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Jan Holeksa, Faculty of Biology,
Adam Mickiewicz University in
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AH planned and conducted the research, performed data analysis and wrote the manuscript; WW contributed to data analysis and manuscript writing; JS contributed to research design and data analysis; all authors critically reviewed and revised the manuscript for content and read and approved the final manuscript

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Competing interests

No competing interests have been declared.

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ORIGINAL RESEARCH PAPER

Long-term growth performance and productivity of Scots pine (*Pinus sylvestris* L.) populations

Anna Maria Hebda^{1*}, Witold Wachowiak^{2,3}, Jerzy Skrzyszewski⁴

¹ Department of Genetics and Forest Tree Breeding, Institute of Forest Ecology and Silviculture, Faculty of Forestry, University of Agriculture in Krakow, 29 Listopada 46, 31-425 Krakow, Poland

² Institute of Dendrology, Polish Academy of Sciences, Parkowa 5, 62-035 Kórnik, Poland

³ Institute of Environmental Biology, Faculty of Biology, Adam Mickiewicz University in Poznań, Umultowska 89, 61-614 Poznań, Poland

⁴ Department of Silviculture, Institute of Forest Ecology and Silviculture, Faculty of Forestry, University of Agriculture in Krakow, 29 Listopada 46, 31-425 Krakow, Poland

* Corresponding author. Email: a.hebda@ur.krakow.pl

Abstract

The phenotypic differentiation of 16 provenances of Scots pine originating from a wide variety of habitats that range from lowland to southern highland locations in Poland was assessed during 47 years of their growth and development in the Carpathian Mountains. The traits, including height, diameter at breast height, stem straightness, and crown width, were used to evaluate the differentiation of the provenances in their juvenile period and at maturity and were examined for patterns of local adaptation. The populations from northern Poland were characterized by the best growth and productivity, whereas provenances from central Poland had the best stem quality. There were some changes in growth between provenances observed during the experiment, but the stand volume (m³/ha) in juvenile trees was closely correlated with that in mature trees ($r = 0.979$). There was a positive relationship between the productivity and the environmental conditions of the geographical origin of provenances with increasing values for the trees' productivity from south to north. Additionally, the elevation above sea level of the original populations was inversely correlated with the growth achieved by the progeny. In general, most populations from the species distribution range in Poland tested in the severe climate conditions of the Carpathian Mountains showed good growth performance under that environment, characterized by low temperatures and short growing periods. Provenances from climatic zones outside mountain regions demonstrated great growth and productivity, which proved to be the most important for competitively outperforming the local populations. Our study demonstrates good adaptive potential of the tested provenances, as selection will favor fast-growing genotypes under the predicted environmental change scenario.

Keywords

quantitative traits; quality traits; local adaptation; forest trees

Introduction

Scots pine (*Pinus sylvestris* L.) is the most widely distributed conifer in Europe and Asia and has huge ecological and economic importance. This species shows good growth and development and thus good adaptation to a broad range of environmental conditions, and it is characterized by a low requirement for soil, rapid growth, and good wood quality [1,2]. In Poland, Scots pine is the most important forest-forming and utility species. Scots pine shows continuous distribution in the lowlands of Poland, where it forms approximately 70% of the total forest area. In the highlands of

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the Carpathians and Sudetes, Scots pine grows in a scattered distribution. Because of its great importance, Scots pine was used in several provenance trial experiments that showed differences in the shape of crown, needle length, cone form, tree habit, and growth as well as the resistance to frost and needle cast of populations originating from various environments [3–8]. Populations located in Poland showed very good growth performance compared to populations from other parts of the species range [3,8–13]. High clinal variation of phenotypic and quantitative traits related to the time of bud burst and bud set and resistance to low temperature, water stress, and pathogens has been observed across the species latitudinal range [14–16]. Several ecotypes and races of the species have been described based on morphological and phenotypical features of the populations across the range [3,5,7,17–19].

Climate is an important factor that affects population growth and productivity and consequently its survival or extinction. Trees are long-lived organisms that need to respond to environmental change during their life span. Plant populations can adapt to environmental changes through several mechanisms such as dispersal to track their preferred environmental conditions, phenotypic plasticity and genetic evolution through natural selection [20–22]. The potential of the adaptive response depends on the population genetic variation as determined by evolutionary and demographic processes including mutations, recombination, selection, and intraspecific gene flow. The above mechanisms affect the ability of a species to adapt to and successfully reproduce under changing environmental conditions.

Provenance trial experiments provide a unique opportunity for monitoring among- and within-population variability and the influence of environmental change on species fitness, including simultaneous assessments of species mortality and growth [23,24]. Such experiments are valuable for evaluating adaptive variability and transfer effects or seed transfer rules [6,25–28]. In this study, 16 provenances representative of the Polish range of native pine stands and established on an experimental plot in the lower part of the Polish Carpathians were analyzed. We present the results of the provenances' differentiation in phenotypic traits observed during 47 years of tree growth and assess potential patterns of local adaptation.

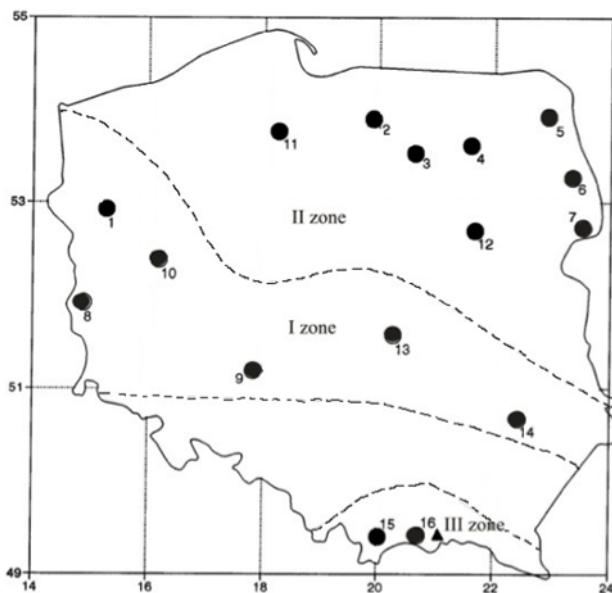


Fig. 1 Locations of the 16 Polish provenances of native Scots pine stands (black circles) grown in the experimental trial in Polish Carpathian Mountains (triangle). Dotted lines divide geographical regions: I – central Poland (lowlands), II – north-eastern Poland (lowlands), and III – southeastern Poland (mountains), referring to climatic zones with different lengths of the growing period (I > 215 days, II of 200 to 215 days, III < 200 days; [32] with modification).

Material and methods

Provenance trial experiment

The trial was established in 1966 in the Carpathian Mountains with 16 Scots pine (*Pinus sylvestris* L.) provenances originating from across the distribution range of this species in Poland (Fig. 1). Seeds were collected from parent trees in natural stands characterized by very good quality and growth [29]. Samples of seeds were mixtures from many mother trees. One-year-old seedlings were planted in a randomized block design with five repetitions (I, III, V, VII, IX; Fig. S1). Between these blocks, Scots pine seedlings representing four populations were planted, but those four populations belong to a separate experiment and will not be further discussed here.

Each plot contains a single provenance and is 17 m × 15 m, where 255 seedlings were planted in a spacing of 1 m × 1 m (17 rows with 15 plants). Plots within each of the five blocks (I, III, V, VII, IX) were separated by isolation strips of 2.0 and 2.4 m (Fig. S1) according to Chodzicki [29]. The sampled provenances include the races of lowland pines such as the populations from Rychtal and Bolewice (Population 9 and 10, respectively), the race of foothill pine from Nowy Targ (Population 15) and mountain pines from Piwniczna (Population 16; Tab. 1, Fig. 1).

Tab. 1 Characteristics of the Scots pine provenances included in the study.

Provenance (population) name	Latitude N	Longitude E	Altitude	Climatic zones	Name of forest
1. Karsko	52°54	15°15	75	I	Gorzów Forest
2. Tabórz	53°52	19°55	110	II	Tabórz Forest
3. Dłużek	53°31	20°38	145	II	Rudzko-Napiwodzkie Forest
4. Ruciane	53°37	21°35	145	II	Nidzka Forest
5. Rozpuda	53°55	22°55	205	II	Augustów Forest
6. Supraśl	53°15	23°20	165	II	Białystok Forest
7. Starzyna	52°38	23°37	170	II	Białowieża Forest
8. Gubin	51°55	14°50	70	I	Nadodrzańskie Forest
9. Rychtal	51°12	17°50	190	I	Namysłowsko-Ostrzeszowskie Forest
10. Bolewice	52°23	16°10	90	I	Nowotomyślki Forest
11. Lipowa	53°44	18°15	130	II	Tuchola Forest
12. Jegiel	52°40	21°40	95	II	Biała Puszcza (Mazovian Forest)
13. Spała	51°35	20°15	150	I	Spała Forest
14. Janów Lubelski	50°40	22°25	250	I	Puszcza Solska
15. Nowy Targ	49°20	20°20	590	III	Nowotarskie Forest
16. Piwniczna	49°20	20°17	500	III	Nadpodpradzkie Forest

I – central Poland (lowlands); II – northeastern Poland (lowlands); III – southeastern Poland (mountains).

The analyzed provenance trial was established in the twentieth century and possesses considerable value and information potential for eco-monitoring [30]. Damage from windstorms and snowfalls required some nursery thinning that was done during the experiment. This minor silvicultural impact on stand dynamics was strictly and consistently maintained under scientific control. This management reduced the number of trees without impacting the crown layer [30]. After 47 years of tree growth and testing, the trial includes approximately 2300 trees.

Climate of the provenance trial experiment

The provenance trial was located at a height of 620 m above sea level in mixed mountain forest on brown soil in the Carpathians. The site is an example of a pluvial-snow area with climate characterized by an average annual temperature of approximately 5.4°C, a total annual precipitation exceeding 1000 mm, and a growing season shorter than 200 days [31].

Climates of seed sources

The length of the vegetation period and meteorological observations from 1931 to 1960 were the basis for defining three climatic zones of the geographical origin of the parental populations (based on [32]). Mean parameters and indexes of climate characteristics of the sites during 1965–2010 were obtained using a climate service [33] and are summarized in a table (Tab. S1). Those three climatic regions covered different seed zones for Scots pine in Poland. Despite only minor differences between climate parameters for the characterized climatic zones, there were still differences in

the length of the vegetation period, which might influence the growth and development of first the seedlings and then the trees growing on the experimental site.

Measurements of phenotypic traits

The historical records [32] and newly gathered data of quantity and quality traits of the studied pine provenances cover 47 years of their development.

In Fall 2011, the heights of all growing trees on the experimental site were measured using a Vertex altimeter with accuracy of 0.1 m. At the same time, diameter at breast height (1.3 m) was measured for all growing trees using a diameter-measuring instrument with accuracy of 0.1 cm. The two characteristics, height and diameter at breast height, along with the breast-height form factor [34], allowed the calculation of the single tree volume (m³; according to Eq. 1), which was used to estimate the productivity of tested provenances per hectare (m³/ha) according to Eq. 4.

$$v = ghf \tag{Eq. 1}$$

$$g = \pi\left(\frac{1}{2}d\right)^2 \tag{Eq. 2}$$

$$f = \frac{1}{1 + \left(\frac{d}{1.2895 + 0.90645d}\right)^4} \tag{Eq. 3}$$

Here, v is the single tree volume (m³), g is the area of a circle, h is the height, f is the breast-height form factor [34], and d is the diameter at breast height.

$$V = \frac{\bar{v}}{0.1275} \tag{Eq. 4}$$

Here, V is the stand volume (m³/ha), \bar{v} is the mean tree volume in the population (m³), and 0.1275 is the area of each provenance at the experimental site (ha).

Those new and historical data (Tab. S2) were used to evaluate the differences between populations. For each trait, each tested provenance was characterized based on the averages (\bar{x}), standard deviation (S) and coefficient of variation ($V\%$), which was calculated according to Eq. 5:

$$V\% = \frac{S}{\bar{x}}100 \tag{Eq. 5}$$

where \bar{x} is the total mean of a specific trait.

The impact of tree density on the differentiation of the traits was assessed using analysis of variance (ANOVA) with a single-factor completely randomized model. Then, analysis of covariance (ANCOVA) was conducted to test for differences of provenances, a block effect and their interaction because of the significant correlation of tested traits with the tree density in the year of measurement [35]. ANCOVA tests populations after the corrections of the values of their traits by including information about the additional variable that disturbs the impact of provenance on the trait. In the ANCOVA, corrected values of traits refer to the same number of trees that were used for the evaluation of impact of the provenance. ANCOVAs were performed according to a completely randomized model [25]:

$$y_{jkn} = \mu + P_k + B_j + PB_{kj} + \beta(x_{kj} - X) + e_{n(jk)} \tag{Eq. 6}$$

where y_{jkn} is the n th observation on the k th population from the j th block, μ is the overall mean, P_k is the effect of the k th population, B_j is the effect of the j th block, PB_{kj} is the interaction of the k th population and the j th block, β is the correlation coefficient between variables: x_{kj} is the number of trees in the k th population from the j th block, and X is the overall mean for number of trees. The size of the covariance effect was estimated using partial eta squared (η^2) following Eq. 7:

$$\eta^2 = \frac{SS_T}{(SS_T + SS_E)} \tag{Eq. 7}$$

where SS_T is the total sum of squares and SS_E is the error of the sum of squares.

If the ANCOVA results allowed the rejection of the hypothesis of no differences between provenances, the post-hoc NIR Fisher test was performed.

Scots pine were characterized by comparisons of height and diameter at breast height in subsequent years of testing. Values of growth traits were standardized in order to compare tested provenances in various ages of trees according to Eq. 8:

$$J_s = \frac{x - \bar{X}}{S} \quad \text{Eq. 8}$$

where J_s is a unit of standard deviation, x is the mean value of a trait for a given population, \bar{X} is the total mean for trait x , and S is the standard deviation.

Additionally, several quality traits were tested for all growing trees on the experimental site including stem straightness (SS), crown width (CW), branch angle (BA) and branch thickness (BT). The diameter (cm) of the thickest Scots pine knot on the trunk at the height of 4 m from the ground was also measured. The phenotypic features and their quality scale are characterized in a table (Tab. S3). The averages of traits were estimated, and the same statistical analyses were performed as for growth traits. ANCOVA was also used because the variation in the number of trees in the plots at the experimental site might perturb the effects of genotype on the quality traits [35].

The relationships between growth and quality traits were evaluated based on the means of provenances following Eq. 9 [25]:

$$r_{xy} = \frac{\text{cov}(xy)}{\sqrt{\text{var}(x)\text{var}(y)}} \quad \text{Eq. 9}$$

where r_{xy} is the coefficient of correlation between two traits x and y , $\text{cov}(xy)$ – components of phenotype covariance, $\text{var}(x)$, $\text{var}(y)$ – components of phenotype variance.

This method was also applied to verify how the shape of trait means depends on the specific environment of the origin of the population. Characteristics including latitude, longitude, and evaluation of parental stands were used for phenotype–environmental correlation.

Furthermore, we investigated how natural selection or selective thinning could affect the growth changes of the pine populations. To do so, we assessed the correlation between the 10 trees achieving the best diameter at breast height in every five repetitions (i.e., approximately 50 trees per provenance) and the diameter of all 47-year-old trees.

Principal component analysis (PCA) was used to demonstrate the relationships between the tested provenances that were differentiated by the studied phenotypic traits. PCA was also used to identify components (traits) that influenced this variation significantly. The PCA method allowed the classification of multidimensional variables that were the means of the tested traits. Those features might be described by using one or more new variables called principal components which constitute some percentage of the trait variation. The data used in this analysis were first standardized according to Eq. 8.

All statistical analyses of measured and scored traits of trees were conducted with the statistical software Statistica 10 [36].

Results

After growing for 47 years in the provenance trial, Scots pine reached an average tree height of 22.4 m and an average diameter of 23.9 cm (Tab. 2). Between provenances, tree ranged from 21.9 m to 23.0 m in height and from 22.3 cm to 25.6 m in diameter. Provenances were characterized by the volume of single trees, which ranged from 0.43 m³ to 0.56 m³ and averaged 0.50 m³ (Tab. 2). The average stand volume was 559.9 m³/ha, with the variation between provenances ranging from 363.2 m³/ha to 676.8 m³/ha (Tab. 2).

The differentiation between provenances in respect to all tested traits was significantly impacted ($p < 0.001$) by the provenances density. Thus, differentiation analysis

Tab. 2 Mean values of growth and productivity parameters determined for individual provenances of Scots pine.

Provenance (population)	Number of trees	Diameter (cm)	Height (m)	Volume of single tree (m ³)	Stand volume (m ³ /ha)
1. Karsko	131	25.58 ^f	22.45	0.56 ^g	576.44 ^{cde}
2. Tabórz	164	23.65 ^{bcd}	22.59	0.50 ^{cdef}	643.37 ^{de}
3. Dłużek	142	24.67 ^{def}	22.18	0.52 ^{cdefg}	575.68 ^{cde}
4. Ruciane	138	24.71 ^{def}	22.54	0.53 ^{defg}	575.72 ^{cde}
5. Rozpuda	162	23.80 ^{bcde}	22.20	0.49 ^{bcd}	620.55 ^{de}
6. Supraśl	173	24.11 ^{cde}	22.30	0.49 ^{bcde}	670.80 ^e
7. Starzyna	135	23.78 ^{bcde}	21.87	0.48 ^{abcd}	512.13 ^{bcd}
8. Gubin	108	22.30 ^a	22.00	0.43 ^a	363.15 ^a
9. Rychtal	156	23.32 ^{abc}	22.44	0.48 ^{abc}	582.79 ^{cde}
10. Bolewice	175	22.69 ^{ab}	22.03	0.44 ^{ab}	609.29 ^{de}
11. Lipowa	158	24.93 ^{ef}	22.92	0.55 ^{efg}	676.78 ^e
12. Jagiel	140	23.82 ^{bcde}	22.34	0.49 ^{bcd}	538.81 ^{bcde}
13. Spała	142	23.19 ^{abc}	21.96	0.47 ^{abc}	518.80 ^{bcd}
14. Janów Lubelski	163	23.41 ^{abc}	22.63	0.49 ^{abcd}	620.71 ^{de}
15. Nowy Targ	102	25.08 ^{ef}	22.99	0.56 ^{fg}	444.39 ^{abc}
16. Piwniczna	112	23.63 ^{abcd}	22.26	0.49 ^{abcde}	428.61 ^{ab}
Sum/Mean	2301	23.92	22.36	0.50	559.88
Standard deviation	-	0.86	0.31	0.04	85.79
Coefficient of variation	-	3.60%	1.41%	7.28%	15.32%

The best provenances for specific traits are marked in bold. The same letters indicate homogenous groups.

was performed using ANCOVA for which the values of traits were corrected to refer to the same number of trees.

Growth traits

Differentiation in quantity traits of tested Scots pine provenances was significant (Fig. 2a, Tab. 2). Diversity in height was small, with coefficients of variation of 1.41% (Tab. 2). ANCOVA showed that the interaction between genotype (provenance) and environment (block) significantly affected the trait development (Tab. 3).

Marked differentiation between provenances observed in diameter at breast height, with a coefficient of variation of 3.6% (Fig. 2b, Tab. 2). This differentiation had a strong genetic component with a high covariance effect (0.637205), which means that nearly 64% of the trait variability was explained by the provenance (Tab. 3). Six homogenous groups were distinguished, but none was separated (Tab. 2). The best values for diameter were characterized for Population 1 and 11 from the lowlands of Poland and for a local population, Population 15.

The above provenances were also the best based on the single-tree volume (m³; Fig. 2c). Differentiation of this trait was mainly due to genotype, as no significant influence of environment (block) and/or interaction between the genotype and block was observed (Tab. 3). Stand volume (m³/ha) is one of the tree characteristics that depend on the ability to survive and on the growth potential of the specific population.

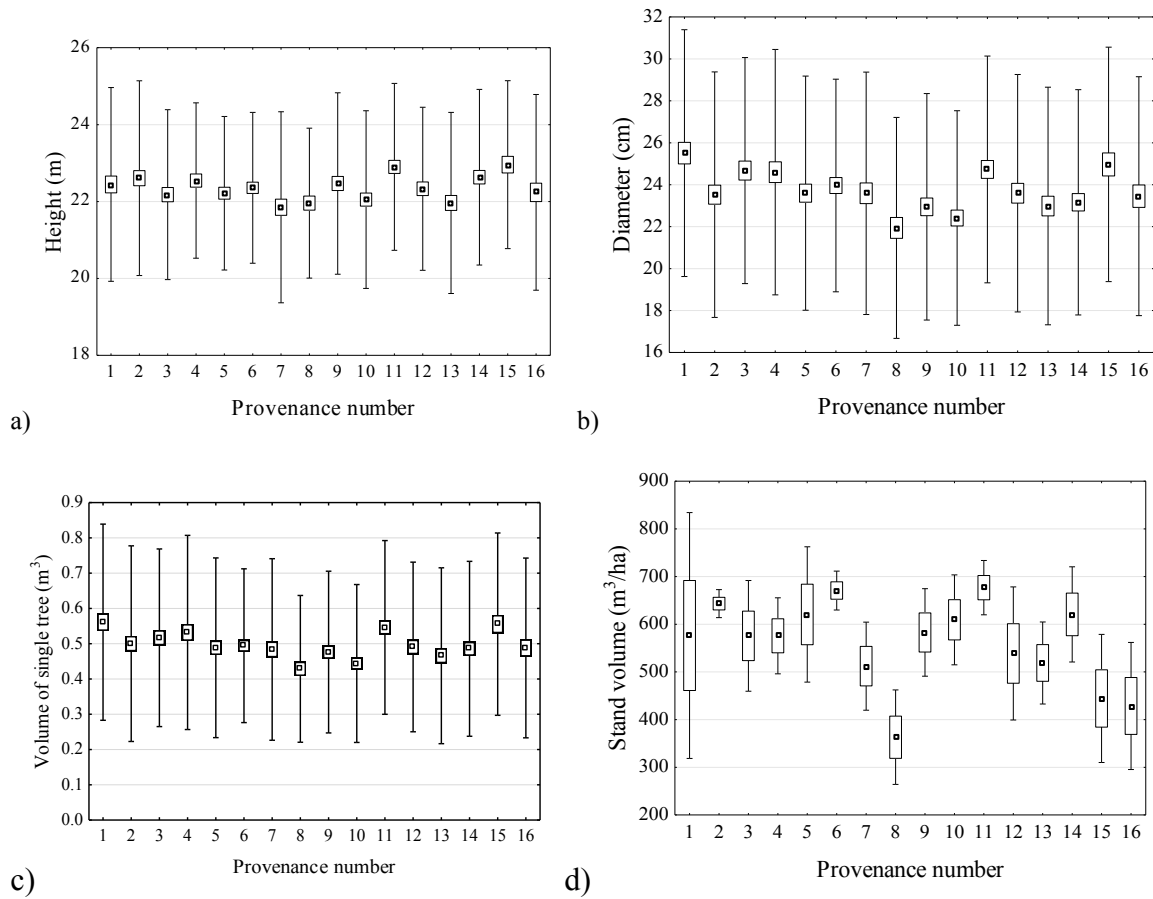


Fig. 2 Variation in height (m; **a**), diameter (cm; **b**), single-tree volume (m³; **c**), and stand volume (m³/ha; **d**) of the individual provenances, shown as the means (small boxes), means ± 1 standard error (larger boxes), and means ± 1 standard deviation (whiskers).

This trait differentiated analyzed provenances than did height or diameter based on the coefficient of variation, and it ranged from 363.15 to 676.78 m³/ha (Tab. 2). The best values were observed for provenances from northeastern Poland: Populations 2, 6, and 11 (Fig. 2d). Local provenances were characterized by weak average stand volume, but one population from Nowy Targ (Population 15) was characterized by very good growth and large single-tree volume. The divergence between the single-tree volume (m³) and the stand volume (m³/ha) for this population resulted from the low number of surviving trees (Tab. 2).

The changes in group of provenances showing the best growth were constantly observed over the 47 years of testing the trees (Fig. S2, Fig. S3). The best and most stable growth over the life span of the experiment was observed for Provenance 1, from central Poland and for Provenances 3 and 11, from northeastern Poland. Growth characteristics for local provenances improved over time. The sources of differentiation in growth traits differed in subsequent years of tree testing, with a substantial impact of environment (block) on tree height. The ranges of trait values and their characteristics in years of experiment are presented in figures (Fig. S2, Fig. S3).

Quality traits

Of the quality traits tested, only the stem straightness and the crown width differed significantly among the analyzed provenances (Tab. 3). The average values of these characteristics are presented in a figure (Fig. 3a,b). Among all of the tested populations, lowland provenances (Populations 9, 10, and 14) from central Poland were characterized by very straight stems. There was a difference in the crown width among provenances: trees with the thin crowns belonged to Populations 2, 6, and 10 from

Tab. 3 Analysis of covariance of a specific trait of Scots pine in the age of 47 on the experimental area.

Source	df	MS	F	p	η^2
Height (m)					
Provenance	15	16	1.30	0.2103	0.2677
Block	4	5	0.40	0.7807	0.0309
Block × Provenance	59	11	2.20	0.0000	0.0559
Error	2221	5			
Diameter (cm)					
Provenance	15	146	5.79	0.0000	0.6372
Block	4	22	0.89	0.4774	0.0673
Block × Provenance	59	25	0.90	0.6911	0.0233
Error	2221	28			
Volume (m³)					
Provenance	15	0.26	4.36	0.0000	0.5644
Block	4	0.04	0.67	0.6039	0.0518
Block × Provenance	59	0.06	1.01	0.4493	0.0262
Error	2221	0.06			
* Stand volume (m³/ha)					
Provenance	15	9455	2.73	0.0028	0.3940
Error	63	3463			
Stem straightness					
Provenance	15	1.27	2.15	0.0199	0.3637
Block	4	2.53	4.25	0.0045	0.2325
Block × Provenance	59	0.57	2.46	0.0000	0.0799
Error	1669	0.23			
Crown width					
Provenance	15	0.73	2.53	0.0065	0.4116
Block	4	3.50	12.08	0.0000	0.4736
Block × Provenance	59	0.29	1.30	0.0622	0.0441
Error	1669	0.22			
Branch angle					
Provenance	15	0.49	0.57	0.8849	0.1310
Block	4	1.62	1.90	0.1236	0.1183
Block × Provenance	59	0.82	2.85	0.0000	0.0917
Error	1669	0.29			
Branch thickness					
Provenance	15	0.80	1.49	0.1393	0.2845
Block	4	9.14	17.10	0.0000	0.5495

Tab. 3 Continued					
Source	<i>df</i>	<i>MS</i>	<i>F</i>	<i>p</i>	η^2
Block × Provenance	59	0.52	2.37	0.0000	0.0774
Error	1669	0.22			
Knots					
Provenance	15	3.38	1.73	0.0719	0.3176
Block	4	5.61	2.86	0.0317	0.1713
Block × Provenance	59	1.90	1.90	0.0001	0.0628
Error	1669	1.00			

Statistically significant values are marked in bold. *df* – number of degrees of freedoms; *MS* – mean of squares; *F* – statistics *F*; *p* – probability; η^2 – partial eta squared. * In the ANCOVA, the impact of block and interaction for stand volume were not possible to be considered.

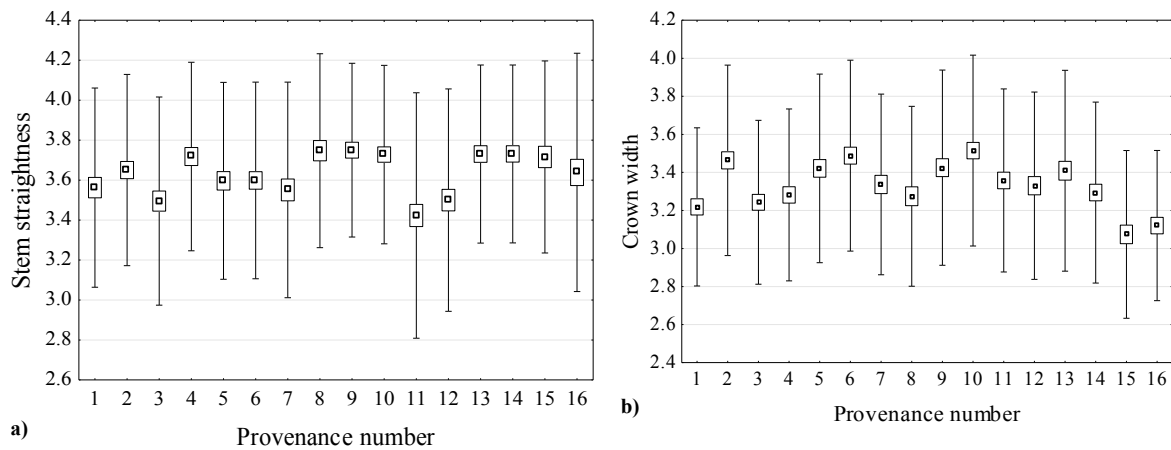


Fig. 3 Variation in stem straightness (SS; **a**) and crown width (CW; **b**) of the individual populations, shown as the means (small boxes), means ±1 standard error (larger boxes), and means ±1 standard deviation (whiskers).

central Poland and northeastern Poland. Provenances 9, 13, and 14 were characterized by the smallest branch angle, while Provenances 4, 8, and 12 had the thinnest branches (not shown). The smallest knots diameters were observed for Provenances 8, 14, and 15 (not shown).

Correlations between phenotypic traits

High and mostly significant correlations were observed between growth traits such as height and diameter (Tab. 4). The highest correlation ($r = 0.979$) was observed between the stand volume (volume m³/ha) evaluated for trees during the late-juvenile (25 years) and mature developmental stage (47 years). For selected trees, these parameters also correlated with diameter with $r = 0.707$ and $r = 0.733$, respectively. The relationships between growth traits and quality features were positive or negative depending on the specific traits. Stem straightness was negatively correlated with all features except the crown width. CW was positively and significantly correlated with stand volume (for both 47-year-old trees and 25-year-old trees). Branch angle was negatively and significantly correlated with stand volume of 47-year-old trees and CW, whereas branch thickness was correlated positively with growth traits and negatively with quality traits. Knot diameter was correlated positively and significantly only with branch angle.

Tab. 4 Phenotypic correlation of the analyzed traits.

Trait	Height_47	Height_36	Diameter_47	Diameter_47 select	Diameter_35	Volume m ³ /ha_47	Volume m ³ /ha_25	SS	CW	BA	BT
Height_36	0.592										
Diameter_47	0.570	0.385									
Diameter_47 select	0.553	0.519	0.824								
Diameter_35	0.557	0.300	0.834	0.722							
Volume m ³ /ha_47	0.340	0.414	0.267	0.707	0.245						
Volume m ³ /ha_25	0.349	0.444	0.343	0.733	0.285	0.979					
SS	-0.096	-0.448	-0.538	-0.554	-0.384	-0.344	-0.408				
CW	-0.270	0.010	-0.447	0.067	-0.344	0.640	0.555	0.035			
BA	-0.063	0.100	0.297	-0.063	0.111	-0.536	-0.491	-0.310	-0.598		
BT	0.369	0.217	0.375	0.356	0.056	0.207	0.285	-0.095	-0.193	-0.168	
Knot	-0.107	0.099	0.449	0.406	0.072	0.102	0.149	-0.467	-0.118	0.554	0.041

The values shown in bold are statistically significant at the level of $p = 0.05$. SS – stem straightness; CW – crown width; BA – branch angle; BT – branch thickness.

Phenotype–environment correlation

Latitude of population origin was positively correlated with almost all growth traits but this correlation was only statistically significant between latitude and diameter for selected trees and between latitude and stand volume (Tab. 5). Latitude was also significantly and negatively correlated with stem straightness and positively correlated with crown width. Elevation of population origin showed positive and negative correlation with different quantity and quality traits (Tab. 5). Elevation of provenances was negatively correlated with crown width and positively correlated with branch thickness.

Based on the PCA analysis, two principal components were distinguished, representing 86.19% of all differentiation of traits (Fig. 4, Tab. S4). Three analyzed traits that were directed against the X-axis, the diameter, the stand volume, and the stem straightness, had the most impact on variability between populations. The provenances from northeastern Poland were clustered on one side of the X-axis, whereas the provenances from the other climatic zones were grouped on the opposite side. Provenances 1 and 8 were the only ones that did not fit into the clustering by climatic zones. Provenance 1 was grouped with trees from northeastern Poland, and Population 8 differed from all other provenances.

The trait that showed the largest impact on the differentiation of provenances was the crown width along the Y-axis. This trait clearly clustered the provenances from central Poland and from southeastern Poland on opposite sides of the Y-axis. The provenances from northeastern Poland were varied and did not form a compact cluster on one side of the Y-axis.

The PCA results showed the differentiation of traits among climatic zones and demonstrated that the provenances from northeastern Poland were characterized by the high values for stand volume and diameter. The provenances from central Poland had the best stem quality. The provenances from southeastern Poland were differentiated from the provenances from northeastern Poland based on growth traits and from the provenances from central Poland based on quality traits.

Tab. 5 Phenotype–environment correlation of the analyzed traits.

Trait	Latitude	Longitude	Altitude
Height_47	-0.102	0.017	0.367
Height_36	0.122	0.053	0.040
Diameter_47	0.203	0.155	0.202
Diameter_47 select	0.519	0.231	-0.135
Diameter_35	0.336	0.089	-0.013
Volume m ³ /ha_47	0.622	0.249	-0.404
Volume m ³ /ha_25	0.576	0.297	-0.333
SS	-0.506	-0.208	0.217
CW	0.573	0.060	-0.652
BA	-0.186	-0.007	0.366
BT	-0.307	0.449	0.612
Knot	0.167	0.026	-0.014

The values shown in bold are statistically significant at the level of $p = 0.05$. SS – stem straightness; CW – crown width; BA – branch angle; BT – branch thickness.

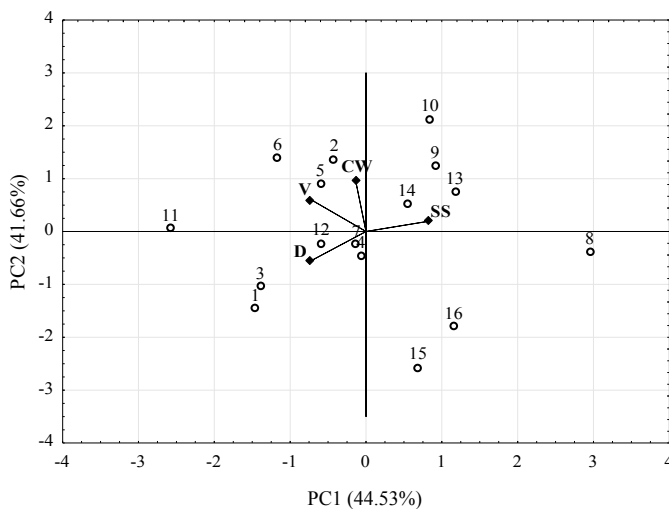


Fig. 4 The grouping of provenances tested on the experimental site using PCA. 1–16 – provenance numbers; D – diameter; V – stand volume (m³/ha); SS – stem straightness; CW – crown width.

Discussion

Population growth in a mountain environment

Provenances from the Polish range of Scots pine growing on the experimental site in the Carpathian Mountains showed continuous changes in the provenances showing the best growth during 47 years of research. However, a high correlation (0.979) was observed between the stand volume (m³/ha) evaluated for provenances at 25 years of growth and the stand volume evaluated for provenances at 47 years of growth. This result showed that the same provenances were the most productive up to the age of 25 (late-juvenile stage) and to the age of 47 (maturity). Moreover, this correlation result showed that the stability, referring to the productivity and adaptation of populations was established by the juvenile stage in the mountain environment. Similar conclusions were obtained by Barzdajn [37,38] and Barzdajn et al. [39]. During 30 years of testing the variability of growth and survival of European provenances of Scots pine growing on the experimental plot in the lowlands of Poland, they observed only minor changes in the group of the most productive populations. These results suggested that conclusions about the productivity of various provenances of Scots pine could be drawn by late-juvenile stage. This is related to the specificity of *Pinus sylvestris*, which is a species characterized by fast growth, fast differentiation of populations, and self-thinning during the juvenile period [40]. Evaluation of differences in the growth rate and productivity of the Polish pine populations showed that the provenances from northeastern Poland (Populations 2, 6, and 11) demonstrated the best productivity. After diameter, the stand volume was most effective for differentiating provenances according to the PCA. The excellent performance of pine provenances from northeastern Poland have also been reported based on previous experiments [3,8,38].

Differentiation of provenances growing on the experimental site in the Carpathians was also evaluated based on the quality traits. This evaluation showed that provenances from the central Poland (Populations 9, 10, and 14) were characterized by the best quality. Much of research

on the variability of Scots pine has shown that quality traits are generally inversely correlated with growth characteristics [8,27]. This relationship was confirmed in the correlation and the PCA, in which the stem straightness was negatively correlated with the stand volume and the diameter. Provenances from central and southeastern Poland were characterized by the lower values for stand volume and diameter and by straighter stems compared with provenances from northeastern Poland. In contrast, crown width was positively correlated with the stand volume and divided provenances from southeastern Poland with wide crowns from provenances from central Poland with narrow crowns. Those results provide opportunity to select provenances from northeastern Poland that are characterized by good growth and good quality of the crown width.

Patterns of phenotypic variation across different environments

The natural distribution of populations depends on phenotypic variation, strength of selection, fertility, interspecific competition, and biotic interactions [41]. Analyzed provenances were exposed to a colder, higher-elevation environment than those in which the populations originated.

The results of the present study indicate that there are differences between provenances from various latitudes in the growth shape and in quality traits. High correlations between the latitude of the origin of the provenances and the productivity (stand volume m^3/ha) of the tested trees may suggest a differentiation in productivity in the native range of Scots pine distribution. In Poland, the local climate does not vary as strongly with latitude as in Scandinavia, but some growth dependence on latitude can be observed and has been described in other studies [7,42–44].

The elevation above sea level of the origin location of each provenance is another environmental factor that may affect the growth and development of provenances tested at the experimental site. This factor was mainly inversely correlated with growth traits and was contributed to lower productivity of a population. These findings are consistent with other studies [16,27], with the reservation that the analyzed populations in the previous publications originated from high and low elevations but were tested under lowland environmental conditions.

Many experiments using multiple provenances show the best growth and performance are associated with phenotypic traits of local populations [3,11,45]. Therefore, we could expect that the local provenances from mountainous areas should be best adapted to the severe climate of their natural habitat in the Carpathian Mountains. However, compared to other provenances, they showed a relatively high mortality rate [also reflected by a weak stand volume (m^3/ha)] during the entire period of juvenile growth [32]. In contrast, pines from lowlands located in northern Poland show good growth performance under the elevation and other climate conditions present in the mountain environment of the experimental site. Provenances from central Poland were characterized by differentiated growth, with high or low productivity, and by very straight stems and thin crowns. Analysis of the experimental results demonstrated that, contrary to expectations, provenances from northeastern Poland did not achieve poorer growth rates than their local competitors [46,47]. Lowland pines from Poland are characterized by very good growth potential and can exclude the genotypes of other populations from their site of origin. Similar phenomena of competitive exclusion have been reported by Reigheltdt et al. [22,48] based on studies of different growth potentials and survival of numerous *Pinus sylvestris* and *P. contorta* populations. Our results also suggest better development of fitness-related traits for populations from environments characterized by milder climatic conditions than the local provenances [49]. A report by Sabor [32] shows that during the juvenile period, the majority of lowland pines (nine of fourteen provenances) demonstrated better survival than the average for all populations, as well as better survival than locally adapted provenances. Additionally, pines from the northeastern Poland had higher than average values for height during the juvenile growth period.

Local stands, represented among others by trees from Nowy Targ, have also been tested in other provenance experiments. In one of these other experiments, progeny of a Scots pine stand from Nowy Targ produced from seeds collected in the winter of 1984–1985 was characterized by the lowest productivity compared to other populations from Poland [35]. There are several possible explanations for this observation. One possibility is weak fitness and fertility of the seeds used from those locations for establishing trial. In general, a small number of trees producing seeds seems characteristic for pines growing in the lowlands and highlands of the Carpathian Mountains [50]. The habitats of Scots pine populations in the highlands show a scattered distribution [17]. Topographical features of the landscape that limit gene flow may narrow the genetic divergence and reduce the adaptive ability of trees [51]. Populations existing at the margin of the distribution may be seriously degraded, inbred and exposed to unknown random effects. To date, the local provenances used in our research have only been analyzed with the use of monoterpene markers such as estimation of the mean percentages of the genetic markers α - and β -pinene and Δ^3 -carene in the total content of the bark tissue [32]. Trees from Nowy Targ and Piwniczna were characterized by

very low levels of α - and β -pinene and a high percentage of Δ^3 -carene. In contrast, pines from central and western Poland showed high α - and β -pinene levels and an increase in the Δ^3 -carene content. Therefore, more detailed studies of the genetic variation and structure of the local provenances compared to lowland stands are needed to provide a better understanding of the reasons underlying their weak fitness.

Conclusions

- Scots pine showed high differentiation based on diameter at breast high and stand volume (m^3/ha) and high variation of stem straightness and crown width according to the provenance.
- Pines from lowland stands from northern and northeastern Poland (Populations 2, 6, and 11) showed very good growth and development during 47 years of growth in the environmental conditions of the Carpathian Mountains. Provenances from central Poland were characterized by the best quality traits.
- Despite constant changes in the group of provenances showing the best growth traits, the most productive provenances at maturity were also the most productive in the late-juvenile stage. Stability in tree production and adaptation of populations were established by the juvenile stage in the mountain environment.
- Local stands were outperformed by better growing lowland pines. Due to their innate growth potential pines from the northeastern Poland were able to compete successfully with the local provenances. Growth potential proved to be more important for pine trees to achieve the best growth and the greatest stand volume (m^3/ha) in the specific climatic conditions than traits related to adaptation to the mountain environment.

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Supplementary material

The following supplementary material for this article is available at <http://pbsociety.org.pl/journals/index.php/asbp/rt/suppFiles/asbp.3521/0>:

Fig. S1 Distribution of the Scots pine populations in the provenance trial experiment.

Fig. S2 The mean heights for provenances at years 5, 10, 14, 21, 25, 36, and 47.

Fig. S3 The mean diameter at the breast height at ages 5, 21, 25, 35, and 47 and the mean diameter evaluated for 50 selected dominant diameter trees.

Tab. S1 Mean parameters and indexes of the three climate zones in Poland between 1965 and 2010.

Tab. S2 Various features of Scots pine tested at the experimental site in the Carpathians used in the presented research.

Tab. S3 Quality traits analyzed.

Tab. S4 Eigenvector scores of tested traits.

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