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Understanding the role of ecotypic factors in the early growth of *Pinus sylvestris* L.

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Abstract: The ecological significance of Scots pine (*Pinus sylvestris* L.) in Europe, especially in areas devastated by bark beetles, has led to its consideration as a substitute for Norway spruce. This pioneering species boasts sun and drought tolerance, fast growth, and wood industry value. To gauge its potential, we examined two ecotypes across two test sites over two years, focusing on height and growth increment. Through statistical analysis employing R software and linear mixed models, we assessed heritability, genotype by environment interaction, and spatial correlations. Both ecotypes exhibited significant differences in height and increment, varying by year and site. Heritability was higher in the second year, with increment showing greater stability. Genetic correlations between sites were evident, suggesting stable increment ranking across locations. These findings underscore the role of ecotypic variation in Scots pine growth, advocating for its consideration in reforestation. Acknowledging such dynamics is vital for effective forest management and reforestation in Central Europe, promoting sustainability and informed decision-making. Further research will enhance this understanding of preserving and enhancing the region's tree populations.

Keywords: early selection; ecotypic variation; genetic correlations; heritability; Scots pine

Scots pine (*Pinus sylvestris* L.) holds a significant position among European tree species due to its ecological importance. In central Europe, particularly in countries such as the Czech Republic, Slovakia, and Poland, where most Norway spruce forests have been devastated by bark beetle infestation, Scots pine is considered a potential substitute, particularly in areas with large clear-cuts. This species, known as a 'pioneer' species, possesses unique key features such as extreme tolerance to sunlight and water deficit, relatively fast growth, and high production value for the wood processing industry (Pickett, White 1985; Mátyás et al. 2004). However, to fully evaluate the potential of Scots pine in the context of massive reforestation efforts, it is crucial to comprehend the impact of genetic variation on its growth and survival, as this factor could either enhance or hinder its potential.

Unique climatic conditions shape the local populations of Scots pine. Daily photoperiod and average annual temperature can greatly influence Scots pine ecotypic variation (Ekvall, Greger 2003). Abiotic factors like temperature, light, and soil type result in specific phenotypes in local populations, referred to as 'geographic races' (Pawlaczyk et al. 2010). Provenance experiments of Scots pine have shown significant growth differences among populations, particularly in long-distance transfers of plants to common gardens. Northern populations are more sensitive to transfer to the south, resulting in evident growth and volume reduction (Giertych 1979; Oleksyn, Giertych 1984). This shift may have a similar impact as transferring the upland ecotype to lower elevations as the morphological forest tree types have been formed through many years of evolution in lo-

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cal conditions, with significant differences observed among ecotypes in needle length, cone size, and seed characteristics (Krzakowa 1979; Szweykowski, Urbaniak 1982; Białobok et al. 1993; Krzakowa et al. 1994; Szweykowski et al. 1994). In the Czech Republic, Scots pine exists in two significant ecotypes: the 'upland' and 'lowland' ecotypes, each shaped by local climatic conditions over time. Populations of each ecotype share common hereditary traits, growth parameters, and patterns (Pospíšil, Kobliha 1998).

Furthermore, these local ecotypes may exhibit differences in crown and tree shape and even physiological traits responsive to water deficit (Čáp et al. 2016). The upland ecotype naturally occurs at higher elevations (up to 800–1 100 m a.s.l.) across Central Europe. Unlike the lowland ecotype, it thrives in mixed forests with spruce, fir, beech, and oak. It exhibits increased resistance to pollution and natural disturbances caused by wind (Kaňák 1999). There is no available literature on juvenile growth differences among these ecotypes. However, this information is crucial for selecting suitable planting material on a larger scale.

The selection of trees for reforestation at the population level depends on the existing genetic variation as the main precursor of future genetic gains. As Jansson (2007) published, selection based on height at the young age of Swedish Scots pine could indicate future volume production. This study examined correlations between height at a young age and volume production at older ages. The genetic correlation between height at age nine and volume production at age 30 was 0.8 (Jansson 2007). Besides the importance of age-to-age correlation for breeding and early testing, interactions among various traits and their further interaction with the environment are key for understanding adaptation. In Sweden, the dynamic relationship between tree (*Pinus sylvestris)* vitality and height was recently examined (Calleja-Rodriguez et al. 2019). The authors evaluated the genotype by environment interaction (G × E) and detected positive correlations between vitality and height. These findings reflect that small tree height in harsh environments correlates with low survival capacity. This phenomenon was further confirmed by Olsson and Ericsson (2002) in their study on correlations between the survival and height of a tree. Genetic correlations reported between height and tree survival were positive, between 0.03 and 0.65. There is still little known about the ecotypic variation in Scots pine and the distinct growth dynamics of the lowland and upland ecotype, especially in the early stages of development. Similarly, studies are lacking on the genetic variation and G × E concerning the ecotypes that practitioners mainly distinguished. Multi-environmental trial (MET) is needed to combine data from multiple sites to account for potential heterogeneity between locations caused by climate, soil, or vegetation differences.

Our study compares growth parameters, specifically height, and growth increment, between two ecotypes tested within two different test sites over two years. We also investigate the narrow-sense heritability of height and annual increment and analyse how it changes across the two sites and between two vegetation seasons. Additionally, we assess spatial autocorrelations for both sites and rank changes concerning G × E through MET relating to annual variation in height and increment.

MATERIAL AND METHODS

Plant material. As our plant material, we used Scots pine seedlings comprising open-pollinated half-sib progenies of the 53 maternal parents located in the first-generation seed orchard Nad Damníkovem (WGS84 49°51'46.8''N, 16°32'53.6''E). This seed orchard serves as a conservation site for upland pine clones *ex-situ*, and the represented upland pine is originally native to the protected area of Žďárské vrchy in the centre of the Bohemian-Moravian Highlands. In addition, seedlings of local origin were used, representing the lowland ecotype.

Trial description. Data were collected from two test sites. The first test site is located near the town of Svitavy (WGS84 49°49'11.726''N; 16°33'0.690''E) with an elevation of 502 m a.s.l., and the second test site is near the city of Telč (WGS84 49°4'33.395''N; 15°30'47.153''E) which is located at approximately 571 m a.s.l. The sites are about 200 km apart. Both sites were established in the fall of 2018. The experiment was set up as a randomised incomplete block design with four replicates, and within each replicate, there were nine blocks (with six families randomly assigned to each block). There were 54 parcels per replicate, each having 4 m × 6 m in size. Each parcel contained 16 seedlings of a specific half-sib progeny. As a comparison, each block contained one lot with the seedlings of the lowland ecotype, which had no information on pedigree. In total, there were 3 456 seedlings at each site present at the establishment date. The replications arrangement at the Svitavy site forms a 2 m × 2 m grid, whereas the Telč site has a linear 1 m × 4 m arrangement.

Climatic description. At the Svitavy site, the average annual temperature in 2021 was 8 °C (9.2 °C in 2022), the yearly precipitation in 2021 was 680 mm (610 mm in 2022), and the growing season spans to approx. 150 days. Telč's annual average temperature in 2021 was 7.6 °C (8.7 °C in 2022), the yearly precipitation in 2021 was 610 mm (630 mm in 2022), and the growing season is about 150 days [average temperature and precipitation were acquired from the Czech Hydrometeorological Institute (CHMI) website]. The test site in Svitavy is situated in natural forest area 31 'Českomoravské mezihoří' and the second test site is in natural forest area 16 'Českomoravská vrchovina'.

Sampling. Tree heights in 2021 (age 5) and 2022 (age 6) were measured at both sites, yielding growth increments between these years. At both locations, the tree height was measured in cm.

Statistical analysis. For statistical analysis, native functions of the R software (Version 3.5.0, 2018; R Core Team 2008) and the ASReml library for R Version 4 (Butler et al. 2017) were used. A single-environment linear mixed model (later referred to as model A) was fitted to evaluate tree heights with the following terms of Equation (1):

$$y = 1\mu + X_1\beta_x + X_1\beta_y + Zm + e \tag{1}$$

where:

y – data vector;

μ – overall mean effect;

β_x, β_y – fixed effects associated with ecotypes and four replications within both study sites;

m – maternal general combining ability effect, with $m \sim \mathrm{N}(0, \sigma_m^2 I_m)$;

e – random vector of errors, with $e \sim \mathrm{N}(0, R)$;

1 – a vector of ones;

X, Z – design matrices associated with fixed effects and random effects, respectively;

I_m – identity matrix of order m.

Within the random vector of errors, R is a matrix of variance-covariance of residuals related to each field position. Two forms of the R matrix were evaluated, one assuming independent errors, i.e. $R = \sigma^2 I_n$, and the other incorporates a separable first-order autoregressive process (AR1) associated with the rows and columns of the experiment. The spatial adjustments are defined as Equation (2):

$$R = [\mathrm{AR1}(p_{\mathrm{col}}) \otimes \mathrm{AR1}(p_{\mathrm{row}})] \tag{2}$$

where:

σ^2 – residual variance;

$\mathrm{AR1}(p_{\mathrm{col}})$, $\mathrm{AR1}(p_{\mathrm{row}})$ – first-order autoregressive correlation matrices.

Several models were fit, considering independent or autoregressive errors with or without polynomial functions. The best model was selected based on likelihood ratio tests (LRT), Akaike information criterion (AIC), and approximate *F*-tests (Isik et al. 2017).

The predicted means of ecotypes and sites were calculated using the R software's predictPlus function (asremlPlus package). This function also yields the least significant difference (*LSD*) used to verify the difference between ecotypes and sites.

Narrow-sense heritability (h^2) was estimated for each response variable using the formula defined by Equation (3):

$$h^2 = \frac{4\sigma_m^2}{\sigma_m^2 + \sigma_{rep:block}^2 + \sigma_R^2} \tag{3}$$

where:

h^2 – narrow-sense heritability;

$\sigma_{rep:block}^2$ – random variation of incomplete blocks nested within the sites;

σ_R^2 – residual variance modelled independently for both sites (residual matrices are modelled as a direct sum).

Approximate standard errors were obtained using the Delta method.

We also fit the above-described model for the multi-environmental trial (MET) to estimate the additive genetic correlation between the two study sites (later called model B). In this model, the site effect was added to fixed terms. The covariance between the two sites was modelled using a correlation matrix with a heterogeneous structure (CORGH). This is also a fully heterogeneous genetic correlation parametrized in terms of correlations instead of covariances between environments (Isik et al. 2017). Narrow-sense heritability (h^2) was estimated for each response variable using two different formulas, see Equations (4–5):

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$$h^2 = \frac{4\left(\sigma^2_{mTel\check{c}} + \sigma^2_{mSvitavy}\right)}{\sigma^2_{mTel\check{c}} + \sigma^2_{mSvitavy} + \sigma^2_{rep:block(Tel\check{c})} + \sigma^2_{rep:block(Svitavy)} + \sigma^2_{R(Tel\check{c})} + \sigma^2_{R(Svitavy)}} \tag{4}$$

$$h^2 = \frac{4\left(\sigma^2_{mTel\check{c}} + \sigma^2_{mSvitavy}\right) \times G_{corr}}{\sigma^2_{mTel\check{c}} + \sigma^2_{mSvitavy} + \sigma^2_{rep:block(Tel\check{c})} + \sigma^2_{rep:block(Svitavy)} + \sigma^2_{R(Tel\check{c})} + \sigma^2_{R(Svitavy)}} \tag{5}$$

where:

$\sigma^2_{mTel\check{c}}, \sigma^2_{mSvitavy}$ – random family variation;

G_{corr} – type-B genetic correlation.

RESULTS

The unique characteristic of this study is the experiment established using half-sib progenies and two contrasting ecotypes. The parental trees exhibited the typical and natural morphotype for the original location. Thus, each provenance was assessed for its relative ecotype at the time of a phenotypic selection of the respective plus trees. The experiment's strength lies in the relatively high number of preserved trees. Despite the notable presence of *Rubus* and various competing weeds on both sites, the actual mortality remained relatively low. At the test site Svitavy mortality was 5% (between 2021 and 2022). At the Telč site, it was even as low as 4%.

Differences in average height at test sites. We compared the average heights of both sites and individual ecotypes within those sites (Table 1). Here, we report the means predicted for both sites individually, including the sites' design effects, random family effects, and autoregressive errors (predicted by model A for each site individually).

The more complex MET model (model B) yielded a significant fixed site effect ($P = 0.01$) for height. In contrast, the predicted means in increments are only approximately one centimeter apart. Thus, the effect size is too small to verify any significant difference (based on the higher *LSD* of 4.6). Similar results could be reported about the mean height of 2021 (the actual difference of 4 cm vs. $LSD = 6$) and 2022, respectively.

Comparison of ecotypes in mean height and increment. The ecotypes at both observed sites and during different seasons showed statistically significant mean height and increment differences. These ecotypic differences varied across the sampling seasons 2021 and 2022. The pairwise differences between ecotypes are site-specific, but the general trend is confirmed across the years and sites. While the lowland ecotype always displayed faster growth than the upland ecotype, the highest predicted differences between ecotypes were recorded at the test site Telč [especially for height in 2022 (*H*22) with a nearly 50 cm difference].

Differences between ecotypes are statistically significant for every variable except for the increment at the test site Svitavy (Table 2). The highest significance of the differences can be observed for height in 2021 (*H*21) and 2022 (*H*22) at the test site Telč.

Narrow-sense heritability in mean height and increment. Narrow-sense heritability as a precursor of the potential response to selection was first assessed for both sites separately with a focus on annual variation in height and also to compare the genetic variation in increment on both sites.

Table 1. Average height (cm) of individual years and increment between 2021 and 2022

Year	Test site Svitavy			Test site Telč		
	whole site	lowland ecotype	upland ecotype	whole site	lowland ecotype	upland ecotype
2021	112.1	121.2	102.9	116.1	133.1	99.0
2022	168.4	180.4	156.5	171.8	193.1	150.3
INCR	57.5	61.5	53.6	56.1	61.1	50.9

INCR – increment

Table 2. Differences between ecotypes in predicted heights and increment with their respective statistical significance

Measured traits	Test site Svitavy			Test site Telč		
	difference (cm)	*LSD*	Wald *P*-value	difference (cm)	*LSD*	Wald *P*-value
*H*21	18.3	12.5	0.00347	34.1	9.3	4.11E^{-10}
*H*22	23.9	20.8	0.02276	42.8	14.2	9.96E^{-10}
INCR	7.8	9.4	0.10703	10.2	6.8	0.002362

*H*21 – height in 2021; *H*22 – height in 2022; *INCR* – increment; *LSD* – least significant difference

Table 3 shows the comparison of the heritability of tested parameters. Results are extracted from model A (two sites evaluated separately, including design effects and spatial auto-correlation). It is clear from both sites that the heritability of height is higher in the second year of measurement. When comparing the test sites regarding heritable variation, Svitavy exhibits a higher narrow-sense heritability than Telč. The estimated heritability of increment also reached relatively high values. At both sites, it surpassed the value of 0.20. The increment seems to be a more stable indicator of genetic variation than the mean height measured annually at single sites. In addition, the site difference in increments heritability is much smaller.

Spatial autocorrelation in growth traits. To account for any potential environmental variation within the incomplete blocks, we modelled the autocorrelation of residuals on both sites (Table 4). This method relies on the complete grid of coordinates that was available. There is a higher impact of the sites' spatial heterogeneity at site Telč, where the maximum correlation (0.21; SE 0.02) in the direction of rows was detected in the mean height 2022, followed by mean annual increment spatial correlation (0.19; SE 0.02). The spatial models exhibited a significantly higher log-likelihood (verified by the LRT) and AIC at both sites.

Spatial and temporal rank changes recorded in half-sib families. A heterogeneous correlation structure between sites was modelled to investigate the genetic correlation between the sites and the existence and extent of G by E interaction. As a result, the genetic variation was modelled separately for both locations. This approach also yielded the type-B genetic correlation. The MET analysis allowed us to investigate spatial family rank changes caused by G by E interaction. In contrast, the temporal rank changes were assessed through model A for both years across the individual sites.

Figures 1 and 2 illustrate the changes in ranking family breeding values across the seasons and sites. The seasonal changes in ranking were quite pronounced, which can be attributed to the juvenile stage of the plants under investigation. The second chart illustrates that at the Telč site, there are more dramatic shifts between the two years, which is reflected by more frequent crossing over of the lines. It is worth noting that a single family (mother clone 20948) stays at the top of the ranking at the Svitavy site.

MET analysis: Two sites modelled together with the heterogeneous correlation. First, based on model B, we estimated the narrow-sense heritability for mean height and annual increment. The heritability values are slightly lower than individual site models (model A). There is also

Table 3. Narrow-sense heritability of mean heights on both studied sites

Measured traits	Estimated narrow-sense heritability			
	test site Svitavy		test site Telč	
	heritability	SE	heritability	SE
*H*21	0.27	0.06	0.15	0.05
*H*22	0.35	0.08	0.19	0.06
INCR	0.26	0.07	0.22	0.06

*H*21 – height in 2021; *H*22 – height in 2022; *INCR* – increment; SE – standard error

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Table 4. Spatial auto-correlations for rows and columns are reported for individual sites and years; standard error is reported, followed by z-ratio

Measured traits	Spatial auto-correlations			
	column/row	correlation	SE	z-ratio
Test site Svitavy				
*H*21	column	0.02	0.02	1.29
	row	0.07	0.02	3.82
*H*22	column	0.04	0.02	1.86
	row	0.12	0.02	6.40
INCR	column	0.04	0.02	1.93
	row	0.13	0.02	6.52
Test site Telč				
*H*21	column	0.11	0.02	5.48
	row	0.16	0.02	7.81
*H*22	column	0.11	0.02	5.18
	row	0.21	0.02	10.24
INCR	column	0.08	0.02	3.80
	row	0.19	0.02	8.84

*H*21 – height in 2021; *H*22 – height in 2022; *INCR* – increment; SE – standard error; the ratio of the correlation and its respective standard error, which serves as an indicator of significance; z-ratio higher than 1.96 indicates the significant correlation

the trend of increasing heritability between two years of measurement. The estimated heritability of *H*22 and the mean annual increment is 0.16 (SE varies only slightly from 0.05 to 0.06). However, this heritability value is penalised for the additive genetic correlation between sites. When we used an alternative calculation (see the description in methods), the same model yielded the narrow-sense heritability of 0.28 (SE 0.06) and 0.24 (SE 0.05), respectively.

Secondly, we investigated how the family breeding values changed in rank between Svitavy and Telč. In 2022, the additive genetic correlation reached 0.59 (SE 0.14). The moderately high value reflects the less pronounced rank change between sites compared to the previous year. This trend complies

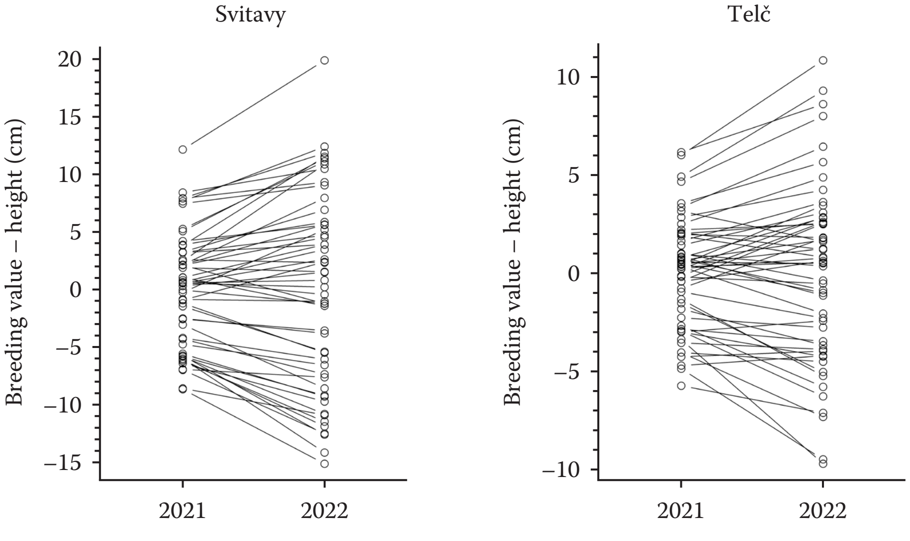

Figure 1. Family rank changes in breeding values between the years 2021 and 2022 at the Svitavy and Telč sites

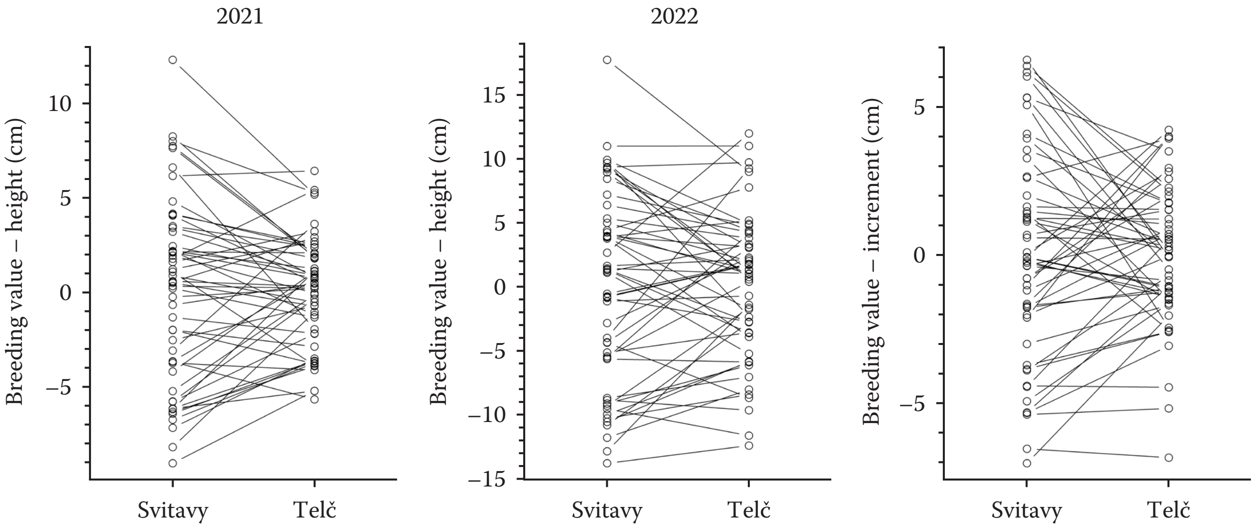

Figure 2. Illustrative family rank changes in breeding values between the sites (from left to right *H*21, *H*22, and increment)

*H*21 – height in 2021; *H*22 – height in 2022

with the lower genetic correlation of 0.53 (SE 0.17). However, the increase is very slight. The mean annual increment exhibits the highest type B genetic correlation (0.66; SE 0.14); thus, the ranking of family breeding values remains more stable in increment than in height. That suggests annual increment could be less prone to G × E.

DISCUSSION

Limitations. It is important to acknowledge a limitation in this experimental design: Currently, only two accessible locations in the Czech Republic possess such a comprehensive structure. Consequently, the experimental setup is constrained to comparing Scots pine ecotypes within a pair of localities, which are relatively distant (200 km apart) yet not extremely contrasting regarding their ecological and climatic conditions. The pedigree structure is present for only the upland ecotype, so this study information on the lowland ecotype is limited to a population level.

Site differences. At the Svitavy site, the trees reached a higher mean height in both years (Table 1) and a higher average increment (the difference between predicted site means was 2 cm). Still, this site effect seems rather small and was not verified by the statistics. This discrepancy could be caused by higher summer temperatures at the test site, which resembles the results of Misi et al. (2019) on Scots pine in Poland and Hungary. The average annual temperature at the Svitavy test site is 8 °C (9.2 °C in the second year), nearly 0.5 °C higher than the second test site. Almost the same annual precipitation during the second year was recorded at both test sites. However, at the test site Svitavy in 2021, the annual rainfall was approx. 680 mm, which is 70 mm higher than at Telč. This fact could have influenced the slight difference in mean annual increment.

Ecotypic variation. The differences observed between the recorded ecotypes were notably robust, as documented in Table 2. Particularly at the Telč site, these differences hold statistical significance for both years, encompassing the mean annual increment. These growth disparities, particularly in height, have been noted by various other researchers, including Giertych (1979) and Oleksyn and Giertych (1984). Their provenance experiments with Scots pine found significant growth differences, such as evident growth and volume reduction in northern populations (ecotypes). This phenomenon was confirmed Galdina and Khazova (2019) study investigating *Pinus sylvestris* provenance trials – the morphological and anatomical structure changes with local ecotypes.

Our results indicate that the lowland ecotype at both sites exhibited higher growth increments, and its total height also reached greater values. Particularly at the Telč site, there was a disparity of nearly 0.5 m in height between the ecotypes. These substantial differences in growth could be attributed to the local adaptation inherent in local ecotypes of Scots pine. Alía et al. (2001) conducted a study on the genetic variability of Scots pine, concluding that the observed variations and disparities among provenances were influenced by divergent gene and genotype frequencies within and between populations.

This finding is further supported by the research of Vizcaíno-Palomar et al. (2019). They stated that the majority of populations in Spain had undergone local adaptation to drought conditions, implying that populations can adjust to their specific local environmental conditions, including drought. The variations observed among provenances underscore the significance of both mass and individual selection, contributing to the remarkable adaptability of the species, as noted by Gülcü and Bilir (2017).

Narrow-sense heritability. We estimated the narrow-sense heritability of height and increment for both observed sites and years. At the Svitavy test site, the heritability values were higher, which can be related to a higher increment and growth variation in general. Estimated heritabilities in our study from the MET model (model B) slightly increased from 0.11 to 0.16 during the two years (Table 5). The MET values not penalised for additive genetic correlation were generally higher and closer to the single-site estimates. The narrow-sense heritabilities estimations from model A (both sites separately) ranged from 0.19 to 0.37 during the two observed seasons. In both models, heritability changed between the two years, which supports the findings of Olsson and Eriksson (2002). Their study also deals with early age trials (6–27 years), with estimated heritability ranging from 0.06–0.13, and has a growing trend. The significant heritability at a young age was also described in trials of *Pinus brutia*, where it reached 0.20 for height (Alan, Isik 2021). In his clonal test in Sweden, Kroon et al. (2011) investigated Norway spruce and Scots pine seedlings between 5 and 20 years of age, and the resulting narrow-sense heritabilities ranged from 0.23 to 0.29, which are also relatively high estimates. The comparison is less relevant as the Swedish clonal trial yielded broad-sense heritability estimates, which generally reach higher values.

We conclude that it is relatively soon to make serious assumptions about heritability at this early age. This conclusion is supported by Haapanen's (2001) study about time trends. Heritability often changes in these early trials before stabilising at a certain value. Dieter et al. (1995), who investigated *Pinus elliotii*, came to the same conclusion. Seedlings in this study were 4 to 15 years old. Average heritability estimates oscillated between 0.07 and 0.12 (from 5 to 14 years).

Spatial auto-correlation. We estimated spatial auto-correlations across both sites to explore the possible reduction of variation caused by environmental heterogeneity. Spatial correlations were calculated for rows and columns in both years and locations (Table 4). In all cases, the correlations in rows were higher than in columns, which can be attributed to the similar orientation of both trials. At the Telč site, spatial auto-correlations were almost twice as high as at the Svitavy site, which is most likely connected with the fact that the replications at Telč are stacked one after another. Consequently, the overall range of environmental conditions was wider at the Telč site. The highest correlation coefficient we found was 0.21 in 2022 at the Telč site across rows; the increment at this site yielded 0.19 spatial correlation in the direction of rows. Chen et al. (2017) also employed an incomplete block design in their study. They claimed that spatial analysis improved the model fitting, accuracy of breeding values prediction, and genetic gain prediction in Norway spruce. They concluded that large trials with great block variance could capitalise from using the spatial model. Saenz Romero (2001) concluded that real loss in genetic gain can occur when selection is based on unadjusted data. Zas (2008) concluded that the loss of genetic gain

Table 5. Estimated heritability for both sites (MET model)

Measured traits	Heritability penalised for genetic correlation		Heritability without accounting for genetic correlation	
	heritability	SE	heritability	SE
*H*21	0.11	0.05	0.22	0.04
*H*22	0.16	0.06	0.28	0.06
INCR	0.16	0.05	0.24	0.05

*H*21 – height in 2021; *H*22 – height in 2022; *INCR* – increment; MET – multi-environmental trial; SE – standard error by selecting unadjusted spatially correlated data is typically between 10% and 30%.

All these studies support adjusting for spatial auto-correlations to prevent incorrect conclusions in breeding programs. However, our data set shows that both sites are relatively homogeneous because correlations across both sites are relatively low. Moreover, the impact of the spatial model on heritability was rather marginal (results not presented). We can conclude that the incomplete block design was sufficient in dealing with the environmental heterogeneity in our trials.

Type B correlations and G × E interactions. Multi-environmental models (MET models) are used predominantly to evaluate G × E. Correlations between the same trait in different environments can show changes among genotypes across different environmental conditions and can also be used to evaluate the degree of G × E (Baltunis et al. 2010; Li et al. 2017).

Type B correlation from our MET model was estimated to be 0.53 in 2021 and 0.59 in 2022. These are relatively high genetic correlations, but the relatively high standard errors of these estimates (0.17 and 0.14) must be considered. In their study, Dieter et al. (1995) compared genetic correlations in years 5 and 14. Correlations from year 5 (0.6) increased to 0.8 at year 14, so the level of G × E interactions decreased with age. Xiang et al. (2003) have also studied the impact and extent of genetic correlations. In their specific case, type B genetic correlations for height ranged from 0.65 to 0.93. Another similar study deals with G × E interactions of Scots pine. Correlations were estimated to be 0.51, and breeding values of families were predicted (Alan et al. 2009). The genetic correlations between vitality and height within sites were generally positive and were driven by the variably harsh environments of the trials under investigation (Calleja-Rodriguez et al. 2019). This finding supports our results of the stable balance between ecotypes' height at both test sites, as various local climates and soils most likely shaped these local adaptations. The sole definition of ecotype is based on this stability in performance underlined by the specific genetic background.

Best linear unbiased prediction (BLUP) and further implications for the early selection. Based on both selected mixed linear models, the parental breeding values for each site and each year were predicted. The BLUP values from model A have greater variance at Svitavy, and values from model B are more dispersed in the second year of measurement (2022) within both sites. Visible shifts in family ranking between years are clear from both models. These shifts are in accordance with the increasing phenotypic and additive variation. Finally, the increase is also mirrored by the rise of narrow-sense heritability.

An early selection for the mean height and mean annual increment in Scots pine would not be efficient enough to supplant long-term field testing. Still, it could reduce the size of field tests via early culling of poor-performing families or screening infusion candidates for minimal breeding value requirements (Surles et al. 1995). Haapanen (2001) supported this methodology in his study on parental selection. The correlated responses per year to early parental (backward) selection peaked approximately at 5 to 7 years and were always greater than the gains from direct selection for tree height at 20 years. Another study examined early selection in the case of wood quality. The early selection proved very effective for wood quality traits (*Pinus sylvestris*), and the optimum selection age was 8 (Hong et al. 2015).

Alan et al. (2009) utilised a similar experimental setting to our study, employing a randomised complete block design with seven blocks and four tree row plots on each site. Strong and statistically significant differences among families on both sites were confirmed. These studies show that massive shifts in family ranking between these relatively young trees (in our case, we reported changes between 3 and 4-year-old trees) are expected and will stabilise in the next few years.

However, some studies about age-age correlations, such as Xiang et al. (2003), presented contrasting results. In their research, age-age correlations significantly increased in the first 3–4 years and then decreased. The trends of heritabilities and age-age correlations indicate that the optimum selection age for height could be as early as 3 years, which seems quite early compared to previously published findings.

CONCLUSION

This study highlights the significant role of ecotypic variation in the early growth of Scots pine in Central Europe. The findings emphasise that ecotypic factors are not fixed but vary over time and space. The observed distinctions between lowland and upland ecotypes underscore the importance of considering such variation during the early selection of progenies.

Considering these results, ecotypic variation should be considered in reforestation efforts. Understanding the existing differences in growth dynamics among ecotypes can profoundly impact the survival and success of trees during their early developmental stages. By factoring in these variations, forest managers and decision-makers can make more informed choices, potentially leading to improved growth and survival rates for Scots pine in the region.

Recognising the dynamic nature of ecotypic factors and their implications for tree growth and survival is crucial for effective forest management and sustainable reforestation practices in Central Europe. Further research in this area will continue to refine our understanding and contribute to preserving and growing valuable tree populations in the region.

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