Ann. For. Res. 68(2): 117-136, 2025
https://doi.org/10.15287/afr.2025.4311

ANNALS OF FOREST RESEARCH
www.afrjournal.org

Genetic parameters of *Abies alba* progenies from seed orchards and natural populations in Romania*

Georgeta Mihai[1]✉, Alin-Madalin Alexandru[1]✉, Paula Gârbacea[1], Emanuel Stoica[1,2], Virgil Scărlătescu[3]

Mihai G., Alexandru A.M., Gârbacea P., Stoica E., Scărlătescu V., 2025. Genetic parameters of *Abies alba* progenies from seed orchards and natural populations in Romania. Ann. For. Res. 68(2): 117-136.

Abstract A total of 204 silver fir open-pollinated families from four first-generation seed orchards and 12 natural stands were tested in a nursery experiment. The performances and genetic parameters of the seed orchards (SO) and natural populations progenies (NP) were determined and compared at ages from 3 to 6 years old. Several traits were assessed such as: the total height, the annual height increment, the root collar diameter, the branch length, the number of branches, and the bud burst evaluated during spring 2015-2016. On average, progenies derived from seed orchards outperformed those from natural stands, exhibiting 8–14% greater height and 4–6% greater diameter. Estimates of genetic variance components indicated that most of the variation was attributable to additive genetic effects. Total height and annual height increment showed the highest proportions of additive variance, ranging from 42 to 91% in NP progenies and from 41 to 78% in SO progenies. Narrow-sense individual heritability estimates were generally higher than those previously reported for silver fir, ranging from 0.12 to 0.83 for SO progenies and from 0.23 to 0.91 for NP progenies. Family heritability exceeded individual heritability in both progeny types investigated. Among the studied traits, total height exhibited the highest heritability for both progenies. Heritability of total height increased moderately from ages 3 to 6, whereas heritability for root collar diameter declined and remained relatively stable for branch-related traits. Phenotypic and genetic correlations between growth traits were relatively high, while those between bud burst and growth traits were positive and weak for both progenies. The correlations between growth traits and branch traits were positive but nonsignificant. A significant correlation was obtained between bud burst in 2016 and elevation of populations. The phenotypic correlations were higher than the genetic ones for both progenies. Genetic gain differed depending on the selection method, intensity, and traits examined. Across all selection methods, total height showed greater genetic gain than root collar diameter. Recurrent selections based on the parental genetic values will bring the greatest genetic gain in the next breeding generation. The genetic gains that could be achieved if the backwards selection will be used at the level of the first-generation seed orchards are between 19–27% for total height, 9–27% for diameter and 40–48% for current height increment. If the backward selection is used in natural populations, a genetic gain of 21–32% for total height, 13–22% for diameter and 42–55% for current height increment could be obtained. The results are discussed linking them to their implications for the development of a silver fir breeding strategy and also for the second-generation seed orchards establishment.

Keywords: silver fir, open-pollinated progenies, early testing, quantitative traits, genetic parameters.

Addresses: [1]Department of Forest Genetics and Tree Breeding, ”Marin Dracea” National Institute for Research and Development in Forestry, Voluntari, Ilfov, Romania. | [2]Faculty of Silviculture and Forest Engineering, Transilvania University of Brasov, Brasov, Romania. | [3]Mihăești Experimental Base, Pitești Research Station, ”Marin Dracea” National Institute for Research and Development in Forestry, Mihăești, Argeș, Romania.

✉ **Corresponding Author:** Georgeta Mihai (gmihai_2008@yahoo.com); Alin-Madalin Alexandru (alexandru.alin06@yahoo.com).

Manuscript: received April 6, 2025; revised October 29, 2025; accepted December 17, 2025.

---

* This article was presented in the framework of the IUFRO Seed Orchards Conference, Brasov (Romania), 20-24 May 2024.

Introduction

In the context of the ongoing and expected climate change, the growth and adaptive capability of economically important tree species have been frequently analyzed. It is unanimously accepted that to increase forest resilience and productivity under climate change, more effort is needed in the selection of more diverse and adapted forest reproductive material intended for the artificial regeneration activity.

European silver fir (*Abies alba* Mill.) continues to be a keystone forest species in Europe, which provides wood for the many economic sectors and more valuable ecosystem services. In Romania, silver fir covers 4% of the national forest area and about two-thirds of the distribution areas are in the Eastern Carpathians, which represents the edge of the species' natural distribution in Europe (Teodosiu et al. 2019).

Many studies indicate that silver fir is generally more resilient, compared with other coniferous species, to previous drought events and therefore could contribute to increase the forest's productivity across Europe under future climate changes (Lévesque et al. 2013, Tinner et al. 2013, Frank et al. 2017, Vitasse et al. 2019, Mihai et al. 2021). However, recent recordings have revealed trends of increasing frequency and severity of droughts in many regions of Europe, including Romania (Mihai et al. 2022, Ionita et al. 2025). In the face of the unprecedented fast warming climate and extreme drought events, reforestation success depends on the profound knowledge of the species' genetic variation of adaptive and growth traits. An understanding of the genetic variation of complex traits like growth and fitness is important for species adaptive evolution and forestry. Tree breeding combining field studies with innovative techniques, can maximize the capability of species to respond to new threats and can ensure the resilience of forest ecosystems for future generations.

In several European countries, national provenance tests were established to assess intraspecific genetic variation of silver fir, but the first significant step towards silver fir breeding was achieved only when the outcomes of the 1st The International Union of Forest Research Organizations (IUFRO) provenances experiment from 1982 became available (Larsen 1982). Later in 2005, the 2nd IUFRO silver fir provenance experiment was established in order to explore the genetic variation of southeastern European provenances (Tabel 2000).

In Romania, the genetic improvement of silver fir had started 45 years ago with the establishment of six provenance trials, one progeny trial and 11 clonal seed orchards (95 ha) from the qualified category. The first-generation of seed orchards comprises 550 vegetative copies of untested plus trees selected from 15 provenance regions across Romania. The main breeding objectives were to improve the wood production in future stands and to reduce vulnerability to environmental conditions. Currently, there is an increasing need to select high-quality forest reproductive materials for this species and the practical way to meet this need is to select superior genetic material at an early stage.

Despite the economic importance of silver fir, there is still a shortfall of results regarding genetic gain realized over the first cycle of selection (first-generation seed orchards) compared with unimproved material (natural populations). In general, limited information is available regarding the genetic variation of silver fir, and this come only from provenance studies (Korpel et al. 1982, Kranenborg 1994, Wolf 1994, Hansen & Larsen 2004, Ballian 2013, Kerr et al. 2015). There are also very few quantitative genetic studies regarding genetic parameters and inheritance of quantitative traits in silver fir (Mihai et al. 2014, Mihai & Mirancea 2016, Frank et al. 2017). Assessing the genetic parameters and their trend over time is very important to select the most efficient breeding strategy to advance to the next seed orchards generation.

Furthermore, for silver fir populations from the southeastern edge of the species range, this knowledge is even less. Marginal tree populations which grow at the edge of species distribution, like silver fir populations in the Romanian Carpathians, often develop specific mechanisms of adaptation, resulting in natural selection of some quantitative traits (Howe et al. 2003, Hampe & Petit 2005, Mátyás et al. 2009). Thus, the marginal populations can represent a valuable source of reproductive materials and a precious forest resource for breeding programs (Fady et al. 2016, Ducci & Donnelly 2017). In the context of climate change, the use of more adapted forest reproductive materials should be mandatory in artificial regeneration activity.

In 2010, in order to evaluate the breeding value of plus trees tested in the first-generation seed orchards and to establish the species breeding strategy, a progeny experiment based on 204 open pollinated families from four silver fir seed orchards and 12 natural populations was carried out. In our progeny experiment, we focused on evaluating the genetic variation and parameters for some characteristics important in species adaptation and breeding, such as phenology, growth, and habitus traits. The progeny tests are an essential tool in tree breeding programs that allow to explore the adaptability of different genotypes to the local environment, quantify the genetic parameters of traits important for selection, estimate the parental genetic values, to select the genetic material for the next breeding generation and the best-matching forest reproductive material for assisted migration. The early testing will allow to predict age-age correlations suitable for use in breeding, which will reduce testing time. The juvenile-adult correlations have both technical tree breeding and silviculture implications because they enable us to estimate early-age genetic gain, avoiding upward bias at optimum rotation age. Early testing, selection at different ages and juvenile–mature correlation are well documented in the literature (Lambeth 1980, Larsen & Wellendorf 1990, Hannerz et al. 1999).

The aim of this study was to: 1) evaluate the genetic variation among and within silver fir populations from the Romanian Carpathians for some quantitative traits at early stage in nursery, 2) estimate and compare the genetic parameters and inheritance of progenies from first-generation seed orchards and natural populations, 3) estimate the genetic and phenotypic correlations among traits, 4) calculate the expected genetic gain under different selection strategies for the two types of progenies, and 5) to make early selection of parental genotypes to advance to the second-generation seed orchards.

This study's findings can offer crucial guidance for the silver fir breeding programs in Romania and in Europe.

Materials and Methods

Genetic material and mating design

In autumn 2010, open-pollinated seeds were collected from four seed orchards (15 clones in each seed orchard) and 12 natural populations (15 trees in each population). The seed orchards are situated in the Avrig, Talisoara, Baia Sprie and Garcina forest districts. The clones involved in open–pollinated families represent the vegetative copies of the plus trees selected in the 1980^s in 6 forest districts from 6 provenance regions of silver fir in Romania. All seed orchards were isolated from foreign pollen. The natural populations were located throughout the Carpathian Chain, in 10 provenance regions, at altitudes between 690 to 1220 m (Fig. 1). All silver fir populations are native to the Romanian Carpathians.

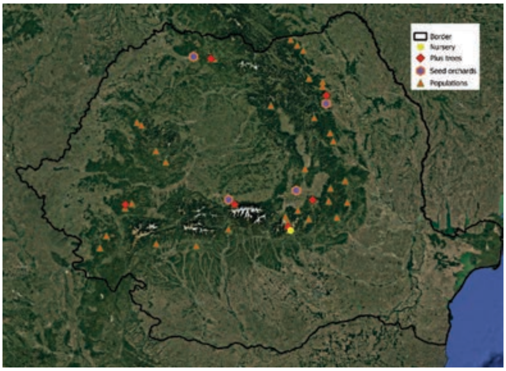


Figure 1 Locations of the silver fir genetic material and nursery experiment.

Nursery design and assessments

The open-pollinated seeds were sown in the Sinaia nursery in autumn 2010. Located at 695 m above sea level in the mountain beech zone, the nursery geographical coordinates are: 45° 29′N latitude, 25° 59′ E longitude. In spring 2013, seedlings resulted from 204 open-pollinated families were transplanted at a 10 x 10 cm distance between individuals in the nursery field. The nursery design was a randomized complete block design with three replications.

The assessed traits were: total height at the ages of 3 (2013), 4 (2014), 5 (2015) and 6 (2016) (HT3, HT4, HT5 and HT6, respectively); annual height increment (HI3, HI4, HI5 and HI6); root collar diameter (RCD3, RCD4, RCD5 and RCD6); branch length (BL3, BL4, BL5 and BL6); number of branches (NB3, NB4, NB5 and NB6), as well as bud burst in the spring of 2015 and 2016 (BB5 and BB6).

We evaluated bud phenology on terminal bud, twice in the spring of 2015 (on April 29th and May 5th) at five-year-old of seedlings and four times in the spring of 2016 (between April 14th and May 19th) at six-year-old of seedlings, using a scoring system, from 1 to 5, where: 1 = unbroken bud and 5 = completely open and fully elongated needles (Ducci et al. 2012). Based on the mean value, the families were classified as early flushing (BB=5) and late flushing (BB=1). All phenological evaluations were made in a single day.

In each open-pollinated family, ten seedlings/plot in each of the three repetitions were measured for quantitative traits and 12 seedlings/plot in each of the three repetitions for bud burst assessments.

Statistical analysis

The statistical analysis was based on individual seedling measurements using the following mathematical model (Nanson 2004 —Eq. 1):

$$Ykijlm = \mu + Rk + Pl + Bi + Fj + FBji + eijklm \qquad (1)$$

where:

Ykijlm = performance of the mth seedling in the kth provenance region, the lth population, the jth family and the ith repetition; μ = overall mean; Rk = effect of the kth provenance region; Pl = effect of the lth population; Bi = effect of the ith repetition; Fj = effect of the jth family; FBji = interaction of the jth family and ith repetition; and ekijlm = random error associated with kijlmth seedlings.

Homogeneity-of-variance assumptions were checked with SPSS (version 20) before analyzing the field data. We visually inspected residual-vs.-predicted plots to verify variance homogeneity; normality of errors was not assessed because it does not affect variance-component estimates (Hallauer & Miranda 1981). Variance components for each trait were estimated with the GLM procedure, in the SPSS version 20, treating every effect as random except the provenance region (fixed); and the expected mean squares were finally computed in R (R core team, Version 3.5.1, 2018).

The open-pollinated seeds used in this experiment were collected from four seed orchards composed of clones from different regions and from different natural mature stands. Many studies in conifers have highlighted that open pollination is a mixture of self and outcrossed zygotes, and the proportion of seeds which originate from selfing varies widely among individual trees and among species. Studies carried out in silver fir populations demonstrate that the percentage of self-fertilization varied between 8 to 54% being an important component of its mating system (Kormutak & Lindgren 1997). Parducci et al. (1996) used allozyme markers in ten natural populations from Italy, and showed a deficiency of heterozygotes, concluding that the partial inbreeding due to restricted pollen could be responsible for this result. Teodosiu et al. (2019), based on seven nuclear microsatellites markers, found values for the inbreeding coefficient between -0.072 to 0.081 ($p<0.001$) for 35 populations from the Romanian Carpathians.

Treating open-pollinated families as pure half-sibs would set $\sigma^2_F = \frac{1}{4}\sigma^2 A$, but we allowed for 30% selfing by applying a coefficient of 2.5 rather than 4 (Squillace 1974), preventing upward bias in variance components and derived genetic parameters (Eq. 2):

$$\sigma^2_A = 2.5\,\sigma^2_F \tag{2}$$

where σ^2_A = additive genetic variance and σ^2_F = family variance.

The narrow-sense individual (h^2_i) and half-sib family heritabilities (h^2_{HS}) were calculated by the following formulas (Nanson 2004—Eqs. 3 and 4):

$$h^2_i = \sigma^2_A / \sigma^2_{Ph1} = 2.5\sigma^2_F / (\sigma^2_F + \sigma^2_{FB} + \sigma^2_e) \tag{3}$$

$$h^2_{HS} = \sigma^2_F / \sigma^2_{Ph2} = \sigma^2_F / (\sigma^2_F + \sigma^2_{FB}/r + \sigma^2_w/m) \tag{4}$$

where σ^2_{Ph1} and σ^2_{Ph2} = phenotypic variances; σ^2_A = additive genetic variance; σ^2_F = family variance; σ^2_{FB} = family × repetition interaction variance; σ^2_e = error variance, $\sigma^2_e = \sigma^2_p + \sigma^2_w / n$; σ^2_p = variance among plots; σ^2_w = within-plot variance; n = number of seedlings per plot; and r = number of repetitions.

Heritability standard errors were approximated using Delta's method (Lynch & Walsh 1998).

The genetic gains were calculated both at the individual ($\Delta G1$, $\Delta G3$) and family levels ($\Delta G2$) for different breeding strategies: forward selection ($\Delta G1$, $\Delta G2$) and backward selection ($\Delta G3$) (Falconer & Mackay 1996):

$$\Delta G1 = ih^2_i\,\sigma^2_{Ph1}$$

$$\Delta G2 = ih^2_{HS}\,\sigma^2_{Ph2}$$

$$\Delta G3 = 2ih^2_{HS}\,\sigma^2_{Ph2}$$

To compare the level of additive genetic variance in each trait independent of their means, we computed the additive genetic coefficient of variation (CVA, %) as described by Cornelius (1994):

$$CVA = (\sigma^2_A / \mu)\ 100$$

Pearson's correlations based on family means and genetic correlations were also calculated to examine correlations among traits. Genetic correlations were derived as the ratio of the additive genetic covariance between traits X and Y, and the square root of the product of their respective additive genetic variances (Falconer & Mackay 1996).

Results

Genetic variation and performance of open-pollinated progenies

The analysis of variance for growth traits, branch traits and bud burst for progenies from the seed orchards and populations is shown in Tables 1 and 2. Highly significant differences among open- pollinated families within seed orchards and populations were found for all studied traits ($p < 0.001$). The effect of provenance region and population were very significant for all traits. Also, the seed orchard effect was significant and reflected the composition of the clones as well as the location of the orchard.

Table 1 Analysis of variance for quantitative traits of silver fir open-pollinated progenies from seed orchards.

Source of variation	DF	Variance (s^2)							
		HT3	HT4	HT5	HT6	HI3	HI4	HI5	HI6
Region of provenance	5	122.19***	381.43***	625.71***	2833.15***	27.56***	168.59***	229.51***	1083.78***
Seed orchard	3	270.27***	3755.78***	19897.80***	36010.51***	75.24***	2334.38***	5998.09***	3860.04***
Family (F)	59	43.71***	129.78***	354.04***	1015.24***	7.41***	60.39***	141.30***	334.17***
Repetition (B)	2	3.46	36.62**	200.58***	387.00**	5.97**	17.82**	39.10*	105.83*
Interaction F x B	118	9.80	19.01	48.19	122.68	1.26	6.48	15.48	43.37
Error	1620	3.36	6.98	23.56	62.28	1.01	3.36	10.56	26.60

Source of variation	DF	Variance (s^2)							
		RCD3	RCD4	RCD5	RCD6	BL3	BL4	BL5	BL6
Region of provenance	9	15.20***	51.88***	34.48***	44.88***	77.67***	89.38***	144.26***	363.12***
Seed orchard	11	53.40***	177.30***	133.63***	79.44***	196.24***	1070.69***	2649.51***	1033.38***
Family (F)	143	3.60***	12.44***	9.64***	10.26***	15.51***	34.17***	71.26***	119.61***
Repetition (B)	2	1.17**	5.18***	1.51	62.80***	15.05***	109.26***	16.44	67.43**
Interaction F x B	286	0.40	1.16	2.36	5.11	2.72	3.89	7.98	11.71
Error	3887	0.19	0.77	1.80	3.06	1.63	2.57	5.74	10.97

Source of variation	DF	Variance (s^2)									
		NB3	NB4	NB5	NB6	BB5-1	BB5-2	BB6-1	BB6-2	BB6-3	BB6-4
Region of provenance	5	11.41***	7.94***	17.11***	13.14***	5.79***	11.69***	13.42***	12.20***	22.13***	10.78***
Seed orchard	3	21.39***	22.12***	53.27***	40.87***	-	-	-	-	-	-
Family (F)	59	2.47***	2.50***	4.65***	5.32***	1.67***	2.82***	3.83***	3.98***	5.42***	2.50***
Repetition (B)	2	2.18**	0.16	0.66	0.40	2.39*	14.98***	0.01	0.12	0.75	2.74**
Interaction F x B	118	0.41	0.46	0.50	0.78	0.06	0.20	0.01	0.07	0.12	0.08
Error	1620	0.34	0.37	0.46	0.74	0.54	1.14	0.16	0.48	0.637	0.42

Table 2 Analysis of variance for quantitative traits of silver fir open-pollinated progenies from natural populations.

Source of variation	DF	Variance (s^2)							
		HT3	HT4	HT5	HT6	HI3	HI4	HI5	HI6
Region of provenance	9	295.90***	978.66***	2458.33***	6757.73***	60.55***	260.67***	563.37***	1921.01***
Provenance	11	212.49***	849.41***	2071.30***	5653.00***	51.64***	245.16***	483.36***	1698.30***
Family (F)	143	38.27***	126.87***	399.57***	994.72***	7.26***	54.32***	123.88***	284.09***
Repetition (B)	2	3.79	5.99	13.93	99.42	0.51	0.27	6.59	39.85
Interaction F	286	6.59	12.32	30.54	100.80	1.42	5.21	13.04	50.01
Error	3887	2.86	6.65	20.41	68.76	0.83	3.23	9.20	37.11

Source of variation	DF	Variance (s^2)							
		RCD3	RCD4	RCD5	RCD6	BL3	BL4	BL5	BL6
Region of provenance	9	6.93***	36.72***	42.85***	56.16***	101.51***	261.83***	231.12***	723.25***
Provenance	11	6.51***	35.06***	43.34***	49.20***	99.69***	236.14***	229.37***	603.11***
Family (F)	143	1.75***	7.27***	8.86***	10.64***	14.56***	43.62***	54.79***	114.73***
Repetition (B)	2	0.04	0.74	14.64***	3.36	10.36***	16.98**	24.93**	38.56*
Interaction F	286	0.35	1.13	3.45	2.72	2.10	3.93	6.90	12.49
Error	3887	0.17	0.68	1.59	2.39	1.47	3.06	4.19	9.64

Source of variation	DF	Variance (s^2)									
		NB3	NB4	NB5	NB6	BB5-1	BB5-2	BB6-1	BB6-2	BB6-3	BB6-4
Region of provenance	9	7.01***	4.53***	6.91***	43.54***	42.33***	71.88***	12.84***	59.33***	53.96***	12.65***
Provenance	11	5.99***	8.65***	5.66***	37.24***	-	-	-	-	-	-
Family (F)	143	1.74***	1.83***	2.76***	5.31***	4.39***	10.19***	2.56***	8.72***	7.96***	4.28***
Repetition (B)	2	0.26	0.74	0.18	1.23	5.06***	38.45***	0.13	0.15	1.70*	9.39***
Interaction F x R	286	0.30	0.32	0.72	0.64	0.11	0.20	0.03	0.08	0.10	0.16
Error	3887	0.24	0.28	0.53	0.60	0.54	1.06	0.17	0.44	0.57	0.58

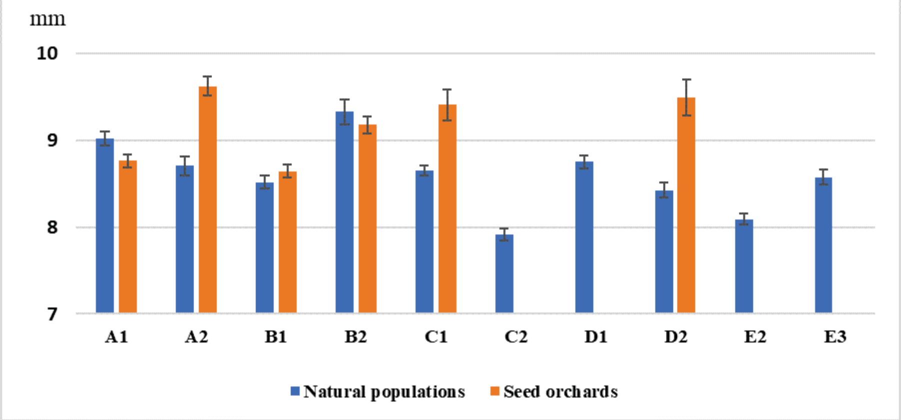


Figure 2 The variation of the total height at 6 years old of the seed orchards and natural populations progenies on provenances regions.

A1: Eastern Carpathians, western cline; A2: Eastern Carpathians, eastern cline; B1: Brașov depression; B2: Curvature Carpathians, outer cline; C1: Southern Carpathians, northern cline; C2: Southern Carpathians, southern cline; D1: Mehedinți/ Cerna/ Semenic Mountains; D2: Țarcu/ Poiana Ruscă Mountains; E2: Western Apuseni Mountains; E3: Eastern Apuseni Mountains.

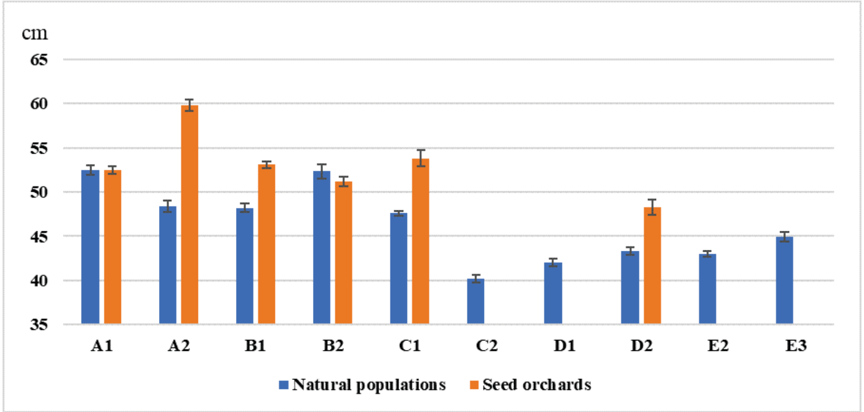


Figure 3 The variation of the root collar diameter at 6 years old of the seed orchards and natural populations progenies on provenances regions.

A1: Eastern Carpathians, western cline; A2: Eastern Carpathians, eastern cline; B1: Brașov depression; B2: Curvature Carpathians, outer cline; C1: Southern Carpathians, northern cline; C2: Southern Carpathians, southern cline; D1: Mehedinți/ Cerna/ Semenic Mountains; D2: Țarcu/ Poiana Ruscă Mountains; E2: Western Apuseni Mountains; E3: Eastern Apuseni Mountains.

Therefore, the SO families which exhibited the best growth traits at 6 years old were from the provenance region A2 - Eastern Carpathians (eastern cline), while the poorly performing families were from the provenance regions D2 - Tarcu/ Poiana Rusca Mountains for HT6 and B1 - Brașov Depression for RCD6 (Figs. 2 and 3).

The best SO families for RCD6 were 12 from Sinaia, 3 from Rusca Montana and 53, 54, 57 and 60 from Varatec (Fig. 4). The families 12 and 3 obtained poor performances regarding HT6, while families 53, 54 and 57 had a very good performance in terms of HT6 and HI6. The weakest growth performances were obtained the families 1, 2 and 3 originated from the Avrig and Rusca Montana forest districts.

For HT6, the best performing SO families were 53 and 52 from Sinaia, 54, 55, 56 and 51 from Varatec (Fig. 5). The lowest values for HT6 were obtained by families 12, 10 and 13 from Sinaia, and families 3 and 4 from Rusca Montana. The differences between the top-ranking SO families (53 for HT6, respectively 12 for RCD6) and the mean on experiment show an increase in total height by 34% and in root collar diameter by 23%. Growth performances in Garcina seed orchard located in the warmer climate and Avrig - the southernmost seed orchard, were higher compared with the other orchards.

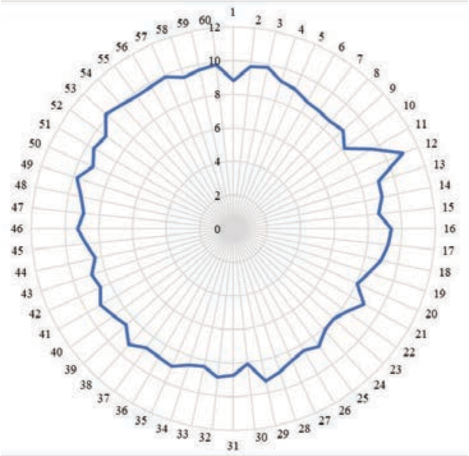


Figure 4 Variation of the root collar diameter for families from seed orchards.

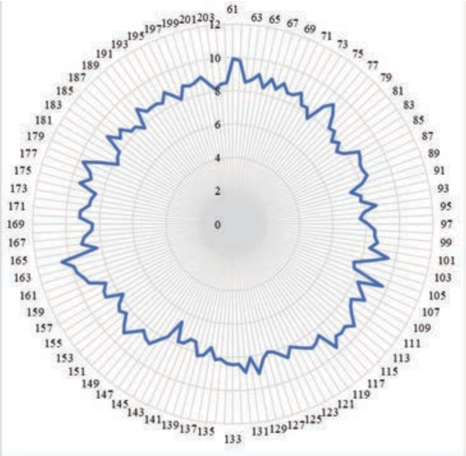


Figure 6 Variation of the root collar diameter for families from natural populations.

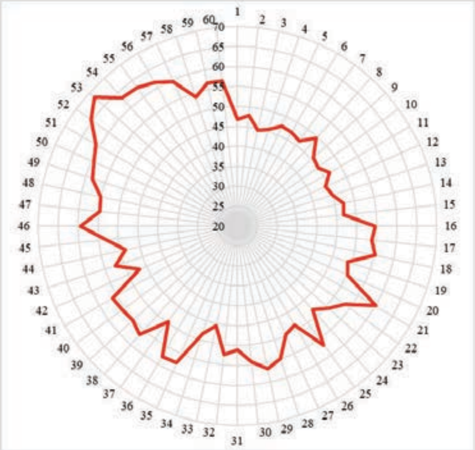


Figure 5 Variation of the total height for families from seed orchards.

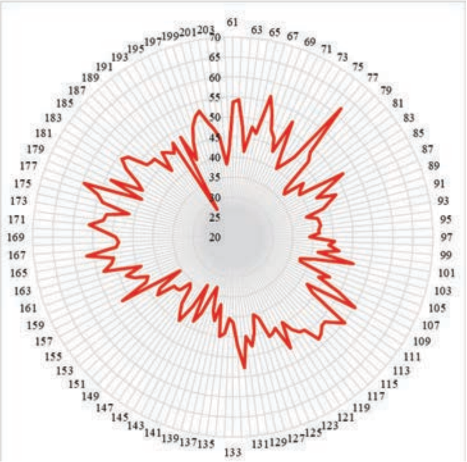


Figure 7 Variation of the total height for families from natural populations.

Regarding the families from natural populations, the best growth performances at 6 years old were exhibited by those from the provenance region A1 - Eastern Carpathians (western cline) and B2 - Curvature Carpathians, while the weakest performances obtained families from the provenance region C2 - Southern Carpathians (Fig. 2 and 3).

The best-performing families regarding HT6 were 77 from Marginea, 177, 171 and 176 from Strambu Baiut and 67, 62 and 61 from Avrig forest districts, while for RCD6 were the families 164 and 163 from Strambu Baiut, 61 and 62 from Avrig, and some families from Anina, Comandau and Rusca Montana forest districts. The weakest growth performances were obtained by some families from the Cozia forest district (Figs. 6 and 7).

The differences between the top-ranking families from natural populations (77 for HT6, respectively 164 for RCD6) and the mean on experiment show an increase in total height by 26% and in root collar diameter by 19%.

When all the data were analyzed together, the differences between families from seed orchards and natural populations were very significant for the growth traits. On average, SO progenies obtained an increase in HT6 between 11 to 22% compared with NP progenies, while for RCD6 the results were highly similar.

Differences among SO families regarding bud flushing were also highly significant in both years assessed. In particular, in 2015, bud flushing evaluation started on April 29 (BB5-1), when 68% of seedlings had their buds in stage 2 and 24% in stage 3, and only 7% of them were unbroken. In 2016, bud flushing evaluation started on 14 April 14th (BB6-1), when 43% of seedlings had their buds in stage 2 and 57% were unbroken. In both years, the earliest families observed were from those the Avrig seed orchard, originating from Avrig and Rusca Montana forest districts. It must be pointed out that all families from Avrig and Rusca Montana, regardless of which seed orchards they were tested in, were the earliest flushing. The latest flushing families come from Garcina seed orchard, having their origin at Varatec and Sinaia forest districts.

Also, very significant differences for BB5 and BB6 have been obtained among regions of provenance for both progenies. The genetic variation within and among natural populations regarding bud burst in 2015-2016 was highly significant, too. The ranking of the different families was quite stable, as indicated by the genetic coefficients of correlations between mean values of phenological scores in 2015-2016. The earliest flushing populations observed were Rusca Montana, Avrig and Marginea while the latest ones were Remeti, Bicaz and Dobra populations. The largest difference was found between the families from Avrig and Rusca Montana populations, located in the Southern Carpathians, and the one from Remeti situated in the Western Carpathians.

Estimates of variance components, heritability, and genetic coefficients of variation

For SO progenies, the variance component estimates are listed in Table 3. The results indicated that the contribution of additive genetic variance (σ^2_A) to the total phenotypic variance (σ^2_{Ph}) varied between 12% for RCD6 and 77% for BB6-1. Among quantitative traits, total height generally had the largest values of additive genetic variance, while the smallest values were obtained for the number of branches. Regarding the growth traits, the additive genetic variance was greater for height than for root collar diameter, ranging from 55–78% for height and 12–83% for diameter. For the analyzed period, the additive genetic variance of RCD decreased with age, increased for HT and HI, and was relatively stable for the branch traits.

The level of genetic variation for each trait was revealed by the additive genetic coefficient of variation (CVA), which ranged from 7 to 35%, depending on the trait. The current height increment had the highest CVA values, while root collar diameter presented the lowest values.

The level of phenotypic variation was calculated by phenotypic coefficients of variation (CV). The CV values were lower than CVA for all traits, but the variation trend was consistent with CVA. Thus, the most variable trait according to CV values was current height increment, while the least variable was root collar diameter. Except for root collar diameter, CVA and CV increased steadily with age for every trait. The variance components for NP progenies are presented in Table 4. The contribution of additive genetic variance (σ^2_A) to the total phenotypic variance (σ^2_{Ph}) varied between 23% for RCD5 and 91% for HT5. Generally, total height had the largest values of additive genetic variance, ranging from 62–91%, while the smallest values were obtained for the number of branches, between 28-51%. Among growth traits, total height recorded greater additive genetic variance compared with root collar diameter. A decreasing trend with age of the additive genetic variance was observed for root collar diameter only, while for the rest of the traits, a certain stability over time was reported.

Table 3 Genetic parameters for studied traits at different ages for silver fir open-pollinated progenies from seed .orchards.

Traits	Mean	CV	CVA	σ^2_A		σ^2_{Ph}	h^2_{HS}		h^2_i	
HT3	13.56 ±0.15	8.83	12.41	2.83	(55)	5.14	0.78	± 0.15	0.55	± 0.03
HT4	21.50 ±0.27	9.59	14.13	9.23	(78)	11.87	0.85	± 0.18	0.78	± 0.03
HT5	36.08 ±0.44	9.44	13.99	25.49	(70)	36.22	0.86	± 0.17	0.70	± 0.03
HT6	52.91 ±0.74	10.90	16.30	74.38	(76)	98.07	0.88	± 0.18	0.76	± 0.03
RCD3	3.17 ±0.04	10.84	16.39	0.27	(83)	0.32	0.89	± 0.19	0.83	± 0.03
RCD4	5.74 ±0.08	11.13	16.89	0.94	(79)	1.18	0.91	± 0.19	0.79	± 0.03
RCD5	7.48 ±0.07	7.52	10.44	0.61	(29)	2.10	0.75	± 0.10	0.29	± 0.02
RCD6	9.12 ±0.07	6.42	7.19	0.43	(12)	3.44	0.50	± 0.06	0.12	± 0.01
HI3	2.87 ±0.06	17.23	24.87	0.51	(41)	1.24	0.83	± 0.12	0.41	± 0.02
HI4	7.29 ±0.18	19.31	29.08	4.49	(82)	5.47	0.89	± 0.19	0.82	± 0.03
HI5	13.16 ±0.28	16.36	24.62	10.49	(69)	15.25	0.89	± 0.17	0.69	± 0.03
HI6	16.83 ±0.43	19.66	29.25	24.23	(64)	37.97	0.87	± 0.16	0.64	± 0.03
BL3	5.45 ±0.09	13.09	18.98	1.07	(49)	2.17	0.82	± 0.14	0.49	± 0.03
BL4	8.33 ±0.14	12.71	19.07	2.52	(68)	3.71	0.89	± 0.17	0.68	± 0.03
BL5	12.73 ±0.20	12.01	18.03	5.27	(65)	8.07	0.89	± 0.17	0.65	± 0.03
BL6	14.67 ±0.26	13.49	20.44	8.99	(61)	14.64	0.90	± 0.16	0.61	± 0.03
BN3	1.55 ±0.04	17.67	26.53	0.17	(41)	0.42	0.83	± 0.12	0.41	± 0.02
BN4	1.91 ±0.04	15.01	21.62	0.17	(38)	0.44	0.81	± 0.12	0.38	± 0.02
BN5	2.59 ±0.05	15.09	22.86	0.35	(57)	0.61	0.89	± 0.15	0.57	± 0.03
BN6	2.30 ±0.05	18.21	26.84	0.38	(43)	0.88	0.86	± 0.13	0.43	± 0.02
BB5-1	2.18 ±0.03	10.18	15.25	0.11	(18)	0.62	0.61	± 0.08	0.18	± 0.01
BB5-2	3.86 ±0.04	7.72	10.99	0.18	(14)	1.29	0.56	± 0.07	0.14	± 0.01
BB6-1	1.45 ±0.04	21.87	25.61	0.27	(47)	0.27	0.93	± 0.23	0.97	± 0.04
BB6-2	3.02 ±0.04	10.61	17.21	0.27	(44)	0.62	0.81	± 0.14	0.44	± 0.02
BB6-3	3.66 ±0.05	10.11	16.61	0.37	(44)	0.83	0.82	± 0.14	0.44	± 0.02
BB6-4	4.69 ±0.03	5.66	8.80	0.17	(32)	0.52	0.76	± 0.11	0.32	± 0.02

Note: Proportion of additive genetic variance in phenotypic variance are given in brackets, CV phenotypic coefficient of variation, CVA additive genetic coefficient of variation, σ^2_A additive genetic variance, σ^2_{Ph} phenotypic variance, h^2_i narrow-sense individual heritability, h^2_{HS} half-sib family heritability

Table 4 Genetic parameters for studied traits at different ages for silver fir open-pollinated progenies from natural populations.

Traits	Mean	CV	CVA	σ^2_A		σ^2_{Ph}	h^2_{HS}		h^2_i	
HT3	12.51 ±0.09	9.00	12.99	2.64	(62)	4.28	0.83	± 0.10	0.62	±0.02
HT4	18.77 ±0.17	10.92	16.47	9.55	(87)	11.03	0.90	±0.13	0.87	±0.02
HT5	31.24 ±0.30	11.64	17.75	30.75	(91)	33.72	0.92	±0.13	0.91	±0.02
HT6	45.88 ±0.48	12.51	18.81	74.49	(73)	101.76	0.90	±0.11	0.73	±0.02
RCD3	2.98 ±0.02	8.09	11.63	0.12	(50)	0.23	0.80	±0.09	0.50	±0.02
RCD4	5.42 ±0.04	9.05	13.18	0.51	(55)	0.93	0.84	±0.10	0.55	±0.02
RCD5	7.03 ±0.05	7.71	9.55	0.45	(23)	1.96	0.61	±0.06	0.23	±0.01
RCD6	8.55 ±0.05	6.95	9.51	0.66	(25)	2.68	0.74	±0.06	0.25	±0.01
HI3	2.64 ±0.04	18.57	26.51	0.49	(45)	1.08	0.80	±0.08	0.45	±0.02
HI4	6.26 ±0.11	21.42	32.31	4.09	(81)	5.07	0.90	±0.12	0.81	±0.02
HI5	10.84 ±0.17	18.68	28.04	9.24	(70)	13.28	0.89	±0.11	0.70	±0.02
HI6	14.65 ±0.26	20.94	30.16	19.51	(42)	46.20	0.82	±0.08	0.42	±0.01
BL3	4.87 ±0.06	14.25	20.92	1.04	(53)	1.95	0.86	±0.09	0.53	±0.02
BL4	7.62 ±0.10	15.76	23.88	3.31	(74)	4.47	0.91	±0.12	0.74	±0.02
BL5	11.29 ±0.11	11.92	17.69	3.99	(66)	6.06	0.87	±0.11	0.66	±0.02
BL6	14.19 ±0.16	13.73	20.57	8.52	(64)	13.33	0.89	±0.11	0.64	±0.02
BN3	1.35 ± 0.02	17.20	25.58	0.12	(41)	0.29	0.83	±0.08	0.41	±0.01
BN4	1.49 ± 0.02	16.32	24.25	0.13	(37)	0.34	0.82	±0.07	0.37	±0.01
BN5	2.69 ± 0.03	11.19	15.30	0.17	(28)	0.62	0.74	±0.06	0.28	±0.01
BN6	2.18 ± 0.04	19.99	28.66	0.39	(51)	0.76	0.88	±0.09	0.51	±0.02
BB5-1	2.20 ± 0.03	15.12	23.58	0.27	(40)	0.68	0.82	±0.08	0.40	±0.02
BB5-2	3.66 ± 0.04	14.41	21.88	0.64	(46)	1.39	0.84	±0.09	0.46	±0.02
BB6-1	1.31 ± 0.02	20.61	31.95	0.18	(70)	0.25	0.89	±0.12	0.70	±0.02
BB6-2	2.87 ± 0.04	16.97	27.01	0.60	(84)	0.71	0.91	±0.13	0.84	±0.02
BB6-3	3.42 ± 0.04	13.78	21.59	0.55	(66)	0.82	0.88	±0.11	0.66	±0.02
BB6-4	4.51 ± 0.03	7.69	11.88	0.29	(39)	0.73	0.80	±0.08	0.39	±0.01

The additive genetic coefficient of variation ranged from 9.51 for RCD6 to 32.31 for HI4. The CV values were lower than CVA for all traits, ranging from 6.95 for RCD6 to 21.42 for HI4. For both CVA and CV, HI recorded the largest values, while RCD reported the lowest values.

The heritability coefficients for the SO progenies are listed in Table 3. The estimates of the narrow-sense individual heritability ranged from 0.12 for RCD6 to 0.97 for BB6-1. The family heritability ranged from 0.50 to 0.93 for RCD6 and BB6-1, respectively. The values of family heritability were higher compared with the individual heritability. In particular, the highest values of heritability were obtained for total height (between 0.55 - 0.78 for h^2_i and 0.78 - 0.89 for h^2_{HS}) and the lowest values for root collar diameter (between 0.12 - 0.83 for h^2_i and 0.50 - 0.91 for h^2_{HS}). Also, bud burst and branch traits showed high heritability values that indicate strong genetic control.

The heritability coefficients for the NP progenies are listed in Table 4. The narrow-sense individual heritability ranged from 0.23 for RCD5 to 0.91

for HT5. The family heritability ranged from 0.61 to 0.92 for RCD6 and BB6-1, respectively. The values of family heritability were higher compared with the individual heritability. The highest values of heritability were obtained for total height (between 0.62–0.91 for h^2_i and 0.83-0.92 for h^2_{HS}) and the weakest values for root collar diameter (between 0.23-0.55 for h^2_i and 0.61-0.84 for h^2_{HS}. Bud burst and branch traits showed very high values for both heritabilities.

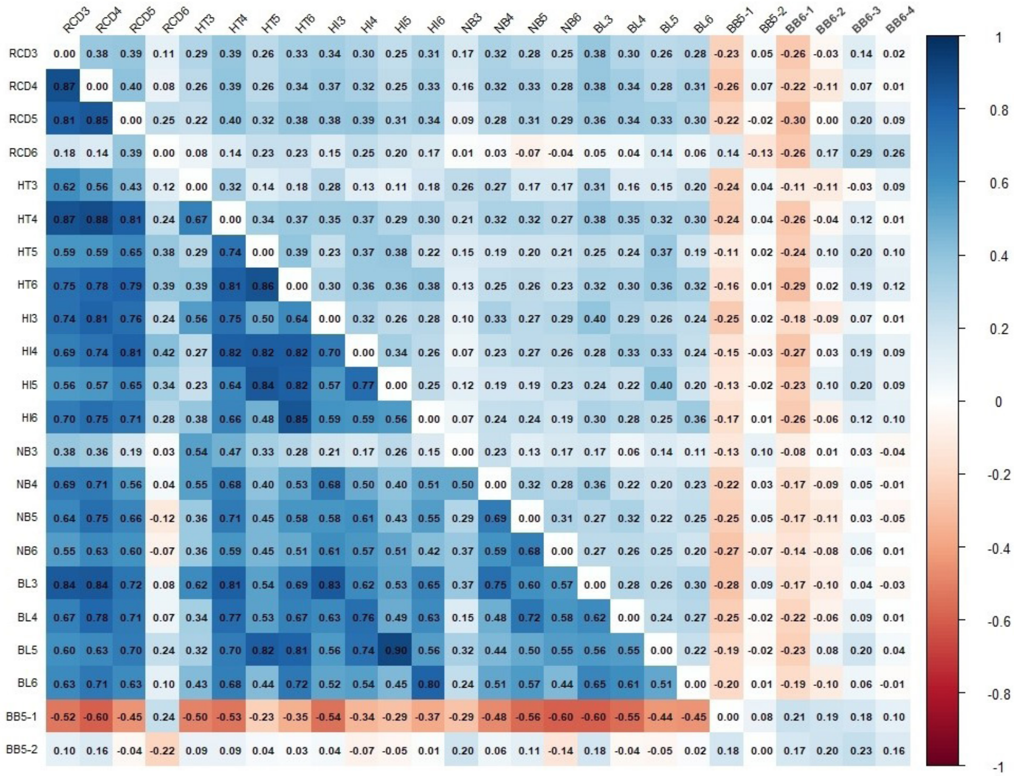
For both progenies, a decreasing trend over the analyzed period was observed related to growth traits, while for branch traits, a stability was noticed.

Genetic and phenotypic correlations

Genetic and phenotypic correlations between analyzed traits for the SO progenies are shown in Table 5. The genetic correlations between growth traits during the measurement period were all positive and, with a few exceptions, significant. Positive and significant genetic correlations were obtained among branch traits and between these and growth traits. Few genetic correlations were obtained between bud burst and growth or branch traits. Positive and significant genetic correlations were obtained between bud burst evaluated in the two consecutive years (2015, 2016).

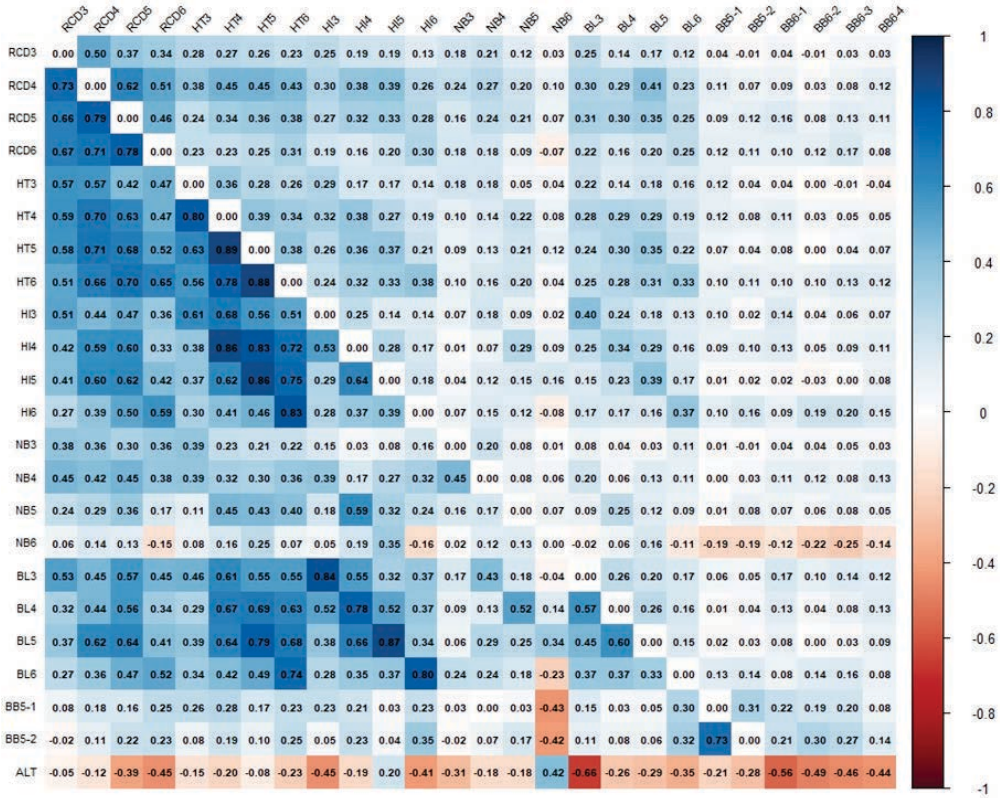
At the NP progenies level, the genetic and phenotypic correlations between analyzed traits are presented in Table 6. Positive and very significant genetic correlations were obtained among growth traits and between these and branch traits. Also, branches number was positively and significantly corelated with branch length. Few genetic correlations were obtained between bud burst and the rest of analyzed traits. The genetic correlations between bud burst evaluated in the two consecutive years were positive and significant.

Table 5 Trait-trait genetic (above line) and phenotypic correlations (below line) for silver fir open-pollinated progenies from seed orchards.



	RCD3	RCD4	RCD5	RCD6	HT3	HT4	HT5	HT6	HI3	HI4	HI5	HI6	NB3	NB4	NB5	NB6	BL3	BL4	BL5	BL6	BB5-1	BB5-2	BB6-1	BB6-2	BB6-3	BB6-4
RCD3	0.00	0.38	0.39	0.11	0.29	0.39	0.26	0.33	0.34	0.30	0.25	0.31	0.17	0.32	0.28	0.25	0.38	0.30	0.26	0.28	-0.23	0.05	-0.26	-0.03	0.14	0.02
RCD4	0.87	0.00	0.40	0.08	0.26	0.39	0.26	0.34	0.37	0.32	0.25	0.33	0.16	0.32	0.33	0.28	0.38	0.34	0.28	0.31	-0.26	0.07	-0.22	-0.11	0.07	0.01
RCD5	0.81	0.85	0.00	0.25	0.22	0.40	0.32	0.38	0.38	0.39	0.31	0.34	0.09	0.28	0.31	0.29	0.36	0.34	0.33	0.30	-0.22	-0.02	-0.30	0.00	0.20	0.09
RCD6	0.18	0.14	0.39	0.00	0.08	0.14	0.23	0.23	0.15	0.25	0.20	0.17	0.01	0.03	-0.07	-0.04	0.05	0.04	0.14	0.06	0.14	-0.13	-0.26	0.17	0.29	0.26
HT3	0.62	0.56	0.43	0.12	0.00	0.32	0.14	0.18	0.28	0.13	0.11	0.18	0.26	0.27	0.17	0.17	0.31	0.16	0.15	0.20	-0.24	0.04	-0.11	-0.11	-0.03	0.09
HT4	0.87	0.88	0.81	0.24	0.67	0.00	0.34	0.37	0.35	0.37	0.29	0.30	0.21	0.32	0.32	0.27	0.38	0.35	0.32	0.30	-0.24	0.04	-0.26	-0.04	0.12	0.01
HT5	0.59	0.59	0.65	0.38	0.29	0.74	0.00	0.39	0.23	0.37	0.38	0.22	0.15	0.19	0.20	0.21	0.25	0.24	0.37	0.19	-0.11	0.02	-0.24	0.10	0.20	0.10
HT6	0.75	0.78	0.79	0.39	0.39	0.81	0.86	0.00	0.30	0.36	0.36	0.38	0.13	0.25	0.26	0.23	0.32	0.30	0.36	0.32	-0.16	0.01	-0.29	0.02	0.19	0.12
HI3	0.74	0.81	0.76	0.24	0.56	0.75	0.50	0.64	0.00	0.32	0.26	0.28	0.10	0.33	0.27	0.29	0.40	0.29	0.26	0.24	-0.25	0.02	-0.18	-0.09	0.07	0.01
HI4	0.69	0.74	0.81	0.42	0.27	0.82	0.82	0.82	0.70	0.00	0.34	0.26	0.07	0.23	0.27	0.26	0.28	0.33	0.33	0.24	-0.15	-0.03	-0.27	0.03	0.19	0.09
HI5	0.56	0.57	0.65	0.34	0.23	0.64	0.84	0.82	0.57	0.77	0.00	0.25	0.12	0.19	0.19	0.23	0.24	0.22	0.40	0.20	-0.13	-0.02	-0.23	0.10	0.20	0.09
HI6	0.70	0.75	0.71	0.28	0.38	0.66	0.48	0.85	0.59	0.59	0.56	0.00	0.07	0.24	0.24	0.19	0.30	0.28	0.25	0.36	-0.17	0.01	-0.26	-0.06	0.12	0.10
NB3	0.38	0.36	0.19	0.03	0.54	0.47	0.33	0.28	0.21	0.17	0.26	0.15	0.00	0.23	0.13	0.17	0.17	0.06	0.14	0.11	-0.13	0.10	-0.08	0.01	0.03	-0.04
NB4	0.69	0.71	0.56	0.04	0.55	0.68	0.40	0.53	0.68	0.50	0.40	0.51	0.50	0.00	0.32	0.28	0.36	0.22	0.20	0.23	-0.22	0.03	-0.17	-0.09	0.05	-0.01
NB5	0.64	0.75	0.66	-0.12	0.36	0.71	0.45	0.58	0.58	0.61	0.43	0.55	0.29	0.69	0.00	0.31	0.27	0.32	0.22	0.25	-0.25	0.05	-0.17	-0.11	0.03	-0.05
NB6	0.55	0.63	0.60	-0.07	0.36	0.59	0.45	0.51	0.61	0.57	0.51	0.42	0.37	0.59	0.68	0.00	0.27	0.26	0.25	0.20	-0.27	-0.07	-0.14	-0.08	0.06	0.01
BL3	0.84	0.84	0.72	0.08	0.62	0.81	0.54	0.69	0.83	0.62	0.53	0.65	0.37	0.75	0.60	0.57	0.00	0.28	0.26	0.30	-0.28	0.09	-0.17	-0.10	0.04	-0.03
BL4	0.67	0.78	0.71	0.07	0.34	0.77	0.53	0.67	0.63	0.76	0.49	0.63	0.15	0.48	0.72	0.58	0.62	0.00	0.24	0.27	-0.25	-0.02	-0.22	-0.06	0.09	0.01
BL5	0.60	0.63	0.70	0.24	0.32	0.70	0.82	0.81	0.56	0.74	0.90	0.56	0.32	0.44	0.50	0.55	0.56	0.55	0.00	0.22	-0.19	-0.02	-0.23	0.08	0.20	0.04
BL6	0.63	0.71	0.63	0.10	0.43	0.68	0.44	0.72	0.52	0.54	0.45	0.80	0.24	0.51	0.57	0.44	0.65	0.61	0.51	0.00	-0.20	0.01	-0.19	-0.10	0.06	-0.01
BB5-1	-0.52	-0.60	-0.45	0.24	-0.50	-0.53	-0.23	-0.35	-0.54	-0.34	-0.29	-0.37	-0.29	-0.48	-0.56	-0.60	-0.60	-0.55	-0.44	-0.45	0.00	0.08	0.21	0.19	0.18	0.10
BB5-2	0.10	0.16	-0.04	-0.22	0.09	0.09	0.04	0.03	0.04	-0.07	-0.05	0.01	0.20	0.06	0.11	-0.14	0.18	-0.04	-0.05	0.02	0.18	0.00	0.17	0.20	0.23	0.16

Table 6 Trait-trait genetic (above line) and phenotypic correlations (below line) for silver fir open-pollinated progenies from natural populations.



	RCD3	RCD4	RCD5	RCD6	HT3	HT4	HT5	HT6	HI3	HI4	HI5	HI6	NB3	NB4	NB5	NB6	BL3	BL4	BL5	BL6	BB5-1	BB5-2	BB6-1	BB6-2	BB6-3	BB6-4
RCD3	0.00	0.50	0.37	0.34	0.28	0.27	0.26	0.23	0.25	0.19	0.19	0.13	0.18	0.21	0.12	0.03	0.25	0.14	0.17	0.12	0.04	-0.01	0.04	-0.01	0.03	0.03
RCD4	0.73	0.00	0.62	0.51	0.38	0.45	0.45	0.43	0.30	0.38	0.39	0.26	0.24	0.27	0.20	0.10	0.30	0.29	0.41	0.23	0.11	0.07	0.09	0.03	0.08	0.12
RCD5	0.66	0.79	0.00	0.46	0.24	0.34	0.36	0.38	0.27	0.32	0.33	0.28	0.16	0.24	0.21	0.07	0.31	0.30	0.35	0.25	0.09	0.12	0.16	0.08	0.13	0.11
RCD6	0.67	0.71	0.78	0.00	0.23	0.23	0.25	0.31	0.19	0.16	0.20	0.30	0.18	0.18	0.09	-0.07	0.22	0.16	0.20	0.25	0.12	0.11	0.10	0.12	0.17	0.08
HT3	0.57	0.57	0.42	0.47	0.00	0.36	0.28	0.26	0.29	0.17	0.17	0.14	0.18	0.18	0.05	0.04	0.22	0.14	0.18	0.16	0.12	0.04	0.04	0.00	-0.01	-0.04
HT4	0.59	0.70	0.63	0.47	0.80	0.00	0.39	0.34	0.32	0.38	0.27	0.19	0.10	0.14	0.22	0.08	0.28	0.29	0.29	0.19	0.12	0.08	0.11	0.03	0.05	0.05
HT5	0.58	0.71	0.68	0.52	0.63	0.89	0.00	0.38	0.26	0.36	0.37	0.21	0.09	0.13	0.21	0.12	0.24	0.30	0.35	0.22	0.07	0.04	0.08	0.00	0.04	0.07
HT6	0.51	0.66	0.70	0.65	0.56	0.78	0.88	0.00	0.24	0.32	0.33	0.38	0.10	0.16	0.20	0.04	0.25	0.28	0.31	0.33	0.10	0.11	0.10	0.10	0.13	0.12
HI3	0.51	0.44	0.47	0.36	0.61	0.68	0.56	0.51	0.00	0.25	0.14	0.14	0.07	0.18	0.09	0.02	0.40	0.24	0.18	0.13	0.10	0.02	0.14	0.04	0.06	0.07
HI4	0.42	0.59	0.60	0.33	0.38	0.86	0.83	0.72	0.53	0.00	0.28	0.17	0.01	0.07	0.29	0.09	0.25	0.34	0.29	0.16	0.09	0.10	0.13	0.05	0.09	0.11
HI5	0.41	0.60	0.62	0.42	0.37	0.62	0.86	0.75	0.29	0.64	0.00	0.18	0.04	0.12	0.15	0.16	0.15	0.23	0.39	0.17	0.01	0.02	0.02	-0.03	0.00	0.08
HI6	0.27	0.39	0.50	0.59	0.30	0.41	0.46	0.83	0.28	0.37	0.39	0.00	0.07	0.15	0.12	-0.08	0.17	0.17	0.16	0.37	0.10	0.16	0.09	0.19	0.20	0.15
NB3	0.38	0.36	0.30	0.36	0.39	0.23	0.21	0.22	0.15	0.03	0.08	0.16	0.00	0.20	0.08	0.01	0.08	0.04	0.03	0.11	0.01	-0.01	0.04	0.04	0.05	0.03
NB4	0.45	0.42	0.45	0.38	0.39	0.32	0.30	0.36	0.39	0.17	0.27	0.32	0.45	0.00	0.08	0.06	0.20	0.06	0.13	0.11	0.00	0.03	0.11	0.12	0.08	0.13
NB5	0.24	0.29	0.36	0.17	0.11	0.45	0.43	0.40	0.18	0.59	0.32	0.24	0.16	0.17	0.00	0.07	0.09	0.25	0.12	0.09	0.01	0.08	0.07	0.06	0.08	0.05
NB6	0.06	0.14	0.13	-0.15	0.08	0.16	0.25	0.07	0.05	0.19	0.35	-0.16	0.02	0.12	0.13	0.00	-0.02	0.06	0.16	-0.11	-0.19	-0.19	-0.12	-0.22	-0.25	-0.14
BL3	0.53	0.45	0.57	0.45	0.46	0.61	0.55	0.55	0.84	0.55	0.32	0.37	0.17	0.43	0.18	-0.04	0.00	0.26	0.20	0.17	0.06	0.05	0.17	0.10	0.14	0.12
BL4	0.32	0.44	0.56	0.34	0.29	0.67	0.69	0.63	0.52	0.78	0.52	0.37	0.09	0.13	0.52	0.14	0.57	0.00	0.26	0.16	0.01	0.04	0.13	0.04	0.08	0.13
BL5	0.37	0.62	0.64	0.41	0.39	0.64	0.79	0.68	0.38	0.66	0.87	0.34	0.06	0.29	0.25	0.34	0.45	0.60	0.00	0.15	0.02	0.03	0.08	0.00	0.03	0.09
BL6	0.27	0.36	0.47	0.52	0.34	0.42	0.49	0.74	0.28	0.35	0.37	0.80	0.24	0.24	0.18	-0.23	0.37	0.37	0.33	0.00	0.13	0.14	0.08	0.14	0.16	0.08
BB5-1	0.08	0.18	0.16	0.25	0.26	0.28	0.17	0.23	0.23	0.21	0.03	0.23	0.03	0.00	0.03	-0.43	0.15	0.03	0.05	0.30	0.00	0.31	0.22	0.19	0.20	0.08
BB5-2	-0.02	0.11	0.22	0.23	0.08	0.19	0.10	0.25	0.05	0.23	0.04	0.35	-0.02	0.07	0.17	-0.42	0.11	0.08	0.06	0.32	0.73	0.00	0.21	0.30	0.27	0.14
ALT	-0.05	-0.12	-0.39	-0.45	-0.15	-0.20	-0.08	-0.23	-0.45	-0.19	0.20	-0.41	-0.31	-0.18	-0.18	0.42	-0.66	-0.26	-0.29	-0.35	-0.21	-0.28	-0.56	-0.49	-0.46	-0.44

Phenotypic correlations were also very significant and stronger than genetic correlations. Growth traits were strongly and positively intercorrelated, as were growth and branch traits; bud flushing was also positively and significantly associated with growth traits. The branch numbers and branch lengths were positively correlated with all traits, except some correlations with the phenology evaluations.

Genetic gain

The genetic gain was calculated as the deviation (%) from population means only for the growth traits, in all years investigated.

For SO progenies, the genetic gain was higher for current height increment and root collar diameter, while for NP progenies, the genetic gain was higher for current height increment and total height (Tables 7 and 8).

In the case of SO progenies, the genetic gain from individual mass selection was higher than the genetic gain from broad sense family selection. In contrast, for NP progenies, the genetic gain from broad sense family selection was higher than the genetic gain based on individual mass selection. For both types of progenies, selection of the best individuals within families brought the highest genetic gain for growth traits.

If the backward selection is used and 20% of the best parents from first-generation seed orchards are mated, a genetic gain of 19 - 27% for total height, 9 - 27% for diameter, and 40 - 48% for current height increment could be achieved.

If the backward selection is used in natural populations and 20% of the best parents are mated, a genetic gain of 21 - 32% for total height, 13 - 22% for diameter and 42 - 55% for current height increment could be achieved.

Selecting at an older stage for total height resulted in a higher genetic gain than if the selection was done at an early stage. In contrast, for root collar diameter, the maximum genetic gains were obtained at the early stage; the differences between the two-year-old and six-year-old were from 5 to 7 times greater, and were larger for SO progenies than for NP progenies.

Table 7 Genetic gain (%) by selection of the best families, individuals, and parents for silver fir open-pollinated progenies from seed orchards.

Character	Family		Individual		Individuals within families			Parents
	10%	20%	5%	10%	5%	10%	20%	20%
HT3	12	12	12	8	17	15	12	19
HT4	14	11	17	11	23	21	17	23
HT5	14	11	16	10	21	20	16	23
HT6	17	13	19	12	26	24	19	27
RCD3	17	13	20	13	27	25	20	27
RCD4	17	14	20	13	28	25	20	28
RCD5	10	8	7	5	10	9	8	16
RCD6	5	4	3	2	5	4	3	9
HI3	25	20	21	14	29	27	22	40
HI4	30	24	35	23	48	44	36	48
HI5	25	20	27	18	37	34	28	40
HI6	30	24	31	21	43	39	32	47
BL3	19	15	18	12	24	22	18	30
BL4	19	16	21	14	29	26	21	31
BL5	18	15	19	13	27	24	20	30
BL6	21	17	21	14	29	27	22	34
BN3	26	21	23	15	31	28	23	42
BN4	21	17	18	12	24	22	18	34
BN5	23	19	23	15	31	29	23	37
BN6	27	22	24	16	32	30	24	43

Table 8 Genetic gain (%) by selection of the best families, individuals, and parents for silver fir open-pollinated progenies from natural populations.

Character	Family		Individual		Individuals within families			Genitors
	10%	20%	5%	10%	5%	10%	20%	20%
HT3	13	11	7	2	19	17	14	21
HT4	18	14	11	3	28	26	21	28
HT5	19	15	12	3	31	28	23	30
HT6	20	16	12	3	29	27	22	32
RCD3	11	9	6	2	15	14	11	18
RCD4	14	11	7	2	18	16	13	22
RCD5	8	7	3	1	8	8	6	13
RCD6	9	7	3	1	9	8	6	15
HI3	27	21	13	3	32	30	24	42
HI4	34	27	21	4	53	49	39	55
HI5	30	24	17	3	43	39	32	47
HI6	31	24	14	3	36	33	27	49
BL3	22	17	11	3	28	26	21	34
BL4	25	20	15	3	38	34	28	41
BL5	19	15	11	3	26	24	19	29
BL6	22	17	12	3	30	28	22	35
BN3	26	17	11	3	28	26	21	41
BN4	24	19	11	3	27	24	20	39
BN5	15	12	6	2	15	13	11	23
BN6	30	24	15	3	37	34	28	48

Discussion

We studied within and among genetic population variation of silver fir from two types of open pollinated progenies, obtained from four seed orchards and 12 natural populations, for growth, branch traits and bud burst at the early stage in the nursery. Results revealed high genetic variation at all levels, including provenance regions, populations, seed orchards and families of silver fir for all studied traits.

Because early selection has an important role in tree breeding, genetic parameters have been calculated for both types of open-pollinated progenies, and the outcomes revealed obvious differences between them. Phenotypic variance and CVA for NP progenies were higher than those of SO progenies. The CVA, which expresses in percentage the level of genetic variation, revealed, in general, medium magnitude for the analyzed traits. Estimates of genetic variance components have indicated that most of the variance associated with studied traits was additive. In particular, the additive genetic variance for NP families was higher for all traits compared with SO families, except for RCD. The traits that have the highest percent of additive variance were HT and HI, ranging from 42 to 91% for NP families and from 41 to 78% for SO families. Our results show a higher percentage of additive variance compared with those reported by Frank et al. (2017) for silver fir populations from Central Europe (24% for heigh and 26% for diameter).

Furthermore, our results are in agreement with other studies that highlight higher within-population variation in growth traits of forest species (Ekberg et al. 1985, Chmura et al. 2012, Skrøppa & Steffenrem 2019, Losch et al. 2025). Remarkable variation within populations of silver fir was also reported by Korpel et al. (1982), Paule (1986) and Sagnard et al. (2002).

The results from this study suggest that a genetic gain can be obtained making the selection based on these traits in the breeding program. The high magnitude of variation within populations makes individual selection more significant than mass selection.

Substantial genetic variation among families and high inheritance were highlighted for the number and length of branches. In general, there are few studies that investigated the inheritance of these traits of tree species, which are very important for stem quality (Magnussen & Yeatman 1987b, Lambeth & Huber 1997, Weng et al. 2017). The values over 0.8 for family heritability and over 0.4 for individual heritability obtained in this study are very encouraging for both genetic selection and breeding.

In addition, large variations were found in this study in bud burst of the silver fir open pollinated progenies. The contribution of additive genetic variance to the total phenotypic variance was between 14 to 47 for SO progenies and 39 to 84 for NP progenies. Observations of bud burst in our study were correlated across years, and the rank of bud burst scores among families remained generally stable in the two years, which suggests strong genetic control. Genetic variation among SO progenies was smaller compared with the NP progenies. The results can be explained by the large geographic variation of the sampled populations, located in different geographic regions from the Romanian Carpathians at variable altitudes ranging between 690 to 1220 meters. The difference between the earliest flushing families and the latest one was 2 days in the case of families from seed orchards and 4 days for families from populations.

A distinct geographic pattern was observed for bud burst at progenies level. The earliest SO families were those from Avrig and Rusca Montana forest districts, regardless of which seed orchards they were tested in. The earliest flushing populations were also Avrig, Rusca Montana and Marginea, located at the lowest altitudes while the latest flushing populations were the Remeti, Bicaz and Dobra and some families originating from Varatec and Sinaia, located at higher altitudes of the tested populations.

A strong correlation was obtained between bud burst in 2016 and elevation of populations (r = -0.560, p < 0:05). Low elevation populations showed earlier flushing than populations from higher elevations. Seedling growth in the nursery test declined linearly with the altitude of seed origin, as shown by the negative correlations obtained.

Variation in bud burst phenology associated with the geographical distribution of tested progenies was noted for many tree species. Numerous studies have shown that provenances of tree species from low altitude flush first (Worrall 1983 for *Abies amabilis*, Beuker 1994 for *Pinus sylvestris* and *Picea abies*, Lavadinovic et al. 2013 for Douglas fir, Sagnard et al. 2002 for silver fir). Other studies have shown that provenances from more continental / harsher climate flush early compared to those originating from milder climates (Chmura 2006, Skrøppa & Steffenrem 2019). This pattern is attributed to natural selection locally favoring fitter phenotypes—and the genotypes that produce them.

The narrow-sense individual heritability that quantifies the inheritance that can be transmitted to the next generation presented, in general, elevated values: from 0.12 to 0.83 for SO progenies and from 0.23 to 0.91 for NP progenies. Only RCD5 for NP progenies and RCD6 for SO progenies presented the lowest values for narrow-sense individual heritability (0.23 and 0.12). The results can be explained by the fact that the quantitative traits like RCD are under strong environment influence at this age. The family heritability was higher than the individual heritability for both progenies types. These high heritability estimates may be slightly inflated by maternal effects (considering the young age of the seedlings), common nursery environments, and dominance effects arising from inbreeding. In general, the values of family heritability for NP and SO progenies were very close. The trait that presented the greatest magnitude for the heritability was HT, suggesting the use of this character for selection. The high individual- and family-level heritabilities indicate a sufficient chance of success when using different selection methods in the breeding program.

The estimates of family heritability were consistent with those obtained by Frank et al. (2017), which found values for family heritability between 0.99 to 0.73 for growth traits and 0.42 to 0.57 for bud burst. The same authors found values for individual heritabilities of 0.13 to 0.33 for growth traits and 0.25 to 0.35 for bud burst. In Bulgaria, the individual heritability and family heritability of height growth at ten years old were 0.20 and 0.24, respectively (Evtimov et al. 2002). Therefore, individual heritabilities in our study were generally higher than those published earlier for silver fir. Also, outcomes of our study for family heritabilities are consistent with other similar studies on conifers at the same age. For example, Hannerz et al. (1999) reported values of family heritability for *Picea abies* between 0.34 to 0.60 for four-year height and 0.75 to 0.78 for bud burst. For *Picea glauca*, the family heritability for three-year-height was 0.82 to 0.91, 0.55 to 0.87 for diameter and 0.44 to 0.83 for bud flushing, while individual heritability varied between 0.54 to 0.78, 0.22 to 0.61 and 0.30 to 0.46 for the same traits (Rweyongeza et al. 2010).

For both progeny types, the heritability of height increased moderately from age 3 to 6, declined for root collar diameter and remained stable for branch traits. The age-related trend seen here in heritability of growth traits has also been observed in other species such as *Pinus taeda* L. (Xiang et al. 2003a), *Pinus sylvestris* and *Picea abies* (Kroon et al. 2011) and *Pinus koraiensis* (Lee et al. 2024).

Phenotypic and genetic correlations between growth traits showed relatively higher values for both progenies. The phenotypic correlations were in both cases higher than the genetic ones. Correlations between bud burst and growth traits were positive and weak, indicating that seedlings with relatively earlier bud burst showed stronger growth than late bud-bursting ones. The correlations between growth traits and branch traits were positive but nonsignificant, suggesting that some families could have small and thin branches. Little information is still available in the literature about correlations between branch and growth traits. Similar results were obtained by Weng et al. (2017) for *Pinus banksiana* and by Wu et al. (2013) for *Eucalyptus* clones.

According to results from this study, the SO progenies performed significantly better than NP progenies in all years of measurement. The performances of seedlings obtained from the first-generation seed orchards were, on average, between 8–14% superior in height and 4–6% superior in diameter compared to seedlings from natural stands, at ages between 3 and 6 years old. For both SO and NP progenies, the best growth performance at 6 years old was obtained by the families of plus trees originating from the Eastern Carpathians.

Comparable results were recorded for *P. abies* in Sweden, where seedlings from first-generation untested seed orchards outperformed unselected material of the same provenance by roughly 10 % (Rosvall et al. 2002). Also, Lundströmer et al. (2020) indicated that trees from *P. abies* seed orchards had 9 to 15% greater growth with respect to tree height and diameter in comparison to trees from Swedish local unimproved stands. The genetic gain achieved in the second-generation seed orchards of *P. sylvestris* is between 10 - 25%, while for *P. abies* it is between 10 - 15%, and for the third generation it is estimated at 25% (Prescher, 2007). Samuel & Johnstone (1997) found that Scots pine seedlings obtained from the first-generation seed orchards in the United Kingdom were 8–12% superior in height and 0–3% superior in stem form compared to unimproved seedlings from registered stands, at age 10 years. In the southern USA, the loblolly pine (*P. taeda* L.) genetically improved trees from the first-generation seed orchards have produced 7-12% more volume per hectare at harvest than trees from natural stands. For the second-generation seed orchards of loblolly pine, the same authors estimated gains in rotation volume ranging from 13% to 21% (Li et al. 1999).

Genetic gain varied depending on the selection method, the intensity and the traits considered across all methods. For each method, total height had a higher genetic gain than root-collar diameter. Recurrent selections for general combining ability or the parental genetic values can be used successfully and will bring the greatest genetic gain in the next breeding generation. Additionally, selecting the most performing individuals within the best families (forward selection) will result in a significant genetic gain.

Conclusions

This study reveals large genetic variation for growth, branch traits and spring phenology at provenance regions, populations, seed orchards and open-pollinated progenies levels, information which can be used in the silver fir breeding program and forest regeneration work. Furthermore, outcomes of this work, highlighted high heritability for the studied traits and supported the strategy based on recurrent selection in the progeny tests at the juvenile age. Early selection will significantly reduce the time required for breeding and will also produce large genetic gain in the next breeding generation.

The higher growth performances obtained by progenies from the first-generation seed orchards compared with progenies from natural stands, and large values of both individual and family heritability, lead to the conclusion that selection based on the progenies from the first-generation seed orchards can bring reasonable gains in the breeding programs.

In conclusion, the findings of the present study enriched the knowledge on quantitative genetic parameters of silver fir and are also crucial in order to establish suitable breeding and conservation strategies for this species under climate change conditions.

Conflict of interest

The authors declare no financial or personal interests that could influence the work presented in this paper.

Acknowledgements

This work was supported by a grant of the Ministry of Research, Innovation and Digitization, CNCS/ CCCDI - UEFISCDI, project number PN-IV-P8-8.1-PRE-HE-ORG-2025-0276, within PNCDI IV, and through the project Nucleu Programme FORCLIMSOC-PN23090303 (2023–2026), contracted with the National Institute for Research and Development in Forestry “Marin Drăcea”.

References

Ballian D., 2013. Genetic overload of silver fir (*Abies alba* Mill.) from five populations from central Bosnia and Herzegovina. Folia Forestalia Polonica 55 (2): 49-5.

Beuker E., 1994. Adaptation to climatic changes of the timing of bud burst in populations of *Pinus sylvestris* L. and *Picea abies* (L.) Karst. Tree Physiology 14: 961-970. https://doi.org/10.1093/treephys/14.7-8-9.961.

Chmura D.J., 2006. Phenology differs among Norway spruce populations in relation to local variation in altitude of maternal stands in the Beskidy Mountains. New Forests 32: 21–31. https://doi.org/10.1007/s11056-005-3390-2.

Chmura D.J., Rozkowski R., Chałupka W., 2012. Growth and phenology variation in progeny of Scots pine seed orchards and commercial seed stands. European Journal of Forest Research 131: 1229-1243. https://doi.org/10.1007/s10342-012-0594-9.

Cornelius J., 1994. Heritabilities and additive genetic coefficients of variation in forest trees. Canadian Journal of Forest Research 24: 372-379.

Ducci F., De Cuyper B., Pâques L.E., Proietti R., Wolf H., 2012. Reference protocols for assessment of trait and reference genotypes to be used as standards in international research projects. Ed. CRA SEL – Arezzo, Italy, pp 82.

Ducci F., Donnelly K., 2017. Forest tree Marginal Populations in Europe. Annals of Silvicultural Research 41 (3): 1-12. https://doi.org/10.12899/asr-1586.

Ekberg I., Eriksson G., Weng Y., 1985. Between- and within-population variation in growth rhythm and plant height in four *Picea abies* populations. Studia Forestalia Suecica 167.

Evtimov I., Gagov V., Zhelev P., 2002. Results of progeny experiments with silver fir in Bulgaria. University of Forestry, Sofia, 1756.

Fady B., Aravanopoulos F.A., Alizoti P., Mátyás C., von Wühlisch G., Westergren M., Belletti P., Cvjetkovic B., Ducci F., Huber G., et al., 2016. Evolution-based approach needed for the conservation and silviculture of peripheral forest tree populations. Forest Ecology and Management. 375, 66-75. https://doi.org/10.1016/j.foreco.2016.05.015.

Falconer D.S., Mackay T.F.C., 1996. Introduction to quantitative genetics. 4th edn. Longman and Co, Harlow, pp 360.

Frank A., Sperisen C., Howe G.T., Brang P., Walthert L., St. Clair J.B., Heiri C., 2017. Distinct genecological patterns in seedlings of Norway spruce and silver fir from a mountainous landscape. Ecology, 98 (1): 211-227. https://doi.org/10.1002/ecy.1632.

Hallauer A.R., Miranda J.B.,1981. Quantitative genetics in maize breeding. Iowa state University Press, Ames, pp 468.

Hampe A., Petit R.J., 2005. Conserving biodiversity under climate change: the rear edge maters. Ecology Letters 8: 461-467. https://doi.org/10.1111/j.1461-0248.2005.00739.x.

Hannerz M., Sonesson J., Ekberg I., 1999. Genetic correlations between growth and growth rhythm observed in a short-term test and performance in long-term field trials of Norway spruce. Canadian Journal of Forest Research. 29: 768-778.

Hansen J.K., Larsen J.B., 2004. European silver fir (*Abies alba* Mill.) provenances from Calabria, southern Italy: 15-year results from Danish provenance field trials. European Journal of Forest Research 123: 127-138. https://doi.org/10.1007/s10342-004-0031-9.

Howe G.T., Aitken S.N., Neale D.B., Jermstad K.D., Wheeler N.C., Chen T.H.H., 2003. From genotype to phenotype: unraveling the complexities of cold adaptation in forest trees. Canadian Journal of Botany 81: 1247-1266. https://doi.org/10.1139/b03-141.

Ionita M., Antonescu B., Roibu C., Nagavciuc V., 2025. Drought's Grip on Romania: A Tale of Two Indices. International Journal of Climatology 45:e8876. https://doi.org/10.1002/joc.8876.

Kerr G., Stokes V., Peace A., Jinks R., 2015. Effects of provenance on the survival, growth and stem form of European silver fir (*Abies alba* Mill.) in Britain. European Journal of Forest Research, 134: 349-363. https://doi.org/10.1007/s10342-014-0856-9.

Kormutak A., Lindgren D., 1997. Mating system and empty seeds in *Abies alba*. Forest Genetics, 3(4): 231-235.

Korpel S., Paule L., Laffers A., 1982. Genetics and breeding of the silver fir (*Abies alba* Mill). Annales Forestales 9(5), 151-184.

Kranenborg K.G., 1994. *Abies alba* provenance research in the Netherlands. 7 IUFRO-Tannensymposium, Deutschland, 369-381.

Kroon J., Ericsson T., Jansson G., Andersson B., 2011. Patterns of genetic parameters for height in field genetic tests of *Picea abies* and *Pinus sylvestris* in Sweden. Tree Genetics & Genomes 7: 1099-1111. https://doi.org/10.1007/s11295-011-0398-y.

Lambeth C.C., 1980. Juvenile–mature correlations in Pinaceae and implications for early selection. Forest Science 26: 571-580.

Lambeth C.C., Dudley A.H., 1997. Inheritance of branching and crown traits and their relationship to growth rate in loblolly pine. Tree Improvement and Genetics, Southern Forest Tree Improvement Conference, 1997.

Larsen J.B., 1982. Provenienzen und Versuchsteilnehmer des IUFRO-Weißtannen-provenienzversuches von 1982. Schriften aus der Forstlichen Fakultät der Universität Göttingen und der Niedersächsischen Forstlichen Versuchsanstalt 80: 239-241.

Larsen J.B., Wellendorf H., 1990. Early test in *Picea abies* full sibs by applying gas exchange, frost resistance and growth measurements. Scandinavian Journal of Forest Research 5: 369-380. https://doi.org/10.1080/02827589009382620.

Lavadinović V., Isajev V., Rakonjac L., Popović V., Lučić A., 2013. Douglas-fir provenance phenology observations. Ekológia (Bratislava) 32 (4): 376-382. https://doi.org/10.2478/eko-2013-0035.

Lee K., Oh Ch., Kim I.S., 2024. Genetic parameter changes and age-age correlations in *Pinus koraiensis* growth over 40-year progeny testing. BMC Plant Biology 24: 86. https://doi.org/10.1186/s12870-024-04752-y.

Lévesque M., Saurer M., Siegwolf R.T.W., Eilmann B., Brang P., Bugmann H., Rigling A., 2013. Drought response of five conifer species under contrasting water availability suggests high vulnerability of Norway spruce and European larch. Glob. Chang. Biol. 19: 3184-3199. https://doi.org/10.1111/gcb.12268.

Li B., McKeand S., Weir R., 1999. Tree improvement and sustainable forestry - impact of two cycles of loblolly pine breeding in the U.S.A. Forest Genetics, 6(4): 229-34.

Losch N., Heer K., Dudschuss B., Semizer-Cuming D., Michiels H.G., Neophytou Ch., 2025. Variation in seed traits, leaf phenology and growth performance among sessile oak provenances from Baden-Württemberg and Alsace. Silvae Genetica 74: 31-43. https://doi.org/10.2478/sg-2025-0005.

Lundströmer J., Bo Karlsson B., Berlin M., 2020. Strategies for deployment of reproductive material under supply limitations – a case study of Norway spruce seed sources in Sweden. Scandinavian Journal of Forest Research, 35 (8): 495-505. https://doi.org/10.1080/02827581.2020.1833979.

Lynch M., Walsh B., 1998. Genetics and analysis of quantitative traits. Sinauer Associates, pp 980.

Magnussen S., Yeatman C.W., 1987. Early testing of jack pine. II. Variance and repeatability of stem and branch characters. Canadian Journal of Forest Research. 17: 460-465. https://doi.org/10.1139/x87-079.

Mátyás C., Božič G., Ivanković M., Gömöry D., Rasztovits E., 2009. Transfer Analysis of Provenance Trials Reveals Macroclimatic Adaptedness of European Beech (*Fagus sylvatica* L.). Acta Silvatica & Lignaria Hungarica, 5 (1): 47-62.

Mihai G., Mirancea I., Duta C.V., 2014. Variation of the quantitative traits in a progeny test of *Abies alba* (Mill.) at the nursery stage. Silvae Genetica 63 (6): 275-284.

Mihai G, Mirancea I., 2016. Age trends in genetic parameters for growth and quality traits in *Abies alba*. iForest 9: 954-959. https://doi.org/10.3832/ifor1766-009.

Mihai G., Alexandru A.M., Stoica E., Birsan M.V., 2021. Intraspecific Growth Response to Drought of Abies alba in the Southeastern Carpathians. Forests 12, pp 387. https://doi.org/10.3390/f12040387.

Mihai G., Alexandru A.M., Nita I.A., Birsan M.V., 2022. Climate Change in the Provenance Regions of Romania over the Last 70 Years: Implications for Forest Management. Forests 13(8), 1203. https://doi.org/10.3390/f13081203.

Nanson A., 2004. Génétique et amélioration des arbres forestiers [Genetics and tree breeding]. Les presses agronomique de Gembloux, Belgique, pp 712.

Parducci L., Szmidt A.E., Villani F., Wang X.R., Cherubini M., 1996. Genetic variation of *Abies alba* in Italy. Hereditas 125:1-18. https://doi.org/10.1111/j.1601-5223.1996.00011.x

Paule L., 1986. Results of provenance experiment with Czechoslovak and Polish silver fir (*Abies alba* Mill.) provenances. Acta Facultatis Forestalls Zvolen - Czechoslovaka, XXVIII.

Prescher F., 2007. Seed orchards-genetic considerations on function, management and seed procurement. Doctoral Dissertation, Swedish University of Agricultural Sciences, Umea.

R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rosvall O., Jansson G., Andersson B., Ericsson T., Karlsson B., Sonesson J., Stener L.G., 2002. Predicted genetic gain from existing and future seed orchards and clone mixes in Sweden. In: Haapanen M. & Mikola J. (eds.): Integrating Tree Breeding and Forestry. Proceedings of the Nordic Group for Management of Genetic Resources of Trees, Meeting at Mekrijärvi, Finland, 23-27 March 2001, Finnish Forest Research Institute, Vantaa, Research, Papers 842: 71-85.

Rweyongeza D.M., Yeh F.C., Dhir N.K., 2010. Genetic Parameters for Bud Flushing and Growth Characteristics of White Spruce Seedlings. Silvae Genetica 59 (4): 151-158. https://doi.org/10.1515/sg-2010-0018.

Samuel C.J.A., Johnstone R.C.B., 1997. A study of population variation and inheritance in Sitka spruce. I. Results of glasshouse, nursery, and early forest progeny tests. Silvae Genetica 28 (1): 26-32. https://doi.org/10.1515/sg-2007-0006.

Sagnard F., Barberot C., Fady B., 2002. Structure of Genetic diversity in *Abies alba* Mill. from southwestern Alps: multivariate analysis of adaptive and non-adaptive traits for conservation in France. Forest Ecology and Management 157: 175-189. https://doi.org/10.1016/S0378-1127(00)00664-2.

Skrøppa T., Steffenrem A., 2019. Genetic variation in phenology and growth among and within Norway spruce populations from two altitudinal transects in Mid-Norway. Silva Fennica 53(1): 10076. https://doi.org/10.14214/sf.10076.

Squillace A.E., 1974. Average genetic correlations among offspring from open-pollinated forest trees. Silvae Genetica 23 (5): 49-155.

Tabel U., 2000. Stand der Vorbereitungen zum 2. IUFRO-Weißtannen-Herkunftsversuch. Proceedings of the 9th International European Silver Fir Symposium, Skopje, Macedonia. IUFRO WP 1.05-16; 2000.

Teodosiu M., Mihai G., Fussi B., Ciocîrlan E., 2019. Genetic diversity and structure of silver fir (*Abies alba* Mill.) at the south-eastern limit of its distribution range. Annals of Forest Research, 62(2): 139-156. https://doi.org/10.15287/afr.2019.1436.

Tinner W., Colombaroli D., Heiri O., Henne P.D., Steinacher M., Untenecker J., Vescovi E., Allen J.R.M., Carraro G., Conedera M., Fortunat J., Lotter A.F., Lutherbacher J., Samartin S., Valsecchi V., 2013. The past ecology of *Abies alba* provides new perspectives on future responses of silver fir forests to global warming. Ecological Monographs 83: 419-439. https://doi.org/10.1890/12-2231.1.

Vitasse Y., Bottero A., Rebetez M., Conedera M., Augustin S., Brang P., Tinner W., 2019. What is the potential of silver fir to thrive under warmer and drier climate? European Journal of Forest Research 138 (4): 547-560. https://doi.org/10.1007/s10342-019-01192-4.

Weng Y., Ford R., Tong Z., Krasowski M., 2017. Genetic Parameters for Bole Straightness and Branch Angle in Jack Pine Estimated Using Linear and Generalized Linear Mixed Models. Forest Science 63(1): 111-117. https://doi.org/10.5849/forsci.16-039.

Wolf H. (editor), 1994. Silver fir provenances: recent results related to provenance research of *Abies alba* Mill. Ecomed-Verlag, Landsberg/Lech, 150.

Worrall J., 1983. Temperature-bud burst relationships in Amabilis and Subalpine fir provenance tests replicated at different elevations. Silvae Genetica, 32: 5-6.

Wu S., Xu J., Li G., Lu Z., Han Ch., Hu Y., Hu X., 2013. Genetic variation and genetic gain in growth traits, stem-branch characteristics and wood properties and their relationships to *Eucalyptus urophylla* clones. Silvae Genetica 62 (4): 218-231. https://doi.org/10.1515/sg-2013-0027.

Xiang B., Li B., Isik F., 2003. Time trend in genetic parameters in growth traits of *Pinus taeda* L. Silvae Genetica 52: 114-121. http://www.lib.ncsu.edu/resolver/1840.2/2068.