Adaptability of twelve European provenances of *Pinus cembra* in two different branches of the Carpathians

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Abstract

Swiss stone pine (*Pinus cembra L.*) is a promising species for afforestation at the upper altitudinal limit of the forests due to its adaptability to more difficult climatic conditions. The study aims to analyze the genetic variability, testing site influence, trait-trait and juvenile-adult correlations across two 27-years-old provenance trials. The primary goal was to identify the best-performing provenances, set the suitable breeding strategies, and predicting the optimal age for forward selection. In the spring of 2024, measurements and evaluations were made for survival, diameter at breast height, tree height (Th), volume, fork occurrences, stem straightness, defoliation, branches diameter and finesse. The results indicated a high level of genetic variability, particularly within provenances, suggesting strong potential for selective breeding and adaptability. In each trial, three provenances were selected for reproduction in the same provenance region and under similar environmental conditions as the trials where they were performed. However, due to significant testing site and site x provenance interactions, extreme caution is recommended when transferring forest reproductive materials. Low QST values highlight the need for maintain high genetic diversity, a serious issue for the long-term resilience of this species. The observed juvenile-adult growth traits correlations and the time-to-time evolution of the 12 provenances indicate that early selection, even at the juvenile stage (17 years), could be effective. Forward selection of the top 30 % trees from the best three provenances, for Th, is recommended to enhance genetic gain. These findings provide valuable insights for developing breeding strategies and optimizing afforestation efforts in high-altitude regions.

Keywords: Alps and Carpathians forests; forward selection strategy; provenance trial; quantitative genetics; Swiss stone pine.

Introduction

Global warming has mitigated forests´protective ecological role, so solutions are being sought to identify species and intraspecific varieties with high resilience (Nabuurs et al., 2013, Liang et al., 2016, Ammer, 2019, Bastin et al., 2020, Chakraborty et al., 2024), while simultaneously implementing actions to increase the resilience of forest ecosystems (Spathelf et al., 2018, Jandl et al., 2019).

A mixture of Swiss stone pine *(Pinus cembra)*, European larch (*Larix decidua*), dwarfed mountain pine (*Pinus mugo*), and occasionally Norway spruce (*Picea abies*) could be a feasible solution for afforestation at the upper limit of the forests and also in the subalpine area of Alps and Carpathians (Paulsen et al., 2000, Li and Yang, 2004, Ulber et al., 2004, Blada and Popescu, 2007, 2012, Caudullo and de Rigo, 2016, Gugerli et al., 2023), due to these species capacity to adapt to the restrictive climatic conditions (Leonelli et al., 2009, Mosca et al., 2016, Neuschulz et al., 2018, Tóth et al., 2019, Dauphin et al., 2021) and their ability to increase the stands' resistance to windfalls and snow breaks. Although Swiss stone pine is well adapted to high altitudes, competition poses a challenge for this slow-growing species, particularly in the shade of fast-growing species such as spruce (Gugerli et al., 2022). This aspect must be considered in afforestation planning.

Genetic analyses have indicated low diversity among Swiss stone pine populations in the Alps and Carpathians, especially in the Tatra Mountains (Dzialuk et al., 2014), as well as in other isolated or fragmented populations (Belokon et al., 2005, Politov et al., 2008, Höhn et al., 2009, Salzer and Gugerli, 2012). This suggests a need to increase the number of genetically improved seed sources of Swiss stone pine (Saura et al., 2008, Funk et al., 2012, Lendvay et al., 2014, Wojnicka-Półtorak et al., 2015, Sonnenwyl et al., 2024) to enhance the genetic diversity of forest reproductive materials used in afforestation.

In Romania, a breeding programme for Swiss stone pine was coordinated by Blada (1987, 2019) between 1979 and 2004. It began with mapping the natural distribution areas of the species in the Romanian Carpathians, selecting phenotypically valuable plus trees, reproducing them generatively or vegetatively, and establishing nine field trials (three half-sib, two full-sib, three of provenances and one clone trial). Additionally, due to a LIFE project, a 50 ha area in the Pietrosul Rodnei

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Mountain (Eastern Carpathians) was planted (Blada, 2019). Conclusions and recommendations from this research were disseminated in important journals (Blada and Popescu, 2007, 2008, 2012, Budeanu et al., 2024), highlighting the significance of these experiments and the need to continue and expand investigations.

This study aims to analyze the genetic variability, testing site influence, trait-trait and juvenile-adult correlations in two 27-years-old provenance trials to select the best-performing provenances, establish the most suitable breeding strategy, and predict the optimal age for forward selection.

Materials and methods

The experiment, designed to test 12 European provenances of Swiss stone pine, 7 from the Romanian Carpathians and 5 originating from the Alps (from Austria, Switzerland and France), is considered unique in Europe. These provenances cover a significant part of the species' natural range, spanning across a latitude range of 4°36' N (from 45°12' to 49°48') and a longitude range of 20°29' E (from 4°48' to 25°17'). The altitudinal amplitude of the provenances varies by 655 m, ranging from 1520 m to 2175 m, a.s.l. Each provenance resulted from mixing seeds harvested from 10 to 20 open-pollinated trees, located at least 50 m apart (Blada and Popescu, 2007).

One provenance originated from France (Bois des Ayes), one from Switzerland (Grachen Walis), three from Austria (Bluhnbach, Imst-Roppen, Sirnitz-Gilendorfer), and seven from Romania (three from the Eastern Carpathians: Călimani, Valea Lalei, Pietrosul, and four from the Southern Carpathians: Gemenele, Pietrele, Stâna de Râu, Păpușa-lezer) (Figure 1A).

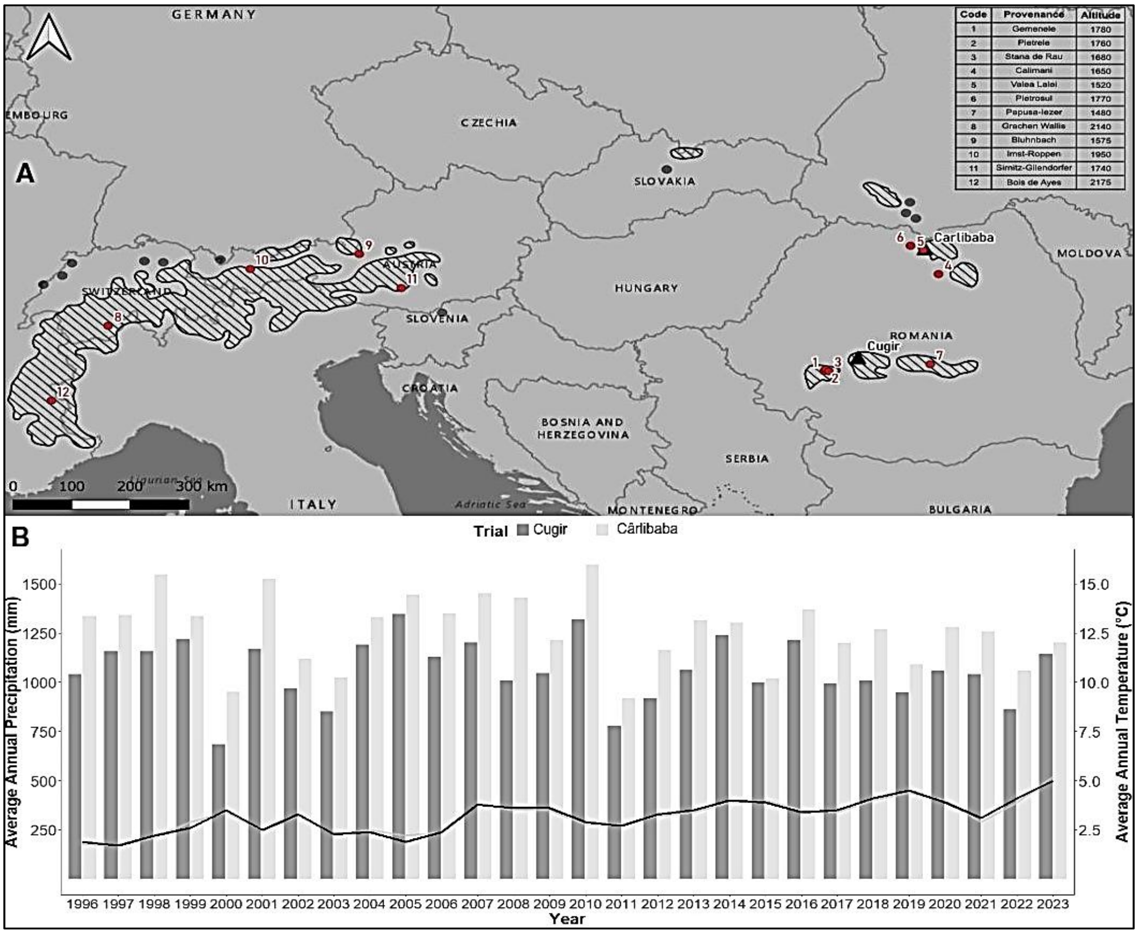

Figure 1
The location of the Cugir and Cârlibaba field trials (black triangle) and provenances origins (red circle, A) on the *Pinus cembra* distribution map (Caudullo et al., 2017). The natural distribution of the species is hatched. Regional climate trends (B) in the mean annual temperature (red) and total precipitation (brown) for the trials over the last 28 years were computed using Climate downscaling tool (B4EST, 2024).

The two comparative trials (Cugir, located in the Southern Carpathians, and Cârlibaba, in the Eastern Carpathians) were established in the autumn of 1997, using 7-year-old seedlings with an average height of 27 cm and a root collar diameter of 12 mm. For both trials a completely randomized block design was utilized with three replications and 30 trees per unitary plot, planted at a spacing of 2.5 x 2.5 m (Blada and Popescu 2007).

The Cugir trial was established in the Şureanu Mountains of the Southern Carpathians and it is currently administered by the Cugir Forest District. It is located in the production unit IV Canciu, plot 65B, covering an area of 0.9 ha. Geographically, it is located at 45˚37′ N latitude, 23˚32' E longitude, and at an altitude of 1550 m. The trial is positioned at the top of a slope on land with an undulating configuration, facing southwest, with a 20˚ inclination. The biotope is of medium productivity, the forest type being represented by high-altitude spruces with mull flora, and the soil is classified as typically districambosoil.

The Cârlibaba trial was located in the Inău Mountains of the Eastern Carpathians and is administered by the Plaiurile Heniului Forest District. It is situated in the production unit IV Leşu, plot 22B, covering an area of 0.85 ha. Geographically, it is located at 47˚33' N latitude, 24˚55' E longitude, and at an altitude of 1445 m. The trial it is positioned at the top of a slope on land with a strongly undulating configuration, facing south, with a 25˚ inclination. The biotope is of medium productivity, the forest type being represented by high-altitude spruces with mull flora, and the soil is classified as typically districambosoil.

While the precipitation showed no clear trend over the last 28 years in both testing regions, temperatures have increased (Figure 1B). The average annual temperature in both trials was 3.2°C, while the sum of annual precipitation averaged 1062 mm in the Cugir trial and 1265 mm in the Cârlibaba test (B4EST, 2024).

In these trials, measurements were taken at 1, 10, and 27 years after the trial's establishment (the years 1998, 2007, and 2024, respectively). At 34 years of trees' age (27 years after the trial's establishment), measurements and evaluations of growth and quality traits were carried out for ten trees per provenance in each replication, randomly selected (every third tree was selected: 1, 4, 7, etc.). The breast height diameter (Dbh), tree height (Th), fork height (Fh), and dominant branch diameter (Bd, measured in the whorl situated at 1.3 m from the ground) were assessed using a forest caliper, a Vertex V instrument, and an electronic caliper, respectively. Fork (F) and the stem straightness (Ss) were evaluated on a scale of 7 (from 1= more forks in the lower third of the stem, to 7= no fork) and 5 (0 = vertical and rectilinear stem, 1 = 1-2 slight curves, 2 = three or more slight curves, 3 = 1-2 big curves, and 4 = three or more big curves.) classes, respectively, according to the Treebreedex protocol (Ducci et al., 2012). Defoliation (D) was evaluated on a scale of 5 classes (from 0= healthy tree, 0-10 % defoliation, to 4= dead tree), following the ICP protocol (Eichhorn et al., 2020). More details related to the three indices can be found in Budeanu et al. (2024). Additionally, tree volume (Tv) was calculated using the regression equation method (Giurgiu et al., 2004), and branches' finesse (Bf) was calculated using the formula Bf=Bd x 100 / Dbh.

Survival (Sr) was calculated in both trials for each provenance and in every replication as the proportion of trees that survived until the trials age of 27 years compared to the number of trees planted.

Statistical analysis

In each trial, the mathematical model used for the analysis was the one recommended by Nanson (2004):

$X_{ij} = m + \alpha_i + \beta_j + \varepsilon_{ij}$

where: m is the average value, α_i is the component of i provenances (i = 1...12), β_j is the component of j replications (j = 1...3), ε_{ij} represents the random error that influences ij plots. A mixed linear model was used, where the replication was integrated as a fixed effect, while the provenance factor had a random effect.

After conducting ANOVA for each trial, the results were cumulated and analyzed using a bifactorial analysis to highlight the influences of the testing site and the interaction between populations x localities, according to Nanson (2004):

$X_{ijk} = m + \alpha_i + \beta_j + \alpha\beta_{ij} + \varepsilon_{ijk}$

where: m and α_i have the same signification as mentioned above, β_j represent component of j localities (j = 1…2), $\alpha\beta_{ij}$ indicates the interaction between provenances and localities, ε_{ijk} is the random error. Again, a mixed linear model was used, with the locality having a fixed effect, while the provenance and provenance x locality factors had a random effect.

The significance level was determined using Fisher (F) test, assessing the transgression probability at levels of 5 %, 1 % and 0.1 %. Provenances ranking and their separation into homogenous groups were conducted using the Tukey HSD test at a 5 % transgression possibility. Additionally, Pearson's simple phenotypic age-age ant trait-trait correlations were determined, along with correlations between traits and the ecological gradients corresponding to origins of the provenances. The ecophysiological latitude (Le) was estimated according to Wiersma (1962) using the formula Le = L + A / 100, where: L represents latitude, A represents altitude (with a 100 m difference in altitude considered equivalent to one degree of latitude).

A graphical method was used to highlight the best-performing provenances, based on the average values recorded for survival rate (stability performance) and trees height (growth performance). mosaic plot, with significant differences marked by different colors, was utilized to visualize and interpret the categorical relationships between provenances regarding the fork index.

To estimate the quantitative genetic differentiation among provenances, the Q_{ST} coefficients were calculated according to Morgan et al. (2005) using the following formula:

$$Q_{ST} = \frac{\sigma_b^2}{\sigma_b^2 + 2\sigma_w^2}$$

where σb^2 and σw^2 represent the genetic variances between and within provenances. The level of genetic divergence among the provenances shows us the level of genetic diversity in the experiment. This is compared with the intra-populational diversity to determine the optimal breeding strategy (population or individual selection). At the same time, it provides information on the genetic diversity that we can transmit to future forests.

The software utilized for data processing includes R (2023), for figures 2-4 and tables 3, 4, 6-9, Statistica 10.0 (2010), for Tukey HSD tests (tables 1-2), Microsoft Office Excel 15, for table 5, and QGIS 10.3 (2024), for figure 1.

Results

Phenotypic variability

In both field trials, the principal growth traits (Th, Dbh, and Tv), highlighted two notable provenances, 4-Călimani (Eastern Carpathians) and 9-Bluhnbach (Austria). In contrast, provenance 6-Pietrosul (Eastern Carpathians) registered low results (Tables 1, 2, Figure 2). ANOVA results (Table 3) revealed a highly significant influence of provenance ($p<0.001$) in both experiments, while the influence of replication was found to be insignificant. The statement is valid for all analyzed traits, except of Bf in the Cârlibaba trial. Factorial ANOVA (Table 4) further confirms a highly significant influence ($p<0.001$) of locality, provenance, and their interaction. The local provenances (3-Stâna de Râu, in Cugir, and 5-Valea Lalei, in Cârlibaba trials) were ranked in the best homogeneous group for all growth traits, especially the local provenance of the Cugir trial, which ranked in third place (Tables 1, 2, Figure 2). For Tv, the provenances from the Carpathians outperformed those from the Alps by 17.3 % in the Cârlibaba trial, while a reverse situation was observed in the Cugir experiment, where the Alpine provenances exceeded the Carpathians origin by 4.5 %. The provenance 11-Sirnitz-Gilendorfer from Austria recorded contrasting results, achieving first place in the Cugir trial but ranking last in Cârlibaba, which emphasizes the need for maximum caution when moving forest reproductive materials.

Table 1
Ranking of the provenances for Dbh and their separation into homogeneous groups (Tukey HSD test, α=5 %)
(Dbh= diameter at breast height, Hg= homogeneous groups. Foreign provenances: Switzerland= red, Austria= green, France= blue. Romanian origins: Eastern Carpathians= orange, Southern Carpathians= black.)

<table>
<tr><th colspan="4">Cugir trial</th><th colspan="5">Cârlibaba trial</th></tr>
<tr><th>Provenance</th><th>Dbh (cm)</th><th colspan="2">Hg</th><th>Provenance</th><th>Dbh (cm)</th><th colspan="3">Hg</th></tr>
<tr><td>11</td><td>17.82</td><td>|</td><td></td><td>4</td><td>16.87</td><td>|</td><td></td><td></td></tr>
<tr><td>9</td><td>17.29</td><td>|</td><td></td><td>9</td><td>16.43</td><td>|</td><td>|</td><td></td></tr>
<tr><td>3</td><td>17.11</td><td>|</td><td></td><td>2</td><td>16.41</td><td>|</td><td>|</td><td></td></tr>
<tr><td>4</td><td>16.98</td><td>|</td><td></td><td>3</td><td>16.31</td><td>|</td><td>|</td><td></td></tr>
<tr><td>7</td><td>16.78</td><td>|</td><td></td><td>5</td><td>16.23</td><td>|</td><td>|</td><td></td></tr>
<tr><td>2</td><td>16.75</td><td>|</td><td></td><td>8</td><td>16.21</td><td>|</td><td>|</td><td></td></tr>
<tr><td>1</td><td>16.61</td><td>|</td><td></td><td>7</td><td>16.06</td><td>|</td><td>|</td><td></td></tr>
<tr><td>12</td><td>16.55</td><td>|</td><td></td><td>1</td><td>15.96</td><td>|</td><td>|</td><td></td></tr>
<tr><td>10</td><td>16.32</td><td>|</td><td></td><td>10</td><td>15.66</td><td>|</td><td>|</td><td></td></tr>
<tr><td>5</td><td>16.03</td><td>|</td><td>|</td><td>12</td><td>15.15</td><td>|</td><td>|</td><td></td></tr>
<tr><td>8</td><td>14.38</td><td></td><td>|</td><td>6</td><td>15.02</td><td></td><td>|</td><td></td></tr>
<tr><td>6</td><td>14.20</td><td></td><td>|</td><td>11</td><td>10.23</td><td></td><td></td><td>|</td></tr>
</table>

Table 2
Ranking of the provenances for Th and their separation into homogeneous groups (Tukey HSD test, α=5 %) Th= trees' height. Hg and provenances color as in table 1.

<table>
<tr><th colspan="7">Cugir trial</th><th colspan="5">Cârlibaba trial</th></tr>
<tr><th>Provenance</th><th>Th (m)</th><th colspan="5">Hg</th><th>Provenance</th><th>Th (m)</th><th colspan="3">Hg</th></tr>
<tr><td>9</td><td>7.69</td><td>|</td><td></td><td></td><td></td><td></td><td>1</td><td>7.29</td><td>|</td><td></td><td></td></tr>
<tr><td>2</td><td>7.59</td><td>|</td><td>|</td><td></td><td></td><td></td><td>8</td><td>7.29</td><td>|</td><td></td><td></td></tr>
<tr><td>3</td><td>7.40</td><td>|</td><td>|</td><td></td><td></td><td></td><td>2</td><td>7.28</td><td>|</td><td></td><td></td></tr>
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<tr><td>11</td><td>7.15</td><td></td><td>|</td><td>|</td><td>|</td><td></td><td>9</td><td>7.03</td><td>|</td><td>|</td><td></td></tr>
<tr><td>7</td><td>7.13</td><td></td><td>|</td><td>|</td><td>|</td><td></td><td>5</td><td>7.03</td><td>|</td><td>|</td><td></td></tr>
<tr><td>12</td><td>7.08</td><td></td><td>|</td><td>|</td><td>|</td><td></td><td>10</td><td>6.99</td><td>|</td><td>|</td><td></td></tr>
<tr><td>10</td><td>6.85</td><td></td><td></td><td>|</td><td>|</td><td></td><td>3</td><td>6.84</td><td>|</td><td>|</td><td></td></tr>
<tr><td>8</td><td>6.78</td><td></td><td></td><td></td><td>|</td><td></td><td>12</td><td>6.54</td><td></td><td>|</td><td></td></tr>
<tr><td>5</td><td>6.75</td><td></td><td></td><td></td><td>|</td><td></td><td>6</td><td>5.94</td><td></td><td></td><td>|</td></tr>
<tr><td>6</td><td>5.70</td><td></td><td></td><td></td><td></td><td>|</td><td>11</td><td>5.87</td><td></td><td></td><td>|</td></tr>
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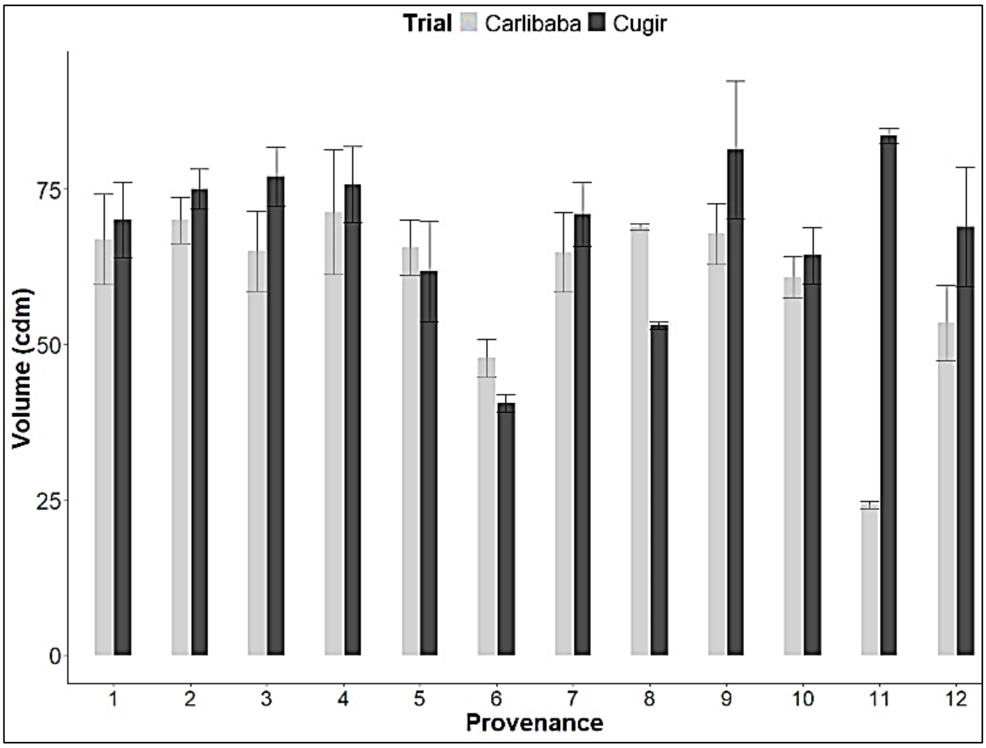

Figure 2
Trees volume variation (mean±SD) among the provenances, in the Cugir and Cârlibaba trials. The provenance codes (1-12) as in figure 1.

Table 3
ANOVA for the principal analyzed traits, by location (DF= degrees of freedom, MS = mean square. Significant influences, * at p<0.05, ** at p<0.01, *** at p<0.001, according to Fisher test. Dbh, Th, Tv, Bd and Bf as in methodology.)

Factor	DF	MS_{Dbh}	MS_{Th}	MS_{Tv}	MS_{Bd}	MS_{Bf}	MS_{Dbh}	MS_{Th}	MS_{Tv}	MS_{Bd}	MS_{Bf}
		Cugir test					Cârlibaba test				
Replication	2	3.33	0.91	602	0.16	1.93	4.97	0.57	399	0.002	3.37
Provenance	11	35.55***	8.14***	4524***	1.29***	112.4***	92.53***	7.22***	5370***	2.26***	23.28**
Error	346	4.88	0.38	497	1.17	6.05	4.23	0.44	417	0.24	8.08

Table 4
Factorial ANOVA for the principal analyzed traits, over locations (DF= degrees of freedom, MS = mean square. Significant influences, * at p<0.05, ** at p<0.01, *** at p<0.001, according to Fisher test. Dbh, Th, Tv, Bd and Bf as in methodology.)

Factor	DF	MS_{Dbh}	MS_{Th}	MS_{Tv}	MS_{Bd}	MS_{Bf}
Locality (L)	1	132.4***	7.22***	11519***	0.098	56.8**
Provenance (P)	11	49.4***	11.56***	4757***	1.764***	97.8***
L x P	11	78.7***	3.79***	5137***	1.783***	37.9***
Error	696	4.6	0.41	457	0.202	7.0

For *Survival rate* (Sr), very high average values were recorded in both trials, respectively 88.6 % in Cugir and 90.1 % in Cârlibaba, with amplitudes of variation between 63.6 % (6-Pietrosul) and 97.8 % (9-Bluhnbach, Austria), in Cugir, and respectively between 79.2 % (5-Valea Lalei, the local provenance) and 98.7 % (12-France), in Cârlibaba. The provenances highlighted for growth, 9-Bluhnbach (Austria) and 4-Călimani, also exhibited high survival rates, ranking oin the first and second places in Cugir, respectively, the fifth and sixth places (but with 90 % survival) in the Cârlibaba trial.

Regarding *branches* (Bd, Bf), the provenances highlighted for growth and survival, 9-Bluhnbach (Austria) and 4-Călimani, also presented thin and fine branches, which are indicative of superior stem wood quality. Both ranked in the best homogeneous group for Bd and Bf across both trials, positioning between the fifth and the second places (Table 5). When considering cumulative data for both trials, these two provenances emerged as the best performers for Bf. In contrast, the local provenances (3-Stâna de Râu, in Cugir, and 5-Valea Lalei, in Cârlibaba trials) registered different branch characteristics. Thus, in the Southern Carpathians field trial (Cugir), the local provenance presented thin and fine branches, ranking third for Bf and sixth for Bd, while in the Eastern Carpathians experiment (Cârlibaba), the local provenance presented thick branches, recording the highest Bd and the fourth-highestr Bf. Almost similar average results were registered in both trials for the Carpathians and Alps provenances, with 3-11 % higher values for Bd and Bf for the Carpathians provenances compared to the Alp's' ones.

The best *fork index* results, for the ensemble of the two trials, was registered by provenance 5-Valea Lalei (5.82, with 1 fork in the upper third of the stem), which is a local provenance in the Eastern Carpathians experiment. This suggests a higher adaptation of the local population to the loss of the terminal bud or shoot due to snow breakage or late frosts. The hypothesis is further supported by the good result (4th place) registered by the local provenance (3-Stâna de Râu) in the Southern Carpathians trial. In the Cugir trial, the fork index was 13 % higher (favorable) compared to the Cârlibaba experiment. Across both trials, the Carpathians provenances registered an 8.8 % higher fork index compared to the Alps provenances. The weakest result was recorded by provenance 11-Sirnitz-Gilendorfer from Austria, due to its performance in the Cugir test, where it ranked last (Figure 3), despite displaying opposite behavior (second place) in the Cârlibaba trial. In the Cugir trial, the above-mentioned provenance registered the highest Dbh.

Table 5
Provenances average results for the branches and stem traits (Foreign provenances: Switzerland= red, Austria= green, France= blue. Romanian provenances: Eastern Carpathians= orange, Southern Carpathians= blank.)

	Cugir			Cârlibaba		
Provenance	**Bd (cm)**	**Bf (%)**	**Ss (index)**	**Bd (cm)**	**Bf (%)**	**Ss (index)**
1	2.36	14.3	0.83	2.45	15.6	1.10
2	2.49	14.9	0.67	2.44	15.0	1.03
3	2.33	13.6	0.57	2.52	15.5	0.93
4	2.29	13.6	0.47	2.38	14.2	0.87
5	2.66	16.7	1.00	2.56	15.8	1.23
6	2.83	20.2	1.23	2.53	16.9	0.93
7	2.50	15.0	0.97	2.55	16.0	0.67
8	2.09	15.0	0.40	2.37	14.7	0.30
9	2.20	12.7	0.33	2.42	14.9	0.77
10	2.27	14.0	1.03	2.23	14.3	0.67
11	2.55	14.5	1.07	1.57	15.7	0.60
12	2.31	14.0	0.47	2.56	16.8	0.87
Average	**2.41**	**14.87**	**0.75**	**2.38**	**15.43**	**0.83**

Figure 3
Fork index variation among the twelve provenances in the Cârlibaba (up) and Cugir (down) trials. The provenance codes (1-12) as in figure 1. The blue color express significantly higher values while the red color mark the significantly lower ones. The grey color suggest no interactions and the intensity of the colors express a higher level of significance.

Stem straightness is another important aspect when establishing stands where high-quality timber production is the main purpose. Likewise, for this trait, the average result recorded in the Cugir trial was clearly more favorable compared to the Cârlibaba test. Thus, the number of trees included in the zero class (perfectly straight stem) was 54 % higher in the Southern Carpathians test, a statistically significant difference. However, good results for this trait were registered in both trials, with over 86 % of the trees classified in the 0-1 classes (with a maximum of 1-2 slight stem curves). For Ss, the provenance from Switzerland, 8-Grachen Wallis, was particularly noteworthy in both experiments, followed by 9-Bluhnbach (Austria) and 4-Călimani (especially in Cugir, see Table 5), both of which also demonstrated good growth performance. Obviously, the two provenances from Romania and Austria will be among those selected and proposed for the region where they stood out, as well as for their regions of origin. In both trials, the Alp's' provenances presented superior stem straightness compared to the Carpathians' origins (20 % in Cugir and 34 % in Cârlibaba). Additionally, for Ss, the local provenances were included in the best homogeneous group.

Defoliation (D), evaluated on a 5-class scale, according to the ICP protocol (Eichhorn et al. 2020), highlighted the high vitality of the 12 provenances in both test sites, with an average value per experiment of 0.55 at Cugir and 0.63 at Cârlibaba. Provenances 4-Călimani (0.20 in Cugir, first place, and 0.43 in Cârlibaba, third place), 5-Valea Lalei (ranking opposite to provenance 4), 7-Păpușa-Iezer and 9-Bluhnbach (Austria) stood out with the lowest defoliation values in both experiments. Conversely, the highest defoliation values were recorded for provenances 12-France (0.77 in the Cugir test) and 11-Sirnitz-Gilendorfer, Austria (1.23 in Cârlibaba). It is well known how sensitive Swiss stone pine is to high concentrations of ozone (Wieser et al., 2006). Additionally, the local provenances were included in the best homogeneous group for D.

Trait-trait, trait-origin and juvenile-adult correlations

Highly significant phenotypic correlations were registered among the growth traits in both trials (r= 0.72*** - 0.96***). A negative but statistically insignificant correlation was registered between growth traits and fork index. The trait-trait phenotypic correlations in the Cugir and Cârlibaba trials (Table 6) suggest that the selection for growth traits (Dbh or Th) also favors the improvement of most other traits, with the exception of fork, where correlations were not significant).

Table 6
Trait-trait phenotypic correlations, in the Cugir (above diagonal) and Cârlibaba (below diagonal) trials Significant correlations: * at p<0.05, ** at p<0.01, *** at p<0.001. Dbh, Th, Tv, F, Bd, Bf, D, and Ss, as in methodology. N= 36.

Traits	Dbh	Th	Tv	F	Bd	Bf	D	Ss
Dbh	-	0.78***	0.96***	-0.31	-0.10	-0.67***	-0.14	-0.17
Th	0.72***	-	0.89***	-0.04	-0.50**	-0.85***	-0.08	-0.41*
Tv	0.95***	0.88***	-	-0.29	-0.25	-0.75***	-0.17	-0.29
F	-0.28	-0.21	-0.28	-	0.01	0.10	0.00	-0.11
Bd	0.80***	0.38*	0.65***	-0.23	-	0.79***	-0.10	0.38*
Bf	-0.26	-0.55***	-0.44**	0.02	0.35*	-	0.01	0.37*
D	-0.54	-0.33	-0.48**	0.00	-0.42*	0.19	-	0.18
Ss	0.23	0.04	0.17	-0.45**	0.29	0.16	0.05	-

Correlations between traits and the geographical coordinates of provenances origin in the Cugir and Cârlibaba trials (Table 7), generally indicated a low and statistically insignificant influences of provenance origin. In the Cugir trial, the highest correlation was found between Bd and longitude (r= 0.54***), suggesting that the provenances from higher longitudes have thicker branches. Altitude had a negative and significant influence on both Dbh (r= -0.37*) and Bd (r= -0.40*), suggesting that provenances from lower altitudes registered superior Dbh and Bd values. In the Cârlibaba trial, longitude showed a positive and distinctly significant influence on stem straightness (r= 0.48**), suggesting that the provenances from the west (Alps) presented better stem straightness. Also, provenances from high altitudes presented superior steam straightness (r= -0.34*). Another interesting correlation, observed in both trials (but significant only in the Cârlibaba trial), was between latitude and Th, where a negative correlation indicated that provenances for southern regions had superior Th values.

The evolution over time of the 12 European provenances of Swiss stone pine in the Cugir and Cârlibaba trials was assessed using juvenile-adult correlations (Table 8), and by analyzing the ranking of the provenances at the two stages (for Dbh and Th). Positive and highly significant correlations were recorded between saplings' heights at the time of the trial establishment and those heights measured 10 years later (r= 0.89*** in Cugir, and r= 0.86*** in Cârlibaba). These correlations remained positive and significant until 2024, although their intensity decreased over time (r= 0.68* in Cugir and r= 0.69* in Cârlibaba for the correlations between initial heights and Th measured in the spring of 2024). Similarly, positive and distinctly significant correlations were obtained between the heights recorded 10 years after trials establishment and Th measured in 2024 (r= 0.76** in Cugir and r= 0.72** in Cârlibaba). For root collar diameters measured at the start of the trials, medium-intensity direct correlations were observed with Dbh measured in 2024. However, these were statistically insignificant (r= 0.37 in Cugir and r= 0.56 in Cârlibaba).

Table 7
Correlations between traits and geographical coordinates of provenances origin, in the Cugir (up) and Cârlibaba (down) trials Significant correlations: * at p<0.05, ** at p<0.01, *** at p<0.001. Dbh, Th, Tv, F, Bd, Bf, D, and Ss, as in methodology. N=36.

Traits/Coordinates	North Latitude	Altitude	North corrected Latitude	East Longitude
		Cugir trial		
Dbh	0.00	-0.37*	-0.01	0.05
Th	-0.22	-0.19	-0.23	-0.08
Tv	-0.10	-0.31	-0.10	-0.02
F	-0.21	-0.20	-0.21	0.43*
Bd	0.11	-0.40*	0.10	0.54***
Bf	0.09	-0.04	0.09	0.34*
D	0.06	0.25	0.07	-0.19
Ss	-0.01	-0.18	-0.01	0.26
		Cârlibaba trial		
Dbh	-0.15	-0.10	-0.15	0.27
Th	-0.41*	-0.07	-0.41*	0.11
Tv	-0.29	-0.12	-0.29	0.24
F	-0.19	-0.06	-0.19	-0.16
Bd	0.01	-0.04	0.01	0.26
Bf	0.27	0.02	0.27	0.07
D	-0.25	0.22	-0.25	-0.14
Ss	0.13	-0.34*	0.12	0.48**

Table 8
Age-age correlations between growth traits, in the Cugir (above diagonal) and Cârlibaba (below diagonal) trials. Significant correlations: * at p<0.05, ** at p<0.01, *** at p<0.001. D7, Th7, Th17, Th34, and Dbh34 are the collar diameter, breast height diameter, and trees height, at the seedlings age of 7, 17, and 34 years (trials age of 1, 10, and 27). N=12.

Traits	Th7	D7	Th17	Th34	Dbh34
Th7	-	0.95***	0.89***	0.68*	0.38
D7	0.95***	-	0.84***	0.74**	0.37
Th17	0.86***	0.84***	-	0.76**	0.58*
Th34	0.69*	0.74**	0.72**	-	0.82***
Dbh34	0.53	0.56	0.62*	0.78**	-

In both comparative trials, the provenances 9-Bluhnbach (Austria) and 4-Călimani consistently ranked at the top for both diameter and tree height, from the establishment of the trials in 1997 until 2024. Conversely, the provenances 5-Valea Lalei and 6-Pietrosul showed modest results in the Cugir trial, while 6-Pietrosul and 11-Sirnitz-Gilendorfer (Austria) ranked lower in the Cârlibaba test. Notably, in both experiments, provenance 3-Stâna de Râu (a local provenance in the Cugir test) exhibited a strong improvement in recent years, after showing only average growths during the juvenile stage.

These results regarding age-age correlations and the time-to-time evolution of the 12 provenances suggest that selection could be effectively carried out from the juvenile stage, at the trees' age of 17 years .

3.3. Forward selection

In the Cugir trial, located in the Southern Carpathians, the mean performance of provenances for the most important growth (Th) and stability (Sr) traits indicated that the best-performing provenances were 9-Bluhnbach (Austrian Alps), 2-Pietrele (Southern Carpathians), and 4-Călimani (Eastern

Carpathians). These provenances outperformed the local provenance, 3-Stâna de Râu, which showed lower stability (Figure 4). In the Cârlibaba experiment, located in the Eastern Carpathians, the best-performing provenances were 8-Grachen-Wallis (Swiss Alps), 1-Gemenele, and 2-Pietrele (both from Southern Carpathians), which all achieved higher performance than the local provenance, 5-Valea Lalei, which also lost points for stability. Even in this trial, the 4-Călimani and 9-Bluhnbach provenances demonstrated very high Th values and high Sr values (> 89 %), close to the trial mean (Figure 4).
The quantitative genetic differentiation (QST) among provenances was, on average, equal in both the Cugir and Cârlibaba trials, with the highest value recorded for the most important growth traits: Th in the Cugir trial, and Dbh in the Cârlibaba test (Table 9). For these important growth traits, within-provenance variances were 1.3 to 4.2 times higher than among-provenances in both trials, suggesting greater variability within the provenances and emphasizing the necessity for promoting individual selection. The breeding program for wood production should prioritize selection based on Th in both trials due to the higher QST values and the critical importance of selecting provenances and individuals with superior Th to ensure competitiveness with other species in the area, especially Norway spruce and European Larch.

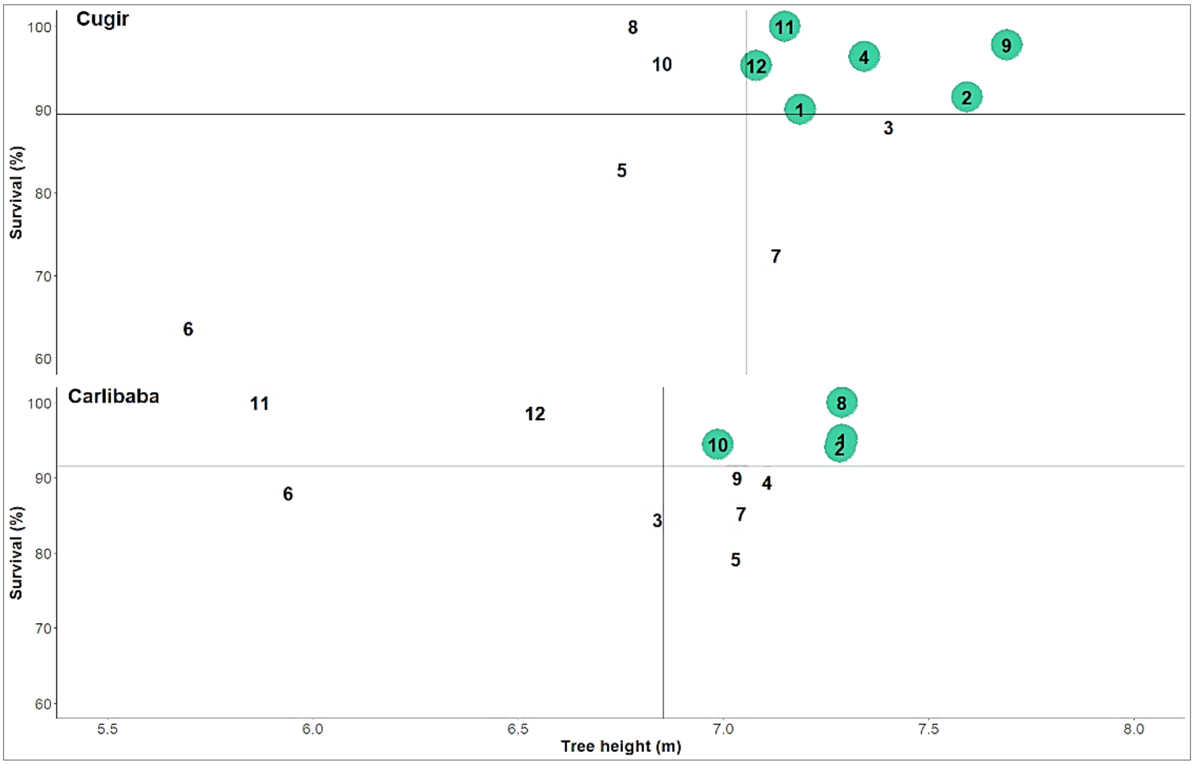

Figure 4. The best-performing provenances in the two trials. The green circles mark the best-performing provenances positioned in the upper right quadrant, and the black lines represent the trial mean for tree height and Survival rate.

Table 9
The quantitative genetic differentiation (Q_{ST}) among provenances. Traits abbreviation as in methodology.

Traits	Q_{ST} Cugir	Q_{ST} Cârlibaba
Dbh	0.11	0.27
Th	0.27	0.22
Tv	0.13	0.18
Bd	0.12	0.14
Bf	0.24	0.05
F	0.10	0.03
D	0.06	0.12
Ss	0.09	0.09

Therefore, the best inheritance rate could be obtained by a mixed selection of the best 30% of trees from the three most valuable provenances in each trial for Th, which would likely lead to improvements in all traits. At the same time, the low QST values suggest reduced genetic diversity, necessitating the combination of seedlings obtained from these experiments with those from similar tests (e.g., from the Păltiniș and Rodna full-sib trials, Budeanu et al., 2024).

Discussion

Phenotypic variability

Significant differences among and within provenances suggests a good potential for adaptation to future difficult climates (Pliura and Eriksson, 2002). However, extreme caution is mandatory when transferring forest reproductive materials, as well as to ensure a high level of genetic diversity, which is a very critical issue for Swiss stone pine populations in the Alp's and Carpathians (Belokon et al., 2005, Politov et al., 2008, Höhn et al., 2009, Salzer and Gugerli, 2012, Dzialuk et al., 2014). Superior results for the majority of the analyzed traits (except for Sr, which had nonsignificant differences) were registered in the Cugir trial, 2.9-13.2 % for the principal growth traits (Dbh, Th, Tv), 9.4 % for Ss, and 12 % for F, compared to the Cârlibaba test. When comparing environmental conditions, no significant differences were observed, with the most relevant factors being two degrees of latitude, one degree of longitude, 100 m of altitude, and a 5° difference in inclination. The genetic component seems to have an important role, as some provenances performed well in both experiments [especially 9-Bluhnbach (Austrian Alps), 2-Pietrele (Southern Carpathians) and 4-Călimani (Eastern Carpathians)], but also one that achieved inferior results in both test sites [especially 6-Pietrosul (Eastern Carpathians)]. However, the contrasting results registered for provenance 11-Imst-Roppen (Austrian Alps), highlights the need for caution in transferring forest reproductive materials.

At the upper altitudinal limit of Romanian forests where the Swiss stone pine is found, promoting specific juvenile provenances with active growth, such as 9-Bluhnbach (Austria) and 4-Călimani, along with local provenances, can enhance the stands' resistance to wind and avalanche. This approach also supports the species survival in the face of intense competition from the fast-growing species, especially spruce (Budeanu et al., 2019). The results from the current study, alongside previous research (Budeanu et al., 2024), and the up-to-date evaluation of all the experiments established over a quarter of century ago by Blada (2019), recommend a two-stage afforestation of mixed species: first, the planting of Swiss stone pine, followed by the addition of Norway spruce and European larch after approximately 10 years. It is also recommended to plant Swiss stone pine in larger clusters, located at the altitudinal limit of the forest. However, to ensure high resistance to strong winds and snow avalanches, detailed research should focus on selecting provenances with either thick or thin branches. Provenance selection will play a key role in improving forest resilience to future climate change (Chakraborty et al., 2024). The continued increase in global temperatures will likely require ongoing adaptation of tree species (Leonelli et al., 2009, Mosca et al., 2016, Gugerli et al., 2022). The global warming seems to offer a competitive advantage to Norway spruce over Swiss stone pine, in subalpine areas of the Western Carpathians (Marčiš et al., 2025). Also, in the Southern Carpathians the highly important role of temperature in the Swiss stone pine resilience was registered (Știrbu et al., 2022).

The best fork results, characterized by the absence of forks or only one fork in the upper third of the stem, were observed for the local provenances, suggesting a higher adaptation of the local population to the loss of the terminal bud or shoot due to snow breakage or late frost events. Overall, all provenances in both trials registered good results for defoliation and stem straightness, with most trees exhibiting healthy characteristics, vertical and rectilinear stems, and only 1-2 slight curves present in some trees.

Correlations

In both trials, the trait-trait phenotypic correlations favor the selection for growth traits (such as Dbh or Th), which promote the improvement of most other traits.

The present results regarding the age-age correlations and the time-to-time evolution of the 12 provenances suggest that selection could begin as early as the juvenile stage, around 17 years of trees' age. Previously, Blada and Popescu (2008, 2012) recommended an even earlier selection age of 12 years, also emphasizing growth traits.

The generally low correlations between traits and the geographic origin of provenances are surprising, considering the large differences in altitude, latitude and longitude among the provenances. It is possible that the climatic conditions in the regions of provenance's origin do not follow any geographic trend. Also in the Romanian Carpathians, the same low trait-gradient correlations were registered for Norway spruce (Budeanu et al., 2014). In contrast, research carried out in the Tatra Mountains indicated a strong influence of altitude and slope inclination on the distribution of Swiss stone pine (Zięba et al., 2019, Izworska et al., 2023).

Forward selection

For the combined results of both trials, the best-performing provenances in terms of stability and growth were 2-Pietrele and 1-Gemenele (both from Southern Carpathians), followed by 9-Bluhnbach (Austria) and 4-Călimani Eastern Carpathians), along with the local provenances. Due to the significant influence of the test site, we must restrict forward selection to the provenance region where the tests were located and to those provenances that performed well in each experiment. For provenance region C1, located in the northern part of the Southern Carpathians, based on the results obtained in the Cugir test, we recommend selecting the provenances 9-Bluhnbach (Austrian Alps), 2-Pietrele (Southern Carpathians) and 4-Călimani (Eastern Carpathians). Simultaneously, for provenance region A2, situated in the eastern part of the Romanian Eastern Carpathians, we recommend selecting 8-Grachen-Wallis (Swiss Alps), along with 1-Gemenele and 2-Pietrele (both from the Southern Carpathians), based on the results from the Cârlibaba test.

The genetic component appears to play the most crucial role in growth traits, especially for Th. Therefore, based on the results obtained in this research, we propose a mixed selection of the best 30 % of trees from the most valuable three provenances, in each trial, specifically for Th. At the same time, the low QST values suggest a reduced genetic diversity, necessitating the combination of seedlings from these experiments with those from similar tests in future seed orchards and plantations. Lendvay et al. (2014) highlight the importance of maintaining sufficiently large population sizes to ensure a high level of genetic diversity, which is an essential component of biodiversity and significantly contributes to the forest resilience.

The implications for forest management plans are related to the desire for replacing spruce monocultures (strongly affected by windfalls) with spruce-cembra mixtures, in the upper altitudinal limit of the Carpathian forests. Unfortunately, the very small growths of the Swiss stone pine in its juvenile stage make it overwhelmed by the Norway spruce, so the strategy must include a planting gap of at least 10 years. The conservation strategies in favor of *Pinus cembra* must include the in-situ conservation of the natural forests, the ex-situ conservation of all trials and seed orchards, together with the expansion of the species at the upper altitudinal limit of the Carpathian forests. The above-mentioned provenances (Bluhnbach, Pietrele, Călimani, for the Southern Carpathians, and Grachen-Wallis, Gemenele, and again Pietrele, for the Eastern Carpathians) could be considered.

Conclusions

The high level of genetic variability both within and among provenances, along with the significant trait-trait and age-age correlations, and the large number of provenances involved in this experiment, ensures the success of the breeding program.

Twenty-seven years after the trials establishment, we successfully managed to select three provenances from each trial (representing a 25 % selection intensity) that could be targeted for forward selection and reproduction in the same provenance region and under similar environmental conditions to the trial where they were evaluated. Given the high influence of the testing site and test site x provenance interaction, extreme caution is mandatory when transferring forest reproductive materials. Additionally, the low values of QST suggest the necessity to ensure a higher level of genetic diversity, which is a very serious issue for Swiss stone pine.

The correlations between juvenile-adult growth traits, along with the time-to-time evolution of the 12 provenances, indicate that early selection, even at the juvenile stage, at 17 years of trees' age, could be effective. Therefore, the forward selection of the best 30 % individual trees from the top three provenances for Th could be applied in each trial.

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Conflicts of Interest

The authors declare no conflict of interest.

References

Ammer C (2019) Diversity and forest productivity in a changing climate. New Phytologist 22:50-66. https://doi.org/10.1111/nph.15263

Bastin J F, de Haulleville T, Maniatis D, Marchi G, Massaccesi E, Mollicone D, Papa C, Pregagno C (2020) Tree Restoration Potential in the European Union. FAO and European Commission Directorate General for Environment (DG ENV) https://doi.org/10.13140/RG.2.2.24811.67368/1

B4EST (2024) Adaptive breeding for better forests. Climate database available online: http:// www.b4est.eu/ (accessed on July, 2024).

Blada I (1987) Cercetări asupra rezistenței genetice la Cronartium ribicola a unor hibrizi interspecifici (Research on the genetic resistance to Cronartium ribicola of some interspecific hybrids). PhD thesis, A.S.A.S., Bucharest, 146 p. (in Romanian)

Blada I (1999) Diallel crossing in *Pinus cembra*. III. Analysis of genetic variation at the nursery stage. Silvae Genetica 48(3-4):179-187.

Blada I, Popescu F (2007) Swiss stone pine provenance experiment in Romania. II Variation in growth and branching traits to age 14. Silvae Genetica 56(3-4):148-158. https://doi.org/10.1515/sg-2007-0023

Blada I, Popescu F (2008) Diallel crossing in *Pinus cembra*. IV. Age trends in genetic parameters and genetic gain for growth and branching traits. Annals of Forest Research 51:89-113. https://doi.org/10.1515/sg-2012-0009

Blada I, Popescu F (2012) Diallel crossing in *Pinus cembra*: age trends in genetic parameters and genetic gain for height. Silvae Genetica 61(1-2):66-79. https://doi.org/10.1515/sg-2012-0009

Blada I (2019) Memoriu de activitate 1961-2007 (Activity memory 1961-2007). Silvică Publishing House, Bucharest, 51 p. ISBN: 978-606-8020-62-4 (in Romanian)

Belokon M M, Belokon Y S, Politov D V, Altukhov Y P (2005) Allozyme polymorphism of Swiss stone pine *Pinus cembra L.* in mountain populations of the Alps and the Eastern Carpathians. Russian Journal of Genetics 41:1268-1280. https://doi.org/10.1007/s11177-005-0228-0

Budeanu M, Apostol E N, Popescu F, Postolache D, Ioniță L (2019) Testing of the narrow crowned Norway spruce ideotype (*Picea abies f. pendula*) and the hybrids with normal crown form (pyramidalis) in multisite comparative trials. Science of the Total Environment 689:980-990. https://doi.org/10.1016/j.scitotenv.2019.06.518

Budeanu M, Şofletea N, Petrițan IC (2014) Among-population variation in quality traits in two Romanian provenance trials with *Picea abies L*. Baltic Forestry 20(1):37-47. https://doi.org/10.1515/sg-2012-0022

Budeanu M, Popescu F, Besliu E, Apostol E N (2024) Adaptability of Swiss stone pine (*Pinus cembra*) in two different environmental conditions of Romanian Carpathians. Applied Sciences 14(16), 7428, 12 p. https://doi.org/10.3390/app14167428

Caudullo G, de Rigo D (2016) *Pinus cembra* in Europe: distribution, habitat, usage and threats: European atlas of forest tree species (ed. San Miguel-Ayanz J., de Rigo D., Caudullo G., Houston Durrant T., Mauri A.). Publication Office of the European Union, Luxembourg City, Luxembourg, pp. 120-121.

Caudullo G, Welk E, San-Miguel-Ayanz J (2017) Chorological maps for the main European woody species. Data in Brief 12:662-666. https://doi.org/10.1016/j.dib.2017.05.007

Chakraborty D, Ciceu A, Ballian D, et al (2024) Assisted tree migration can preserve the European forest carbon sink under climate change. Nature Climate Change 14:845-852. https://doi.org/10.1038/s41558-024-02080-5

Dauphin B, Rellstab C, Schmid M, Zoller S, Karger DN, Brodbeck S, Guillaume F, Gugerli F (2021) Genomic vulnerability to rapid climate warming in a tree species with a long generation time. Global Change Biology 27:1181-1195. https://doi.org/10.1111/gcb.15469

Ducci F., De Cuyper B., Proietti R., Pâques L., Wolf H., 2012. TREEBREEDEX, research infrastructure network 2006-2011. Reference protocols for assessment of traits and reference genotypes to be used as standards in international research projects. CRA SEL Publishing House, Arezzo, Italy, 82 p.

Dzialuk A, Chybicki I, Gout R, Maczka T, Fleischer P, Konrad H, Curtu A L, Şofletea N, Valadon A 2014. No reduction in genetic diversity of Swiss stone pine (Pinus cembra L.) in Tatra Mountains despite high fragmentation and small population size. Conservation Genetics 15:1433-1445. https://doi.org/10.1007/s10592-014-0628-6

Eichhorn J, Roskams P, Potočić N, Timmermann V, Ferretti M, Mues V, Szepesi A, Durrant D, Seletković I, Schröck H-W, Nevalainen S, Bussotti F, Garcia P, Wulff S (2020) Part IV: Visual assessment of crown condition and damaging agents. Version 2020-3. In: UNECE ICP Forests Programme Coordinating Centre (ed.): Manual on methods and criteria for harmonized sampling, assessment, monitoring and analysis of the effects of air pollution on forests. Thünen Institute of Forest Ecosystems, Eberswalde, Germany, 49 p. (+Annex). Available at: http://www.icp-forests.org/manual.htm.

Funk W C, McKay J C, Hohenlohe P A, Allendorf F W (2012) Harnessing genomics for delineating conservation units. Trends in Ecology & Evolution 9:489-496. https://doi.org/10.1016/j.tree.2012.05.012

Giurgiu V, Decei I, Drăghiciu D (2004) Metode şi tabele dendrometrice (Methods and dendrometrical tables). Ceres Publishing House, Bucharest, Romania, 575 p. ISBN: 973-40-0639-8 (in Romanian)

Gugerli F, Brodbeck S, Bebi P, Bollmann K, Dauphin B, Gossner M, Krumm F, Peter M, Queloz V, Reiss G, Rellstab C, Stofer S, von Arx G, Wasem U, Zweifel R (2022) Swiss stone pine - portrait of a mountain forest tree. Fact sheet 72, 16 p. https://doi.org/10.55419/wsl:32467

Gugerli F, Brodbeck S, Lendvay B, Dauphin B, Bagnoli F, van der Knaap WO, Tinner W, Höhn M, Vendramin GG, Morales-Molino C, Schwörer C (2023) A range-wide postglacial history of Swiss stone pine based on molecular markers and palaeoecological evidence. Journal of Biogeography 50:1049-1062. https://doi.org/10.1111/jbi.14586

Höhn M, Gugerli F, Abran P, Bisztray G, Buonamici A, Cseke K, Hufnagel L, Sebastiani F, Quintela-Sabaris S, Vendramin G G (2009) Variation in the chloroplast DNA of Swiss stone pine (*Pinus cembra L*) reflects contrasting postglacial history of populations from the Carpathians and the Alps. Journal of Biogeography 36:1798-1806. https://doi.org/10.1111/j.1365-2699.2009.02122.x

Izworska K, Muter E, Matulewski P, Zielonka T, (2023) Tree rings as an ecological indicator of the reaction of Swiss stone pine (*Pinus cembra L.*) to climate change and disturbance regime in the extreme environment of cliff forests. Ecological Indicators 148, 110102, 12 p. https://doi.org/10.1016/j.ecolind.2023.110102.

Jandl R, Spathelf P, Bolte A, Prescott CE (2019) Forest adaptation to climate change-is non-management an option? Annals of Forest Science 76, 48, 13 p. https://doi.org/10.1007/s13595-019-0827-x

Lendvay B, Höhn M, Brodbeck S, Mîndrescu M, Gugerli F (2014) Genetic structure in *Pinus cembra* from the Carpathian Mountains inferred from nuclear and chloroplast microsatellites confirms post-glacial range contraction and identifies introduced individuals. Tree Genetics & Genomes 10:1419-1433. https://doi.org/10.1007/s11295-014-0770-9

Leonelli G, Pelfini M, Battipaglia G, Cherubini P (2009) Site-aspect influence on climate sensitivity over time of a high-altitude *Pinus cembra* tree-ring network. Climatic Change 96:185-201. https://doi.org/10.1007/s10584-009-9574-6

Li M-H, Yang J (2004) Effects of microsite on growth of *Pinus cembra* in the subalpine zone of the Austrian Alps. Annals of Forest Science 61:319-325. https://doi.org/10.1051/forest:2004025

Liang J, Crowther T, Picard N, et al (2016) Positive biodiversity-productivity relationship predominant in global forests. Science 354(6309), https://doi.org/10.1126/science.aaf8957

Marčiš P, Rybár J, Šebeň V, Murgaš V, Sitková Z (2025) *Picea abies* and *Pinus cembra* at high altitudes show different growth reaction to rising temperatures: Study from the Western Carpathian subalpine forests. Dendrochronologia 91(4), 126325. https://doi.org/10.1016/j.dendro.2025.126325

Morgan T J, Evans M A, Garland T, Swallow J G, Carter P A (2005) Molecular and quantitative genetic divergence among populations of house mice with known evolutionary histories. Heredity 94:518-525. https://doi.org/10.1038/sj.hdy.6800652

Mosca E, Gugerli F, Eckert A J, Neale D B (2016) Signatures of natural selection on *Pinus cembra* and *P. mugo* along elevational gradients in the Alps. Tree Genetics & Genomes 12, 6. https://doi.org/10.1007/s11295-015-0964-9

Nabuurs G, Lindner M, Verkerk H, Gunia K, Deda P, Michalak R, Grassi G (2013) First signs of carbon sink saturation in European forest biomass. Nature Climate Change 3:792-796. https://doi.org/10.1038/nclimate1853

Nanson A (2004) Genetic and forest trees breeding. Ed. Gembloux, Belgium, 712 p. ISBN: 978-287-0160-70-1 (in French)

Neuschulz EL, Merges D, Bollmann K, Gugerli F, Böhning-Gaese K (2018) Biotic interactions and seed deposition rather than abiotic factors determine recruitment at elevational range limits of an alpine tree. Journal of Ecology 106:948-959. https://doi.org/10.1111/1365-2745.12818

Paulsen J, Weber UM, Körner C (2000) Tree growth near treeline: abrupt or gradual reduction with altitude? Arctic, Antarctic, and Alpine Research 32:14-20. https://doi.org/10.1080/15230430.2000. 12003334

Pliura A, Eriksson G (2002) Genetic variation in juvenile height and biomass of open-pollinated families of six *Castanea sativa* Mill. populations in a 2 x 2 factorial temperature x watering experiment. Silvae Genetica 51(4):152-160.

Politov D V, Belokon M M, Belokon Y S (2008) Alloenzymatic variation in *Pinus cembra* and *P. sibirica*: differentiation between populations and species. Annals of Forest Research 51:143-144.

QGIS Development Team (2024) QGIS Geographic Information System. Open-Source Geospatial Foundation Project. Available online: http://qgis.osgeo.org (accessed on 10 August 2024)

R Core Team (2023) R: A Language and Environment for Statistical Computing; R Foundation for Statistical Computing: Vienna, Austria. Available online: https://www.r-project.org/ (accessed on August 12, 2024).

Salzer K, Gugerli F (2012) Reduced fitness at early life stages in peripheral versus core populations of Swiss stone pine (*Pinus cembra*) is not reflected by levels of inbreeding in seed families. Alpine Botany 122:75-85. https://doi.org/10.1007/s00035-012-0106-z

Saura M, Perez-Figueroa A, Fernandez J, Toro M, Caballero A (2008) Preserving population allele frequencies in ex situ conservation programs. Conservation Biology 22:1277-1287. https://doi.org/10.1111/j.1523-1739.2008.00992.x

Sonnenwyl V, Dauphin B, Fragnière Y, Clément B, Grünig S, Brodbeck S, Parisod C, Kozlowski G, Gugerli F (2024) Genetic underpinning of historical afforestation with allochthonous *Pinus cembra* in the northwestern Swiss Alps. Alpine Botany 134:1-13. https://doi.org/10.1007/s00035-023-00304-6

Spathelf P, Stanturf J, Kleine M, Jandl R, Chiatante D, Bolte A (2018) Adaptive measures: integrating adaptive forest management and forest landscape restoration. Annals of Forest Science 75, 55, 6p. https://doi.org/10.1007/s13595-018-0736-4

Statistica 10.0 (2010) StatSoft Inc., Tulsa, OK, USA.

Știrbu M-I, Roibu C-C, Carrer M, Mursa A, Unterholzner L, Prendin AL (2022) Contrasting climate sensitivity of *Pinus cembra* tree-ring traits in the Carpathians. Frontiers in Plant Science 13, 855003, 11 p.
https://doi.org/10.3389/fpls.2022.855003

Tóth E G, Tremblay F, Housset J M, Bergeron Y, Carcaillet C (2019) Geographic isolation and climatic variability contribute to genetic differentiation in fragmented populations of the long-lived subalpine conifer *Pinus cembra L.* in the western Alps. BMC Evolutionary Biology 19, 190, 17 p. https://doi.org/10.1186/s12862-019-1510-4

Ulber M, Gugerli F, Bozic G (2004) EUFORGEN. Technical Guidelines for genetic conservation and use for Swiss stone pine (*Pinus cembra*). Biodiversity International. Available at: https://hdl.handle.net/10568/104342

Viersma Wiersma J H (1962) Enkete kwantitatieve aspecten van het exotenvraagstuk. Nederlands Bosbouw Tijtschrift 34(5):175-184.

Wieser G, Manning W J, Tausz M, Bytnerowicz A (2006) Evidence for potential impacts of ozone on *Pinus cembra L*. at mountain sites in Europe: An overview. Environmental Pollution 139(1):53-58. https://doi.org/10.1016/j.envpol.2005.04.037

Wojnicka-Półtorak A, Celiński K, Chudzińska E, Prus-Głowacki W, Niemtur S (2015) Genetic resources of *Pinus cembra L*. Marginal populations from the Tatra mountains: implications for conservation. Biochemical Genetics 5:49-61. https://doi.org/10.1007/s10528-015-9670-4

Zięba A, Różański W, Bukowski M, Ciesielska B, Szwagrzyk J (2019) Distribution and habitat conditions of *Pinus cembra* forests in the Tatra Mountains. Dendrobiology 81:86-96. http://dx.doi.org/10.12657/denbio.081.010