declined from 7.01 cm² per tree in 2018 to 5.05 cm² per tree in 2019, a decrease of 1.96 cm² (28%), whereas it declined by 0.26 cm² (4%) from 6.25 cm² in 2020 to 5.99 cm² in 2021. In Tuusula, mean annual BAI declined by 1.28 cm² (14%), from 9.23 cm² in 2018 to 7.95 cm² in 2019, compared with a decrease of 2.07 cm² (26%), from 7.93 cm² in 2020 to 5.86 cm² in 2021. The complete raw annual mean BAI values and their 95% confidence intervals are shown in Fig. 2.

Phenotypic variation in resilience indices and overall growth

The two sites showed distinct drought-response profiles (Table 1). For the 2019 drought, mean recovery, resilience, and relative resilience were 1.30, 0.89, and 0.18 in Hankasalmi, compared with 1.00, 0.86, and -0.002 in Tuusula, respectively. Mean resistance was higher in Tuusula (Rt1=0.86) than in Hankasalmi (Rt1=0.72), with an SD of 0.17 at both sites. The standard deviation of the

Table 1 Summary statistics of the analyzed traits in the two trial sites

Trait	Tuusula (n=713)			Hankasalmi (n=730)		
	Mean	SD	Range (Min–Max)	Mean	SD	Range (Min–Max)
Rt ₁	0.86	0.17	0.33–1.80	0.72	0.17	0.29–1.30
Rc ₁	1.00	0.21	0.31–1.90	1.30	0.28	0.39–2.80
Rs ₁	0.86	0.21	0.26–2.10	0.89	0.21	0.29–1.50
RRs ₁	-0.002	0.17	-0.72 to 0.82	0.18	0.17	-0.63 to 0.88
D ₁	-0.19	0.28	-1.60 to 0.86	-0.20	0.35	-1.80 to 0.77
Rt ₂	0.74	0.19	0.26–1.60	0.94	0.19	0.41–1.60
Rc ₂	1.20	0.30	0.32–3.60	1.20	0.22	0.41–2.50
Rs ₂	0.84	0.29	0.31–5.60	1.10	0.25	0.25–2.50
RRs ₂	0.10	0.24	-0.75 to 4.10	0.15	0.19	-0.74 to 1.50
D ₂	-0.28	0.39	-1.90 to 3.00	0.06	0.27	-1.20 to 1.50
DBH	101.0	15.1	54–147	95.9	22.7	30–163
Height	69.0	6.5	51–87	75.9	10.1	41–102

Rt: resistance; Rc: recovery; Rs: resilience; RRs: relative resilience; D: deviation from the full-resilience boundary. Subscripts 1 and 2 refer to the first (2019) and second (2021) drought events, respectively. DBH: diameter at breast height (mm); Height: total tree height (dm). Rt, Rc, Rs, RRs, and D are dimensionless

resilience indices ranged from 0.17 to 0.30. For the 2021 drought, mean resistance and resilience were higher in Hankasalmi ($Rt_2=0.94$; $Rs_2=1.10$) than in Tuusula ($Rt_2=0.74$; $Rs_2=0.84$), whereas mean recovery was 1.20 at both sites and mean relative resilience was 0.15 in Hankasalmi and 0.10 in Tuusula; SDs across these indices ranged from 0.19 to 0.25 in Hankasalmi and from 0.19 to 0.30 in Tuusula (Table 1).

Phenotypic correlations between drought-response traits and conventional growth traits were generally weak at both sites (Table 2), with absolute correlations not exceeding 0.24. Genetic correlations were more variable in direction and magnitude and were generally estimated with substantial uncertainty, with no consistent pattern across traits, sites, or drought events. Complete tree-level and family/test-entry mean phenotypic correlation matrices, including DBH, height, BAI reference traits, and drought-response traits, are provided in Tables S4–S7.

At the individual-tree level, event-to-event Pearson correlations for R_s and D were negative in Hankasalmi (R_s : $r_p = -0.281 \pm 0.040$; D : $r_p = -0.236 \pm 0.044$) and weaker in Tuusula (R_s : $r_p = -0.149 \pm 0.051$; D : $r_p = -0.131 \pm 0.055$). Additional family/test-entry mean correlations are provided in Tables S2–S3.

The bivariate GBLUP analyses provided no precise evidence of stable genetic ranking across the two drought events. In Hankasalmi, genetic correlations were negative for R_s ($r_g = -0.22 \pm 0.21$) and D ($r_g = -0.25 \pm 0.22$). In Tuusula, the corresponding estimates were positive but imprecise for R_s ($r_g = 0.98 \pm 1.01$) and D ($r_g = 0.87 \pm 0.92$), with standard errors approximately as large as the point estimates. Full event-to-event genetic-correlation estimates are provided in Supplementary Table S8.

A descriptive inverse pattern between resistance and recovery was observed in both sites and drought events

(Fig. 3): trees with higher R_t generally showed lower R_c , whereas trees with lower R_t tended to show larger recovery responses. Most observations across the site-by-event combinations fell below the full-resilience boundary ($R_c = 1/R_t$), indicating that post-drought BAI generally remained below the observed pre-drought BAI level after one year. Because the analyzed trees were relatively young, underlying age-related growth trends may also have influenced pre- to post-drought differences; therefore, this pattern should not be interpreted as evidence of persistent physiological damage attributable solely to drought.

The model-adjusted mean D was negative in Tuusula in 2019 (-0.194 ± 0.011 , 95% CI -0.215 to -0.173) and 2021 (-0.278 ± 0.017 , 95% CI -0.313 to -0.243). In Hankasalmi, the model-adjusted mean D was negative in 2019 (-0.201 ± 0.021 , 95% CI -0.243 to -0.158) but slightly positive in 2021 (0.067 ± 0.016 , 95% CI 0.035 to 0.100). By definition, $D=0$ represents the full-resilience boundary, whereas negative and positive values indicate post-drought growth below and above the observed pre-drought growth level, respectively. In Hankasalmi, recovery values were higher for the 2019 event at lower resistance levels ($R_t \approx 0.4$ – 0.7), whereas at higher resistance levels ($R_t \approx 1.0$ – 1.3), recovery values were slightly higher for the 2021 event. In Tuusula, the fitted recovery curve for 2021 was higher than that for 2019 across the common observed resistance range ($R_t \approx 0.33$ – 1.64).

Heritability

For the first drought, heritability estimates for the resilience indices ranged from $h^2 = 0.03 \pm 0.03$ to 0.05 ± 0.04 in Tuusula and from $h^2 = 0.13 \pm 0.05$ to 0.25 ± 0.06 in Hankasalmi (Table 3). For the second drought, the corresponding

Table 2 Phenotypic (r_p) and genetic (r_g) correlations between drought-response traits and conventional growth traits (DBH and height) in Tuusula ($n=713$) and Hankasalmi ($n=730$)

Trait	Tuusula				Hankasalmi			
	DBH		Height		DBH		Height	
	r_p	$r_g \pm SE$	r_p	$r_g \pm SE$	r_p	$r_g \pm SE$	r_p	$r_g \pm SE$
Rt_1	0.030	-0.43 ± 0.36	0.120	0.03 ± 0.29	0.007	0.63 ± 0.55	-0.055	0.42 ± 0.25
Rc_1	-0.002	-0.23 ± 0.38	0.066	-0.19 ± 0.35	-0.040	-0.22 ± 0.55	-0.044	-0.20 ± 0.28
Rs_1	0.040	-0.72 ± 0.59	0.166	-0.15 ± 0.39	-0.027	0.48 ± 0.59	-0.091	0.28 ± 0.24
RRs_1	0.018	-0.24 ± 0.44	0.082	-0.27 ± 0.42	-0.041	-0.16 ± 0.55	-0.059	-0.12 ± 0.27
D_1	0.042	-0.70 ± 0.53	0.165	-0.17 ± 0.37	-0.002	0.48 ± 0.58	-0.059	0.31 ± 0.24
Rt_2	0.077	0.34 ± 0.29	0.147	0.49 ± 0.27	0.238	-0.59 ± 0.40	0.210	-0.18 ± 0.23
Rc_2	-0.104	-0.46 ± 0.26	-0.020	-0.12 ± 0.20	-0.155	-0.46 ± 0.83	-0.047	0.17 ± 0.24
Rs_2	0.002	-0.09 ± 0.28	0.115	0.34 ± 0.26	0.103	-0.50 ± 0.57	0.173	0.10 ± 0.22
RRs_2	-0.057	-0.30 ± 0.26	0.025	0.03 ± 0.21	-0.104	-0.18 ± 0.55	0.017	0.22 ± 0.23
D_2	0.012	-0.12 ± 0.28	0.165	0.40 ± 0.26	0.115	-0.54 ± 0.64	0.184	0.22 ± 0.23

r_p : tree-level Pearson phenotypic correlation; r_g : additive-genetic correlation estimated using bivariate GBLUP; SE: standard error of r_g . R_t : resistance; R_c : recovery; R_s : resilience; RR_s : relative resilience; D : deviation from the full-resilience boundary. Subscripts 1 and 2 refer to the first (2019) and second (2021) drought events, respectively. DBH: diameter at breast height (mm); Height: total tree height (dm)

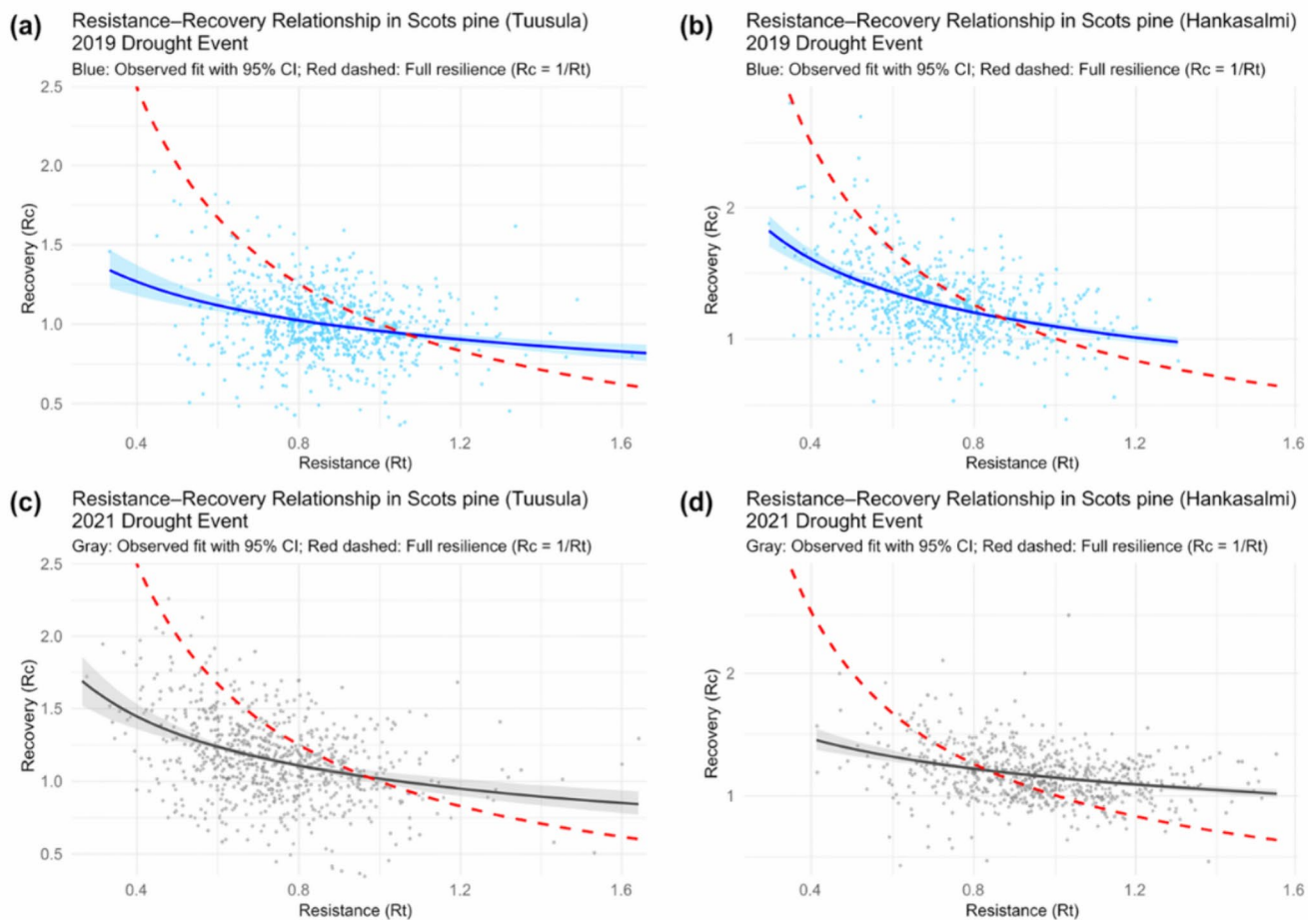


Fig. 3 The relationship between phenotypic values of resistance and recovery in Scots pine for **a** Tuusula, 2019 drought event; **b** Hankasalmi, 2019 drought event; **c** Tuusula, 2021 drought event; and **d**

Hankasalmi, 2021 drought event. Solid curves show the LOESS fit, shaded bands represent the 95% confidence interval, and the red dashed line indicates the hypothetical full-resilience boundary

Table 3 Genetic and environmental variances and heritability for growth and resilience traits

Trait	Tuusula			Hankasalmi		
	$\sigma_A^2 \pm SE(\sigma_A^2)$	$\sigma_E^2 \pm SE(\sigma_E^2)$	$h^2 \pm SE(h^2)$	$\sigma_A^2 \pm SE(\sigma_A^2)$	$\sigma_E^2 \pm SE(\sigma_E^2)$	$h^2 \pm SE(h^2)$
Rt ₁	0.002±0.001	0.028±0.002	0.05±0.04	0.007±0.002	0.02±0.001	0.25±0.06
Rc ₁	0.002±0.002	0.045±0.003	0.04±0.03	0.01±0.004	0.06±0.004	0.13±0.05
Rs ₁	0.001±0.001	0.043±0.003	0.03±0.03	0.01±0.003	0.03±0.002	0.25±0.06
RRs ₁	0.0009±0.001	0.03±0.002	0.03±0.03	0.003±0.001	0.02±0.001	0.13±0.05
D ₁	0.002±0.002	0.07±0.004	0.03±0.03	0.03±0.009	0.08±0.007	0.26±0.06
Rt ₂	0.003±0.002	0.033±0.002	0.09±0.04	0.008±0.003	0.03±0.002	0.21±0.06
Rc ₂	0.015±0.005	0.078±0.006	0.16±0.05	0.009±0.003	0.03±0.002	0.20±0.05
Rs ₂	0.007±0.004	0.081±0.005	0.08±0.04	0.02±0.005	0.04±0.004	0.29±0.06
RRs ₂	0.008±0.003	0.05±0.003	0.13±0.05	0.008±0.002	0.03±0.002	0.22±0.06
D ₂	0.01±0.007	0.14±0.009	0.09±0.04	0.02±0.005	0.05±0.004	0.26±0.06
DBH	63.5±17.7	167.50±14.2	0.28±0.06	10.7±15.3	462.6±27.8	0.02±0.03
Height	20.5±4.1	21.38±2.5	0.49±0.06	16.3±50.6	70.6±5.3	0.19±0.05

Rt: resistance; Rc: recovery; Rs: resilience; RRs: relative resilience; D: deviation from the full-resilience boundary. Subscripts 1 and 2 refer to the first (2019) and second (2021) drought events, respectively. DBH: diameter at breast height (mm); Height: total tree height (dm). Rt, Rc, Rs, RRs, and D are dimensionless

estimates ranged from $h^2 = 0.08 \pm 0.04$ to 0.16 ± 0.05 in Tuusula and from $h^2 = 0.20 \pm 0.05$ to 0.29 ± 0.06 in Hankasalmi.

Consistent with these patterns, our analyses of the signed deviation from the full-resilience boundary ($D = R_c - 1/R_t$) indicate that the signed deviation from the boundary showed heritable variation in Hankasalmi (both events: $h^2 \approx 0.26$), whereas heritability estimates in Tuusula were smaller than those in Hankasalmi (D_1 : $h^2 \approx 0.03$; D_2 : $h^2 \approx 0.09$). For DBH and height, h^2 estimates were 0.28 ± 0.06 and 0.49 ± 0.06 in Tuusula, respectively, compared with 0.02 ± 0.03 and 0.19 ± 0.05 in Hankasalmi (Table 3).

Heritability of the underlying BAI reference traits was also site- and year-dependent. Annual BAI h^2 ranged from 0.02 ± 0.03 to 0.14 ± 0.05 in Hankasalmi and from 0.05 ± 0.04 to 0.20 ± 0.05 in Tuusula. Mean BAI across 2016–2022 had $h^2 = 0.06 \pm 0.04$ in Hankasalmi and 0.12 ± 0.05 in Tuusula. For the drought years, BAI h^2 was 0.14 ± 0.05 in Hankasalmi and 0.05 ± 0.04 in Tuusula in 2019, and 0.10 ± 0.05 and 0.12 ± 0.05 , respectively, in 2021. These estimates provide reference context for interpreting the heritability of the derived drought-response metrics. Full annual and mean BAI heritability estimates are provided in Supplementary Table S9.

Discussion

Drought responses vary across sites and years

Our results show distinct annual BAI responses to the 2019 and 2021 drought events across the two trial populations (Fig. 2), with corresponding variation in the derived drought-response traits summarized in Table 1. Although converting ring width to BAI accounts for the increasing stem circumference, annual BAI may still retain age- or time-related trends. Detrending substantially reduced the BAI–SPEI correlation in Tuusula, whereas the correlation remained similar in Hankasalmi, indicating that the influence of temporal trends differed between the two sites. Given the seven-year time series, both raw and detrended correlations should be interpreted as exploratory. June SPEI-1 showed the strongest positive raw Pearson association with annual mean BAI at both sites among the tested SPEI windows, but this pattern was not consistently maintained across detrending approaches and correlation measures. June SPEI-1 was therefore retained as the focal early-summer drought indicator, while its selection should not be interpreted as evidence that it was uniquely superior to the other tested SPEI windows as a climatic driver of annual BAI. The use of an early-summer moisture indicator is consistent with earlier findings that early-summer water availability, along with temperature, influences radial

growth in Scots pine in northern regions (e.g., Mäkinen et al. 2022; Merlin et al. 2024; Henttonen et al. 2014; Hökkä et al. 2025). Similar climate sensitivity patterns have been observed across boreal conifers, where Scots pine shows relatively buffered growth responses compared with more drought-sensitive species, such as Norway spruce (*Picea abies* (L.) Karst), under increasing water limitation (Szejner et al. 2025). Additional physiological evidence, such as carbon isotope composition ($\delta^{13}\text{C}$), metabolomics or wood anatomical traits, could strengthen the mechanistic interpretation of drought responses by providing insight into underlying carbon balance and hydraulic processes.

The two study sites differed in soil characteristics, and DBH and height were measured at different ages among trials. In T1, these measurements were taken in 2018, 12 years after planting; H1 was measured in 2020, 15 years after planting; and H2 in 2021, 14 years after planting. Therefore, direct comparisons of absolute growth between the two trial populations should be interpreted cautiously. In Tuusula, the trees had on average larger diameters but were shorter, whereas in Hankasalmi, the trees showed greater variation in growth traits. Overall, drought-response patterns differed between the two trial populations, with Hankasalmi generally showing higher mean values for the resilience indices, except for resistance during the 2019 drought, which was higher in Tuusula. These contrasts may reflect multiple, non-exclusive differences between the trial sites, including site moisture conditions and drought severity, genetic material, and trial design.

Similar environment-dependent variation in resistance, recovery, and resilience has been reported across European forests (Bose et al. 2020; Pardos et al. 2021). Our results also align with recent findings from southern Finland indicating that drought impacts in Scots pine vary with site conditions (Szejner et al. 2025). Comparable patterns have been reported in the Baltic region, where Scots pine radial growth in Estonia and Lithuania has shown sensitivity to water availability and early-summer drought, with climate–growth relationships varying among sites (Henttonen et al. 2014; Vitas and Erlickytė 2007; Metsläid et al. 2018). These findings further support the interpretation that local environmental conditions modulate drought responses within Scots pine.

By positioning each tree on a resistance–recovery (R_c – R_t) plane (Fig. 3), we observed a phenotypic trade-off between drought resistance and recovery across all site-by-event combinations. A similar resistance–recovery trade-off was recently observed among Scots pine families, where families maintaining greater growth during drought tended to show lower subsequent recovery (Chaudhary et al. 2026). Similar trade-offs have also been documented in several other tree species (Lloret et al. 2011; Carnwath and Nelson

2017; Hoffmann et al. 2018). In maritime pine (*Pinus pinaster* Ait.), the resistance–recovery trade-offs were found to depend on site type, with trees from drier environments tending to exhibit lower resistance but faster recovery, whereas trees from mesic sites showing higher resistance but slower post-drought recovery (Sánchez-Salguero et al. 2018). Trade-offs have also been reported for Scots pine in stand-structure contexts, such as stronger resistance but lower recovery in mixtures versus monocultures (Steckel et al. 2020). However, unlike these stand- or site-based comparisons, our material consisted of progeny trials with test materials from different breeding populations; therefore, the observed differences between Tuusula and Hankasalmi may not be solely attributed to site conditions.

In this study, we used the signed deviation from the full-resilience boundary (D) as an additional quantitative descriptor of drought response. Compared with considering Rt or Rc separately, D provides a single signed descriptor of their combined position relative to the full-resilience boundary, facilitating comparison among different resistance–recovery combinations. The predominance of negative values across three of the four site-by-event combinations indicates that post-drought BAI generally remained below the observed pre-drought level after one year in these cases, whereas Hankasalmi in 2021 showed a positive deviation. The positive D in Hankasalmi in 2021 may partly reflect the relatively mild growth reduction during that event, together with favorable post-drought growth relative to the 2020 pre-drought reference level. However, because the metric was based on only one pre-drought and one post-drought year, the positive deviation may also be sensitive to year-specific variation in the reference and recovery years rather than reflecting a persistent difference in drought response.

The implications of these one-year recovery patterns for longer-term forest growth remain uncertain and will depend on how drought responses accumulate over time. Incomplete recovery within one year represents a short-term growth deficit, but the present data do not allow us to determine its long-term consequences for wood productivity, tree health, or survival. Trees with stronger recovery may compensate more rapidly for short-term growth reductions, whereas greater resistance may reduce the initial growth loss. These considerations highlight the importance of evaluating drought-response traits together with long-term growth trajectories rather than in isolation, as the relative contributions of resistance and recovery to resilience may vary across traits, species, and environmental contexts (Crespo-Antia et al. 2025). Recent multi-species evidence indicates that conifer drought responses are strongly conditioned by pre-drought growth levels and post-drought moisture conditions (Zhang et al. 2026), reinforcing the need to

interpret short-window resilience metrics within their event-specific climatic context.

Genetic variation in drought responses in Scots pine

Heritability estimates for drought-response traits were generally higher in Hankasalmi than in Tuusula, although the differences varied among traits and drought events. The heritability of the underlying BAI reference traits was also year- and site-dependent, providing important context for interpreting the heritability of the derived drought-response metrics. In Hankasalmi, several drought-response traits showed higher heritability than the annual BAI traits from which they were derived; annual BAI heritability during the event windows was generally low to moderate, whereas drought-response heritabilities reached 0.25–0.29. In Tuusula, the correspondence was also not direct: for example, BAI in the pre-drought year 2018 had a heritability of 0.17, whereas the drought-response traits derived for the 2019 event had heritabilities of only 0.03–0.05. Thus, the genetic variation detected in the drought-response metrics does not appear to simply mirror the heritability of annual BAI, although these metrics are mathematically derived from annual BAI and their genetic variation is necessarily influenced by variation in the underlying annual growth measurements. Because our two sites represent different regional breeding populations and trial structures, these differences cannot be attributed solely to environmental conditions. Similar low-to-moderate GBLUP-based narrow-sense heritability estimates were recently reported for tree-ring-derived drought-response traits in a mature Swedish Scots pine progeny trial, with estimates of 0.22 for resistance, 0.15 for recovery, and 0.07 for resilience (Chaudhary et al. 2026). Together, these results illustrate that heritability of drought-response traits can vary among traits, populations, environments, and drought events.

For DBH and height, heritability estimates were higher in Tuusula than in Hankasalmi. For height, the additive-genetic variance was of broadly similar magnitude in the two trial populations, whereas the environmental variance was substantially higher in Hankasalmi, supporting the interpretation that the lower heritability in Hankasalmi partly reflects greater environmental heterogeneity. A further limitation is the relatively small number of blocks in the Tuusula trial, which was established with only two randomized complete blocks. This may have limited the ability to account for within-site environmental heterogeneity and may have reduced the precision of some variance-component, heritability, and genetic-correlation estimates. This should be considered when interpreting estimates with large standard errors. In addition, although more than 700 individual trees were analyzed at each site, the effective sample

size for genetic parameter estimation was constrained by the family structure of the trials. The Tuusula material comprised 64 full-sib families with 12 sampled trees per family, whereas the combined Hankasalmi material comprised 49 full-sib families with 15 sampled trees per family. Consequently, the amount of independent family-level information was substantially smaller than the total number of individual trees. This limited effective sample size, together with environmental heterogeneity and differences in experimental design, may have contributed to the large standard errors and broad uncertainty observed for some genetic correlations and variance-component estimates. At the same time, the broad phenotypic ranges and standard deviations may also reflect genuine biological variation among trees and families.

This pattern may suggest that genetic variation in drought-related traits becomes more apparent under drier site conditions, where moisture limitation can exert a stronger influence on tree growth (Pardos et al. 2021; Szejner et al. 2025). Such context dependence is consistent with Pardos et al. (2021), who reported variation in drought resistance, recovery, and resilience associated with stand structure and site aridity across European forests. Comparable long-term work in European larch detected provenance differences in resistance and resilience across four drought periods, with repeatability estimates reaching 0.39 but varying among provenances (George et al. 2017). This further indicates that stability of drought response across events may itself depend on genetic background. In Hankasalmi, the negative event-to-event associations for R_s and D were retained using both Pearson and Spearman correlations and after aggregation to family/test-entry means, indicating that the pattern was not restricted to the individual-tree Pearson correlations. In contrast, the weak negative tree-level associations in Tuusula were not reproduced at the family-mean level. The corresponding genetic correlations were imprecise. However, the two event windows were not fully independent because BAI in 2020 served as both the post-drought year for the 2019 event and the pre-drought year for the 2021 event. This overlap may partly influence the observed cross-event associations and should therefore be considered when interpreting the stability of drought-response rankings across the two events. Taken together, the tree-level, family/test-entry mean, and genetic correlations provide limited evidence for stable drought-response rankings across the two events; however, this pattern should be evaluated using additional independent drought events. This interpretation is consistent with broader evidence that drought-related growth responses depend on interacting climatic and tree-level factors (Anderson-Teixeira et al. 2022; Bottero et al. 2021). Similar evidence of genetic variation and heritability in drought-response traits has been reported

in other boreal conifers (Depardieu et al. 2020, 2021). Population- and family-level genetic variation in resistance, recovery, and resilience was detected using tree-ring-derived metrics in common garden experiments (Depardieu et al. 2020). Tree-ring analyses from provenance trials have shown that climate-growth responses in trees vary depending on their genetic background (Suvanto et al. 2016). Studies combining tree-ring phenotypes with genomic analyses demonstrate that drought-response traits are heritable and polygenic (Depardieu et al. 2021; Novikova et al. 2023; Peach et al. 2024; Krutovsky 2022; Heer et al. 2018). This reinforces the broader view that tree rings constitute a functionally meaningful class of phenotypes for analysing genetic basis of climate adaptation in conifers (Housset et al. 2018).

Scots pine breeding has traditionally emphasized growth and quality-related traits (Haapanen and Mikola 2008; Ruotsalainen and Persson 2013). The goal of this study was to evaluate whether drought-response traits could provide complementary information for future breeding evaluations. Height and diameter are commonly assessed growth traits in Scots pine progeny trials and breeding programs and provide cumulative measures of tree volume growth (Haapanen et al. 1997; Haapanen and Mikola 2008). When assessed across diverse environments, they provide an indication of yield stability that can be interpreted as one aspect of resilience. However, single-time-point growth measurements do not reflect the effect of year-specific stress events the same way that resilience metrics derived from tree rings can do. Therefore, these metrics could potentially complement the conventional traits, although their values may depend on analytical resolution and measurement approach (Björklund et al. 2019).

The genetic correlations did not suggest a consistent relationship between drought-response traits and conventional growth traits. The direction and magnitude of the estimates varied among traits, sites, and drought events, and uncertainty was generally substantial. In another boreal conifer, a multi-site white spruce progeny study reported generally low and non-significant genetic correlations between drought-response components and conventional traits, except for a positive association between resistance and tree height (Laverdière et al. 2022). In contrast, Chaudhary et al. (2026) reported positive genetic correlations of resistance and recovery with BAI and height in a mature Swedish Scots pine progeny trial. The contrasting patterns between studies indicate that genetic relationships between drought-response and growth traits may be context-dependent and should be evaluated across additional populations, environments, and drought events. The weak phenotypic correlations and variable, but imprecise genetic correlations between growth traits and drought-response metrics suggest

that the latter traits could be useful complementary indicators in breeding evaluations, especially if they are associated with productivity under long-term drought.

To our knowledge, phenotypic variation in the position of individual trees relative to the full-resilience boundary in the R_c – R_t plane (Schwarz et al. 2020) has not previously been quantified in forest trees. Our results show that the heritabilities of the D metrics were similar to those of the individual resilience indices for each site-by-event combination. Because D is derived from R_t and R_c and showed limited or negative cross-event stability, it is more appropriately treated as an interpretive/descriptive index of position relative to the full-resilience boundary rather than as an operational selection criterion. However, operational use would require further validation of stability across drought events and sites, genetic relationships with growth and survival or damage traits, and efficient phenotyping in breeding populations. Alternatively, genomic selection could offer a promising approach for such “expensive phenotypes” (Meuwissen et al. 2001). Recent work in Scots pine showed that genomic prediction for drought-response traits was feasible and produced prediction efficiencies broadly comparable to pedigree-based prediction, although prediction performance for drought-response traits was lower than for several wood-anatomical traits (Chaudhary et al. 2026).

Beyond possible breeding applications, drought-response information may also contribute to climate-adaptive forest management by supporting the evaluation of genetic material for different environmental conditions. Scots pine provenance trials have shown variation in drought sensitivity, recovery, and resilience among provenances and across trial environments, highlighting the relevance of provenance and site conditions when considering future deployment strategies (Taeger et al. 2013; Matisons et al. 2019).

Future directions

The relatively short tree-ring time series and the interval between the two drought events limited the pre- and post-drought reference periods to single years, restricting inference about longer-term recovery and the persistence of drought effects. Longer time series would allow better separation of drought responses from age-related growth trends and background climatic variation (D’Orangeville et al. 2025). Future multi-site analyses could build on existing regional evidence, including studies from the Baltic region, to place drought responses observed in progeny trials within a broader climatic and site context and to improve the generalizability of the findings. Longer-term growth trends should also be considered when interpreting these short-term responses, as recent national-scale analyses indicate less favorable growth conditions for Scots pine in Finland

despite earlier positive trends (Henttonen et al. 2024). Additional independent drought events and larger sample sizes would allow more robust evaluation of cross-event stability and more precise estimation of genetic correlations among drought-response traits and between drought-response traits and conventional growth, survival, and damage traits.

The contrasting resistance–recovery combinations observed in this study may reflect differences in water transport and carbon balance during and after drought (McDowell et al. 2008; Martínez-Vilalta et al. 2009). However, the present analyses do not allow these mechanisms to be identified directly. Further integration of drought-response metrics with complementary wood or physiological traits could help clarify the mechanisms underlying these response patterns.

Conclusions

The drought-response patterns indicated incomplete one-year recovery in most site-by-event combinations and large variation among trees, sites, and drought events. Within-site analyses identified additive genetic variation and low to moderate heritability in several drought-response traits. Cross-event phenotypic correlations were generally weak, while genetic correlations were variable and often imprecise, suggesting limited evidence for stable drought-response rankings across the two events. However, because the event windows shared the year 2020, these cross-event comparisons were not fully independent and should be interpreted cautiously. The deviation-from-boundary metric provided a simple descriptor of the combined resistance–recovery response relative to the full-resilience boundary.

Information on resilience traits is likely to become increasingly important if drought periods become more frequent. Longer time series and complementary physiological data could further clarify the biological significance and longer-term stability of these drought-response traits. Exploratory analyses also indicated a positive association between annual growth and June moisture availability, although this relationship was sensitive to detrending and the short temporal series. Our findings should be regarded as a first step toward evaluating the value of drought-response traits in Scots pine breeding; further validation is needed to assess the stability of these traits across independent drought events and sites and their relationships with growth, survival, and damage traits.

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Data availability The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

Code availability The code used for the analyses in this study is available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare no conflict of interest.

Consent for publication Not applicable.

Ethical approval Not applicable.

Consent to participate Not applicable.

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