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Research Article

Variation in survival and stem quality of Douglas-fir provenances: Insights from 47-year-old common garden experiments in Romania

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Abstract

Understanding the genetic variation of wood quality traits is essential for developing breeding strategies to improve the quality of Douglas-fir plantations. This study assessed the performance of 61 Douglas-fir provenances established in 1977 established in three Romanian common garden experiments (Aleșd, Făget and Padeș). A mixed linear model was applied to estimate the variance components, and Pearson correlations were used to explore trait relationships. The results revealed significant provenance effects for branch angle, branch diameter, number of branches, and survival at Aleșd, and for branch angle and diameter at Făget. Survival and branch traits, particularly branch angle and diameter, were the most stable traits across the field trials and hence suitable for early selection and breeding across similar site conditions. Over 50% of trait variance was accounted by stem form, forking index, and number of branches due to strong environmental effects. Provenance-by-environment interaction was significant only for branch diameter, suggesting that this trait is more sensitive to site-specific conditions. The other traits had stable provenance rankings across environments due to non-significant interaction effects. These findings highlight the potential to use selected provenances as a genetic base for renewing the Douglas-fir breeding program in Romania. Selecting provenances with high survival and favourable branch traits improves timber quality and plantation resilience. The study also demonstrates the relevance of long-term provenance trials in identifying climate-resilient genetic resources, which is critical for maintaining forest productivity and stability under future climate change scenarios.

Keywords: adaptation; common garden experiments; Douglas-fir; genetic variance; wood quality

Introduction

Forest genetic improvement represents the systematic application of genetic principles integrated with silvicultural practices to establish forest plantations that are productive, resilient, or sustainable forest plantations depending on management objectives (Lantz, 2008; White *et al.*, 2009; Castellanos-Hernández *et al.*, 2011). In the context of climate change, identifying species that are threatened is essential for guiding species

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selection in reforestation and breeding programs, and for prioritizing management strategies that promote forest ecosystem resistance (Liu *et al*., 2021), resilience (Falk *et al*., 2022), or adaptation (Aitken *et.al*, 2016; Nagel *et al*., 2017; Ghirardo *et al*., 2022).

Provenance trials constitute a fundamental experimental framework in forest genetics, providing two important functions: the establishment of scientifically-based seed transfer protocols and the identification of superior genetic sources for reforestation (White *et al.*, 2009; Pâques, 2013). These trials enable the evaluation of genetic variability and local adaptation, allowing breeders to identify seed sources to site conditions across varying environments (Risk *et al*., 2021; Sestras *et al*., 2025).

Among commercial conifers in North America, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) has the largest north-south range geographic distribution (Konnert and Alizoti, 2016). Most non-native forest tree species introduced in Europe exhibit extensive geographic variation within their native range. Consequently, provenance performance and survival may vary significantly when planted outside their natural distribution (Cannell *et al*., 1984; Eilmann *et al*., 2013). The most commonly planted non-native forestry species in Europe tend to be fast-growing, such as Sitka spruce (*Picea sitchensis* (Bong.) Carr.), Douglas-fir (*Pseudotsuga menziesii* (Mirb). Franco), Grand fir (*Abies grandis* (Douglas ex D. Don) Lindley), Black locust (*Robinia pseudoacacia*), Lodgepole pine (*Pinus contorta* Douglas), Eucalypts (*Eucalyptus* spp.), Northern red oak (*Quercus rubra* L.), Tree of heaven (*Ailanthus altissima* (Mill.) Swingle), and hybrid polars (e.g., *Populus x euramericana, P. x canadensis*) (Zerbe, 2003; Schmidt *et al*., 2016).

Douglas-fir transitioned from ornamental use in the late 1800s to become a major reforestation species in Western Europe after World War II, supported by government reforestation subsidies (Ronch *et al.*, 2016). In Europe, non-native tree species extend over approximately 8.54 million hectares, equivalent to 4.0% of the total forest area, with the five most common species representing as much as 77% of this total (Brus *et al*., 2019). Douglas-fir now covers 800,000 ha across Europe, with approximately 400,000 ha - around 50% of the continental area - in France, roughly 200,000 ha (25%) in Germany, and the remainder distributed across other countries, including the United Kingdom (which accounts for approximately 45,000 ha) (Nicolescu *et al*., 2023). The species has also been greatly extended across Southern Hemisphere countries, including South Africa, South America, New Zealand, and Australia (Bastien *et al*., 2013; Nicolescu *et al*., 2023).

Beginning in 1972, Romania participated in IUFRO's international provenance trials for Douglas-fir, testing diverse native-range seed sources under a common garden experimental design (Enescu, 1975). Douglas-fir is recognised as the most valuable introduced coniferous species (Enescu,1975; Şofletea and Curtu, 2007; Leskinen *et al*, 2020) in Romania, occupying approximately 7300 ha, and accounting for 0.12% of the national forest area. Romania had a Douglas-fir tree breeding program, which was discontinued around the year 2000. These trials provide the principal genetic base for identifying seed sources adapted to Romanian conditions, which could serve as the starting point for future breeding efforts.

Douglas-fir timber exhibits excellent mechanical properties suitable for many uses: exterior cladding (heartwood only), joinery, veneer production, engineered wood panels, and pulp manufacturing (Bastien, *et al*., 2013). It is suitable for premium appearance-grade applications, encompassing architectural millwork, fenestration products, and specialised structural components. The commercial significance of Douglas-fir stems from its inherent dimensional stability and superior strength properties compared to many used conifers, such as Norway spruce and Scots pine, establishing it as a preferred material for high-performance specialty lumber applications (Ross, 2021). Given its importance in the global industry, understanding the genetic architecture of wood quality and adaptive traits is essential for implementing breeding programs. This knowledge enables prediction of correlated responses to selection, prevents undesirable indirect effects from single-trait selection, and maintains tree health and wood quality for future markets and reforestation efforts (Ukrainetz *et al*., 2008).

The commercial value of Douglas-fir is significantly influenced by the morphological variation in stem form and branching characteristics that directly affect wood quality (Temel and Adams, 2000; Vargas-Hernández *et al.*, 2003; Magalska and Howe, 2014). Research has shown that, after volume growth, stem defects are the second most important factor that determines tree value, while branch traits play a critical role in timber quality (Magalska and Howe, 2014). Quantitative genetic studies have revealed substantial variation among families in key morphological traits, like branch number, branch length, and branch angle, and heritable genetic control, especially for the branch angle (Vargas-Hernández *et al.*, 2003).

Results from international common garden experiments have confirmed significant variation in quality traits across Douglas-fir. For instance, in a 19-year-old provenance trial in New Zealand, significant variation was observed among provenances for wood density, branch size per log, branch angle, and stem form (Lausberg *et al.*, 1996). A 46-year-old IUFRO provenance experiment in Slovenia revealed strong provenance differences in survival, growth, and log quality (including stem straightness and knot attributes), underscoring the influence of provenance on timber quality (Smolnikar *et al.*, 2021). Additionally, older international provenance tests in Germany documented clear provenance-driven variation in branch and stem characteristics across different environments (Seho and Kohnle, 2014).

Wood quality traits critically influence the end-product value in the commercial industry. Structural defects from branch knots, stem crook, and epicormic branching are primary factors causing lumber downgrading and economic losses in sawn wood products (Climent *et al.*, 2024). Despite the commercial and ecological importance of Douglas-fir, studies assessing genetic variability assessment in morphological quality traits in mature provenance trials (≥ 40 years) remain limited in Eastern European contexts. A deeper understanding of the genetic variability in morphological traits that directly influence wood quality is essential for optimizing selection strategies and improving timber performance. Traits like as branch number, branch diameter, branch angle, stem straightness, and forking are known to significantly affect stem form, knot size, sawn timber quality, and structural performance.

The objectives of this study were to 1) evaluate the genetic variability of wood quality and adaptive traits among Douglas-fir provenances, 2) analyze the phenotypic correlations among these traits, 3) assess provenance x environment interaction, and 4) identify the best provenances in terms of quality and adaptive traits for reforestation and inclusion in breeding programs.

Materials and Methods

Common garden experiments and tested provenances

Between 1977 and 1980, a total of five common garden experiments were established across Romania to evaluate the performance of Douglas-fir provenances under local environmental conditions (Enescu, 1984). These trials were part of a broader effort to assess the adaptability, growth potential, and wood quality traits of this non-native conifer species in Romania. The remaining common garden experiments are located in Aleșd (Bihor County), Făget (Timiș County), and Padeș (Gorj County), all established in the year 1977 (Enescu, 1984). Although five common garden experiments were initially installed, only these three remain suitable for evaluation, as the other two were disaffected.

The Douglas-fir provenance included in common garden experiments originated from a broad range of geographic regions, reflecting a broad genetic and ecological diversity. A total of 34 provenances were sourced from the United States, specifically from the states of Idaho (5), California (2), Oregon (6), Washington (20), and Wyoming (1). Additionally, 10 provenances were obtained from Canada, 6 from Germany, 3 from France, and 8 from various locations within Romania (Figure 1).

The number of Douglas-fir provenances tested varied among the three common garden experiments: 55 provenances were evaluated at Aleșd, 49 at Făget, and 48 at Padeș (Table A1) Despite these differences, 38 provenances were common across the three common garden experiments, enabling a comparative analysis of provenance-environment interactions and site-specific performance.

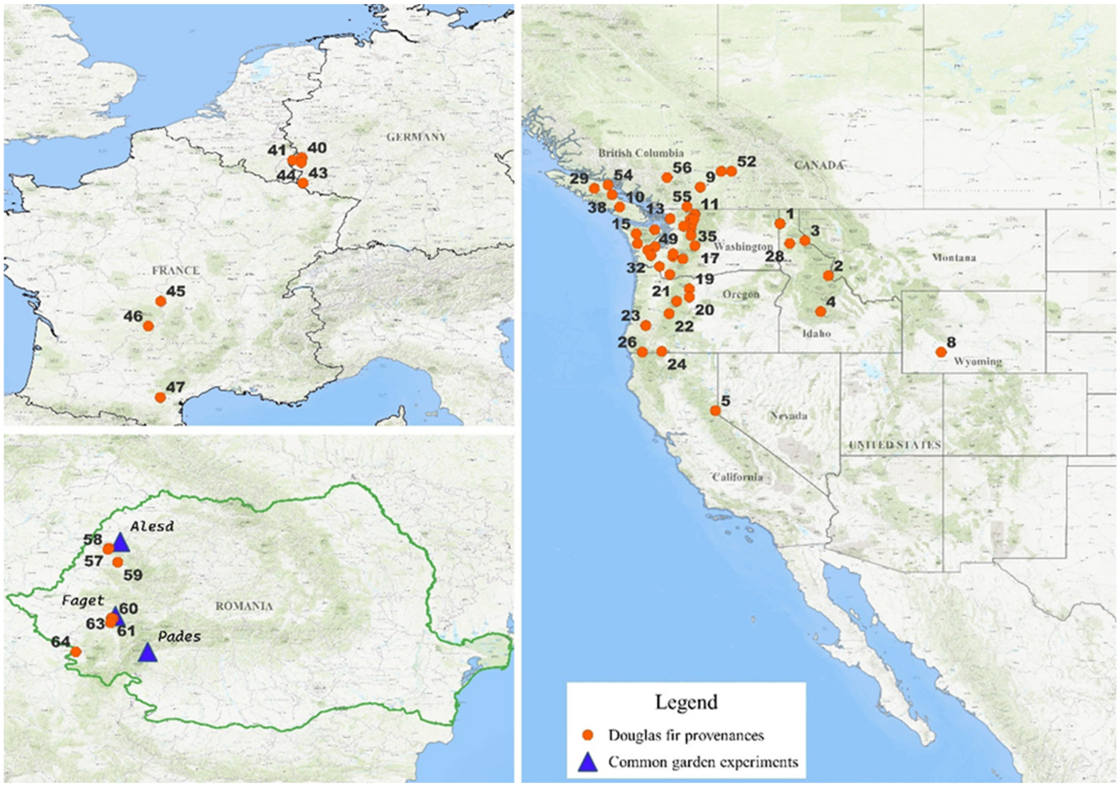

Figure 1. Geographic location of the tested Douglas fir provenances (orange points) and common garden experiments (blue triangles)

Site conditions and field measurements

The geographic, site and climate characteristics of the three Douglas-fir common garden experiments over the period 1977-2023 (Table 1) are detailed below. Mean climatic values were calculated using data from ClimateEU (Marchi *et al.*, 2020). Precipitation and mean temperature are reported both as annual averages and as averages for the growing season (May-September).

Table 1. Geographic, climatic, and edaphic characteristics of the three Douglas-fir common garden experiments in Romania

Characteristics	Aleşd	Făget	Padeş
Coordinates	47.15° N, 22.33° E	45.76° N, 22.29° E	45.09° N, 22.89° E
Elev. (m a.s.l.)	670	330	720
Soil type	Eutricambosol	Luvisol	Eutricambosol
MAT (°C)	7.9	10.4	7.8
GST (°C)	15.3	17.9	15.4
MAP (mm)	71.6	70.9	81.3
GSP (mm)	90.0	90.9	100.5

*Elev - Elevation (m a.s.l. - meters above sea level), MAT - Mean Annual Temperature, GST - Mean Temperature in Growing Season, MAP - Mean Annual Precipitation and GSP - Growing Season Precipitation

The three common garden experiments were planted in a partially balanced block design. Each provenance was represented by a plot of 25 trees, arranged in a 5 x 5 grid with 2 x 2 meter spacing, replicated across three blocks.

The analyzed traits were grouped into the following categories: 1) wood quality traits: stem form (SF), forking index (FI), branch angle (BA), number of branches (NB), diameter of branch (DB), and 2) adaptive trait - survival (SV).

The evaluation of wood quality and adaptive traits was carried out according to the Treebreedex protocol (Ducci *et al.*, 2012; Opgenoorth *et al.*, 2021), with the assessment methodology for each trait described in Table 2.

Table 2. Scoring methodology for wood quality and adaptive traits

Wood quality traits	**Score**	**Description**
1. Stem form	5	Straight (no visible crooks)
	4	Fairly straight (weak crooks, 1-2)
	3	Slight to moderate bend in different directions (≥ 3 weak crooks)
	2	Moderate or strong bends (1-2, strong curvature)
	1	No straight stem (≥ 3 severe crooks)
2. Forking index	4	No forking
	3	Forking in the upper third of the tree
	2	Forking in the middle third of the tree
	1	Forking in the lower third of the tree
3. Branch angle	1	Angle < 90°
	2	Angle ≃ 90°
	3	Angle > 90°
4. Branch diameter	1	Diameter of branches < 2 cm
	2	Diameter of branches between 2 - 5 cm
	3	Diameter of branches > 5 cm
Quantitative trait	**Score**	**Description**
5. Number of branches	-	Number of branches per whorl
Adaptive traits	**Score**	**Description**
6. Survival	-	Survival was calculated as the percentage of live trees to the total number of trees initially planted per provenance.

Data analyses

Statistical analysis of phenotypic variation was performed both at individual trial sites and among sites. For each site, a linear mixed-effects model was applied, treating provenance as a random effect and block as a fixed effect (Nanson, 2004):

$$Y_{jkl} = \mu + P_j + B_k + ejkl \qquad (1)$$

Where, Y_{jkl} is the observed trait (SF, FI, BA, NB, DB, SV), μ is the overall mean, P_j is the random effect of provenance, B_k is the fixed block effects, and $ejkl$ is the residual error.

Models were fitted using the *lmerTest* package in R (A. Kuznetsova, *et al.*, 2020).

For the across-site analysis of variance, a similar model was used, where site, provenance and the site-by-provenance interaction were treated as fixed factors:

$$Y_{ijkl} = \mu + S_i + P_j + B_k + S_i \, x \, P_j + e_{ijkl} \qquad (2)$$

Where S_i is the site effect and $S_i \, x \, P_j$ the interaction between site and provenance.

Pearson correlation coefficients were calculated to describe the linear relationship between traits. The analysis assumes normally distributed variables and evaluates correlations ranging from − 1 (negative) to +1 (positive), with 0 indicating no linear association. In addition to the six traits, diameter at breast height (DBH), total height (HT) and pruned height (PH) were also included in the correlation analysis, as these traits were analyzed in a previous study (Stoica *et al.*, 2025) and are important indicators of tree growth. Correlation matrices were visualised using ellipse-based correlograms generated with the *corrplot* package in R (Wei and Simko, 2021). All statistical analyses were conducted using the *R environment* (R Core Team, 2024).

Results

Statistical analysis of provenance variation

Analysis of random and fixed effects for Douglas fir across common garden experiments revealed distinct patterns of genetic and environmental variability for quality and adaptive traits, as presented in Table 3.

Table 3. Results of random and fixed effects in each Douglas fir common garden experiments

Trial	Trait	LRTp	Vp	Vr	MSb
Aleșd	SF	1.67 ^{ns}	0.005 (1.8%)	0.28 (98.2%)	0.007 ^{ns}
	FI	2.81 ^{ns}	0.008 (2.5%)	0.31 (97.5%)	0.04 ^{ns}
	BA	26.18 ***	0.03 (6.7%)	0.42 (93.3%)	0.45 ^{ns}
	NB	6.68 **	0.04 (3.4%)	1.14 (96.6%)	3.15 ^{ns}
	DB	14.53 ***	0.04 (6.7%)	0.56 (93.3%)	1.71 ^{ns}
	SV	35.56 ***	39.96 (48.3%)	42.77 (51.7%)	108.04 ^{ns}
Făget	SF	0.54 ^{ns}	0.005 (1.1%)	0.45 (98.9%)	0.79 ^{ns}
	FI	4.60 ^{ns}	0	0.90 (100%)	0.01 ^{ns}
	BA	15.38 ***	0.35 (44.3%)	0.44 (55.7%)	0.06 ^{ns}
	NB	0.44 ^{ns}	0.01 (0.6%)	1.58 (99.4%)	2.07 ^{ns}
	DB	12.34 ***	0.05 (7.4%)	0.63 (92.6%)	2.97 *
	SV	0 ^{ns}	0	92.14 (100%)	254.74 ^{ns}
Padeș	SF	0.34 ^{ns}	0.002 (0.7%)	0.27 (99.3%)	0.33 ^{ns}
	FI	0.23 ^{ns}	0.0009 (0.8%)	0.11 (99.2)	0.01 ^{ns}
	BA	8.60 **	0.03 (5.9%)	0.48 (94.1%)	0.12 ^{ns}
	NB	0.99 ^{ns}	0.02 (1.4%)	1.46 (98.6%)	0.08 ^{ns}
	DB	2.50 ^{ns}	0.01 (1.7%)	0.57 (98.3)	2.96 *
	SV	0.01 ^{ns}	0.55 (0.9%)	63.40 (99.1%)	26.04 ^{ns}

*Significance levels: $p \leq 0.05$ (*), $p \leq 0.01$ (**), and $p \leq 0.001$ (***); ^{ns}: not statistically significant with $p > 0.05$; LRTp-likelihood ratio test for provenance effect; Vp-variance for provenance random effect; Vr-residual variance; MS-mean squares for block (b); SF - Stem form, FI - Forking index, BA - Branch angle, NB - Number of branches, DB - Diameter of branch and SV - Survival; values in brackets report the proportion of variance accounted by each effect

In the Aleșd trial, provenance effects were highly significant for most analyzed traits. BA had an LRTp = 26.18, NB = 6.68, DB = 14.53 and SV = 35.56. The provenance variance component (Vp) was substantial for SV = 48.3% and DB = 6.7%, indicating a strong genetic contribution of these traits. Residual variances (Vr) for these traits were also notable, such as 51.7% for SV and 93.3% for DB. Block effects (MS b) were non-significant for all traits in Aleșd, with values like 0.45 ns for BA and 108.04 ns for SV.

In the Făget trial, significant variation among provenances was found for BA (LRTp = 15.38 and Vp = 44.3%) and DB (LRTp = 12.34 and Vp = 7.4%). The block effect was significant only for DB (MSb = 2.97), while other traits showed non-significant block effects.

In the Padeș, only the BA (LRTp = 8.60 and Vp = 5.9%) showed a significant provenance effect, with a Vr = 94.1% and a non-significant block effect (MSb = 0.12 ns). For all other traits at Padeș, provenance and block effects were not significant.

For the Aleșd trial, the provenances with the highest proportion of BA Score 1 (< 90°) are as follows: 24 - Jakson-Ashland, Oregon (59%), 38 - Oyster R, British Columbia (56%) and 21 - Marion Forks, Oregon (53%).

At Făget, the provenance with the highest proportion of BA Score 1 (< 90°) are as follows: 57 - Pădurea Neagră, Romania (76%), 28 - Chatcolet, Idaho, USA (71%), and 31 - Elma, Washington, USA (64%).

At Padeș, the provenance with the highest proportion of BA Score 1 (< 90°) are as follows: 28 - Chatcolet, Idaho, USA (75%), 37 - Concrete-Presentin Creek USA, Washington (71%) and 26 - Siskiyou-Hawkinsville, California, USA (70%). These percentages indicate the proportion of trees with Score 1 within each provenance, calculated based on the total number of trees (Figure 2).

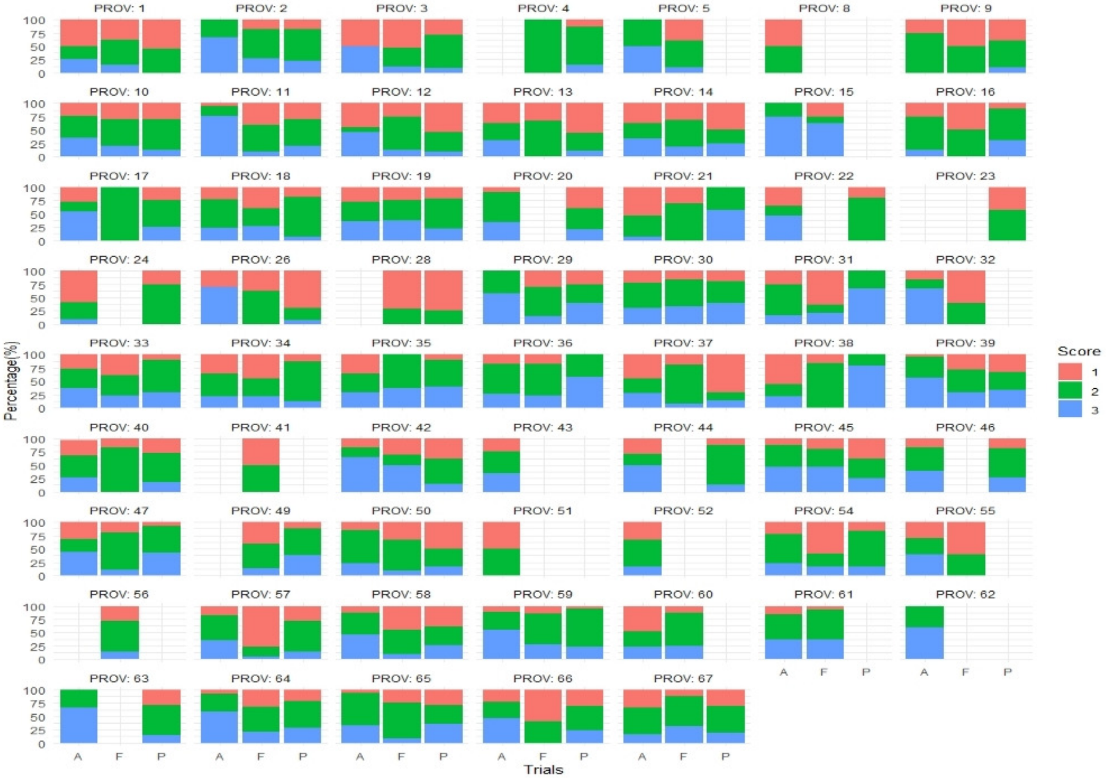

Figure 2. Percentage distribution of branch angle (BA) scores for each provenance and field trial
Each facet displays a different provenance, while the stacked bars represent the proportion of each score within each trial (A - Aleșd, F - Făget, and P - Padeș).

According to the random and fixed effects, the DB was significant in the Aleșd and Făget trials. For the Aleșd trial, the provenance with the highest proportion of DB Score 1 (thin branches) are as follows: 24 - Jakson-Ashland, Oregon (58%), 38 - Oyster R, British Columbia, Canada (55%) and 21 - Marion Forks, Oregon, USA. For the Făget trial, the provenance with the highest proportion of DB Score 1 are as follows: 28 - Chatcolet S, Idaho, USA (86%), 17 - Washington, Kittitas - Cle Elum, USA (83%), and 54 - Morton Lake, British Columbia, Canada. In the Padeș trial, DB was not statistically significant. These percentages indicate the proportion of trees with Score 1 within each provenance, calculated based on the total number of trees (Figure 3).

Figure 3. Percentage distribution of branch diameter (DB) scores for each provenance and field trial
Each facet displays a different provenance, while the stacked bars represent the proportion of each score within each trial (A - Aleșd, F - Făget, and P - Padeș)

At age 47, the survival rate (SV) varied among the common garden experiments and provenances. The highest average SV was recorded at the Aleșd trial ($\bar{x}$ = 18.45%), followed by Făget ($\bar{x}$ = 16.80%) and Padeș ($\bar{x}$ = 16.66%). According to the random and fixed effects, the SV was very significant only in the Aleșd trial.

The provenances with the highest SV in the Aleșd trial were: 39 - Daun Ost, Germany (32%), 20 - Benton - Corvallis, Oregon - USA (29%), 37 - Concrete, Presentin Creek, Washington - USA (29%), 61 - Sub Vîrful Dăii, Lugoj - România (29%) and 43 - Wittlich West, Abt. 1B - Germany (28%).

The provenances with the highest SV in the Făget trial were: 64 - Anina - Buhui - România (27%), 37 - Concrete, Presentin Creek, Washington - USA (29%), 58 - Piatra Albă, România (25%), 18 -Lewis - Packwood, Washington - USA (24%) and 36 - Skycomish - Beckler Peak, Washington - USA (24%). These percentages indicate the proportion of live trees to the total number of trees initially planted per provenance (Figure 4).

The provenances with the highest SV in the Padeș trial were: 20 - Benton - Corvallis, USA, Oregon (25%), 47 - Moussans II - France (24%), 49 - Darrington III, Washington - USA (24%), 18 - Lewis - Packwood, Washington - USA (23%), and 63 - Nădrăgel - România (23%).

Figure 4. Survival rate (SV) for each provenance across all field trials (A - Aleșd, F- Făget and P - Padeș)

Provenance - environment interaction

To evaluate sources of variation in survival and quality traits, variance components were estimated for genetic (provenance), environmental (location), and provenance-by-environment interaction (P x L) effects across common garden experiments Table 4.

Table 4. Analysis of variance for studied traits in the Douglas fir common garden experiments

Source of variation	s^2						
	D.F.	SF	FI	BA	NB	DB	SV
Provenance (P)	37	0.098 ^{ns}	0.071 ^{ns}	0.248 ^{ns}	0.263 ^{ns}	0.261 *	74.642 *
Location (L)	2	0.889 ***	1.098 ***	1.494 **	1.176 *	0.292 ^{ns}	195.991 *
Interaction P x L	74	0.100 ^{ns}	0.074 ^{ns}	0.164 ^{ns}	0.409 ns	0.261 *	0.699 ^{ns}
Error	188	0.095	0.084	0.195	0.453	0.190	48.611

*Significance levels: $p \leq 0.05$ (*), $p \leq 0.01$ (**), and $p \leq 0.001$ (***); ^{ns}: not statistically significant with $p > 0.05$; SF - Stem form, FI - Forking index, BA - Branch angle, NB - Number of branches, DB - Diameter of branch and SV - Survival.

Regarding the provenance (P) factor, significant variance was observed only for DB and SV, indicating a genetic determinism for these traits. The other traits did not show significant provenance effect, suggesting stronger influence of other factors in phenotypic expression.

Location (L) had a highly significant effect on most traits, especially for SF, FI and BA, highlighting a strong environmental influence.

The Provenance × Location interaction (P × L) was significant only for DB, indicating that the provenances' performance depends on environmental conditions. For other traits, the interaction was not significant, suggesting high stability for provenance characteristics across locations.

Phenotypic correlations between traits

Phenotypic correlations among the studied traits reveal distinct patterns across experimental sites, with greater number of significant correlations in the Aleșd trial compared to the Făget and Padeș trials. Phenotypic correlations among Douglas fir traits in the Aleșd trial are presented below (Figure 5).

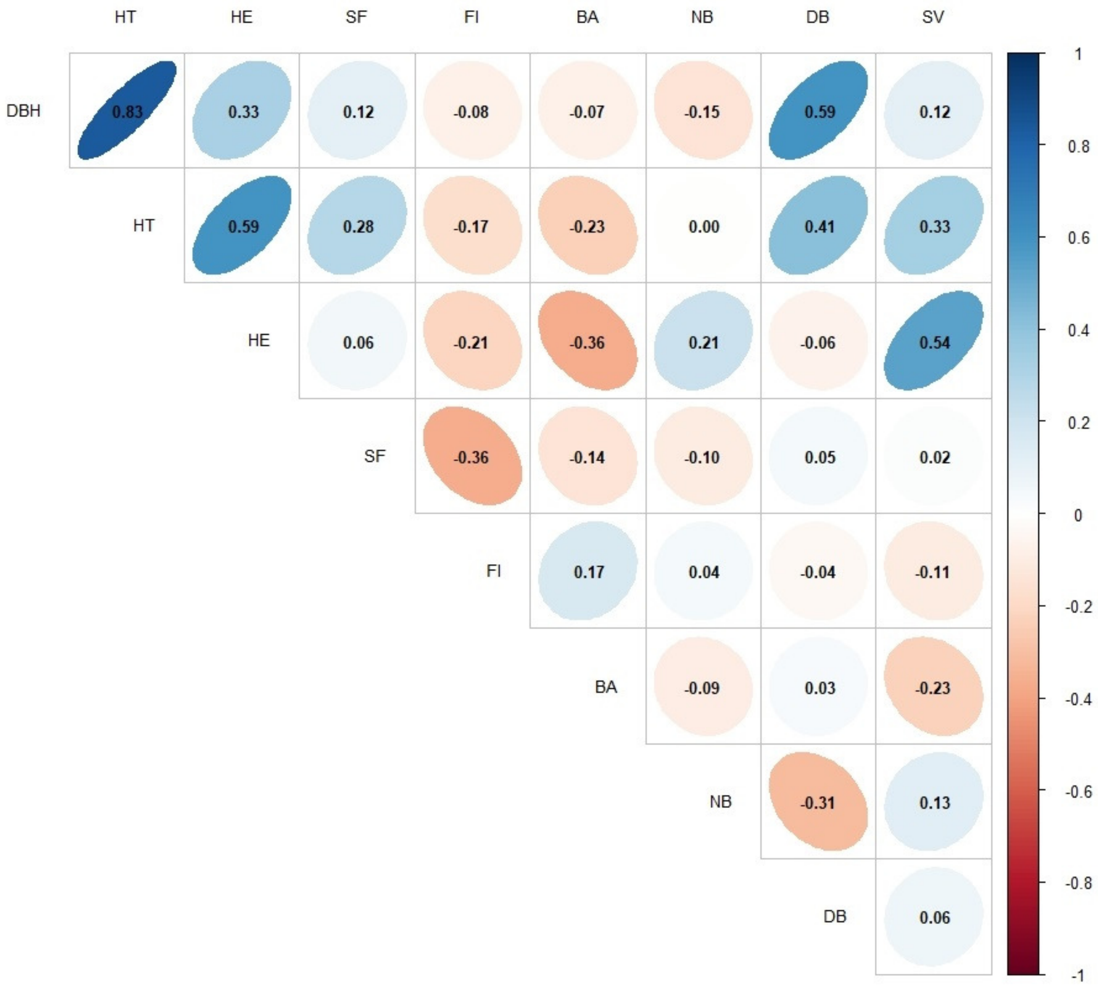

Figure 5. Pearson correlations of traits in the Aleșd common garden experiment

Ellipse direction indicates the sign of the correlation (↗ positive - blue, ↘ negative - red), and ellipse shape reflects strength (narrow = strong, round = weak). DBH - Diameter at breast height, HT -Total height, HE - Pruned height, SF - Stem form, FI - Forking index, BA - Branch angle, NB - Number of branches, DB - Diameter of branch and SV - Survival

At Aleșd, significant correlations were identified among analyzed traits: a very strong positive correlation was observed between DBH and HT, while DBH and DB also showed a significant positive correlation. HT and HE had significant positive correlation, as were HE and SV. Among the negative correlations, a significant relationship was found between SF and BA, as well as between NB and DB.

In the Făget trial, the following significant correlations were identified among the analysed traits: a strong positive correlation was observed between DBH and HT, while DBH and DB also showed a significant positive correlation. HT and DB had a significant positive correlation. Additionally, SF and NB, as well as SF and SV, showed significant positive correlations (Figure 6).

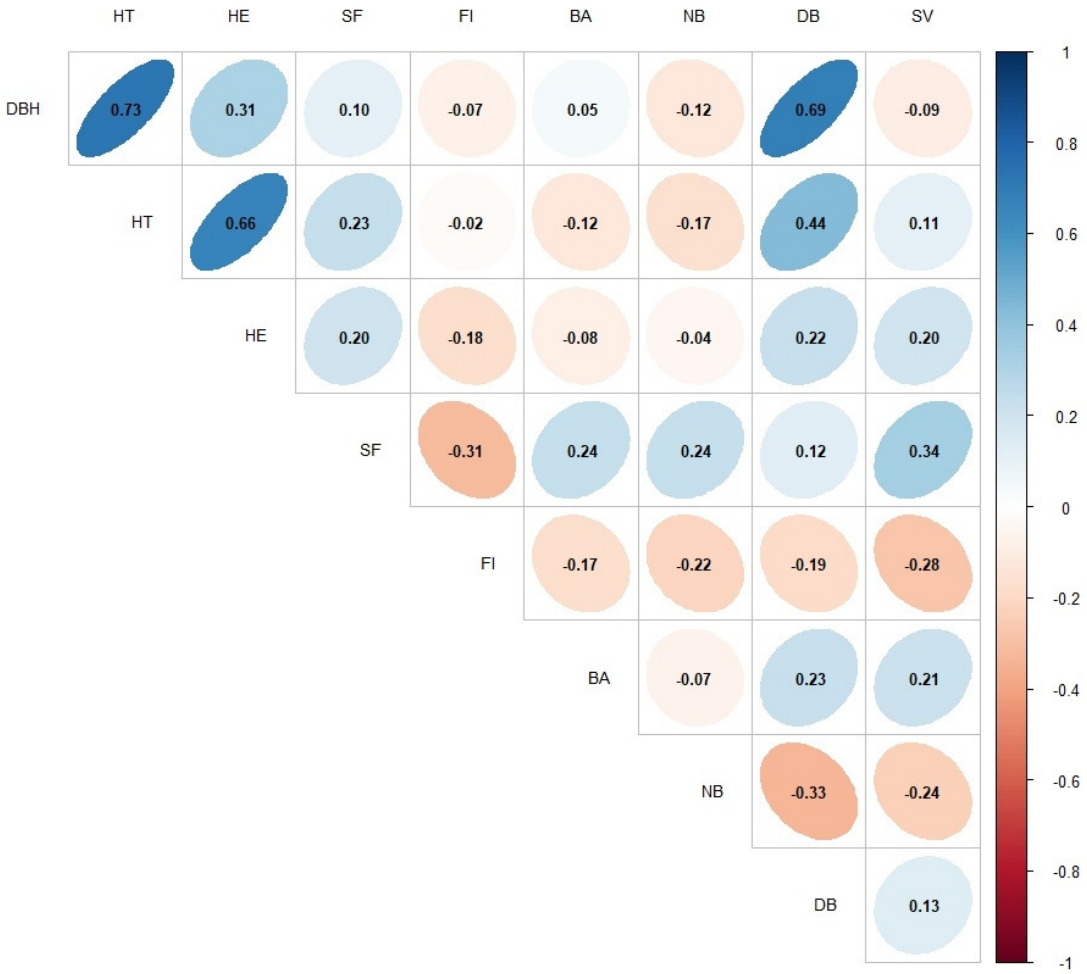

Figure 6. Pearson correlations of traits in the Făget common garden experiment

Ellipse direction indicates the sign of the correlation (↗ positive - blue, ↘ negative - red), and ellipse shape reflects strength (narrow = strong, round = weak). DBH - Diameter at breast height, HT -Total height, HE - Pruned height, SF - Stem form, FI - Forking index, BA - Branch angle, NB - Number of branches, DB - Diameter of branch and SV - Survival

In the Padeș trial, the following significant correlations were identified among the analyzed traits: a strong positive correlation was observed between DBH and HT, while DBH and DB also showed a significant positive correlation. DBH and SV showed a significant negative correlation. HT and HE were positively and significantly correlated. SF and FI showed a significant negative correlation, as did HE and NB (Figure 7).

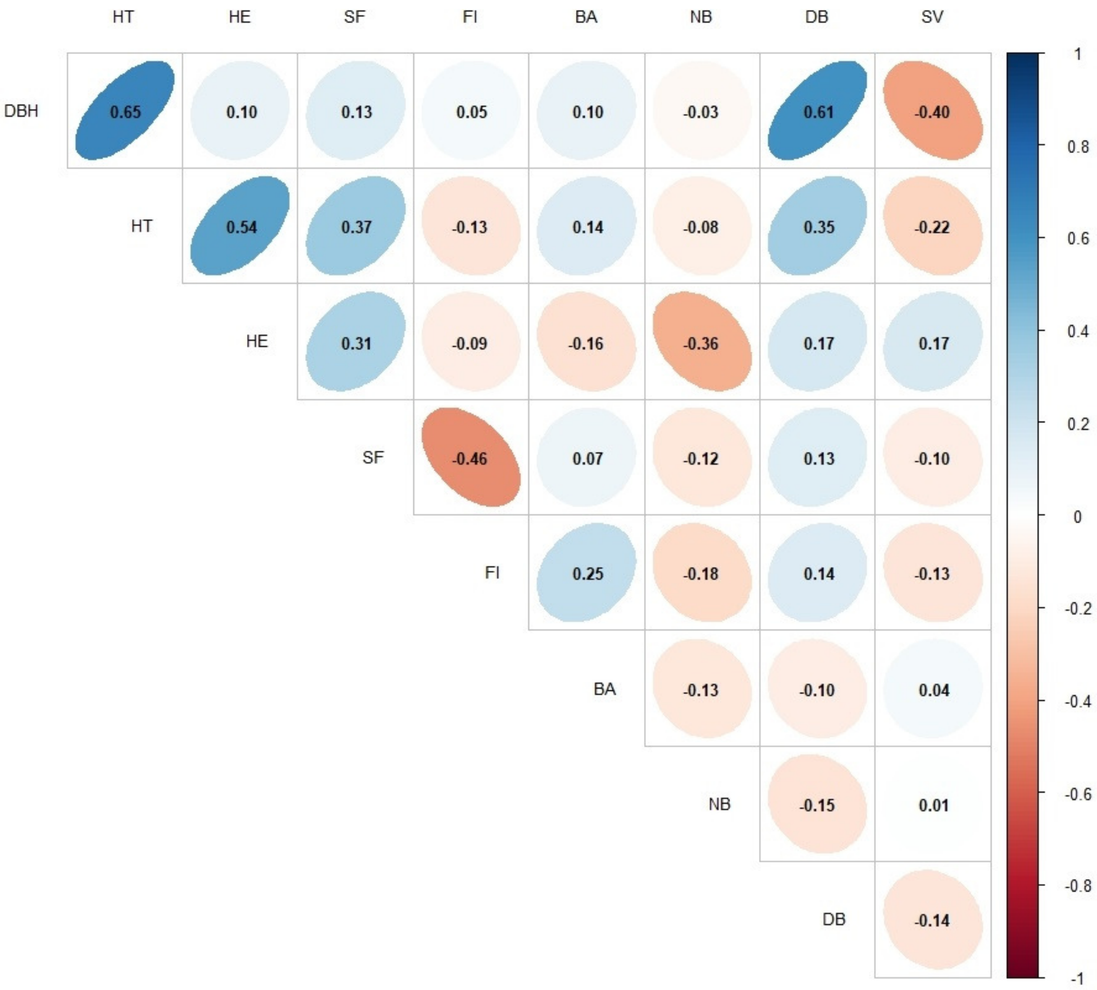

Figure 7. Pearson correlations of traits in the Padeș common garden experiment

Ellipse direction indicates the sign of the correlation (↗ positive - blue, ↘ negative - red), and ellipse shape reflects strength (narrow = strong, round = weak). DBH – Diameter at breast height, HT -Total height, HE - Pruned height, SF - Stem form, FI - Forking index, BA - Branch angle, NB - Number of branches, DB - Diameter of branch and SV – Survival

Discussion

Across three Romanian common garden experiments, Douglas fir provenances showed distinct site-specific genetic signals for key adaptive and wood-quality traits.

Analysis of random and fixed effects for Douglas fir in each common garden experiments revealed significant provenance effects at Aleșd for four of six traits (BA, NB, DB, SV), at Făget for two traits (BA and DB), and a single significant trait (BA) at Padeș (Table 3). These traits are of critical importance in evaluating timber quality and structural integrity in breeding programs, as they influence knot formation, wood stiffness, and board grade. Osborne and Maguire (2016) showed that BA strongly correlates with internal knot geometry and volume in Douglas-fir, enabling early selection for improved log quality. Similarly, Lowell *et al.* (2014) found the NB and DB significantly affect veneer recovery and structural lumber grade, and these traits exhibit both genetic and silvicultural control. Macdonald and Hubert (2002) reinforced that branch-related features reduce mechanical performance in structural applications, supporting the use of form traits in quality improvement. Further evidence from CT-scan studies by Todoroki *et al.*, (2005) and Longo *et al.*, (2019) confirms that the knot size and frequency, strongly influenced by crown architecture, are the primary defects driving downgrades in structural timber classification and modulus of elasticity. These findings collectively support the inclusion of wood quality traits, particularly branch-related variables, in selection indices for Douglas-fir.

The pronounced genetic effect observed at Aleșd may be attributed to its intermediate elevation, eutricambosoil, and moderate precipitation (≈ 72 mm/month), which together likely reduced environmental stress and allowed clearer expression of genetic variance in adaptive (SV) and wood quality traits (BA, DB). Such mesic site conditions are known to favour the detection of genetic differentiation by limiting phenotypic plasticity and environmental variation (Mátyás, 1996; St Clair *et al.*, 2005). In contrast, Făget, a lower and warmer site (10.4 °C) on luvisol, expressed some provenance effects (BA, DB), but also exhibits significant block-level heterogeneity, possibly due to local variability in soil properties or moisture availability, which can obscure genetic signals. At Padeș, the highest elevation site with the wettest growing season (≈ 81 mm/month), alternating periods of drought and excessive rainfall likely imposed stress conditions that reduced trait differentiation among provenances, with only BA showing a detectable genetic component. These patterns are consistent with findings that climatic extremes, particularly drought and precipitation variability, reduce variation expression in conifers (Depardieu *et al.*, 2020; Schueler *et al.*, 2021).

At the Aleșd trial, a positive correlation was found between BA and DB, confirming that flatter crowns tend to carry thicker branches. This relationship was only moderate in strength. Therefore, selecting provenances with smaller BA results in a substantial correlated reduction in knot size, accelerating saw-log grade improvement without incurring additional measurement costs. Osborne and Maguire (2016) modelled this relationship and highlighted the predictive value of BA and knot size. A moderate negative correlation emerged between BA and SV, indicating that wider and thicker branches are associated with reduced survival rates, likely due to increased mechanical stress or competition under dense stand conditions (Macdonald and Hubert, 2002). HT - DBH were correlated; however, neither growth trait showed a strong link to wood-quality traits, suggesting early vigour can be pursued without compromising branch architecture. Overall, the Aleșd trial supports two types of selection that could be applied: (1) indirect selection based on BA that will also bring an increase in the volume and wood quality, and (2) selection based on an index selection. Index selection refers to the use of a weighted combination of multiple traits to guide selection decisions, rather than relying on a single characteristic. The objectives appear to be compatible, and the provenance-level differentiation observed indicates that the genetic improvement across multiple traits is achievable through selection. These earlier studies applied multi-trait selection tools such as MGIDI and MTSI to identify stable, superior provenances in Romanian Douglas-fir populations (Stoica *et al.*, 2025), Norway spruce (Alexandru *et al.*, 2023), and European beech (Liepe *et al.*, 2024).

Făget trial presents a correlation pattern that reshapes breeding priorities compared with the other common garden experiments. HT-DBH remain positively correlated, showing a consistent phenotypic relationship between the two growth traits across provenance. By contrast, BA and DB are only weakly correlated. These low correlations mean that selecting provenances with BA less than 90° will lead to only a small, indirect reduction in knot size. This pattern differs from the Aleșd trial, where BA and DB showed a positive correlation, although the relationship was weak. A more consequential relationship is the moderate negative correlation between NB–DB. This suggests that provenances with fewer branches also tend to produce thinner ones, providing a second opportunity to reduce knot size without compromising overall crown density (Macdonald and Hubert, 2002). Based on this pattern, an effective selection index for Făget should assign equal weight to BA and DB for assessing wood quality, include NB as a secondary level for future quality improvement, and use HT or DBH as the primary driver of volume gains. Indirect selection based on BA is recommended, as it can lead to increased height growth (due to negative correlations) and improved wood quality (through thinner branches and smaller knots). In addition, selection can be applied using a selection index.

Padeș trial shows a distinctly different correlation pattern from the other two sites. The HT-DBH remains strongly correlated. However, the strong positive correlation between DBH-BA implies that gains in growth may be accompanied by an increase in knot size - unless branch traits are explicitly integrated into the selection index. Overall, a balanced multi-trait selection index that includes height, DBH and wood quality should be used in the breeding program.

Provenance-by-environment interactions further clarified the relative influence of genetic and site on the phenotypic expression of traits. The variance component analysis reveals distinct patterns of genetic and environmental control across Douglas-fir traits, with important implications for breeding programs and the transfer of forest reproductive materials.

Among all the studied traits, only two - BA and SV - are significantly influenced by the provenance. For DB, provenance accounts for 26% of total variance, indicating a moderate level of genetic control, suggesting that selecting based on origin could be beneficial for improving traits (Aitken and Bemmels, 2016; Milesi *et al.*, 2019; Schueler *et al.*, 2021). Survival shows even stronger provenance influence (23.3% of variance), suggesting the importance of seed source in ensuring persistence over time (Kerns *et al.*, 2020; Hankin *et al.*, 2023; Di Fabio *et al.*, 2024; Pedlar *et al.*, 2024). The remaining traits-SF, FI, BA, and NB-show non-significant provenance effects, which may reflect high environmental plasticity, strong within-provenance variation, or insufficient expression even at the age of 47 years in the Padeș trial.

The non-significant results for SF aligns with the natural tendency of Douglas-fir to develop straight stems and good form (Schermann *et al.*, 1977), potentially reducing detectable genetic variation in our 47-year-old common garden experiments compared to younger populations, where stem form defects are more pronounced (Temel and Adams, 2000)

Environmental effects dominate most traits, with highly significant variance for SF, FI, BA, and NB. Similar findings were reported by Temel and Adams (2000), who observed that the stem defects and crown traits in Douglas-fir showed substantial site-revealed variation, often masking genetic signals. Li *et al.* (2017) also find that environmental effects can account for up to 80% of total phenotypic variance in forest trees across common garden experiments, especially for form and branching. Similarly, a large-scale analysis of 22 Douglas-fir breeding programs confirmed that trunk defect traits are predominantly influenced by location, with site effects exceeding 60-70% of total variance (Magalska and Howe, 2014). SV also shows significant location effects (61.3% of variance), confirming that environmental stress is a major determinant of the variation. Only DB lacks significant location effects, suggesting this trait is relatively stable across environments. The sharp decline in survival between 18 and 47 years highlights the importance of long-term monitoring. At age 18, survival levels exceeded 64% at all sites, with a maximum of 81.20% at Făget (Moise Maria, 1998). By age 47, however, survival dropped to around 16-18% across trials. The Douglas-fir breeding program in Romania was discontinued more than two decades ago, leaving the suitability of provenances insufficiently validated under present conditions. In this context, the long-term provenance trials analyzed in our study and previously, together with earlier (Stoica *et al.*, 2025), represent the principal scientific foundation for developing recommendations on seed source selection adapted to Romanian forestry.

Significant P x M interaction appears only for BD, where interaction effects account for 26% of total variance. All other traits show non-significant interactions, suggesting that provenance rankings remain relatively stable across locations.

Overall, Douglas-fir breeding programs should focus mainly on testing different provenances to identify those with better survival rates and higher branch quality, defined as having fewer and thinner branches that minimize knot formation and enhance timber value. In our study, survival (SV) and branch-related traits-particularly branch angle (BA) and diameter (DB)-exhibited the strongest genetic control or most stable expression across environments, making them reliable targets for selection. Given the significant environmental influence observed for many growth traits, selecting provenances that combine resilience with favorable branching characteristics will enhance both stand persistence and timber quality in future plantations.

Conclusions

The analysis of long-term common garden experiments revealed significant genetic variation in survival and branch traits of Douglas-fir, particularly branch angle and diameter, suggesting these are reliable targets for selection across different environmental conditions. Site conditions were the primary driver of variation for traits such as stem form, forking index, and number of branches. Survival has changed with age, from 64-81% at age 18 to only 16-18% at age 47 across the three sites. These results demonstrate the value of testing multiple provenances under varying site conditions to identify genetic materials with consistent performance and highlight the potential for selecting resilient, high-quality planting stock. The findings underscore the importance of provenance choice in future breeding programs and suggest that survival and branching traits can support both timber quality and climate resilience in Douglas-fir plantations.

Authors' Contributions

Conceptualization: ES, AMA, GM and ALC; Formal analysis: ES; Methodology: ES; Map: ES; Supervision: GM and ALC; Project administration: GM; Funding acquisition: GM; Writing: ES, GM, ALC, and AMA.

All authors have read and agreed to the published version of the manuscript.

Ethical approval (for researches involving animals or humans)

Not applicable.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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Appendix

Table A1. Details about the tested Douglas fir provenances

Prov.	**Name of provenance**	**Country**	**Lat. N**	**Long. E**	**Altd. (m)**
1	Idaho (var. glauca)	SUA	48°00’	-116°95’	780
2	Idaho (var. glauca)	SUA	47°48’	-113°61’	1389
3	Idaho (var. glauca)	SUA	47°52’	-115°68	1356
4	Boise (var. galuca)	SUA, Idaho	44°00’	-115°00’	1829
5	El Dorado	SUA California	39°17’	-120°08’	1387
8	South End Pass	SUA, Wyoming	50°07’	-120°85’	900
9	Merrit	Canada, Columbia Britanică	50°04’	-120°51’	900
10	Franklin River	Canada, Columbia Britanică	49°06’	-124°46’	150
11	Duncan	Canada, Columbia Britanică	48°75’	-121°17’	450
12	Diablo Dam – Whatcom	SUA, Washington	48°72’	-121°17’	450
13	Skagit – Sedro Wooley	SUA, Washington	48°53’	-122°31’	60
14	Snohomish -Sloan Creek	SUA, Washington	48°08’	-121°18’	650
15	Jefferson – Hoh River	SUA, Washington	47°48’	-123°58’	240
16	Grays Harbour – Humptulips	SUA, Washington	47°19’	-123°54’	140
17	Kittias – Cle Elum	SUA, Washington	47°13’	-121°07’	640
18	Lewis – Packwood	SUA, Washington	46°34’	-121°42’	300
19	Pine Grove	SUA, Oregon	45°06’	-121°23’	730
20	Benton – Corvallis,	SUA, Oregon	44°42’	-121°23’	76
21	Marion Forks	SUA, Oregon	44°30’	-122°00’	1060
22	Lane – Oakridge	SUA, Oregon	43°54’	-122°22’	880
23	Rosenburg	SUA, Oregon	43°19’	-123°30’	280
24	Jakson – Ashland	SUA, Oregon	42°05’	-122°39’	1500
26	Siskiyou – Hawkinsville,	SUA, California	41°47’	-123°40’	1060
28	Chatcolet, S., (var. galuca)	Idaho, SUA	47°20’	-116°30’	700
29	Vancouver	Canada, Columbia Britanică	50°00’	-126°00’	150
30	Hoodsport	SUA, Washington	47°10’	-123°03’	300
31	Elma, Washington	SUA, Washington	47°00’	-123°30’	300
32	Pe Ell-Sand Creek, Mc. Donald	SUA, Washington	46°45’	-123°15’	200
33	Yacolt – Spotted Deernt – Battle G.	SUA, Washington	45°48’	-122°20’	600
34	Vicinity, Mineral Walker Road	SUA, Washington	46°40’	-12°15’	500
35	Darrington – Texas Pond	SUA, Washington	48°18’	-121°15’	280
36	Skycomish – Beckler Peak	SUA, Washington	47°42’	-121°20’	500
37	Concrete – Presentin Creek	SUA, Washington	48°30’	-121°20’	110
38	Oyster R.	Canada, Columbia Britanică	49°42’	-125°08’	400
39	Daun Ost – Abt. 39 A – Rezervație	Germania	50°12’	-06°50’	520
40	Daun Ost – Abt. 46 C.	Germania	50°11’	-06°52’	500
41	Prüm Süd – Abt. 79 C – Rezervație	Germania	50°13’	-06°25’	380
42	Wittlich West – Abt. 3B	Germania	49°47’	-06°54’	230
43	Wittlich West – Abt. 1B	Germania	49°47’	-06°55’	230
44	Manderscheid – Abt. 36 B2 – Rezervație	Germania	50°06’	-06°50’	400
45	Poinsat – Puy de Dome	Franța	46°04’	-02°43’	750
46	Les Farges III	Franța	45°32’	-02°07’	665
47	Moussans II	Franța	43°26’	-02°42’	750
49	Darrington III	SUA, Washington	48°10’	-121°40’	200
50	Clallam Contry – Louella	SUA, Washington	48°00’	-123°04’	330

51	Pinetan	Canada, Columbia Britanică	50°50'	-119°50'	830
52	Shuswape Lake	Canada, Columbia Britanică	50°50'	-119°20'	530
54	Morton Lake	Canada, Columbia Britanică	50°10'	-125°20'	150
55	Centre Creek – Chilliwack Valey	Canada, Columbia Britanică	49°07'	-121°30'	460
56	Devine – Dist.	Canada, Columbia Britanică	50°32'	-122°28'	380
57	Pădurea Neagră	România	47°03'	22°17'	500
58	Piatra Albă	România	47°01'	22°15'	580
59	Toplița	România	46°46'	22°20'	330
60	Aninoasa Mare	România	45°43'	22°15'	550
61	Vîrful Dăii	România	45°44'	22°13'	825
62	Vîrful Dăii	România	45°44'	22°13'	420
63	Nădrăgel	România	45°43'	22°13'	560
64	Anina – Buhui	România	45°10'	21°55'	650
65	Sedro Wooley	SUA, Washington	48°30'	-122°10'	720
66	Elbe	SUA, Washington	46°50'	-122°10'	720
67	Kelso	SUA, Washington	46°12'	-122°50'	609

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