



What Can We Learn from an Early Test on the Adaptation of Silver Fir Populations to Marginal Environments?

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Abstract: In order to determine the adaptive potential of silver fir in the southeast of Poland, the stability of the height of its five-year-old progeny was analyzed. The study was conducted in two different population groups in a total of four environments, including one ecologically marginal environment. The linear mixed model was used to evaluate the differentiation of populations in terms of height growth. The genotype and genotype-by-environment interaction biplot (GGE) were used to verify the stability of height. The climate of populations origin, in relation to actual fir distribution in Poland, was verified based on principal components analysis (PCA) of bioclimatic parameters. The highest total variability was explained by the genotype-environment interaction effect (GE) (54.50%), while the genotype effect (G) explained 41.27% and only 4.23% was explained by the site effect. The result of height growth variations revealed the Komańcza site as the most representative among study sites, while the Lesko site characterized the highest discriminating ability. The progeny occurring in climatic conditions most different from the average testing conditions showed a heterogeneous growth reaction, only adapting to the marginal environment, while the progeny of the second population in this region as well as the northernmost one was characterized by a mean but stable growth. The westernmost population revealed maladaptation. The assessment of the adaptability of silver fir depends on the broad spectrum of test conditions considering the ecologically marginal environments.

Keywords: genotype \times environment interaction; phenotypic plasticity; multi-environment trials; bioclimatic indexes; maladaptation

1. Introduction

Populations of species within the natural range and on its periphery often occupy marginal environments in which a specific factor or factors are close to the limit of physiological tolerance of individuals, contributing to the reduced reproduction, survival, and abundance. Groups of individuals of a species occurring in marginal environments are referred to as marginal populations [1]. In such



populations, natural selection may be targeted for the selection of genotypes to increase the tolerance to certain environmental factors [2]. Attempts to determine the potential climate range of silver fir (Abies alba Mill.) in Europe have demonstrated divergent results [3,4]. In Poland, A. alba seems to be well adapted to climate conditions outside its natural range [5]. This is probably due to the fact that the silver fir recovery process from glacial refuges has not yet finished [6]. In both cases, the potential climatic ranges are much wider than the previously recognized range of the natural occurrence of this species. According to the "central-marginal hypothesis", genetic diversity decreases as it approaches the periphery of the species range [7]. This principle is also confirmed for the silver fir, which reaches the northeastern range in Poland [8,9]. According to Larsen [10], low adaptability to the changing environmental conditions may be explained by the lower genetic diversity. Marginal populations are characterized by the synchronicity of the growth reaction in response to the extreme climatic events [11,12]. The observed phenotypic plasticity determines the survival of genotypes [13]. Adaptation opportunities of in-situ populations outweigh the potential of alien populations, as long as the environmental conditions are stable. But, if climate changes trigger a "shift" of growth conditions, this rule is falsified [14]. According to Frank et al. [15], the adaptation strategy of fir to climate change seems opportunistic, manifesting itself in the low sensitivity to climate-related maladaptation. Furthermore, silver fir, whose height growth is mainly associated with soil water availability, seems to be an adaptive generalist [15]. The predicted rise in global temperatures over the next century is similar in value to the changes that have occurred over 5000 years since the last glacial maximum, but it runs 50 times faster [16]. Many geographic modeling studies point to the potentially high risk of shifting ecological niches and the extinction of populations and species [17–19]. The modeling methods developed so far [20] treat all positions equally, without considering many environmental factors and the adaptability of the population. This could lead to the overestimation of the tolerance of climatic conditions and the potential range of species. On the other hand, the realized niche, smaller than the potential, can be the result of biotic effects such as competition or herbivore pressure. The abovementioned problems related to the modeling of a potential niche mean that these methods, although undoubtedly useful in environmental research, do not answer how individual, genetically different populations react to the changes in climatic conditions. To better understand the adaptation of the population to climate change, it is advisable to use provenance experiments [21]. These studies are particularly important in view of the current climate change, as they may allow for the selection of genotypes that are more resistant to drought [22,23]. Provenance areas also allow phenotypic assessment through multiple environments and thus provide the basis for determining the interaction of genotype \times environment (GE) [24].

The use of early tests in assessing the adaptive potential of fir to growth conditions in southern Poland has been the subject of a number of studies [25,26]. In "The Carpathian Gene Bank" experiment [27], a wider composition of the population group was included (40). However, the scope of testing conditions (location of experiments) did not cover the periphery of the fir range in southeastern Poland. On the other hand, experiments on the adaptability of the fir population were limited to the location of experiments in the Sudety Mountains due to the question about the possibility of restoring this species [25]. Previous research focused mainly on testing the fir population in close to optimal growth conditions. They did not give the opportunity to evaluate the growth response in marginal conditions.

Verification of the adaptation to local environmental conditions and potential climatic range of species is possible through multi-environment population tests covering peripheral and/or marginal testing locations [27]. Whereas, experiments conducted under controlled growth conditions in environmental chambers, simulating projected warming and drought, only allow the verification of the potential climatic range [28]. In studies on the adaptation potential of forest trees, it is particularly important to include the composition of a tested population group that is from outside the tested region. Such populations allow one to trace the different directions of adaptation (or maladaptation) to marginal conditions [29]. In the absence of the representativeness of the test conditions and omission

of marginal conditions, there is a risk of incorrect or incomplete assessment of the adaptability in marginal environments [26,30].

Current knowledge about the adaptability potential of fir on the eastern edge of Europe to marginal conditions of growth is, however, insufficient to estimate the impact of the potential climate change on the condition of the population. Hence, the purpose of this study is to determine the requirements for early tests to assess the adaptability of the fir populations to growth conditions in marginal environments.

2. Materials and Methods

For the needs of a series of four population experiments, seeds representing 19 populations of silver fir from the eastern range of southeastern Poland, VIII and VI Nature-Forestry Country, were collected (Table 1). The populations, originally represented by selected seed stands, are characterized by the best phenotypic characteristics for this part of Poland [27]. As a reference population, a "national standard", located in the Forest Experimental Station in Krynica (LZD), outside the region of southeastern Poland, was chosen based on the breeding value known from previous studies [27]. Thanks to this, it was possible to compare local populations with outgroup populations. To collect seeds, transects have been designated at a distance of not less than 25 m, covering 50 randomly selected fir trees. The seed collection was performed between 1998 and 2005, collecting 12.5 kg of cones from each healthy tree, which gave 300 g of seeds per tree.

Table 1. Characteristics of the tested silver fir populations. Production cycle: 1.5/1.5 (after replanting
for 1.5 years) and $2/1$ (after nurturing for two years); latitude and longitude in WGS84 expressed in
decimal degrees (DD).

Population ID	Forest Base Material ID	Forest District	District Production Cycle (Year/Year) Elevation (m a.s.l.)		Latitude	Longitude
BAL1	11625	Baligród	2/1	631	49.3226	22.2699
BAL2	11626	Baligród	1.5/1.5	624	49.3226	22.1912
BIR1	27146	Bircza	1.5/1.5	506	49.5667	22.5713
KRA1	11270	Krasiczyn	2/1	399	49.6918	22.5931
KRA2	11271	Krasiczyn	1.5/1.5	374	49.6919	22.5961
KRA3	11273	Krasiczyn	1.5/1.5	365	49.7168	22.6460
LES1	30320	Lesko	1.5/1.5	456	49.4862	22.1964
LES2	30326	Lesko	1.5/1.5	363	49.5056	22.2871
LES3	30327	Lesko	1.5/1.5	491	49.5150	22.4125
LES4	30328	Lesko	2/1	450	49.4548	22.3039
LES5	30329	Lesko	1.5/1.5	499	49.4590	22.2859
LES6	30330	Lesko	2/1	396	49.4489	22.3366
LUT1	30205	Lutowiska	1.5/1.5	516	49.3151	22.5550
LUT2	30212	Lutowiska	1.5/1.5	599	49.3129	22.6590
LZD	MP/2/45114/06	LZD Krynica	2/1	670	49.3750	20.9870
NAR	10995	Narol	1.5/1.5	314	50.3837	23.3674
RYM1	36145	Rymanów	1.5/1.5	580	49.3810	21.9499
RYM2	36146	Rymanów	1.5/1.5	536	49.4380	21.8773
STU	10691	Stuposiany	1.5/1.5	688	49.1613	22.6977

Seedlings with covered root systems were produced from the seeds harvested in the Oleszyce container nursery (50.1778 N, 22.9688 E) in a three-year cycle of 1.5/1.5 (after replanting for 1.5 years) and 2/1 (after nurturing for two years) (Table 1). Robbin's Styrofoam containers were used for the production (cell volume, 285 cm³/38 in.3). In the first stage of the production, the seedlings were kept in polyhouses. After three years of growth in the nursery, the seedlings were transported to the target planting sites. Planting took place in April 2009 in four locations of southeastern Poland: Bircza (BIR) (49.6376 N, 22.4908 E), Cisna (CIS) (49.1671 N, 22.4671 E), Komańcza (KOM) (49.3734 N, 22.0231 E), and Lesko (LES) (49.4979 N, 22.2909 E) (Figure 1). When selecting the location of study sites, the criterion of the highest diversification of environmental conditions was applied, while taking into account the range of silver fir distribution in south-eastern Poland.



Figure 1. Locations of the experimental sites and the tested populations. Experimental sites (squares), populations (dots), and weather stations (triangles). Distribution range of silver fir (main map: in beige, upper left map: in gray) according to http://www.euforgen.org/. Experimental sites: BIR—Bircza, KOM—Komańcza, CIS—Cisna, LES—Lesko. Weather stations: PML—Przemyśl, LSK—Lesko, KRN—Krosno, KMC—Kamenica nad Cirochou. Acronyms for populations according to Table 1.

The climate of the experimental areas is characterized by the average annual temperatures of 8.5 to 9.8 °C (KOM and CIS, respectively) and annual precipitation from 568 to 667 mm (KOM and CIS, respectively), mainly concentrated in May–July (climate data from the National Oceanic and Atmospheric Administration (NOAA) agency, weather stations in Przemyśl (PML) (distance to BIR: 26 km), Lesko (LSK) (distance to LES: 4.5 km), Krosno (KRN) (distance to KOM: 40 km), and Kamenica nad Cirochou (KMC) (distance to CIS: 42 km), the reference period 1952–2016) (NOAA/NCEI/CWC, http://www.noaa.gov/) (Figure 2).

Soil conditions occurring at the four experimental sites were differentiated from pseudogley lessive soil to leached brown soil (Bircza and Cisna, Komańcza and Lesko, respectively). According to the Polish forest typology, the Bircza and Lesko sites were an upland broadleaved forest (Lwyż); and the Cisna and Komańcza sites were a fresh montane broadleaved forest (LMG). For all areas intended for the experiment, no forest management was undertaken before. Full ground cultivation was made as a form of land preparation in 2006. In 2007, two years ahead of fir planting, European larch seedlings were planted with 1.5×1.5 m spacing to create the preferable ecological/growing conditions for fir. Losses in larch trees were replenished with new seedlings until the planting of fir seedlings. Experimental sites were established based on the population plot design of 10-trees × 10-trees with 1.5×1.5 m spacing between larch trees. For BIR, KOM, and LES experiments, all populations were represented by 400 trees (100 trees × four replicates); only in the case of CIS experiment BAL1, KRA3, LES4, and LES6 populations were samples omitted due to seedling shortages. In 2009 (May) and 2013 (May), some of the seedlings were damaged from late frosts [31]. After five years of growth, in September 2013, height measurements were made (Table 2).



Figure 2. Climatic diagrams for experimental sites. Plots of the precipitation and temperature monthly averages, annual averages of both elements (in the upper part), and monthly averages of the daily maximum and mini- mum temperatures of the warmest and coldest months, respectively (at the left margin); rectangle under the 0 °C axis—frost likelihood (darker blue when the average daily minimum is zero or negative, lighter blue when absolute monthly minimum is zero or negative); blue vertical pattern depicts the humid months.

Bernalation		Mean	Height (c	m) (CV (%	5))		Μ	ean Sur	vival (%	5)
Population	BIR	КОМ	CIS	LES	Across Sites	BIR	КОМ	CIS	LES	Across Sites
BAL2	55 (12)	52 (14)	58 (13)	50 (6)	54 (12)	93.3	90.5	98.5	94.8	94.3
BIR1	57 (13)	57 (5)	59 (10)	55 (10)	57 (9)	93.5	95.8	96.3	93.0	94.7
KRA1	38 (36)	30 (46)	55 (14)	44 (4)	42 (32)	77.7	90.9	95.2	94.7	89.6
KRA2	52 (26)	55 (11)	61 (9)	51 (2)	55 (15)	87.8	90.0	96.3	88.3	90.6
LES1	53 (29)	63 (7)	49 (14)	48 (17)	53 (20)	92.8	93.8	93.5	94.0	93.5
LES2	57 (11)	56 (11)	53 (15)	57 (10)	55 (11)	94.8	88.5	94.5	91.0	92.2
LES3	61 (10)	54 (16)	61 (9)	55 (14)	57 (13)	96.3	84.5	96.0	94.3	92.8
LES5	55 (28)	56 (4)	60 (4)	51 (13)	56 (15)	93.3	90.3	96.0	83.6	90.8
LUT1	55 (18)	53 (6)	56 (15)	53 (16)	54 (13)	94.8	91.0	98.0	94.3	94.5
LUT2	57 (19)	54 (14)	64 (2)	52 (7)	57 (13)	94.8	89.8	97.3	95.3	94.3
LZD	42 (10)	46 (16)	48 (5)	38 (38)	44 (18)	88.8	88.8	98.3	92.3	92.1
NAR	55 (13)	55 (6)	54 (5)	51 (8)	54 (8)	91.3	92.0	95.3	95.0	93.4
RYM1	57 (8)	58 (13)	58 (11)	56 (7)	57 (9)	94.5	91.5	98.0	93.5	94.4
RYM2	52 (14)	49 (9)	57 (4)	46 (14)	51 (12)	92.0	87.0	95.8	94.8	92.4
STU	56 (6)	58 (10)	60 (14)	47 (26)	55 (16)	94.8	94.8	96.5	89.0	93.8
BAL1	30 (63)	63 (16)		76 (16)	59 (38)	55.1	91.8		93.3	80.1
KRA3	66 (11)	56 (12)		50 (16)	58 (17)	96.3	89.8		92.5	92.9
LES4	49 (16)	28 (48)		39 (17)	39 (33)	92.3	91.8		95.0	93.0
LES6	45 (29)	61 (35)		89 (11)	65 (36)	87.1	80.3		95.5	87.6
fulti-population mean	53 (22)	53 (23)	57 (12)	53 (25)	54(21)	90.1	90.2	96.4	92.9	91.9

Table 2. Mean values and coefficients of variation (CV) of tree heights and survival in 19 populations of fir at four experimental sites: BIR—Bircza, KOM—Komańcza, CIS—Cisna, LES—Lesko.

Poland were used. Their location was determined by the geographical coordinates of centroids of forest units obtained from the State Forest Information System (SILP). Based on the vector-based map of silver fir coverage (http://www.euforgen.org), out-of-range positions were excluded from the analysis. Next, 20 raster maps from the BIOCLIM 1.4 [32] with a 2.5 arcmin resolution (www.worldclim.org) were selected. These include values related to the altitude and annual and seasonal values of precipitation and temperatures. These data, as the main climatic determinants of species distribution, are widely used in studies on the modeling of a potential niche of species and the limitation of their occurrence or areas of possible introduction [33–36]. Extraction of bioclimatic coefficient values for each of the stations was performed using the DIVA-GIS 7.5 software [37]. Due to the local high density of stands, in many cases, there was more than one point per one raster cell, resulting in duplicate extractions. After removing such duplicate records, a set of 1164 stands was obtained, which was used to identify the main climatic factors that differentiate silver fir stands in Poland. Identification of these factors was made using principal component analysis (PCA) on the correlation matrix (Figure 3) using PAST 3.15 software [38].



Figure 3. Climate-related variability between provenances and experimental sites. For the input data extraction of the altitude and 19 BIOCLIM indexes (http://worldclim.org/bioclim) for 1164 records, the included study sites and localities of silver fir from the native ranges of Poland were used. The ellipse includes 95% of the climate variability associated with PC1 and PC2. BIR—Bircza, CIS—Cisna, KOM—Komańcza, LES—Lesko experimental sites.

A number of statistically significant components were determined using bootstrap analysis $(1000 \times)$. The variables most strongly influencing the distribution of silver fir were identified by Pearson's correlation coefficients between the climatic variables and principal components (PCs) (Table 3).

Bioclimatic Variables	Abbreviation	PC 1	PC 2	PC 3
Altitude	Alt	0.99	0.04	-0.05
Annual Mean Temperature	bio1	-0.88	0.42	0.10
Mean Monthly Temperature Range	bio2	0.07	0.81	0.49
Isothermality (BIO2/BIO7) (\times 100)	bio3	0.45	0.85	-0.11
Temperature Seasonality (STD $ imes$ 100)	bio4	-0.67	-0.51	0.52
Max Temperature of Warmest Month	bio5	-0.87	0.33	0.34
Min Temperature of Coldest Month	bio6	-0.56	0.63	-0.47
Temperature Annual Range (5–6)	bio7	-0.56	-0.14	0.81
Mean Temperature of Wettest Quarter	bio8	-0.92	0.25	0.25
Mean Temperature of Driest Quarter	bio9	-0.61	0.76	-0.17
Mean Temperature of Warmest Quarter	bio10	-0.92	0.25	0.25
Mean Temperature of Coldest Quarter	bio11	-0.51	0.80	-0.24
Annual Precipitation	bio12	0.91	0.34	0.19
Precipitation of Wettest Month	bio13	0.85	0.46	0.20
Precipitation of Driest Month	bio14	0.94	0.05	0.14
Precipitation Seasonality (CV)	bio15	-0.32	0.71	0.04
Precipitation of Wettest Quarter	bio16	0.85	0.47	0.21
Precipitation of Driest Quarter	bio17	0.94	0.10	0.20
Precipitation of Warmest Quarter	bio18	0.85	0.47	0.21
Precipitation of Coldest Quarter	bio19	0.93	0.04	0.21
Eigenvalue		11.87	4.97	2.02
Variance explained		59.37	24.85	10.08

Table 3. Pearson correlation coefficients between climatic variables and the first three principal components, eigenvalues, and variation explained. Absolute values of correlation coefficients greater than 0.057 are statistically significant at the 95% confidence level.

In this study, the "population" term was used to define the genotype as many of the previous studies point to significant genetic diversity between closely localized populations distributed in the Carpathian Mountains [9,39,40].

In recent years, analysis of variance in multi-environment trials (MET) has been performed according to the mixed model framework [41–44]. Depending on the needs, the effects of genotypes (in this study populations) and environments (in this study experimental sites) are treated as fixed or random [43–46]. In order to investigate the environmental impact and the differentiation of genotypes in terms of height, a linear mixed model was considered:

$$y_{iik} = \mu + r_k(e_i) + g_i + e_j + ge_{ij} + \varepsilon_{iik} \tag{1}$$

where y_{ijk} is the trait value observed on the experimental plot for the *i*-th genotype (*i* = 1, ..., G) in the *j*-th site (*j* = 1, ..., E) and in the *k*-th block (*k* = 1, ..., R), μ is the general mean, g_i is the fixed effect of the *i*-th genotype, e_j is the random effect of the *j*-th site, ge_{ij} is the random effect of the genotype × site interaction, $r_k(e_j)$ is the random effect of the *k*-th block in the *j*-th site, and ε_{ijk} is the random residual containing the effect of a block-within site × genotype interaction (i.e., plot effect) and some tree-within-plot experimental error. In MET data analysis, the analysis of variance according to the model with effects of the genotype, the environment, and their interactions is a standard approach, preceding the application of GGE biplot analysis. If based on the analysis of variance a significant interaction of G × E is confirmed, studying the stability of genotypes using GGE biplot analysis finds justification.

As four genotypes (BAL1, KRA3, LES4, and LES6) did not occur in the CIS environment (Table 2), the analysis of model 1 (Equation (1)) was performed for unbalanced data with empty cells (missing combinations). F statistics for genotype and environment effects of model 1 (Equation (1)) were determined using Hocking's approach [47].

Genotype and genotype-by-environment interaction biplot (GGE) graphs were obtained by the two-dimensional table of means (Table 2) and PCA analysis on the covariance matrix [48–51]. In order to account for all 19 studied populations together with four non-present populations in CIS

environments, PCA analysis was performed on the data supplemented by mean values (at least one value in combination) or imputed all values (in case of missing combination). When the percentage of the missing data is very small, it is possible to fill in the missing values with the mean value [52,53]. In contrast, when all values in the combination are missing, data could be calculated according to the EMB algorithm (expectation-maximization with bootstrapping). In our case, imputed values for missing combinations were calculated in the Amelia II R package, which assumes that data are jointly distributed as multivariate normal [54].

To investigate the similarities between the environments, the AEC method was used [55,56]. Based on the GGE1 and GGE2 components, the average environment (AE) was determined independently for complete and incomplete variants. Then, by the AE point and the center of the coordinate system, the average environment axis (AE axis) was passed through. Similarities between environments were determined by the angles between the vectors of the environments. The smaller the angle between the vectors, the greater the similarity between the environments.

The population stability ranking was based on the location of the population on the GGE biplot. Population rank in relation to the height was determined based on its location along the GGE1 axis. The zero value of GGE1 determines the mean value of the trait through the environment over the years. The highest populations are those for which GGE1 values are the largest. Population stability was determined by their position relative to the GGE2 axis. Genotypes with the largest absolute values of GGE2 are unstable and their interactions with the environment are important. In other words, stable genotypes are characterized by a similar height regardless of the environmental conditions, while unstable ones show a high variability of the analyzed trait between environments. The term stability determined on the basis of the GGE biplot allows a relative reference of one genotype to the others.

Using the GGE biplot graph, one can look for an ideal genotype (IG) that could have a high mean trait value and exhibit good stability in the studied environments [43,56]. For this purpose, the end of the vector lying on the AE axis should be determined as the highest value among the orthogonal projection of the genotype positions on the AE axis. The AE axis determines the zero value of the GE interaction effect for the average AE environment. In order to find the genotypes closest to the end of the vector, the circles centered at the point defining the end of the vector on the AE axis and arbitrary radii were drawn.

Statistical analyses and presented biplots were done with SAS/STAT 13.1 (SAS Institute Inc., Cary, NC, USA) and specifically the GLM, PRINCOMP, and GPLOT procedures [57,58].

3. Results

3.1. Bioclimatic Analyzes

Silver fir sites (1164) used for the analysis, including PCA-analyzed surfaces, were sorted by 20 components, of which only the first two are statistically significant and account for 84.22% of the variance (Figure 3, Table 3). The first component (PC1), explaining 59.37% of the variance (Table 3), was strongly positively correlated (r > 0.7) with the elevation above the sea level and annual and seasonal rainfall (bio12–14, bio16-19), and strongly negatively correlated (r < -0.7) with the annual temperatures and growing season (bio1, bio5, bio8, bio10). The location of fir stands, according to PC1, was correlated (negatively) with seasonal temperature distribution (bio4, bio7) to a lesser degree and with winter temperatures (bio6, bio7, bio9, bio11). The second PC2 component explained 24.85% of the variance (Table 3) and was strongly positively correlated (r > 0.7) with monthly and annual temperature amplitudes for the coldest and at the same time the driest quarter (bio9, bio11) and seasonality of the precipitation (bio15). To a lesser extent, the location of fir stands, relative to that component, corresponded to the temperature seasonality (r = -0.51) and the temperature and precipitation of the coldest month (bio6 and bio14). The third (PC3) component, which was statistically insignificant, explained 10.07% of the variance (Table 3) and was correlated with the annual temperature amplitudes (bio7, r = 0.81) and temperature seasonality (bio4, r = 0.52). Except for the CIS and LZD sites, all the others formed a cluster, indicating a significant similarity to the climatic conditions of most of the fir sites (Figure 3). The position

of the CIS site draws attention, and a small number of the fir sites outside the ellipse, which determines 95% of the variability of climatic conditions associated with PC1 and PC2.

3.2. Analysis of Variance

The population (G) and population \times environment interaction (GE) effects were significant (p = 0.019; p < 0.001 respectively; Table 4). In total, 54.50% of the total height variation (G + E + GE) was explained by the GE interaction effect, 41.27% by the G genotype effect, and only 4.23% by the E environment effect. The reason for the insignificant site effect (E) may be the relatively small variability of the climatic conditions of the growing season prevailing at the experimental sites (Figure 2). PCA analysis of the bioclimatic indexes confirmed high similarity for the three experimental sites located at a lower elevation and at the same time differentiated them with respect to the CIS experimental site (Figure 3).

Table 4. Results of the analysis of variance for tree heights for 19 populations at four experimental sites, along with the percentage of the variation explained (F statistics for genotype and site effects are calculated according to Hocking's approach).

Source of Variation	Df	Mean Square	F	р	% (G + E + GE)
Genotype (G)	18	518.08	2.11	0.019	41.27
Site (E)	3	318.56	0.69	0.564	4.23
Block (Site)	12	274.96	4.79	< 0.001	
Genotype \times Site (GE)	50	246.31	4.29	< 0.001	54.50
Experimental error	201	57.38			

3.3. Similarity of Environments

Based on the position of the environments with respect to the average environment position (AE) (Figure 4), the less representative were LES and BIR sites (large angle between the AE axis and the environmental vector). The closest to the average environment AE was the KOM site with stable growth conditions. The CIS site characterized low representativeness, similar to LES and BIR, while having a low discrimination ability (the shortest environmental vector).



Figure 4. View of average environment coordination (AEC) on the GGE-type biplot based on principal components of the environments. AE in the circle is the "average environment" for BIR, CIS, KOM, and LES designated for the comparison. BIR—Bircza, CIS—Cisna, KOM—Komańcza, LES—Lesko experimental sites.

3.4. Similarity and Stability of Populations and Ideal Genotype

Populations LES6 and BAL1 were characterized by the largest average heights, while LES4, KRA1, and LZD by the smallest average heights (Figure 5, Table 2). At the same time, all these populations and the KRA3 population were the most unstable (Figure 5).

The highest and most stable were RYM1 and BIR1. The position of the RYM1 and BIR1 populations closest to the IG point denoting a theoretically ideal genotype on the GGE biplot (Figure 6) makes it possible to recognize the RYM1 and BIR1 populations as ideal populations (IG).



Figure 5. Distribution of genotypes on the GGE-type biplot. Principal component GGE1 describes the height, while GGE2 describes the size of the GE interaction. Position of the BIR1 and RYM1 populations, closest to the IG point marked in red.



Figure 6. Comparison of all genotypes with the theoretical ideal genotype (IG). Position of the BIR1 and RYM1 populations, closest to the IG point marked in red.

4. Discussion

We confirmed the hypothesis about the influence of the testing conditions due to peripheral and/or marginal testing locations, on the assessment of adaptability of silver fir in early tests. The CIS site, defined by the results of bioclimatic analysis as marginal to the climatic conditions of silver fir growth in Poland, allowed the identification its high discriminatory strength (Figure 3). However variance analysis did not confirm significant environmental differentiation, confirming the low percentage of variation explained by the environmental effect (4.23%) which may be related to the relatively restricted area occupied by testing sites. However, similar studies on half-sib families collected from 15 French silver fir provenances provided opposite results, indicating that most of the phenotypic variability was attributed to the environmental factors [59]. The reverse trend obtained in the presented studies may be related to slight variation in the altitude of testing sites and populations (from 380 to 670 and from 314 to 688 m, respectively). Also, the diversity of climatic conditions characterizing the testing site was relatively low compared to those presented by Latreille and Pichot [59]. It is possible that when the silver fir population reaches a climatological limit for this species, unfavorable environmental conditions determine the phenotypic traits to such an extent that the genetic diversity of the population does not matter [60]. Perhaps the niche modeling approach would help to better explain the lack of impact of the environmental effect on the population variation by identifying potential areas ensuring stable fir cultivation [61]. However, the uncertainty of estimates of future climate niches requires a careful interpretation of the results [62]. In previous studies using early tests to evaluate the adaptability of fir trees, the focus was on the proper selection of testing sites [25,26]. Less attention was paid to the composition of the tested populations. The results of our studies show the impact of the selection of the tested population on their stability manifesting in height growth and on the results of adaptability in marginal environments (Figures 5 and 6). Our studies indicate the need to preserve the principle of broad composition of the surveyed populations, to assess the adaptability of silver fir to growth conditions in marginal environments. In addition, they gave us the opportunity to overcome the limitations of previous fir experiments related to their location in close to optimal growth conditions [25,26] Moreover, they provide important insights into adaptability to the potential climatic conditions that we face in experiments under controlled growth conditions [28].

According to our assumptions, the KRA1, KRA2, KRA3, NAR, and LZD populations occurring in climatic conditions most different from the average climatic conditions of the populations should result in unfavorable growth under all test conditions or good growth only under specific conditions. This reaction should be determined by the vector of climate change, assuming that the shift toward better conditions should result in improved growth. The results of these studies, however, indicate the heterogeneous response of these populations. The KRA1 population only adapted to the specific growth conditions of the CIS site (Table 2), while achieving low values of height at the remaining experimental sites, which explains its unstable position on the biplot (Figure 6). On the other hand, the second population (KRA2) and the northernmost population (NAR) were characterized by an average but stable growth. Such a varied adaptive response of populations occurring in close geographical and climatic locations may be the mixed effect of natural differences in the genetic structure and introduction of new genes resulting from forest management [63,64]. Therefore, neighboring stands possibly defined as one population will represent different gene pools. Given the above, different degrees of adaptation of the KRA1 and KRA2 populations may have genetic backgrounds. Undoubtedly, a diversified pattern of adaptation of the northernmost populations provides an important contribution to the discussion about the potential range of silver fir in Poland [65]. Probably, the potential climatic range of the species obtained from the bioclimatic envelope models should be verified with the results from common garden experiments. In addition, the climatic distribution model for silver including only temperature, precipitation, etc., creates inaccurate results as the species, being resistant to drought, characterize sensitivity to soil water potential rather than precipitation [15,66].

Interesting results in the context of variability of adaptability of fir trees provided the analysis of the westernmost LZD population. The lowest position in terms of height was occupied by the LZD population together with KRA1 and LES4 (Figure 5, Table 2), serving as a reference population in testing the progeny of fir in Poland. At the beginning of the breeding program, the stands whose progeny had the best results in national provenance research, in terms of genetic and breeding value, were selected as a reference population [27,63]. However, not all the results of later studies in respect to this population confirmed its high ratings. Under growth conditions similar to those presented in the study, their progenies were characterized by varying degrees of adaptation, whereas on the gene conservation trail of the Carpathian Gene Bank in the Bircza District, the LZD population was characterized by an average increase in height [26]. In contrast, in the Baligród Forest District, it achieved the highest value on the comparative site [67]. The above-mentioned contradictory findings may result from differences in the age of tested trees. It cannot be excluded that the declining adaptability of LZD in the described experiment in relation to the Carpathian Gene Bank experiment, both located in the Bircza District, could have been due to the progressive erosion of the gene pool of the parental stand. Similar conclusions have been made in the study by Willi et al. [68] on the reduction of adaptive potential in small populations.

Our results are in contradiction with the theory of adaptive strategies to marginal conditions of silver fir [15]. Populations with the climate of origin the most different from the testing condition (Figure 3), LZD and KRA1, were manifested by high sensitivity to a shift of climatic condition. For KRA1, it seems to be related to different selective pressures in the lowland (north of the studied area) and experimental sites (high elevation). However, the maladaptation of the LZD population (the highest location among tested populations) seems to be surprising and may be related to the reaction to bioclimatic (out-group in Figure 3) and non-climatic environmental factors.

The composition of populations in a common garden significantly modifies the assessment of their adaptation potential. The populations characterized by the most unstable growth strongly determine the discriminatory strength of the environments (testing sites). The discriminatory strength may be indicative of the marginal conditions of growth in a given area. Because at the beginning of the experiment it is hardly possible to predict the growth response of progenies, the most complete composition of the population group should be considered. Only the least stable population could be excluded.

5. Conclusions

When determining the silver fir populations' adaptation to growth in marginal environments, the level of trait stability seems to affect assessment quality. The composition of the tested populations determines the accuracy of assessing the population adaptation to growth in marginal environments. Early tests appear to be useful for evaluating the silver fir adaptation to growth conditions in marginal environments. The adaptive potential of fir population seems to be related to its sensitivity to elevation and climatic conditions, in particular to: annual and seasonal rainfall, annual temperatures, growing season and seasonal temperature distribution, and maladaptation to marginal growth conditions.

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Abbreviations

AE	Average environment
AEC	Average environment coordination
BIR	Bircza experimental site
CIS	Cisna experimental site
Е	Effect of environment
G	Effect of genotype
$G \times E$	Genotype-environment interaction
GGE	Genotype and genotype-by-environment interaction biplot
KOM	Komańcza experimental site
LES	Lesko experimental site
MET	Multi-environment trial
PC1	First principal component
DCO	Concerned anning singel community

- PC2 Second principal component
- PCA Principal components analysis
- SVD singular value decomposition

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