142. Jahrgang (2025), Heft 3, S. 191–214

Austrian Journal of Forest Science
Centralblatt für das gesamte Forstwesen

# Phenotypic variability, inheritance rate and selection strategy of *Pinus cembra* half-sib families in two common garden experiments in the Southern Carpathians

# Phänotypische Variabilität, Vererbungsrate und Selektionsstrategie von *Pinus cembra*-Halbsippen in zwei Freilandversuchen in den Südkarpaten

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**Keywords:** Alpine region, breeding strategy, field trial, quantitative genetics, Subalpine forests, Swiss stone pine

**Schlüsselbegriffe:** Alpenraum, Zuchtstrategien, Feldversuche, quantitative Genetik, Subalpine Wälder, Zirbe

## Abstract

In the interest of facilitating the reintroduction of Swiss stone pine (*Pinus cembra* L.) in the Lotrului and Șureanu mountains (Southern Carpathians), where the species naturally existed in the past, two half-sib comparative trials were conducted at Cugir and Voineasa. In total, 71 and respectively 65 families were tested (41 common in both trials), which belong to 7 provenances (4 common) originating from two countries (Romania and France) and three mountain divisions (French Alps, Eastern and Southern Carpathians). This study aims to analyze genetic variability by examining testing site influences, inheritance rates, and trait correlations in two 27-year-old half-sib trials with the goal of identifying the best-performing families and developing an optimal breeding strategy to enhance desired characteristics in future generations At the trial's 27 years of age, measurements and evaluations of the breast height diameter, tree height, branch diameter and finess of branches, stem straightness, and survival were performed, while the trait-trait, trait-origin, and inheritance rate were estimated. The high level of genetic variance and heritability (especially for tree

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height), along with the significant correlations among traits, and the large number of families, ensures the success of the breeding program. The MGIDI index (multi-trait genotype-ideotype distance) allowed us to select ten to eleven families in each trial that could be promoted in the Southern Carpathians and under similar ecological conditions to those in the trial where they were performed. A forward selection of the top 30% of individual trees from the best selected families, based on tree height, could be applied in each trial. Given the strong effects of the testing site and site x family interaction, extreme attention is required when transferring reproductive materials. Our findings provide a constructive approach for management plans, as we recommend transition from Norway spruce monocultures to structurally more diverse stands with codominant Swiss stone pine, at the upper altitudinal limit of the Southern Carpathian forests.

## Zusammenfassung

Zur Wiederansiedlung der Zirbelkiefer (*Pinus cembra* L.) in den Lotrului- und Șureanu-Gebirgen (Südkarpaten), wo die Art in der Vergangenheit natürlich vorkam, wurden in zwei Halbsippen-Vergleichsversuchen – Cugir und Voineasa – 71 bzw. 65 Familien getestet (davon 41 in beiden Versuchen gemeinsam). Diese Familien stammen aus sieben Herkünften (vier davon gemeinsam), die aus zwei Ländern (Rumänien und Frankreich) und drei Gebirgsregionen (Französische Alpen, Ost- und Südkarpaten) stammen. Ziel der Studie ist es, die genetische Variabilität, den Einfluss des Prüfstandorts, die Vererbungsraten sowie die Korrelationen zwischen Merkmalen und zwischen Merkmalen und Herkünften zu analysieren, um die leistungsfähigsten Familien auszuwählen und die geeignetste Züchtungsstrategie vorzuschlagen. Nach 27 Jahren Versuchsdauer wurden der Brusthöhendurchmesser, die Baumhöhe, die Aststärke und -feinheit, die Geradschaftigkeit sowie das Überleben der Bäume gemessen und bewertet. Gleichzeitig wurden die Merkmalskorrelationen, Herkunftsabhängigkeiten und Erblichkeiten geschätzt. Der hohe Grad an genetischer Varianz und Heritabilität (insbesondere bei der Baumhöhe), die signifikanten Merkmalskorrelationen sowie die große Zahl getesteter Familien bilden eine solide Grundlage für ein erfolgreiches Züchtungsprogramm. Der Einsatz des MGIDI-Index (multi-trait genotype-ideotype distance) ermöglichte die Auswahl von zehn bis elf Familien je Versuch, die für eine Förderung in den Südkarpaten und unter ähnlichen ökologischen Bedingungen wie am Prüfstandort geeignet sind. Bei jedem Versuch konnte eine Vorwärtsauswahl der besten 30 % der Einzelbäume aus den am besten ausgewählten Familien auf Grundlage der Baumhöhe vorgenommen werden. Aufgrund der starken Einflüsse des Prüfstandorts sowie der Standort-Familien-Interaktion ist jedoch bei der Übertragung von Vermehrungsmaterialien größte Sorgfalt geboten. Unsere Ergebnisse liefern einen konstruktiven Ansatz für Managementpläne, da wir den Übergang von Fichtenmonokulturen zu strukturell vielfältigeren Beständen mit kodominanter Zirbelkiefer an der oberen Höhengrenze der Wälder der Südkarpaten empfehlen.

## 1 Introduction

Subalpine forests of the Alps and Carpathians represent highly sensitive ecosystems (Körner, 2012) which have experienced a more significant temperature change than the global average (Jochner, 2017), a trend expected to persist, with both potential pressures and opportunities for tree species (Ulber *et al.*, 2004; Tranquillini, 2012; Ponocná *et al.*, 2016; Jandl *et al.*, 2019; Dauphin *et al.*, 2021; Obojes *et al*., 2024; Marčiš *et al.*, 2025). In this situation, it is necessary to identify species and intraspecific varieties that show adaptability to climate change. The genetic plasticity, gene flow, comigration and demographic dynamics of these species/ varieties could reinforce resilience by accelerating the adaptive reactions (Kremer *et al.*, 2025).

Swiss stone pine (*Pinus cembra* L.) is an important tree species at the alpine treeline of the European Alps and Carpathians (Tóth *et al.*, 2019; Gugerli *et al.*, 2022). The species' weak apical dominance enables flexible growth responses to environmental stresses, such as frost and snow, thereby enhancing its survival in challenging alpine conditions (Oberhuber *et al.*, 2019). Nevertheless, a strong reaction of Swiss stone pine to climate limiting factors, was registered (Carrer *et al.*, 2007). The low temperature during the growing season (< 5°C) is a limiting factor (Körner, 2012; Etzold *et al.*, 2021), but the most restrictive issue seems to be the water regime, especially the drought (Casalegno *et al.*, 2010; Unterholzner *et al.*, 2024). However, Swiss stone pine exhibits a remarkable potential for adaptation to drought events (Știrbu *et al.*, 2022; Izworska *et al.*, 2023; Muter *et al.,* 2024), which is superior to that of other species, such as Norway spruce (Popa *et al.*, 2017). A careful consideration of genetic diversity, assisted gene flow, environmental factors, and seasonal dynamics is required to ensure the species' adaptability and the long-term viability (Farjon, 2013; Mosca *et al.*, 2016; Spathelf *et al.*, 2018; Ammer, 2019; Bastin *et al.*, 2020; Fragnière *et al.*, 2022; Budeanu *et al.*, 2024, 2025a,b; Chakraborty *et al.*, 2024; Sonnenwyl *et al.*, 2024).

In the past, Swiss stone pine had a much broader distribution across Europe and Siberia. After the last ice age and during warmer periods, its range became fragmented, causing it to retreat to higher elevations in the Alps and Carpathians. Researchers have identified *Pinus cembra* as a species of five-needle pine in Europe and *Pinus cembra sibirica* as a subspecies distributed especially in Siberia, the differentiation is likely caused by gradual adaptation. A new relative to Swiss stone pine, *Pinus pumila*, appears in tundra climate, and extends from Siberia to North Korea and Japan (European Wilderness Society, 2023; Gugerli *et al.,* 2023).

In Romania, a breeding programme for promoting Swiss stone pine was coordinated by Blada (1987, 1999, 2019), which have involved the establishment of nine field trials: three half-sib, two full-sib, three of provenances, and one of clones (Blada & Popescu, 2007, 2008, 2012; Budeanu *et al.*, 2024, 2025a, b). The importance of the species, in Romania and in Europe, is mainly due to its ability to adapt to the difficult conditions at the upper altitudinal limit of the forests, but the high-quality wood with industrial use (the best among pines), the edible seeds with pharmaceutical uses, and the pleasant ornamental appearance should not be neglected (Şofletea & Curtu, 2007). The Swiss stone pine could be an alternative three species for the future in order to replace the spruce monocultures (affected by windfalls and snowbreaks) with species mixtures. Previous research has highlighted very significant growth and adaptation differences among the different provenances tested in the Romanian Carpathians (Blada & Popescu, 2007, 2008, 2012), which confirms the importance of conducting comparative studies.

This study aims to analyze genetic variability by examining the effects of testing sites, inheritance rates, and trait correlations in two 27-year-old half-sib trials, with the goal of identifying the best-adapted families and developing an optimal breeding strategy to enhance desirable traits in future generations. For the two half-sib trials that have reached the age of 27 years, nothing has been published until this article, even though they are part of the breeding program mentioned above, and can contribute with valuable families and populations to ensure a high level of genetic diversity in the future afforestation.

*Figure 1: Aspects from the Cugir (left) and Voineasa (right) trials (the authors, 2024).*

Abbildung 1: Aspekte aus den Prozessen Cugir (links) und Voineasa (rechts) (die Autoren, 2024).

## 2 Materials and methods

In the interest of facilitating the reintroduction of Swiss stone pine in the Lotrului and Șureanu mountains (Southern Carpathians), where the species naturally existed in the past, two half-sib comparative trials were conducted at Cugir and Voineasa. In total, 71 families were tested in the Cugir trial, while 65 families were tested in the Voineasa trial, with 41 families being common to both trials. These families belong to 7 provenances (4 common) originated from two countries (Romania and France) and from three mountain divisions (French Alps, Eastern and Southern Carpathians). The place of origin (including altitude) of the seven provenances is shown in Figure 2, while a more detailed presentation can be found in the previous articles (Blada & Popescu, 2007; Budeanu *et al.*, 2025a, b). Significant differences in latitudinal (4°27′), longitudinal (20°29′), and altitudinal (695 m) amplitudes exist among the provenances (Blada & Popescu, 2007; Figure 2). In each of the seven provenances, seeds were harvested from 4 to 20 open-pollinated trees, located at least 50 m apart (Blada & Popescu, 2007), and the seeds were kept separately per tree, so that each family represents the descendants of a single tree.

The experiments were established in the autumn of 1997, using 7-year-old seedlings, planted at a distance of 2.5 x 2.5 m, in a completely randomized block design, with 71 families x 3 replications x 10 seedlings/unitary plot, in Cugir trial, and respectively 65 x 3 x 10, in Voineasa test.

The Cugir half-sib trial is located in the Șureanu Mountains, and it is currently administered by the Cugir Forest District (Alba County), being located in the production unit IV Canciu, plot 65B, covering an area of 1.3 ha, near to the provenance trial analyzed in Budeanu *et al.* (2025a,b). Geographically, it is located at 45˚37′ N latitude, 23˚32′ E longitude, and at an average altitude of 1500 m. The trial is situated at the middle of a slope on land with an undulating configuration, facing southwest, with a 23˚ inclination. The biotope is of medium productivity, with the forest type being represented by high-altitude spruces with mull flora, and the soil is typically dystric Cambisol.

The Voineasa half-sib trial was installed in the Lotrului Mountains of the Southern Carpathians, and it is administered by the Voineasa Forest District. It is situated in the production unit VII Haneș, plot 141B, covering an area of 1.5 ha (including an important area with reserves). Geographically, it is located at 45˚30′ N latitude, 23˚47′ E longitude, and at an average altitude of 1650 m. The trial is situated at the top of a slope on land with an undulating configuration, facing north-east, with a 23˚ inclination. The biotope is of medium productivity, with the forest type being represented by high-altitude spruces with mull flora, and the soil is classified as typically dystric Cambisol.

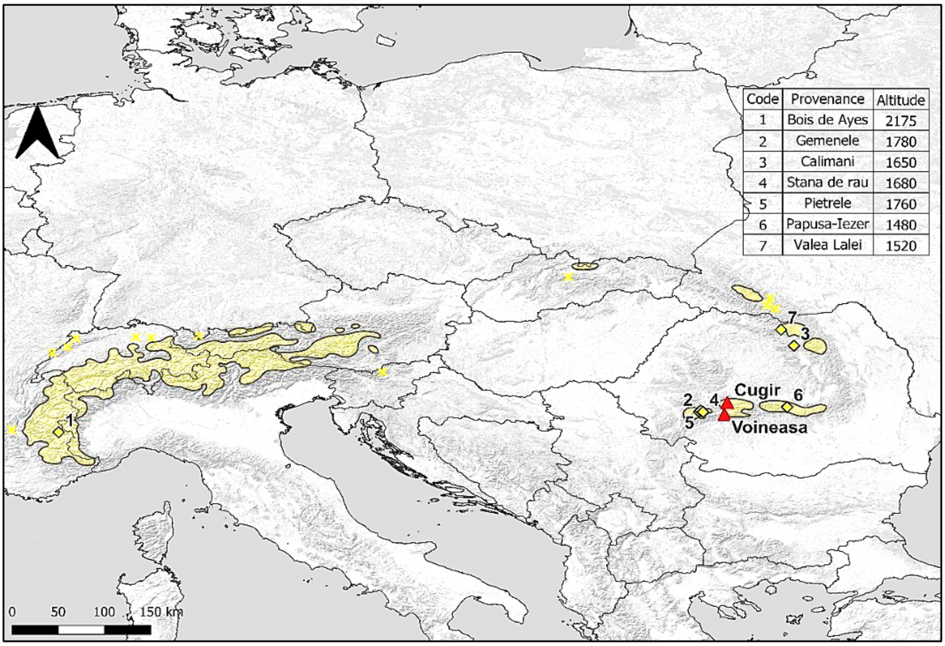


*Figure 2: The location of the Cugir and Voineasa trials (red triangle) and the provenance origins (yellow diamonds) on the Pinus cembra distribution map (Caudullo et al., 2017). The species' natural distribution is indicated by the yellow color. This file contains European countries boundaries in a shapefile format (Sevdari & Marmullaku 2023).*

Abbildung 2: Lage der Versuchsflächen Cugir und Voineasa (rote Dreiecke) sowie der Herkunftsgebiete (gelbe Rauten) auf der Verbreitungskarte von Pinus cembra (Caudullo *et al*., 2017). Das natürliche Verbreitungsgebiet der Art ist schraffiert dargestellt. Die Datei enthält europäische Länder im Shapefile-Format (Sevdari & Marmullaku, 2023).

According to the European forest type classification (2007), the both trials are included in the Subalpine and mountainous spruce forests, into the Subalpine - mountainous Carpathian mountains forest type (Ozenda, 1988). The mull flora is represented especially by *Oxalis acetosella*, *Asperula odorata*, *Dentaria bulbifera*, and *Vaccinium myrtillus* (Beldie & Chiriță 1967).

In both testing regions, while the precipitation showed no clear trend over the last 30 years, temperatures have exponentially increased (from 2.6°C and 1.9°C, in 1996-1999, period to 4.2°C and 3.9°C, in 2020-2024 period, in Cugir and Voineasa respectively). The average annual temperature of the last three decades were 3.8°C in Cugir, and 3.0°C in Voineasa, while the sum of annual precipitation averaged 1080 mm in Cugir and 1190 mm in Voineasa (B4EST, 2025).

At the trial's 27 years of age (34 years tree age), measurements and evaluations of growth and quality traits were carried out for all existing trees. The breast height diameter (Dbh) measured at 1.3 m from the ground, tree height (Th), and dominant branch diameter (Bd, measured at 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. The stem straightness (Ss) was evaluated on a scale of 5 classes (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), according to Ducci et al. (2012). Additionally, the finesse of branches (Bf) was calculated as Bf=Bd x 100 / Dbh. Survival (S) was calculated in both trials and for each family as the proportion of surviving trees from the total number of planted trees.

## 2.1 Statistical analysis

In each trial, the mathematical model used for analyses of the variance (ANOVA) was the one recommended by Nanson (2004), with the replication (environmental factor, integrated in the model as a fixed effect), provenance and family, as genetic factors (as random effect in the mathematical model). After that, the results for common families were cumulated and analyzed using a bifactorial analysis to highlight the influences of the testing site (locality, integrated as a fixed effect), family, and their interactions (integrated in the model as a random effect), according to Nanson (2004). Before applying ANOVA, the Kolmogorov-Smirnov test was applied to check the normal distribution of variables, and the assumptions of ANOVA were verified using Levene's test. The significance level was determined using Fisher (F) test, assessing the transgression probability at 5%, 1% and 0.1% levels. Provenances and families ranking, the differences among them, and their separation into homogenous groups were conducted using the Tukey HSD test at a 5% transgression possibility. Additionally, Pearson's simple phenotypic correlations were determined, along with correlations between traits and the ecological gradients of the provenance's origins. The ecophysiological latitude (Le) was estimated according to Wiersma (1962): Le = L + A / 100, where L represents the north latitude and A represents the altitude (a.s.l.).

A graphical method was used to highlight the best-performing provenances, based on the average values recorded for survival (stability performance) and trees' height (growth performance), using the R programming language (R Core Team, 2025). The metan package (Olivoto & Lúcio, 2020) was used to perform a multi-trait genotype-ideotype distance analysis (MGIDI index) for selecting the best-performing families based on all the analyzed traits (Th, Dbh, S, Bd, Bf, Ss) and to calculate the genetic parameters, including genotypic variances, broad-sense and mean-based heritabilities, as well as the genotypic coefficient of variation.

The software utilized for data processing includes R 4.5.0 (2025), for figures 3-6 and tables 2-4, Statistica 10.0 (2010), for Tukey HSD test (table 1), and QGIS 3.44.1 Solothurn (2024), for Figure 2.

# 3 Results

## 3.1 Survival and phenotypic variability

For Survival (S), a high average value was recorded in the Cugir trial (87%), significantly superior to the average of the Voineasa test (69.2%). No significant differences among the five provenances were registered in the Cugir trial, with the highest result (90.3%) obtained by the Alps provenance (Bois de Ayes, France). In the Voineasa common garden, two groups of provenances were separated, with the fourth common provenances (Gemenele, Călimani, Stâna de Râu, and Pietrele) included in the best group, while the provenances Păpușa-lezer and Valea Lalei being part of the second group (Figure 3). At the family level, a high homogeneity has resulted in the Cugir test, with 70 of the 71 families included in the best group, and nine families (four from France, three from SC, and two from EC) achieving maximum survival (100%). In Voineasa's experiment, the best result (96.7%) was obtained by a family originating from Valea Lalei, although the average of that provenance was the lowest in the trial (Figure 3). Nineteen of the sixty-five families tested in the Voineasa trial registered a survival of more than 80%, indicating that the selection can be successfully applied.

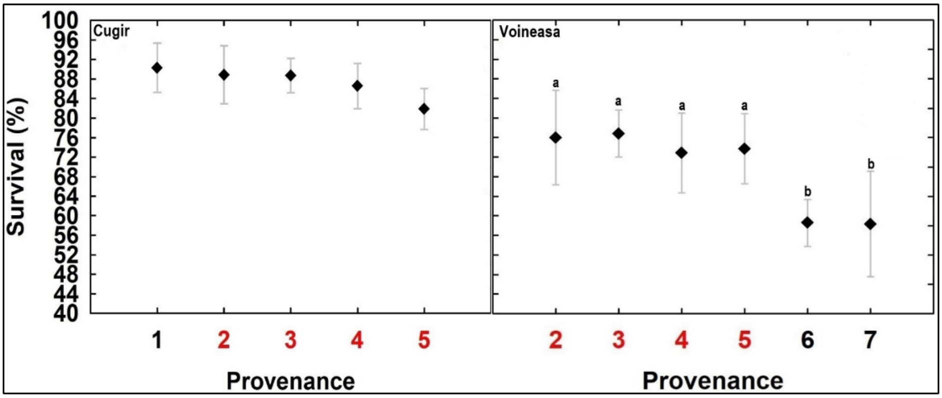


*Figure 3: Survival (mean ± 0.95CI) of the provenances, in the Cugir (A) and Voineasa (B) trials. Common provenances in red. Significant differences expressed by different letters were resulted by applying Tukey's HSD post-hoc test. The provenance codes are as in Figure 2.*

Abbildung 3: Überlebensrate (Mittelwert ± 0,95 % Konfidenzintervall) der Herkünfte in den Versuchen Cugir (A) und Voineasa (B). Gemeinsame Herkünfte sind in Rot. Signifikante Unterschiede, ausgedrückt durch unterschiedliche Buchstaben, ergaben sich durch die Anwendung des Tukey-HSD-Post-hoc-Tests. Herkunftscodes wie in Abbildung 2.

In Cugir trial, analyses of the variance (ANOVA, Table S1) show a highly significant influence ($p < 0.001$) of the family factor, and a significant ($p < 0.05$) impact of the provenance factor, while the microenvironmental factor (replication) played a non-significant role ($p > 0.05$) for survival. In the common garden of Voineasa, all three factors played a highly significant role. Factorial ANOVA highlighted a highly significant influence of locality, while family had a non-significant role (Table S1).

In both field trials, for the principal growth traits (Th and Dbh), the Pietrele provenance registered the highest results, clearly distinguished from all others. In contrast, among the four common provenances, Gemenele exhibited consistently low performance, particularly in terms of tree height (Figure 4). An identical Th average values were registered in both trials (6.8 m), but with a higher variability (expressed by standard deviation, and by 13, compared to 5, homogeneous groups) in the Cugir trial. For Dbh, a 4% higher average value was registered in the Cugir common garden experiment, with the best provenance, Pietrele, getting almost the same result in both trials (Figure 4). Some provenances exhibited a strong reaction to the changing environment, with good results in Cugir and low in Voineasa (Stâna de Râu provenance) and vice versa (Călimani provenance). At the family level, the Tukey HSD test emphasizes a higher variability for Th than Dbh, in both trials, but especially in the Cugir test, and different families obtained good results (top 10%) in the two trials, highlighting the need for caution when making recommendations regarding specific provenances for afforestation. ANOVA and factorial ANOVA support this conclusion, as the majority of genetic and environmental factors showed a significant influence ($p < 0.05$) on the growth traits (Table S1).

The provenance highlighted for growth in both trials, Pietrele (SC), also exhibited high survival, ranking as the best homogeneous group in both experiments, and being the first candidate for selection.

Regarding branches (Bd, Bf), the provenances highlighted for growth and survival, Pietrele (SC), in both trials, seconded by Stâna de Râu (SC) and Bois de Ayes (France Alps), in the Cugir test, and by Călimani (EC), in the Voineasa test, also presented thin and fine branches, which are indicative of superior stem wood quality (Figure 4, Table 1). In general, no significant influences of the environmental factor (replication) on the branches' traits were registered in both trials (except for Bd, in Voineasa), while the genetic factors (family and provenance) played a significant role (Table S1). Factorial ANOVA revealed that all the genetic and environmental factors had a highly significant influence ($p < 0.001$) on the finesse of branches, while for Bd, the influence of family and Locality x family interaction was insignificant (Table S1).

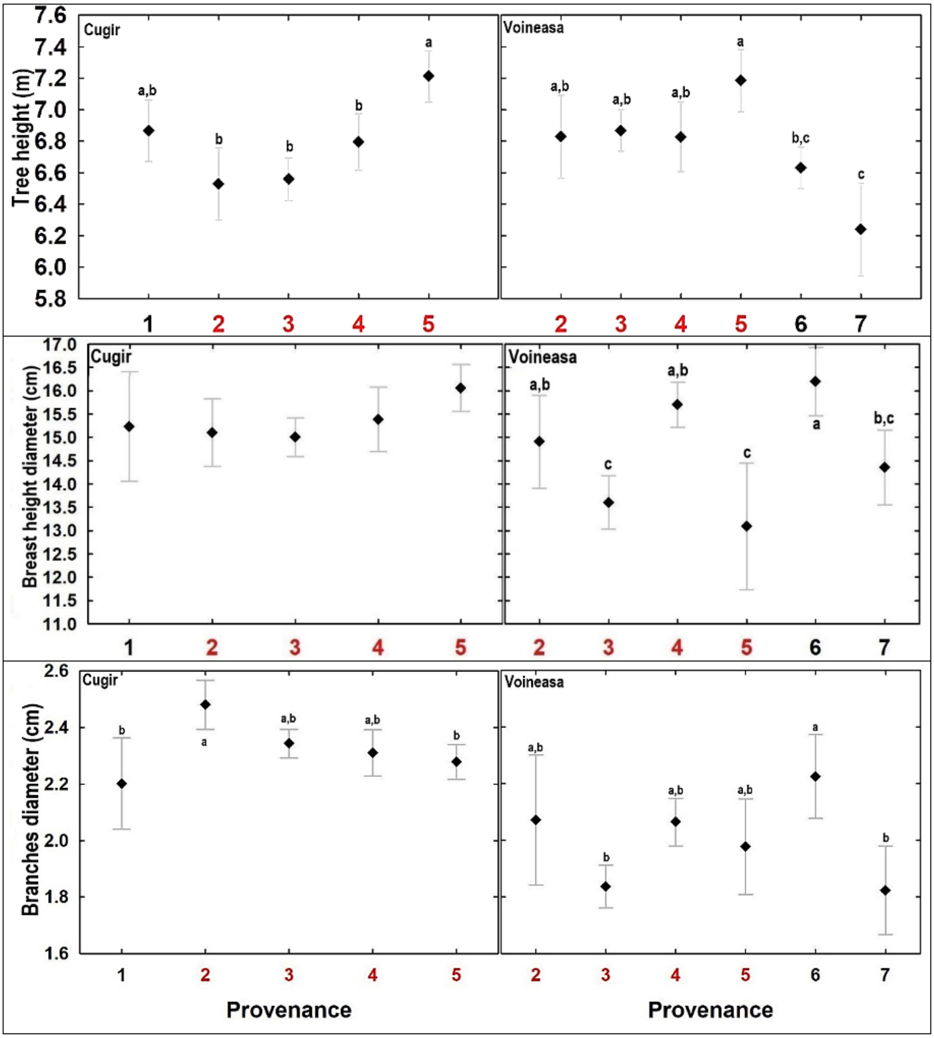


*Figure 4: Variation of tree height, diameter at breast height, and branches diameter (mean±0.95CI) among the provenances in the Cugir and Voineasa trials. Significant differences expressed by different letters were resulted by applying Tukey's HSD post-hoc test. The provenance codes are as in Figure 2.*

Abbildung 4: Variation der Baumhöhe, des Brusthöhendurchmessers und des Astdurchmessers (Mittelwert ± 0,95 % Konfidenzintervall) der Herkünfte in den Versuchen Cugir und Voineasa. Signifikante Unterschiede, ausgedrückt durch unterschiedliche Buchstaben, ergaben sich durch die Anwendung des Tukey-HSD-Post-hoc-Tests. Herkunftscodes wie in Abbildung 2.

*Table 1: Provenances and trials' average results (mean±SD) for the finesse of branches (Bf) and stem straightness (Ss). Common provenances with #. * The best homogeneous group (Tukey HSD test, α=5%)*

Tabelle 1: Durchschnittliche Ergebnisse der Provenienzen und Versuche (Mittelwert ± SD) für die Feinastigkeit (Bf) und die Geradschaftigkeit (*Ss*). Gemeinsame Herkünfte sind #. * Die beste homogene Gruppe (Tukey-HSD-Test, α = 5 %).

| Provenance | Cugir | | Voineasa | |
|---|---|---|---|---|
| | Bf (%) | Ss (index) | Bf (%) | Ss (index) |
| Gemenele# | 17.0 | 1.22 | 14.2* | 0.36* |
| Pietrele# | 14.5* | 0.79* | 13.8* | 0.40* |
| Stâna de Râu# | 15.5* | 0.85* | 12.8* | 0.50* |
| Călimani# | 16.0 | 0.83* | 13.2* | 0.37* |
| Valea Lalei | - | - | 15.5 | 0.53* |
| Păpușa-Iezer | - | - | 13.7* | 0.31* |
| Bois de Ayes | 14.7* | 0.67* | - | - |
| **Average trial** | **15.5±1.9** | **0.85±0.4** | **13.6±1.7** | **0.38±0.3** |

Stem straightness (*Ss*) is an important trait for high-quality wood production. Likewise, for the branches traits and in contrast to the growth traits, the average result recorded in the Voineasa trial (0.38) was clearly more favorable compared to the Cugir test (0.85). Thus, a total number of 49 families are included in the zero class (perfectly straight stem, *Ss* < 0.5) in the test located at a higher altitude, compared to only five families in the Cugir experiment. However, good results for this trait were observed in both trials, with all of the families classified in the 0-1 classes (with a maximum of 1-2 slight stem curves). For *Ss*, the provenance from the Franch Alps (Bois de Ayes) was the best in the Cugir test, followed by Pietrele (SC). In the Voineasa trial, a high homogeneity was registered with all the provenances included in one homogeneous group (Table 1). ANOVA and factorial ANOVA revealed that all the genetic and environmental factors had a significant ($p < 0.05$) to highly significant influence ($p < 0.001$) on the stem straightness (Table S1).

## 3.2 Trait-trait and trait-origin correlations

Highly significant phenotypic correlations were registered among the principal growth traits (Th and Dbh), and in both trials (r= 0.72*** - 0.74***), while both were also direct and significant correlated with Bd, but with a low intensity for Th (r= 0.15* in Cugir, and 0.39*** in Voineasa). The survival was also positively correlated with all growth traits, including Bd (Table 2). The trait-trait correlations in the two trials suggest that the selection for Th also favors the improvement of most other growth and stability traits, with the smallest negative impact on Bd.

*Table 2: Trait-trait phenotypic correlations, in the Cugir (above diagonal) and Voineasa (below diagonal) half-sib trials. Significant correlations: * at p < 0.05, ** at p < 0.01, *** at p < 0.001. S, Dbh, Th, Bd, Bf, and Ss, as in methodology.*

Tabelle 2: Phänotypische Merkmals-Korrelationen zwischen den Merkmalen in den Halbsippenversuchen Cugir (oberhalb der Diagonalen) und Voineasa (unterhalb der Diagonalen). Signifikante Korrelationen: * bei p < 0,05, ** bei p < 0,01, *** bei p < 0,001. S, Dbh, Th, Bd, Bf und Ss, wie in der Methodik.

| Traits | S | Dbh | Th | Bd | Bf | Ss |
|---|---|---|---|---|---|---|
| S | - | 0.32*** | 0.21** | 0.25*** | -0.11 | 0.11 |
| Dbh | 0.34*** | - | 0.72*** | 0.60*** | -0.57*** | 0.12 |
| Th | 0.27*** | 0.74*** | - | 0.15* | -0.70*** | -0.12 |
| Bd | 0.20** | 0.74*** | 0.39*** | - | 0.29*** | 0.38*** |
| Bf | -0.16* | -0.25*** | -0.42*** | 0.46*** | - | 0.26*** |
| Ss | -0.06 | -0.14* | -0.27*** | 0.06 | 0.27*** | - |

Correlations between traits and the geographical gradients of the provenance's origin (Table 3), generally indicated a low and statistically insignificant influence of provenance origin in the Cugir trial, while a positive and highly significant influence of the altitude was registered in the Voineasa test, located at a higher altitude. The highest correlation was found between Dbh and altitude (r= 0.39***), suggesting that the provenances from higher altitudes registered superior growth in the Voineasa experiment. Altitude had a negative and significant influence on stem and branches traits (r= -0.15* to r= -0.19**), in the Cugir trial, suggesting that provenances from higher altitudes registered favorable qualitative traits. An opposite result was registered in the Voineasa trial, for Bd (r= 0.31***). Longitude showed a positive and distinctly significant influence on stem and branches traits (r= 0.18** - 0.19**), in the Cugir trial, suggesting that the families from the west (France Alps) presented better stem and branches traits. An opposite effect of longitude on all traits was observed in the Voineasa trial, where French families were not represented.. Another interesting and significant correlation, observed in both trials, was between latitude and survival (Table 3), indicating that provenances from northern regions presented a superior stability.

*Table 3: Correlations between traits and geographical coordinates of provenances origin, in the Cugir (up) and Voineasa (down) half-sib trials. Significant correlations as in table 2. S, Dbh, Th, Bd, Bf, and Ss, as in methodology.*

Tabelle 3: Korrelationen zwischen Merkmalen und geographischen Koordinaten der Herkunftsgebiete in den Halbsippenversuchen Cugir (oben) und Voineasa (unten). Signifikante Korrelationen wie in Tabelle 2. S, Dbh, Th, Bd, Bf und Ss, wie in der Methodik.

| Traits/ Coordinates | North Latitude | Altitude | North corrected Latitude | East Longitude |
|---|---|---|---|---|
| Cugir trial | | | | |
| S | 0.14* | 0.06 | 0.14* | -0.07 |
| Dbh | -0.09 | 0.01 | -0.09 | 0.00 |
| Th | -0.10 | 0.11 | -0.09 | -0.09 |
| Bd | -0.14* | -0.16* | -0.14* | 0.18** |
| Bf | -0.07 | -0.19** | -0.07 | 0.19** |
| Ss | -0.22** | -0.15* | -0.22** | 0.19** |
| Voineasa trial | | | | |
| S | 0.15* | 0.35*** | 0.15* | -0.15* |
| Dbh | 0.15* | 0.39*** | 0.15* | -0.16* |
| Th | -0.06 | 0.32*** | -0.06 | -0.24*** |
| Bd | 0.13 | 0.31*** | 0.13 | -0.16* |
| Bf | 0.02 | -0.07 | 0.02 | 0.00 |
| Ss | 0.05 | 0.09 | 0.05 | -0.09 |

### 3.3 Inheritance rate and selection strategy

The percentage of total phenotypic variance explained by genotype, Gen (%), registered the highest values for Th, 25.3% in Cugir, and 37.5% in Voineasa, generating also the highest broad-sense ($h^2$) and mean-base ($h^2mg$) family heritabilities (Table 4). Superior variability for Th in the Cugir test, expressed by ANOVA (Table S1) and Tukey tests, is due to microenvironment and within-family interactions, since the genetic variance has a greater weight in the Voineasa test. Also, the highest accuracy of genotypic value prediction (0.71 in Cugir and 0.80 in Voineasa, closest to the ideal value of 1), and the stronger genetic signal [CV ratio, expressed by ratio of genotypic coefficient of variation to residual (environmental) coefficient of variation; 0.58 in Cugir, and 0.77 in Voineasa trials, again the closest to the ideal value of 1], were obtained for Th (Table 4).

*Table 4: Estimates of variances and heritabilities (h2) based on family selection. Gen_var and Gen (%) are the genotypic variance; Res_var and Res (%) are the residual (error) variance: variation due to environment/ unexplained sources; Phen_var is the total phenotypic variance = Gen_var + Res_var; h2, h2mg, are the broad-sense and mean-base family heritabilities; Accuracy of genotypic value prediction (closer to 1 = better); CVg, CVr, CV ratio are the Genotypic coefficient of variation (relative genetic variability), residual (environmental) coefficient of variation, and the ratio of CVg to CVr (higher values, closer to 1 = stronger genetic signal); Traits abbreviation as in methodology*

Tabelle 4: Schätzungen der Varianzen und Heritabilitäten ($h^2$) basierend auf der Familientrachtselektion. Gen_var und Gen (%) sind die genotypische Varianz; Res_var und Res (%) sind die Residualvarianz (Fehlervarianz), die auf Umwelt- oder unerklärte Faktoren zurückzuführen ist; Phen_var ist die gesamte phänotypische Varianz = Gen_var + Res_var; $h^2$ und $h^2$mg sind die Heritabilitäten im weiteren Sinne und auf Mittelwertbasis der Familie; Genauigkeit der Genotypwertvorhersage (je näher an 1, desto besser); CVg, CVr und CV-Verhältnis sind der genotypische Variationskoeffizient (relative genetische Variabilität), der residuale (umweltbedingte) Variationskoeffizient und das Verhältnis von CVg zu CVr (höhere Werte, näher an 1, bedeuten ein stärkeres genetisches Signal); Abkürzungen der Merkmale wie in der Methodik.

| **Trials** | **Cugir** | | | | | **Voineasa** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Parameter/Trait** | **Th** | **Dbh** | **Bd** | **Bf** | **Ss** | **Th** | **Dbh** | **Bd** | **Bf** | **Ss** |
| Gen_var | 0.09 | 0.57 | 0.001 | 0.31 | 0.005 | 0.12 | 1.49 | 0.02 | 0.50 | 0.02 |
| Gen (%) | 25.3 | 11.7 | 0.7 | 7.4 | 2.6 | 37.5 | 31.0 | 15.5 | 16.7 | 21.7 |
| Res_var | 0.26 | 4.28 | 0.125 | 3.87 | 0.165 | 0.19 | 3.31 | 0.10 | 2.47 | 0.07 |
| Res (%) | 74.7 | 88.3 | 99.3 | 92.6 | 97.4 | 62.5 | 69.0 | 84.5 | 83.3 | 78.3 |
| Phen_var | 0.35 | 4.85 | 0.126 | 4.18 | 0.17 | 0.31 | 4.80 | 0.11 | 2.97 | 0.09 |
| $h^2$ | 0.25 | 0.12 | 0.01 | 0.07 | 0.03 | 0.38 | 0.31 | 0.16 | 0.17 | 0.22 |
| $h^2$mg | 0.50 | 0.28 | 0.02 | 0.19 | 0.07 | 0.64 | 0.57 | 0.36 | 0.38 | 0.45 |
| Accuracy | 0.71 | 0.53 | 0.14 | 0.44 | 0.27 | 0.80 | 0.76 | 0.60 | 0.61 | 0.67 |
| CVg | 4.36 | 5.00 | 1.34 | 3.81 | 10.62 | 5.03 | 8.27 | 6.68 | 5.17 | 37.76 |
| CVr | 7.50 | 13.73 | 16.40 | 13.49 | 65.12 | 6.49 | 12.33 | 15.60 | 11.55 | 71.81 |
| CV ratio | 0.58 | 0.36 | 0.08 | 0.28 | 0.16 | 0.77 | 0.67 | 0.43 | 0.45 | 0.53 |

In the Cugir trial, located in the Șureanu mountains of the Southern Carpathians, the mean performance of provenances for the most important growth (Th) and stability (S) traits indicated that the best-performing provenances were Bois de Ayes (from the Franch Alps), Stâna de Râu and Pietrele (both from the Southern Carpathians). Due to the high survival of all provenances, the most important is Pietrele, which registered the highest Th (Figure 5). In the Voineasa experiment, located also in the Southern Carpathians but at a higher altitude, the best-performing provenance was Pietrele, followed by Călimani (from Eastern Carpathians), Gemenele and Stâna de Râu. In both trials, the local provenances, Stâna de Râu and especially Pietrele, registered very high Th values and high Sr values (> 70%), being the most important for the selection strategy (Figure 5).

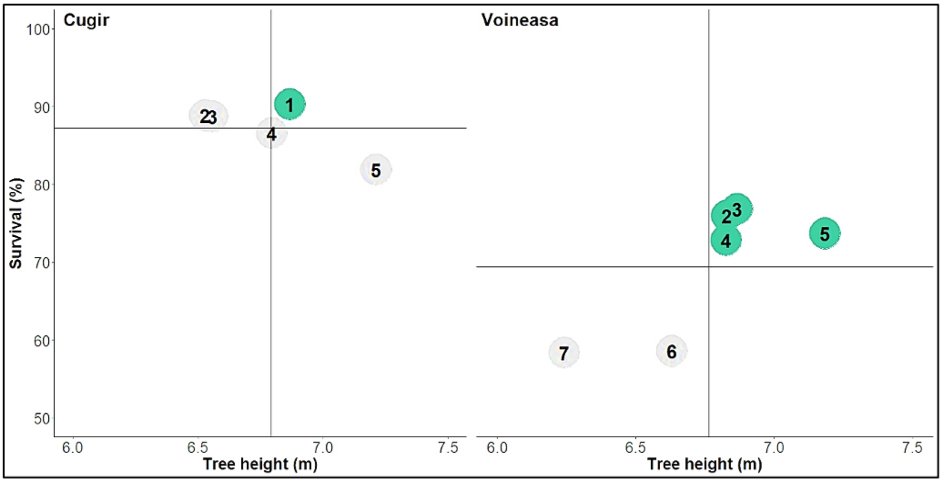


*Figure 5: The best-performing provenances in the two trials (the green circles mark the best-performing provenances and the black lines represent the trial mean for trees' height and survival). The provenance codes are as in Figure 2.*

Abbildung 5: Die leistungsstärksten Herkünfte in den beiden Versuchen (die grünen Kreise markieren die besten Herkünfte, die schwarzen Linien stellen den Versuchs-Mittelwert für Baumhöhe und Überleben dar). Herkunftscodes wie in Abbildung 2.

At the family level, in the Cugir common garden experiment, the multi-trait genotype-ideotype distance index (MGIDI) allows us to select the best eleven most performing families (Figure 6) based on all the analyzed traits (Th, Dbh, S, Bd, Bf, Ss). The best families belong mainly to Bois de Ayes (3) and Pietrele (6), while two other provenances, Călimani and Stâna de Râu, are each represented by only one family. In the Voineasa trial, MGIDI index indicates the selection of the top ten best-performing families (Figure 6), which are part of Călimani (4), Pietrele (1), Stâna de Râu (2), Gemenele (1), and Păpușa-Iezer (1) provenances. Consequently, the best inheritance rate could be obtained by a mixed selection of the best 30% of trees from the ten (Voineasa) and eleven (Cugir) most valuable families for Th, which could ensure improvements in all growth and stem quality traits.

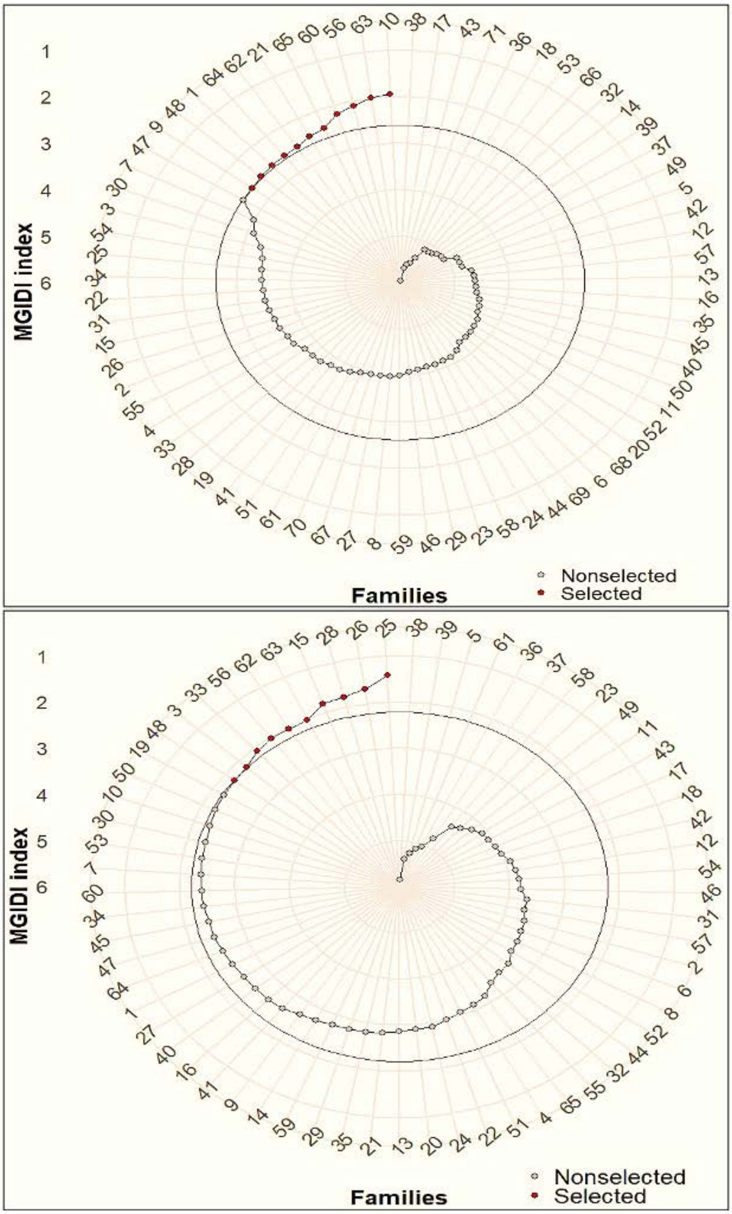


*Figure 6: Multi-trait genotype-ideotype distance index (MGIDI) for selecting the best performing families based on all the analyzed traits (Th, Dbh, S, Bd, Bf, Ss), in Cugir (up) and Voineasa (down) trials.*

Abbildung 6: Multi-Trait Genotyp-Ideotyp-Distanz-Index (MGIDI) zur Auswahl der leistungsstärksten Familien basierend auf allen analysierten Merkmalen (Th, Dbh, S, Bd, Bf, Ss) in den Versuchen Cugir (oben) und Voineasa (unten).

# 4 Discussion

## 4.1 Phenotypic variation

In the present paper, the last in a series of five articles concerning the variability of Swiss stone pine conserved ex situ in common garden experiments, we analyzed the 65 to 71 families originated from seven provenances (one from Alps, two from Eastern Carpathians, and four from Southern Carpathians), in two different environments of the Southern Carpathians (different mountains, 150 m difference in altitude, opposite exposition, sunny vs. shady, slope position, *etc.*). These differences contributed to enhanced adaptability in the more favorable conditions of the Cugir test (survival was superior with 18%, compared to the Voineasa trial). Almost the same survival was registered in the European provenances trial Cugir (established beside of the family experiment, on top of it), while in the paired trial (Cârlibaba, located in the Eastern Carpathians), situated at 100 m lower altitude, a slightly superior survival was registered (Budeanu *et al.*, 2025b), which could suggest a good adaptation at lower altitude, and a feasible solution for mixture with Norway spruce. The growth traits' results, especially for Dbh, were also superior in the Cugir trial, again in accordance with the other trials' results (Budeanu *et al.*, 2025b), while the qualitative traits of the stem and branches were higher in the Voineasa experiment. The genetic factor seems to have a significant role, as a provenance Pietrele achieved good performances in both experiments (actually, in all six testing sites, Budeanu *et al.*, 2024, 2025a,b), but the necessity for attention when transferring the reproductive materials is emphasized by the opposing results recorded in the two trials by provenances Călimani and Stâna de Râu. A similar concern was underlined in the previous papers (Budeanu *et al.*, 2024, 2025a). ANOVA confirms the strong influence of the microenvironment, in each trial, and a highly significant influence of the testing site conditions. The high variability, among and within families, is encouraging for the success of selection, while the adapted families could play an essential role in forest resilience to global warming (Chakraborty *et al.*, 2024), which will demand constant adaptation of the tree species (Leonelli *et al.*, 2009; Mosca *et al.*, 2016; Neuschulz *et al.*, 2018; Gugerli *et al.*, 2022).

## 4.2 Trait-trait and environmental Correlations

In Cugir and Voineasa half-sib trials, the phenotypic correlations favor the selection for growth traits (Dbh or Th), which also ensures the improvement of the majority of stem and branches qualitative traits (except of Bd). Similar results were previously registered for the same species (Budeanu *et al.*, 2024, 2025a,b). The positive correlations between growth traits and the altitude of the family's origin, registered in both trials but highly significant only in Voineasa's higher altitude test, indicate a strong influence of altitude on the Swiss stone pine distribution, results similar to the research performed in the Tatra Mountains (Zięba *et al.*, 2019; Izworska *et al.*, 2023). It appears that populations from higher altitudes exhibit superior adaptive traits, more pronounced in the test at the highest altitude (Voineasa). Previously, in experiments located at slightly lower altitudes, such correlations were not significant (Budeanu *et al.*, 2024, 2025a,b). The global warming may limit the Swiss stone pine distribution at lower altitudes, in accordance with the findings from the Western Carpathians (Marčiš *et al.*, 2025).

### 4.3 Inheritance rate and forward selection

In both experiments, the highest heritabilities were registered for Th, the most important growth trait for this hard growing species, so, the breeding program should prioritize the selection based on Th, which will ensure the competitiveness of Swiss stone pine with the others tree species of the high altitude phytoclimatic area, especially the Norway spruce and European larch.

For the joint results of both trials, the best-performing provenance in terms of stability and growth was Pietrele, which originates from the same region where the trials were established. However, the selection only in favor of local provenances is not justified, since in the Cugir and Voineasa trials, the second Th result was obtained by the Bois de Ayes provenance (from the French Alps, in Cugir), and the Călimani provenance (from Eastern Carpathians, in Voineasa). Due to the highly significant influence of the testing site, we must restrict forward selection to the provenance region of the testing sites (C1, the northern part of the Southern Carpathians) and recommend the best families of the above-mentioned provenances for use in similar environmental conditions. To increase the genetic diversity, all 21 families highlighted by MGIDI could be selected, with special attention to Th. Thus, we propose the selection of the best 30% of trees from the most valuable 21 families for Th. Moreover, to increase the genetic diversity in future afforestation, it is necessary to combine seedlings from these common gardens with those highlighted in the other four trials (Budeanu *et al.*, 2024, 2025a,b). Lendvay *et al*. (2014) underline the importance of a sufficiently large population size to guarantee a high level of genetic diversity, which is a critical problem for *Pinus cembra* in Europe (Belokon *et al.*, 2005; Höhn *et al.*, 2009; Salzer & Gugerli, 2012; Dzialuk *et al.*, 2014; Wojnicka-Półtorak *et al.*, 2015).

Our findings provide a constructive approach for management plans, as we recommend transition from Norway spruce monocultures to structurally more diverse stands with codominant Swiss stone pine, at the upper altitudinal limit of the Southern Carpathian forests. The conservation plans in favor of Swiss stone pine must include the preservation of the natural forests, of all trials and seed orchards, and ensure the extension of the species in the spruce phytoclimatic floor of the Southern Carpathian (Budeanu *et al.*, 2025b). The establishment of a monitoring network at the upper altitudinal limit of the forests would be useful, as would be the highlight of the economic value of Swiss stone pine timber (Koeck *et al.* 2025).

## 5 Conclusions

The high level of genetic variances and heritabilities (especially for tree' height), along with the significant correlations among traits, coupled with the large number of families involved in this experiment, firmly establishes the foundation for a successful breeding program.

Following 27 years of testing, ten to eleven families of Swiss stone pine were successfully identified in each trial, reflecting a selection intensity of 15%. These families are now considered the most suitable candidates for promotion in the northern region of the Southern Carpathians, where the ecological conditions closely resemble those of the experimental sites. Furthermore, a forward selection of the top 30% of individual trees from the best selected families, based on tree height, could be applied in each trial. Given the strong effects of the testing site and site x family interaction, extreme attention is required when transferring reproductive materials.

## Authors' contributions

Conceptualization, M.B. and E.B.; methodology, M.B. and E.B.; formal analysis, M.B. and E.B.; investigation, M.B. and E.B.; writing-original draft preparation, M.B.; writing-review and editing, E.B.; visualization, M.B. and E.B. All authors have read and agreed to the published version of the manuscript.

## Funding and Acknowledgments

This paper was financed by the Romanian UEFISCDI, in the frame of 71PHE-Carmine project contracted by National Institute for Research and Development in Forestry "Marin Drăcea". We wish to express our gratitude to Gabriela Grosu and Dan Pepelea for their help with field measurements.

## Declarations

The authors declare no competing interests. The authors declare that they have no known conflicts of interest.

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