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PHENOTYPIC VARIATION OF SEED TRAITS IN NATURAL POPULATIONS OF *ABIES ALBA* MILL. IN BOSNIA AND HERZEGOVINA AND ITS CORRELATION TO GROWTH IN THE FIRST TWO YEARS IN NURSERY

SUMMARY

Abies alba Mill. is one of the most prevalent tree species in Bosnia and Herzegovina. This study aimed to assess the morphological variability of seeds within silver fir natural populations in Bosnia and Herzegovina. Silver fir cones were collected in thirteen natural populations (in situ). Ten trees per population and 30 cones per tree were sampled. Twenty-five well-developed scales and seeds per tree were measured. The seeds were sown in February 2021. The heights and root collar diameters of one-year-old and 2-year-old seedlings were measured. The Kruskal-Wallis non-parametric test showed statistically significant differences among populations for all analyzed traits. A positive correlation was found between some of scale and seed traits, and traits of growth in the first two years. The determined correlation among traits can be used for the selection of the seed for producing fast-growing seedlings. Grouping of populations according to examined traits did not show any geographical pattern, so it is recommended to use the best populations in terms of growth.

Keywords: silver fir, natural populations, seed morphological traits, seedlings growth

INTRODUCTION

The Central Dinarides (Western Balkans) represent one the most important regions for understanding the genetic and morphological diversity of silver fir (*Abies alba* Mill.). Early phylogenetic studies reported unexpected alleles within this area, suggesting a complex evolutionary and postglacial history. Konnert and Bergmann (1995) identified alleles are not typical for the Balkan Peninsula, and similar findings were later documented in the Carpathian region (Longauer, 1996).

Research into mitochondrial DNA revealed that the Dinarides form a major postglacial suture zone where lineages of different biogeographical origins

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converge (Gömöry *et al*., 2004). This work identified two parallel clines: allele 2 dominating along the Adriatic coast and allele 1 prevailing inland. In Bosnia and Herzegovina, both alleles occur; allele 1 primarily in western Bosnian populations, and allele 2 elsewhere, marking the contact zone between the Balkan and Apennine haplotypes (Gömöry *et al.,* 2004; Liepelt *et al*. 2002; Liepelt *et al*. 2009). Later observation of Balkan haplotype alleles west of the contact zone and Apennine alleles east of it suggested hystorical hybridization (Ballian *et al.,* 2012), yet it remains unclear whether such genetic patterns are reflected in morphological traits.

Morphological variation in *Abies alba* cones, seeds, and scales has long been documented across Europe (Gudeski 1966; Hegi, 1981; Aas *et al.,* 1994; Tracz and Barzdajn 2007). In Bosnia and Herzegovina, earlier studies reported pronounced intra- and inter-population variabiliy in cone, seed, and scale traits (Ballian, 2000a; Ballian and Čabaravdić, 2005; Ballian and Halilović, 2016).

Silver fir studies form neighboring Croatia also demonstrated significant provenance-level differences in early seedling growth (Ivanković and Marjanović, 2005). More recent research in Bosnia and Herzegovina confirms that both morphological and growth-related traits vary significantly among populations (Ballian, 2005; Halilović *et al*., 2009b; Halilović *et al*., 2013; Ballian and Halilović, 2016; Višnjić *et al*., 2019; Memišević Hodžić *et al.,* 2021).

In the last few years, new studies from the Balkan region have further highlighted substantial phenotypic variation in silver fir. A recent investigation of needle morphology across the Balkan peninsula demonstrated clear spatial variability linked to climatic factors (Miljković, 2022; Popović *et al*., 2022). Another recent study from Southeastern Europe reported considerable anatomical variability of needles among natural populations, reflecting adaptations to local ecological gradient (Popović *et al*. 2024). Studies in broader Central European and temperate forests have also emphasized variability in growth responses (Bončina *et al.,* 2023) and the ecological importance of early seedling development under different substrate and nutrient conditions (Błońska *et al*., 2023). Work on reproductive performance has additionally shown notable variability in cone production within clonal seed orchards (Teodosiu *et al*., 2023). Provenance-test research from Bosnia and Herzegovina continues to show marked differences among provenances in morphological and growth traits (Memišević Hodžić *et al*., 2021). These findings underscore the continuing importance of understanding regional variability, particularly in genetically complex zones such as the Dinarides.

Ballian (2000b) reported no correlation between seed mass and early growth, but this has not been re-examined using more detailed measurements on larger population samples. Meanwhile, recent studies emphasize the need for identifying early-growth indicators that support forest regeneration, conservation, and climate-resilient management in silver fir populations (e.g. Popović *et al.,* 2022; Popović *et al*. 2024).

This study addresses this gap by exploring whether morphological traits of cones, seeds, and scales correlate with the early growth of seedlings originating from natural populations of silver fir in Bosnia and Herzegovina. Establishing such correlations could help identify seed sources with superior early-growth potential. Therefore, the aims of this research are: (1) to determine the morphological variability of silver fir within and among natural populations in Bosnia and Herzegovina, and (2) to examine the relationship between cone, seed, and scele morphological traits and seedling growth during the first two years.

The results may contribute to improved management, conservation, and regeneration strategies for silver fir in a region of high genetic complexity and ecological importance.

MATERIAL AND METHODS

During the autumn of 2020, silver fir cones were collected from thirteen natural populations in Bosnia and Herzegovina, representing a range of ecological conditions (Figure 1).

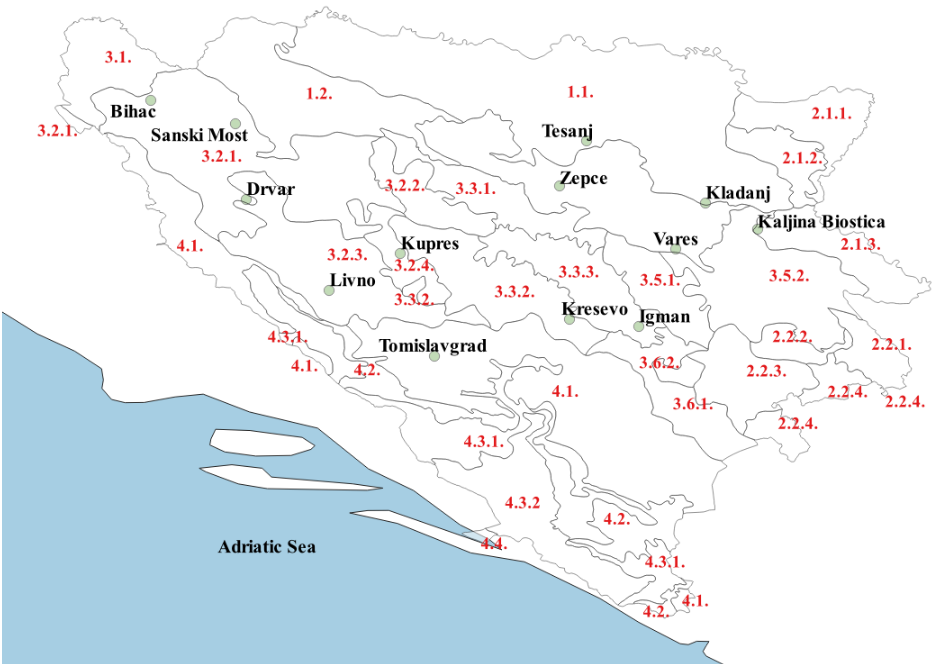

Figure 1. Distribution of researched silver fir populations in Bosnia and Herzegovina

Basic information about each population, including geographical coordinates, altitude, ecological-vegetation regions (Stefanović *et al*., 1983), and approximate tree ages, is presented in Table 1.

Table 1. Investigated populations of silver fir in Bosnia and Herzegovina

No	Population	Locality	Longitude	Latitude	Altitude (m)	Ecological-vegetation area	Area label	Age of trees
1.	Bihać	Risovac	16º03'40"	44º48'19"	898	Inner Dinarides region; West Bosnia limestones-dolomites area; Ključ – Petrovac raion	3.2.1.	100-150
2.	Drvar	Klekovača	16º30'31"	44º24'04"	1169	Inner Dinarides region; West Bosnia limestones-dolomites area; Ključ – Petrovac raion	3.2.1.	51-88
3.	Igman	Crni vrh	18º16'24"	43º47'22"	1245	Inner Dinarides region; Central Bosnia area; Sarajevo – Zenica raion	3.3.3.	69-139
4.	Kaljina Bioštica	Petrovići	18º44'46"	44º07'58"	971	Inner Dinarides region; East Bosnia plateau; Romanija raion	3.5.2.	46-102
5.	Kladanj	Karaula	18º36'11"	44º15'52"	1059	Inner Dinarides region; Zavidovići – Teslić area	3.4.	80-130
6.	Kreševo	Lopata	18º00'09"	43º50'16"	1285	Inner Dinarides region; Central Bosnia area; Vranica raion	3.3.2.	46-148
7.	Kupres	Rastičevo	17º13'20"	44º03'43"	1363	Inner Dinarides region; West Bosnia limestones-dolomites area; Koprivnica raion	3.2.4.	unknown
8.	Livno	Golija	16º52'32"	43º55'32"	1507	Inner Dinarides region; West Bosnia limestones-dolomites area; Glamoč – Kupres raion	3.2.3.	46-146 (208)
9.	Sanski Most	Korčanica	16º26'38"	44º41'23"	889	Inner Dinarides region; West Bosnia limestones-dolomites area; Ključ – Petrovac raion	3.2.1.	129-270
10.	Tešanj	Mekiš	17º59'42"	44º34'37"	360	Pripanonian region; North Bosnia area	1.1.	55-97
11.	Tomislav grad	Vran	17º25'03"	43º39'23"	1471	Mediterranean-Dinarides region; Submediterranean mountain area	4.1.	93-125
12.	Vareš	Dolovi	18º25'29"	44º09'14"	1180	Inner Dinarides region; Zavidovići – Teslić area	3.4.	95-135
13.	Žepče	Mahnjača	17º54'29"	44º27'08"	861	Inner Dinarides region; Zavidovići – Teslić area	3.4.	unknown

Each population was represented by ten mature trees, located 30-50 m appart to minimize spatial autocorrelation. From each tree, thirty medium-sized, well-developed cones were collected.

Morphological measurements

From the central part of medium-sized cone for each tree, twenty-five scales and seeds were selected for measurement. Measured traits of scales and seeds are listed in Table 2 and ilustrated in Figure 2 and 3 (figures modified from Ballian and Halilović, 2016).

Table 2. Measured traits of seeds and scales

No	Scale trait	No	Seed traits
1.	Length (figure 2, trait 1)	1.	Seed length (with wing)
2.	Width (figure 2, trait 2)	2.	Seed width (with wing)
3.	The width of the scale part outside the cone	3.	Seed length
4.	Bract length	4.	Seed width
5.	Bract width at the top of the scale	5.	Seed thickness
6.	Bract tip length		
7.	Scale thickness at the boundary with the outer scale		

All measurements were performed using a digital caliper, with accuracy of 0.01 mm.

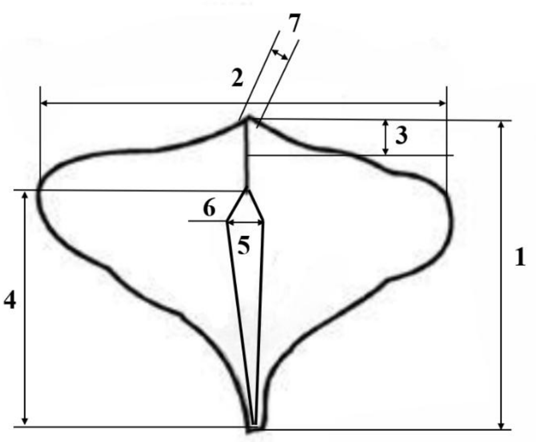

Figure 2. Scale traits

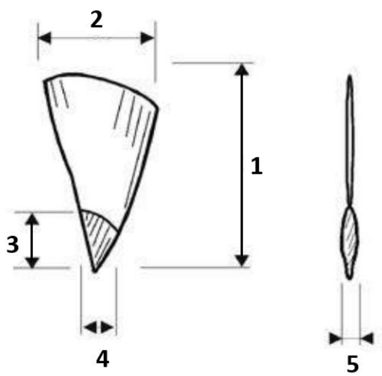

Figure 3. Seed traits.

Seed storage and nursery experiment

After selecting seed for measurement (from the medium-sized cone), the remaining seeds from each population were dried and stored at 0ºC in a cool, dry environment until sowing, with seeds from each population kept separate.

Sowing was conducted on 19 February 2021 at the Busovača Nursery (44°06'11"N, 17°52'44"E; altitude 385 m) in fluvisol soil. Seed were sown 1 cm apart at a depth of 2 cm, and covered with sawdust. Seeds from each population were sown in separate plots in the nursery, ensuring that seeds from different populations were not mixed.

Seedling growth measurement

The height and root collar diameters were measured in all seedlings after the first and second growing seasons using a digital caliper (accuracy 0.01 mm).

Experimental design and replication

The experimental design was completely randomized, with seedlings from each population kept separate to maintain provenance identity. The design ensured ten trees per population x twenty-five seeds/scales per tree for morphological measurements. Seedlings growth measurements were replicated for all individuals grow under the same nursery coniditions, providing a controlled environment for comparison among populations.

Statistival analyses

Normality of data was first tested. Since the data were not normally distributed, non-parametric analyses were performed. Descriptive statistics and the Kruskal-Wallis test were used to assess differences among populations for each trait. Hierarchical cluster analysis was applied to explore grouping patterns among populations based on morphological and growth traits. Pearson’s correlation coefficient was calculated to assess relationsips between seed and scale traits and early seedling growth. All statistical analyses were performed using SPSS version 20.0 (IBM Corp., 2011).

RESULTS AND DISCUSSION

Average values of scale traits per population are shown in Table 3. Population Livno had the lowest average values of scale length and scale width (Table 3). Population Bihać had the lowest average value of the width of the scale part outside the cone, and population Kupres had the lowest average of the scale thickness (Table 3). The highest average value of scale length had population Kreševo, scale width population Žepče, the width of the scale part outside the cone population Vareš, and scale thickness population Kladanj (Table 3). The lowest average value of bract length had population Livno, bract width, and bract tip length population Bihać (Table 3). The highest average value of bract length had population Žepče, and bract width and tip length population Livno (Table 3).

Table 3. Average values of scale traits per population (highest average values highlighted in dark grey, lowest average values in light grey)

No	Population	Scale length		Scale width		The width of the scale part outside the cone		Scale thickness		Bract length		Bract width		Bract tip length	
		Average (mm)	Std. error	Average (mm)	Std. error	Average (mm)	Std. error	Average (mm)	Std. error	Average (mm)	Std. error	Average (mm)	Std. error	Average (mm)	Std. error
1.	Bihać	23.1	0.17	26.2	0.11	5.0	0.04	1.3	0.01	11.1	0.10	5.8	0.03	3.8	0.02
2.	Drvar	22.7	0.19	27.0	0.14	5.3	0.04	1.4	0.01	11.3	0.11	6.2	0.03	4.1	0.03
3.	Igman Sarajevo	27.1	0.18	27.8	0.14	5.4	0.04	1.4	0.01	14.1	0.13	6.1	0.03	4.0	0.02
4.	Kaljina Bioštica	24.7	0.14	27.3	0.15	5.4	0.04	1.3	0.01	12.8	0.09	6.0	0.02	4.0	0.02
5.	Kladanj	26.5	0.19	29.0	0.20	5.8	0.04	1.7	0.01	13.2	0.12	6.1	0.04	4.0	0.02
6.	Kreševo	28.2	0.23	26.7	0.14	5.7	0.05	1.4	0.01	13.9	0.15	6.1	0.04	4.1	0.03
7.	-Kupres	23.8	0.14	27.5	0.17	5.1	0.04	1.3	0.01	12.8	0.11	5.9	0.02	3.9	0.02
8.	Livno	21.7	0.13	26.2	0.10	5.0	0.03	1.4	0.01	10.9	0.09	6.3	0.03	4.2	0.02
9.	Sanski Most	25.1	0.18	27.1	0.18	5.6	0.04	1.6	0.01	12.2	0.13	5.9	0.05	3.9	0.03
10.	Tešanj	25.8	0.24	29.9	0.17	5.4	0.05	1.4	0.01	13.4	0.13	6.1	0.02	4.0	0.01
11.	Tomislavgr ad	22.1	0.16	27.5	0.19	5.1	0.03	1.4	0.01	11.0	0.10	6.3	0.03	4.2	0.02
12.	Vareš	26.8	0.16	28.2	0.11	6.2	0.04	1.7	0.01	12.1	0.08	6.1	0.04	4.1	0.03
13.	Žepče	28.0	0.18	30.4	0.18	5.6	0.04	1.3	0.01	14.5	0.13	6.1	0.03	4.1	0.03
-	Total	25.1	0.06	27.8	0.05	5.4	0.01	1.4	0.004	12.6	0.04	6.1	0.01	4.0	0.01

Average values of seed traits per population are shown in Table 4. The lowest average values of seed length (with wing), seed length, seed width, and seed thickness population Livno and population Bihać had the lowest average value of seed width (with wing) (Table 4). The highest average values of seed length (with wing) and seed width (with wing) had population Žepče, seed thickness population Žepče and Tešanj, and seed width population Igman Sarajevo (Table 4).

Table 4. Average values of seed traits per population (highest average values highlighted in dark grey, lowest average values in light grey)

		Seed length (with wing)		Seed width (with wing)		Seed length		Seed width		Seed thickness	
No	Population	Average (mm)	Std. error	Average (mm)	Std. error	Average (mm)	Std. error	Average (mm)	Std. error	Average (mm)	Std. error
1.	Bihać	20.9	0.14	11.5	0.08	10.4	0.05	4.8	0.04	2.9	0.02
2.	Drvar	22.6	0.95	12.0	0.09	10.2	0.05	4.6	0.03	2.9	0.14
3.	Igman Sarajevo	23.8	0.15	12.2	0.09	10.4	0.06	6.4	0.03	2.9	0.02
4.	Kaljina Bioštica	21.9	0.18	12.2	0.12	10.4	0.06	4.8	0.03	3.0	0.02
5.	Kladanj	23.8	0.21	12.7	0.11	11.3	0.08	4.9	0.04	3.0	0.03
6.	Kreševo	24.9	0.18	11.6	0.09	10.9	0.07	4.9	0.03	3.0	0.03
7.	Kupres	22.3	0.14	11.9	0.12	9.9	0.05	4.9	0.04	2.9	0.02
8.	Livno	20.2	0.13	11.8	0.08	9.6	0.06	4.5	0.03	2.6	0.02
9.	Sanski Most	22.3	0.16	12.8	0.12	11.7	0.08	4.8	0.03	2.9	0.02
10.	Tešanj	23.8	0.22	13.0	0.12	11.3	0.08	5.0	0.04	3.3	0.03
11.	Tomislavgrad	20.4	0.18	11.7	0.12	10.1	0.07	4.7	0.03	2.9	0.03
12.	Vareš	23.9	0.15	12.4	0.08	11.6	0.06	5.2	0.03	3.0	0.01
13.	Žepče	25.5	0.17	13.5	0.13	11.4	0.07	5.0	0.04	3.3	0.04
-	Total	22.8	0.09	12.6	0.02	10.7	0.02	5.0	0.01	3.0	0.01

Kruskal-Wallis test of scale and seed traits showed statistically significant differences among populations for all traits (df 12, Sig. <0.005).

Hierarchical cluster analysis based on scale and seed traits (Figure 4) showed that populations Kaljina Bioštica, Kupres, Sanski Most, Bihać, Tomislavgrad, Drvar, and Livno, formed the first cluster, and populations Kladanj, Tešanj, Vareš, Igman, Kreševo and Žepče formed the second cluster.

The clusters did not follow any geographical pattern. Most of populations in the first cluster belong to Inner Dinarides region; West Bosnia limestones-dolomites area (different raions), and area of East Bosnia plateau (population Kaljina Bioštica), but population Tomislavgrad belong to Mediterranean-Dinarides region; Submediterranean mountain area. The second cluster is composed of populations from Inner Dinarides region Central Bosnia area (Igman and Kreševo) and Inner Dinarides region, Zavidovići – Teslić area (Kladanj, Vareš and Žepče). Population Tešanj belongs to Pripanonian region, North Bosnia area (according to Stefanović *et al*., 1983).

In table 5, the mean values of morphological traits of one-year-old and two-year-old seedlings per populations are shown. The lowest average value of height of seedlings had population Kupres, and the highest population Vareš. The lowest average value of root collar diameter had population Bihać and the highest population Igman Sarajevo.

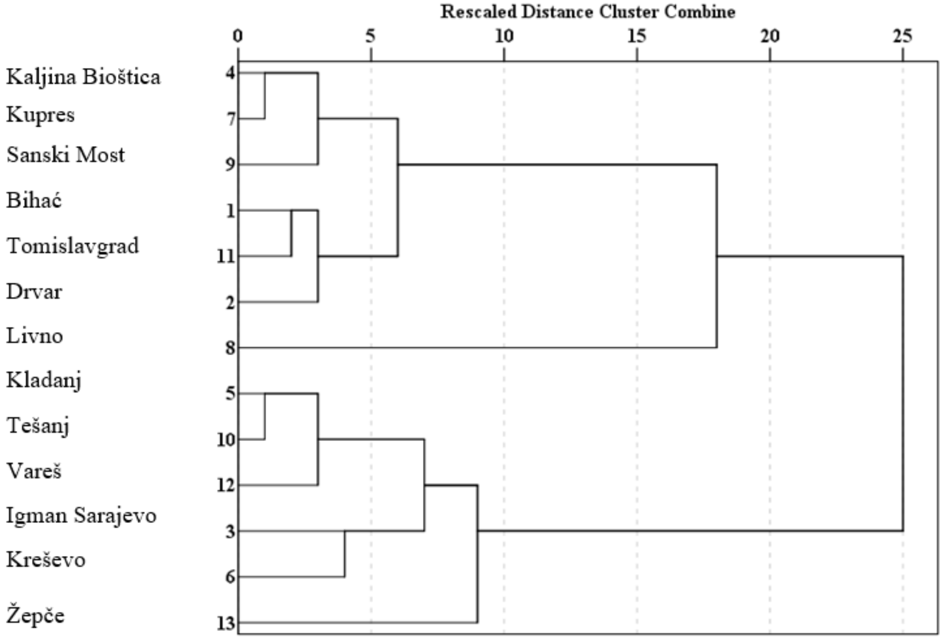

Figure 4. Hierarchical cluster of scale and seed traits

Table 5. Mean values of seedlings' heights and root collar diameters per populations (highest average values highlighted in dark grey, lowest average values in light grey)

No	Population	N 1-y-o	Mean height 1-y-o (cm)	Std. Deviation 1-y-o (cm)	Mean root collar diameter 1-y-o (cm)	Std. Deviation 1-y-o (cm)	N 2-y-o	Mean height 2-y-o (cm)	Std. Deviation 2-y-o (cm)	Mean root collar diameter 2-y-o (cm)	Std. Deviation 2-y-o (cm)
1.	Bihać	296	3.97	1.09	0.87	0.14	276	11.25	2.91	2.90	0.75
2.	Drvar	293	4.26	0.97	1.01	0.13	283	11.90	2.51	3.43	0.69
3.	Igman Sarajevo	236	3.75	0.94	1.23	5.87	170	8.89	2.79	2.71	1.05
4.	Kaljina Bioštica	295	4.14	0.94	0.88	0.14	252	11.15	4.09	2.93	0.75
5.	Kladanj	300	4.08	0.98	0.89	0.17	297	11.23	2.37	3.03	0.73
6.	Kreševo	299	4.12	0.91	0.91	0.14	296	12.88	2.41	3.65	0.78
7.	Kupres	220	3.55	1.66	1.21	5.27	160	10.92	3.22	3.40	1.34
8.	Livno	274	4.30	0.93	0.91	0.16	247	6.73	3.50	6.71	4.18
9.	Sanski Most	300	4.17	1.01	1.01	0.15	297	11.25	2.50	3.41	0.85
10.	Tešanj	300	4.11	2.03	0.93	0.18	281	10.63	2.75	2.95	0.78
11.	Tomislavgrad	192	4.48	0.93	1.01	0.16	172	11.02	2.64	3.14	0.90
12.	Vareš	224	4.25	1.03	0.89	0.17	197	11.25	4.00	3.41	0.93
13.	Žepče	299	5.00	4.54	1.07	0.17	297	16.26	2.92	3.89	0.80
-	Total	3528	4.18	1.76	0.98	2.01	3225	11.35	3.65	3.52	1.72

Results of Kruskal-Wallis test for morphological traits of one-year-old and two-year-old seedlings showed statistically significant differences among populations for both height of plants and root collar diameter (df 12, Sig. <0.005).

The results of hierarchical cluster analysis for morphological traits of one-year-old and two-year-old seedlings are shown in Figure 5. The hierarchical cluster results for morphological traits of seedlings are not similar to those found for seed and scale traits. Populations Kaljina Bioštica, Kladanj, Bihać, Vareš, Tomislavgrad, Tešanj, Kupres, and Drvar are the most alike. The Žepče population was separated from all other populations.

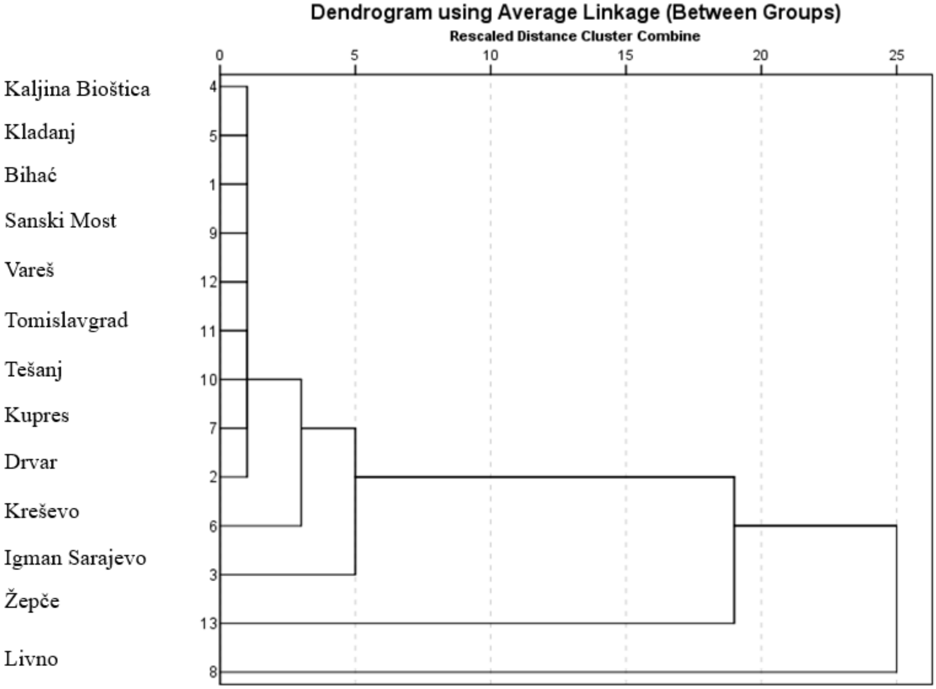

Figure 5. Hierarchical cluster for morphological traits of one-year-old seedlings.

Table 6. Pearson's correlation coefficient among the traits (seeds and scales) and growth in the first two years in the nursery. Significant correlations at the 0.01 level are highlighted in dark grey and significant correlations at the 0.05 level in light grey.

Traits	Traits/Correlation	Scale length	Scale width	Bract length	Seed length with wing	Seed width with wing	Seed length	Seed width	Seed thickness	Height 1-y-o seedlings	Root collar diameter 1-y-o seedlings	Height 2-y-o seedlings	Root collar diameter 2-y-o seedlings
Scale length	Pearson Correlation	1											
	Sig. (2-tailed)												
Scale width	Pearson Correlation	0.446**	1										
	Sig. (2-tailed)	0.000											
Bract length	Pearson Correlation	0.898**	0.492**	1									
	Sig. (2-tailed)	0.000	0.000										
Seed length with wing	Pearson Correlation	0.857**	0.534**	0.822**	1								
	Sig. (2-tailed)	0.000	0.000	0.000									
Seed width with wing	Pearson Correlation	0.013	0.167	0.018	0.041	1							
	Sig. (2-tailed)	0.886	0.057	0.838	0.644								
Seed length	Pearson Correlation	0.687**	0.554**	0.533**	0.676**	0.072	1						
	Sig. (2-tailed)	0.000	0.000	0.000	0.000	0.414							
Seed width	Pearson Correlation	0.508**	0.471**	0.427**	0.444**	0.059	0.533**	1					
	Sig. (2-tailed)	0.000	0.000	0.000	0.000	0.506	0.000						
Seed thickness	Pearson Correlation	0.500**	0.572**	0.497**	0.653**	0.081	0.612**	0.480**	1				
	Sig. (2-tailed)	0.000	0.000	0.000	0.000	0.358	0.000	0.000					
Height 1-y-o seedlings	Pearson Correlation	0.148	0.282**	0.058	0.199*	0.087	0.241**	0.085	0.143	1			
	Sig. (2-tailed)	0.093	0.001	0.515	0.023	0.328	0.006	0.335	0.105				
Root collar diameter 1-y-o seedlings	Pearson Correlation	0.202*	0.118	0.299**	0.220*	0.031	0.114	0.109	0.109	0.040	1		
	Sig. (2-tailed)	0.021	0.180	0.001	0.012	0.730	0.195	0.218	0.216	0.650			
Height 2-y-o seedlings	Pearson Correlation	0.316**	0.266**	0.301**	0.321**	-0.197*	0.326**	0.221*	0.421**	0.223*	0.062	1	
	Sig. (2-tailed)	0.000	0.003	0.001	0.000	0.027	0.000	0.013	0.000	0.012	0.495		
Root collar diameter 2-y-o seedlings	Pearson Correlation	-0.147	-0.156	-0.129	-0.132	0.455**	-0.171	-0.103	-0.188*	0.086	0.034	-0.217*	1
	Sig. (2-tailed)	0.101	0.081	0.149	0.140	0.000	0.056	0.253	0.035	0.336	0.704	0.015	

**. Correlation is significant at the 0.01 level (2-tailed).

*. Correlation is significant at the 0.05 level (2-tailed).

Results of Pearson's correlation coefficient among the traits (seeds and scales) and growth in the first two years in the nursery are shown in table 6.

DISCUSSION

All investigated seed and scale traits of silver fir showed statistically significant differences among populations, consistent with earlier findings by Ballian and Čabaravdić (2005). The grouping of populations into two main clusters based on scale and seed traits revealed only a weak geographical pattern, with one cluster predominaly from western Bosnia and Herzegovina and the other group from central and eastern regions. This pattern partially corresponds with the molecular differentiation observed by Liepelt *et al.* (2002), who identified distinct haplotypes in Central/Western Europe versus Southeastern Europe and with Gömöry *et al*. (2004), who reported allele 1 in Western Bosnian populations and allele 2 in other Bosnian-Herzegovinian populations. The placement of Kaljina Bioštica population (eastern region) within the western cluster may reflect historical hybridization of different silver fir haplotypes in the Central Dinarides contact zone.

These findings are also consistent with broader biogeographical interpretations. Longauer (1996) suggested multiple refugia along the Dinaric range, while other authors stated that the junction of migration streams from the Balkans and the western refugia was at the eastern limit of Hercynian range (Krippel, 1986; Samek, 1967, in Gömöry *et al*., 2004). Other authors (Horvat-Marolt and Kramer, 1982, in Gömöry *et al.,* 2004) proposed the migration of silver fir from the refugia in Macedonia along the Dinarian range to northern Bosnia and Croatia. Konnert and Bergmann (1995) provided evidence of introgression zones between Balkan and Central European origins. Ballian *et al*. (2012) could not determine the extent of the influence of gene pools from both refugia, but their results supported the established impact of the Apennine pool east of the contact zone through the historical and present hybridization. Research conducted across the species' range supports this complex evolutionary history. For example, Belletti *et al*. (2017) detected substantial intrapopulation and interpopulation variability in Italian silver fir, reinforcing the idea of long-lasting isolation and multiple refugial lineages. Balkans specifically, Miljković (2022) reported significant spatial variation in needle morphology linked to climatic gradients, confirming that morphological traits in the region can reflect both environmental heterogeneity and historical gene flow. Our findings of mixed clustering across regions support this interpretation.

Seedling traits also showed statistically significant differences among populations, similar to earlier studies conducted in Bosnia and Herzegovina (Ballian, 2000b; Ballian, 2005; Halilović *et al*., 2009b, 2013) and neighboring Croatia (Ivanković and Marjanović, 2005). Morar *et al*. (2023) found that silver fir from different provenances vary in tolerance to low-temperature stress, further supporting the importance of provenance-specific responses. Comparisons with recent studies reinforces this: Błońska *et al*. (2023) demonstrated that environmental conditions, such as substrate quality, strongly influence root development and nutritional status of silver fir seedlings, which aligns with out interpretation that nursery conditions and maternal effects likely contributed to the variation we observed. Similarly, Teodosiu *et al*. (2023) found provenance-related variation in cone production, indicating strong reproductive trait differentiation, while Bončina *et al*. (2023) showe that stem growth of silver fir differs significantly among Central European regions. Collectively, these studies emphasize the influence of both genetic background ad local ecological factors, supporting the patterns detected in our seedling growth traits.

The average height of one-year-old seedlings (4.18 cm) was lower than the value reported by Dorofeeva *et al*. (2021), 7.2 cm, who observed that growth depends on temperature sums early in the season and on precipitation later. Given that all populations were grown under identical nursery conditions, the variation observed here most likely reflects genetic differences among populations combined with maternal and micro-environmental effects.

The hierarchical cluster results for morphological traits of one- and two-year-old seedlings differed from those based on seed and scale traits. This is expected, as seedling growth can be influenced not only by genetic factors but also by environmental conditions on the nursery and maternal provisioning effect.

Significant correlations were found between severas seed and scale traits and early seedling growth, suggesting that some reproductive traits may have predictive value for initial seedling vigor. Although most correlations were moderate, they warrant further investigation. Ballian (2000b) found no correlation between seed mass and seedling performance, indicating that seed size does not straightforwardly predict growth, a pattern partly echoed in our results.

No clinal morphological variability was detected, likely reflecting the ecological heterogeneity of the Dinaric region, where silver fir occurs in fragmented subpopulations except in the more continuouts western and eastern Bosnian ranges (Fukarek, 1970; Stefanović *et al*., 1983). The observed diversity and grouping of populations are consistent with the influence multiple glacial refugia and the long-term hybridization documented in previous studies (Konnert and Bergmann, 1995; Gömöry *et al*., 2004; Liepelt *et al*., 2002; Ballian *et al*., 2012). The grouping of both western and easter populations in our dendrograms, along with exceptions, likely reflects historical gene flow, hybridization processes, and the complex demographic history characteristic of silver fir in the Central Dinarides.

CONCLUSIONS

This study provides new evidence of substantial intra- and inter-population morphological variability in silver fir across Bosnia and Herzegovina, confirming the species' high adaptive potential and supporting its long term preservation in naturraly fragmented Dinaric habitats.

A key scientific contribution of this work is the identification of two major morphological clusters of seed and scale traits, broadly reflecting western versus central-eastern population groups. The atypical grouping of the Kaljina Bioštica population with western populations further supports earlier genetic findings that the Central Dinarides represent an active contact zone where Balkan and Appenine haplotypes have historically hybridized.

Another important contribution is the discovery of several statistically significant correlations between seed and scale morphology and early seedlings growth, suggesting that certain cone-related traits may serve as indicators for early selection in nursery conditions.

Despite these contributions, the study has limitations. Seedling growth was assessed in a single nursery environment, which may not fully represent filed performance, and maternal or environmental effects during cone development could not be completely separated from genetic factors. In addition, the study relied exclusively on morphological traits; integrating molecular markers would allow stronger inferences about the genetic structure of populations and the extent of hybridization.

Future research should therefore combine morphological, physiological, and genomic analyses across broader environmental gradients. Long-term provenance trials and reciprocal transplants would help verify whether early growth-morphology correlations persist later in development and under field conditions. Such integrated approaches would substantially improve selection strategies and conservation planning for silver fir in the Dinaric region.

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