DOI: 10.1515/frp-2015-0005
Available online: www.lesne-prace-badawcze.pl

ORIGINAL RESEARCH ARTICLE

Leśne Prace Badawcze / *Forest Research Papers*
March 2015, Vol. 76 (1): 49–58

e-ISSN 2082-8926

Evaluating the progeny of European beech (*Fagus sylvatica* L.) in the early years of growth

Jacek Banach*, Kinga Skrzyszewska, Mateusz Smętek, Kamil Kubacki

Hugon Kołłątaj Agricultural University in Krakow, Faculty of Forestry, Institute of Forest Ecology and Silviculture, Department of Genetics and Forest Tree Breeding, Al. 29 Listopada 46, 31–425 Kraków, Poland.

* Tel./fax +48 12 662 51 28, e-mail: rlbanach@cyf-kr.edu.pl

Abstract. This research was carried out on two experimental plots located in the Rymanów and Nawojowa forest districts. In the second and fifth year after planting, at three and six years of age respectively, survival and height of 25 beech progenies of selected seed stands were measured. Furthermore, we show the effect of beech origin and growth environment (significant 'provenance × block' and 'provenance × test plot' interactions). Beeches from both experimental plots differed significantly in growth and survival and this difference increased with tree age. The highest provenance heritability was obtained for the tree height after two years of growth in Rymanów. In Nawojowa, the heritability of beech survival reached zero after five years of growth. An evaluation of the stability of beech provenances (genotypes) in terms of survival and height under the habitat conditions of our experimental plots was done using the Finlay and Wilkinson method. The beech provenances of 469–Nawojowa and 452–Lesko (regional standard) were included as a stable basis for reference. A high degree of stability and high average values for the characteristics investigated indicate high progeny quality within these stands.

Keywords: testing program, survival, tree height, heritability, stability of genotypes

1. Introduction and study aims

The variability of individuals comprising the tree populations of forests is an essential condition for the effective selection of the most valuable provenances. It is the basis for the adaptability, stability and sustainability of forest ecosystems in the face of changing climates and environmental stress.

For a better understanding of the growth potential of specific populations of the most important forest species, we have been implementing 'A programme of testing the progeny of selected seed stands, high quality trees, seed plantations and seed stand planting stock' (Sabor et al. 2004) since 2004 in Poland. Knowledge of the breeding value of the progeny of each seed provenance, as well as an analysis of the interaction of adaptive traits to growing conditions is very important for proper forest management. Establishing plantations by using the offspring of the best seed sources growing in a particular region could provide progeny stands with good parameters of growth, quality and health. For each species in the testing programme, the area of Poland was divided into test regions of the seed base. The four test regions established for the European beech are presented in Figure 1.

Poland's first test plantations of beech were established in 2006 in region III (south-west) and region IV (south-east). Currently, there are 28 test plantations where beech progeny of randomly chosen trees from selected seed stands and parent trees are being tested, and this number is steadily increasing.

This study presents the results of an assessment of the adaptive traits of survival and height in the second and fifth years of age of European beech progeny from selected seed stands. The study was conducted in the south-eastern region of beech testing in experimental plantations located in the Rymanów and Nawojowa Forest Districts.

2. Materials and methods

The first test stand in the Rymanów Forest District was established in Lipowiec Forest Range (subdivision

Received: 13.06.2014, reviewed: 30.06.2014, accepted after revision: 11.07.2014.

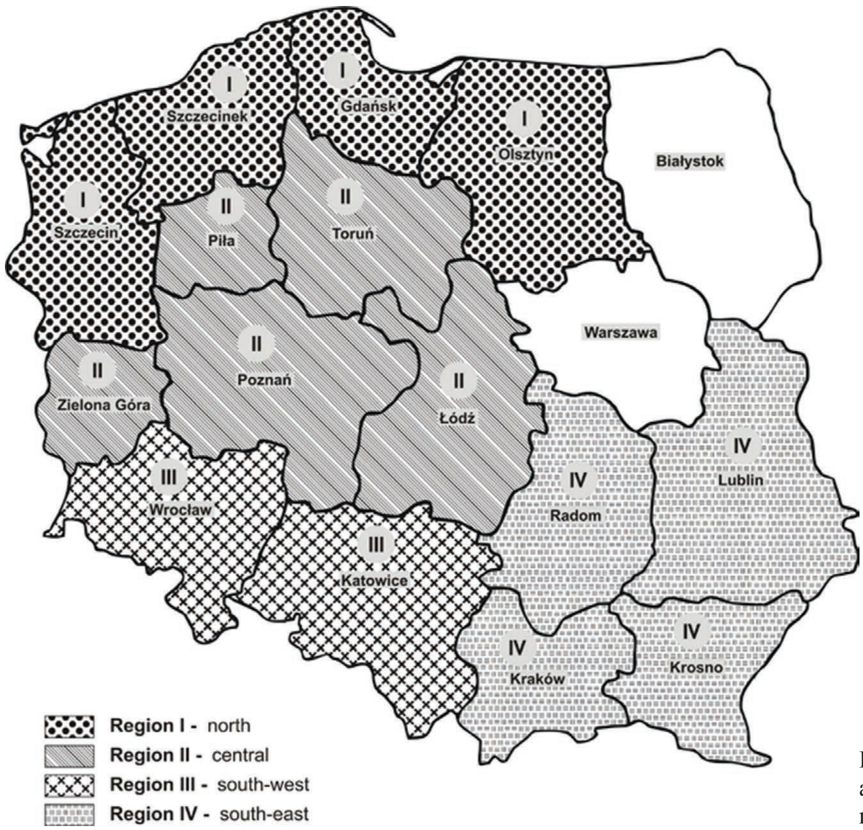

Figure 1. Testing regions of European beech against the division of the State Forests into regional directorates (Sabor et al. 2004)

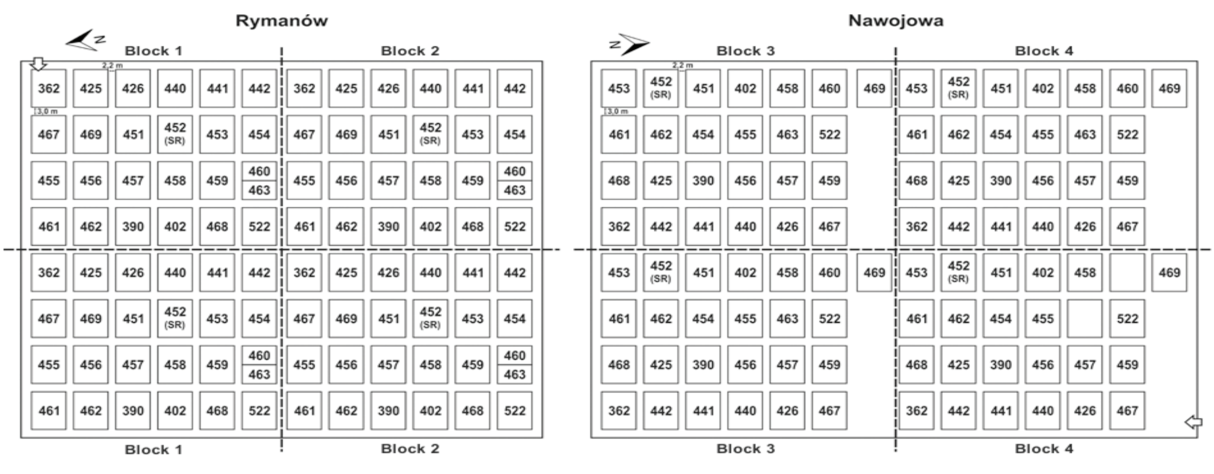

Figure 2. Distribution of replication and provenance plots on the test area with offspring of the European beech, situated at Rymanów and Nawojowa forest districts; 362–522 – numbers of stands according to the Table 1

147Anp) on flat, uncultivated land, formerly used as a meadow. In terms of natural-forest regionalisation, this is the Low Beskid subregion of the Carpathian region. The second test plantation is in the Berest Forest Range (subdivision 152k) of the Nawojowa Forest District, also in the Carpathian region, in the Gorce and Beskid Sądecki subregion. The stand was established on an eastern facing slope in an area cleared of a deteriorating spruce stand. Both plots were fenced in 2005 and planted the following spring with the test material.

Table 1. Characteristics of the selected seed stand of whose offspring is studied in south-eastern region of testing

RDLP*	No and name of provenance	Sub-compartment	Area (ha)	Geographical coordinates		Altitude	Region symbol
				longitude	latitude		
Kraków	362 –Gromnik	110c	15.06	21°11′	49°51′	399	852
	425 –Łosie	25b	30.00	21°07′	49°37′	540	854
	426 –Łosie	14a	21.19	21°00′	49°29′	554	854
	440 –Stary Sącz	134ac,135ikmn, 136c	36.64	20°36′	49°29′	641	803
	441 –Brzesko	100d	7.00	20°31′	49°50′	431	852
	442 –Brzesko	101b	7.00	20°31′	49°50′	431	852
	467 –Nawojowa	354m	4.91	20°48′	49°29′	775–850	803
	469 –Nawojowa	340c	21.48	20°49′	49°28′	894	803
Krosno	451 –Lutowiska	63b	20.14	22°34′	49°12′	620–860	806
	452 –Lesko (SR)	81c, 82c, 83ac	39.22	22°15′	49°23′	537	806
	453 –Bircza	166c, 167af	14.70	22°38′	49°37′	373–530	804
	454 –Bircza	62c, 63bc, 64abc	76.40	22°34′	49°41′	409–573	804
	455 –Krasiczyn	173a, 176a	19.27	22°35′	49°41′	421	804
	456 –Krasiczyn	131a	10.48	22°36′	49°48′	369	804
	457 –Rymanów	9a	5.00	22°01′	49°33′	388	806
	458 –Rymanów	15a	11.00	21°57′	49°34′	385	806
	459 –Strzyżów	250bd, 251c	19.51	21°46′	49°58′	383	854
	460 –Kańczuga	126a	10.98	22°14′	49°55′	339	852
	461 –Leżajsk	205a	7.00	22°16′	50°15′	232	661
	462 –Leżajsk	213c	6.10	22°16′	50°15′	230	661
	463 –Narol	89Aa, 89b	25.35	23°15′	50°20′	324	606
Radom	390 –Kielce	156b, 157d	23.00	20°25′	50°59′	334	604
	402 –Suchedniów	110g	8.87	20°55′	50°01′	346	604
	468 –Staszów	198bcdf, 199ac	35.96	21°09′	50°38′	269	658
	522 –Łagów	44abc, 45a, 46a, 47a, 50b, 51a, 52ab, 53a	148.31	21°07′	50°50′	417	604

*RDLP – Regional Directorate of State Forests; (SR) – regional standard

Tests are being conducted on the offspring of 25 selected seed stands growing on land managed by three regional State Forest Directorates: Kraków, Krosno and Radom. Table 1 presents the characteristics of the parent beech stands of the tested progeny.

One-year-old beech seedlings were planted using the container seedlings (1/0k), spaced at 1.5 × 1.1 m, with 100 trees in each provenance plot. The trees were planted in the centres of 60 × 60 cm holes. Due to the insufficient number of seedlings from the 460-Kańczuga and 463-Narol stands, their progeny was not tested in block 4 in Nawojowa. Figure 2 presents a schematic diagram of the two plantations showing the placement of the blocks (repetitions) and provenance plots. For both plantations, the regional standard is the progeny of stand number 452-Lesko, whereas the progeny of stands 457 and 458 (Rymanów Forest District) served as the local standard for Rymanów, and stands 467 and 469 (Nawojowa Forest District) were the local standard for the progeny in Nawojowa.

Survival and height of the beech seedlings were evaluated in the second and fifth year after planting in the test plantations, that is, in the third and sixth years of life. Each plantation was tested separately for the influence of provenance (genotype), block (repetitions), and the interaction of the two sources of variability. A multifactorial analysis of the data with the following formula was used:

$$y_{kjn} = \mu + B_j + P_k + PB_{kj} + E_{n(jk)}, \qquad (1)$$

where: y_{kjn} – value of the observation of the kjn number, μ – overall average, B_j – influence of block j, P_k – influence of provenance k, PB_{kj} – influence of interaction with provenance k and block j, $E_{n(jk)}$ – error.

The influence of plantation location was analysed using the same formula, substituting the effect of block (B_j) with the effect of location (L_i). The heritability of both survival and height was also calculated separately for each plantation. Due to the use of a mixed model (block – a random effect, provenance – a fixed effect), heritability was calculated using a formula based on the variance of components. The expected mean squares for the analysis of two-way interaction were taken from Żuk (1989).

Provenance heritability was calculated by dividing the provenance variance component (σ_P^2) by the provenance variance (V_P) (Giertych 1991). After inserting the provenance variance into the general formula for heritability in the two-way analysis of variance, and dividing it by the k_3 factor of the provenance component, the model for provenance heritability (h_P^2) assumes the following form:

$$h_P^2 = \frac{\sigma_P^2}{\frac{\sigma_E^2}{k_3} + \frac{k_2 \sigma_{PB}^2}{k_3} + \sigma_P^2}, \qquad (2)$$

where: σ_P^2 – provenance variance component, σ_E^2 – error variance component, σ_{PB}^2 – variance component of the interaction, k_2 – average number of trees in a block and provenance, k_3 – average number of trees in the provenance.

The Pearson correlation coefficients (r) were calculated to determine the strength of the relationship of beech survival and height in specific years at both test plantations with the geographic coordinates and altitude of parent stands.

Finlay and Wilkinson's (1963) method was used to assess the stability of beech provenances. It uses the regression coefficient b to describe the nature of the adaptation of the provenance in different years and growth environments. The value of coefficient b at a level of 1.0 indicates progeny with an average ability to adapt. A value of less than 1.0 indicates a stable provenance that adapts well in many environments, whereas if the value is greater than 1.0, the progeny is highly reactive and only able to adapt to very specific environmental conditions (Finlay, Wilkinson 1963; Giertych 1988). The calculations were performed on average values, which were logarithmically transformed. The interpretation of the degree of adaptability of the studied beech provenances to growing conditions is illustrated in graphs, showing the relationship between the size of the regression coefficient b and the average value of the traits calculated separately for each provenance.

3. Results

The average survival of beech seedlings cultivated in Rymanów in the second year after planting was 90.2% and dropped to 63.6% over the next 3 years. In turn, the average survival rate in Nawojowa for the same period was high, at 94.6 and 92.4% for the second and fifth years after planting, respectively. The highest survival rates in Rymanów after 5 years of growth were found for beech originating from 469-Nawojowa, 451-Lutowiska and 452-Lesko. The lowest survival rates were found for the beech population from 362-Gromnik, 462-Leżajsk and 459-Strzyżów. The best progeny stands in Nawojowa were 467-Nawojowa, 455-Krasiczyn and 452-Lesko. The lowest survival rates at this plantation were found for beech from 440-Stary Sącz, 426-Łosie and 461-Leżajsk (Table 2).

The average height of beech seedlings in Rymanów 2 years after planting was 46.4 cm, increasing to 66.1 cm (an increase of 42.5%) in the next 3 years. The average height of beech in the Nawojowa test plantation was significantly higher than in Rymanów, at 56.2 cm in the second year and 121.6 cm in the fifth year of growth (an increase of 116.4%). In Rymanów, the highest average height at 5 years after planting was found for beech originating from 451-Lutowiska, 452-Lesko and 455-Krasiczyn, while the lowest was found for 362-Gromnik, 462-Leżajsk and 442-Brzesko. In Nawojowa, the best height results were achieved by progeny from the selected seed stands of 469-Nawojowa, 453-Bircza and 522-Łagów, while worst results were from 440-Stary Sacz, 426-**Łosie** and the 441- and 456-Brzesko Krasiczyn (Table 2).

An assessment of the influence of provenance and block on the tested traits (survival, height) showed a statistically significant interaction of 'provenance × block' regardless of the location of the test plantation (Rymanów, Nawojowa) or year of measurement. In Rymanów, we also found a significant influence of block on the size of both analysed traits, which was sustained as the trees aged. However, provenance was significant only for the second year after planting, as it was not confirmed after 5 years. In contrast to Rymanów, the effect of progeny on the observed differences in height significantly increased between the second and fifth years of growth of the beech in the Nawojowa plantation (Table 3).

We also found that test plantation location and the interaction of 'progeny × test plantation' also significantly influenced survival and height of the beech. The response of progeny to habitat conditions was varied. Provenance did not significantly affect the variance of the studied traits for both measurement periods (Table 4).

The heritability of the analysed beech traits calculated for the test plantations and year of measurement varied. The heritability of survival after 2 and 5 years was high and at a similar level for both periods in Rymanów, but in Nawojowa, heritability of survival after 2 years was low and decreased to zero during the second measurement period, after 5 years of growth in the plantation. The heritability of height achieved the opposite result. The high heritability of this trait, comparable for both periods of measurement, was noted in Nawojowa,

Table 2. Survival and height of European beech tested on experimental plots in Rymanów and Nawojowa (2 and 5 years after planting)

RDLP	No. and name of provenance	Survival (%)				Height (cm)			
		Rymanów		Nawojowa		Rymanów		Nawojowa	
		2	5	2	5	2	5	2	5
Kraków	362–Gromnik	89.5	47.3	95.8	94.3	38.9	55.5	56.9	122.5
	425–Łosie	88.0	58.8	94.3	92.8	47.9	67.2	56.9	119.2
	426–Łosie	92.8	67.5	91.3	88.8	47.2	71.6	55.2	110.0
	440–Stary Sącz	92.0	62.0	90.8	88.8	45.2	68.2	51.8	104.8
	441–Brzesko	86.8	59.0	94.5	92.3	47.2	62.6	57.2	112.1
	442–Brzesko	87.0	62.3	94.3	92.3	47.6	60.0	61.3	127.0
	467–Nawojowa	88.8	66.5	97.5	96.3	45.5	65.8	59.0	125.6
	469–Nawojowa	93.0	77.3	94.0	92.3	44.1	75.9	56.0	142.8
Krosno	451–Lutowiska	96.8	76.3	94.3	93.0	46.6	75.9	52.0	117.1
	452–Lesko (SR)	96.5	72.0	96.8	95.5	50.0	75.5	56.1	126.9
	453–Bircza	92.3	68.0	92.8	90.5	47.2	61.5	59.9	136.1
	454–Bircza	88.0	63.5	98.0	94.8	46.1	64.6	56.9	124.3
	455–Krasiczyn	96.0	68.8	97.5	95.8	48.8	73.0	57.1	121.1
	456–Krasiczyn	95.0	66.0	95.8	94.3	45.0	66.0	51.2	112.3
	457–Rymanów	91.8	68.8	92.5	89.0	49.8	68.1	56.4	113.3
	458–Rymanów	89.8	66.3	94.3	92.0	48.3	64.9	58.7	124.9
	459–Strzyżów	86.8	55.5	95.5	93.5	48.4	68.4	59.0	120.3
	460–Kańczuga	89.0	61.5	92.7	90.7	43.7	65.8	54.7	131.7
	461–Leżajsk	86.0	57.3	92.3	88.0	46.5	62.0	54.0	121.4
	462–Leżajsk	85.0	51.3	96.8	93.3	41.4	58.2	53.0	119.6
	463–Narol	87.0	62.0	93.7	89.3	43.8	66.3	55.7	119.3
Radom	390–Kielce	88.5	61.8	94.0	93.5	50.2	66.2	56.4	117.7
	402–Suchedniów	88.7	58.0	93.8	92.8	46.2	61.5	55.9	118.4
	468–Staszów	93.5	69.0	96.3	95.0	47.6	65.7	58.8	122.2
	522–Łagów	85.7	64.3	95.3	92.3	45.9	62.9	54.9	129.4
Mean		90.2	63.6	94.6	92.4	46.4	66.1	56.2	121.6
Standard deviation		3.5	6.8	1.9	2.3	2.6	5.2	2.5	8.1
Coefficient of variance		3.9%	10.7%	2.0%	2.5%	5.6%	7.9%	4.4%	6.7%

whereas in Rymanów, height heritability clearly decreased after 5 years of growth, amounting to 0.296 (Table 5).

The correlation between the average value of each analysed trait for specific progeny and the geographical location and altitude of parent stand location was low and not statistically significant in the Nawojowa test plantation. However, in Rymanów, the correlation between altitude and survival, as well as altitude and average beech height in the fifth year after planting was positive and significant. A similar correlation was found for these traits and the latitude of the parent-stand location, except that it was negative (Table 6).

The Finlay and Wilkinson method, used to evaluate the stability of the adaptive traits 5 years after planting, showed that the most stable beech in terms of survival was the progeny from the provenance of 469-Nawojowa (b = 0.47), 451-Lutowiska (0.53), and 457-Rymanów (0.69). Particularly noteworthy is the 469-Nawojowa provenance, which among all studied provenances, simultaneously achieved the highest value for the trait and a low value of coefficient b. On the other hand, height was a significantly stable trait for the provenances of 440-Stary Sącz (0.70), 426-Łosie (0.70), and 451-Lutowiska (0.71). In terms of both the regression coefficient b and average height, the best were found to be 469-Nawojowa and 452-Lesko. This latter population is the regional standard for the south-eastern test region. In the case of both provenances, but especially in the case of the regional

Table 3. The variance analysis of height and survival of European beech tested on experimental plots in Rymanów and Nawojowa (2 and 5 years after planting)

Trait	Source of variance	Years after planting	Rymanów		Nawojowa	
			F-test	significance level (*p*)	*F*-test	significance level (*p*)
Survival	Block	2	6.551	**<0.001**	1.801	0.156
		5	4.292	**0.008**	2.510	0.066
	Provenance	2	2.205	**0.005**	1.333	0.185
		5	1.734	0.039	0.850	0.655
	Block × Provenance	2	2.618	**<0.001**	3.570	<0.001
		5	5.133	**<0.001**	3.810	**<0.001**
Height	Block	2	5.812	**0.001**	7.816	<0.001
		5	4.856	**0.004**	15.542	**<0.001**
	Provenance	2	3.047	**<0.001**	2.066	0.013
		5	1.421	0.129	2.192	**0.008**
	Block × Provenance	2	4.857	**<0.001**	6.495	**<0.001**
		5	8.334	**<0.001**	9.735	**<0.001**

Table 4. Results of the multifactorial variance analysis for analysed traits of beech together for the testing plots in Rymanów and Nawojowa

Trait	Source of variance	Degree of freedom	Years after planting	*F*-test	Significance (*p*)
Survival	Plot	1	2	**18.25**	**<0.001**
			5	**732.48**	**<0.001**
	Provenance	24	2	1.04	0.463
			5	0.75	0.759
	Plot × provenance	24	2	**5.05**	**<0.001**
			5	**3.67**	**<0.001**
Height	Plot	1	2	**257.25**	**<0.001**
			5	**1120.35**	**<0.001**
	Provenance	24	2	1.90	0.062
			5	1.55	0.145
	Plot × provenance	24	2	**8.88**	**<0.001**
			5	**9.02**	**<0.001**

Table 5. Heritability of analyzed traits of European beech tested on plots in Rymanów and Nawojowa (2 and 5 years after planting)

Trait	Years after planting	Heritability for plot	
		Rymanów	Nawojowa
Survival	2	0.523	0.213
	5	0.423	0.000
Height	2	0.661	0.511
	5	0.296	0.485

Table 6. Correlation of average values of the characteristics of beech populations tested on experimental plots in Rymanów and Nawojowa with geographic coordinates and altitude mother stands locations (correlations significant at $p = 0.05$ are in bold)

Trait	Years after planting	Rymanów			Nawojowa		
		geographical coord.		altitude	geographical coord.		altitude
		longitude	latitude		longitude	latitude	
Survival	2	0.1468	**–0.5214**	**0.4026**	0.1614	0.0829	–0.0066
	5	0.0290	**–0.3901**	**0.5716**	–0.0770	0.0071	0.1468
Height	2	–0.0610	–0.0449	0.0010	–0.1924	0.0236	–0.0282
	5	0.0569	**–0.4488**	**0.5851**	0.0620	0.0209	0.2026

standard, the values of the traits were high, while regression coefficient *b* was low, indicating stability and high adaptability. Both local standard provenances for Rymanów (457 and 458) had very stable, high survival values. The survival rates in both test plantations differed for provenances 362-Gromnik ($b = 1.84$), 462-Leżajsk (1.59), and 459-Strzyżów (1.40). In the case of the regression coefficient *b* for height, provenances 453-Bircza (1.28), 442-Brzesko (1.23), and 362-Gromnik (1.30) significantly exceeded the value of 1. The lowest level of stability was found for provenance 362-Gromnik, both in terms of survival and height (Figures 3–4).

4. Discussion

The evaluation of the adaptive abilities of progeny from selected seed stands of European beech from the south-eastern test region found large differences in the analysed traits between the test plantations, as well as among specific provenances.

Average beech survival after 2 years of growth at the test plantations was similar; however, after 3 more years, the observed differences were greater. The survival rate in Rymanów was 63.6%, while in Nawojowa, it was 92.4%. Such a large variance may be related to the conditions prevailing at each site. The Nawojowa Forest District site was established in the forest, on a plot formed after the removal of a spruce stand, while the Rymanów Forest District site is on former agricultural land – a meadow, though unused for many years. The progeny from this site exhibited a greater effect of the genetic properties of particular provenances (significant effect of provenance) than in Nawojowa, where all of the progeny was assessed similarly after 5 years of growth (no significant differences). The best average survival rate regardless of test plantation or year of observation was found for the progeny of the 455-Krasiczyn tree stand, which was only slightly better than the regional standard (452-Lesko). The worst result of this trait was found for the progeny of stand 461-Leżajsk, which usually ranked at the bottom of the list. When both measurement periods for each plantation were analysed separately, we found that the best results were attained by 451-Lutowiska in the Rymanów test plantation and 467-Nawojowa at Nawojowa. The latter provenance was one of the best in terms of survival assessed in the second and fifth years of growth, regardless of conditions at the test plantations. The analysis of correlation showed no relationship between the plantations, which may result from differences in the adaptive response of specific populations to various environments.

Such a pattern of variability is confirmed by the results of Barzdajn (2006) at the Siemianice experimental plantation. The significance of the interaction 'provenance × test plantation' indicates that some of the provenances responded differently in each of the test plantations, and therefore, are characterised by low plasticity, understood as a comparative response of the same genotype growing in different environmental conditions. Barzdajn (2009) also reached a similar conclusion when analysing the progeny of beech seed stands from Złotoryja and Lądek Zdrój plantations in the south-western test region.

The large difference between the two plantations allowed us to assess the stability of genotypes using the Finlay–Wilkinson (1963) method. Analyses show that the most stable progeny after the first 5 years of growth were the beeches from 469-Nawojowa, which was further characterised by a very high average survival rate. The least stable provenance, and also the worst in terms of average value, was the progeny of stand 362-Gromnik. The progeny of stand 452-Lesko was very stable; therefore, the standard for the south-eastern region is one of the best stands of this species. According Barzdajn (2009), who studied beech progeny, the standard for the south-western region is an average provenance.

Average height, as with survival, was very diverse. The difference between plantations was approximately 10 cm after 2 years and nearly 60 cm after 5 years since planting. In both cases, the results were better for the beech trees growing in the Nawojowa plantation. The reason for such a big difference may be the large disparity in the conditions at each plantation, as evidenced by the significant effect of the 'provenance × test plantation' interaction. Considering the

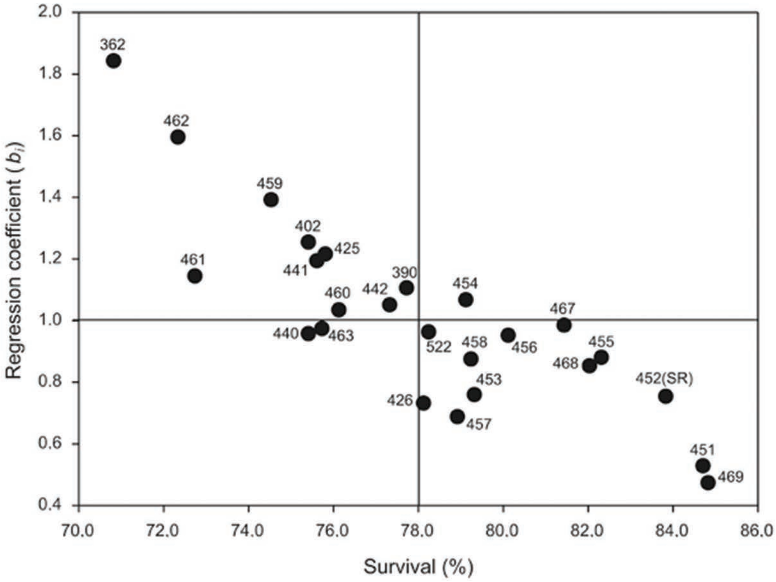

Figure 3. Mean survival 5 years after planting and the regression coefficient (b_i) for individual provenances of the European beech tested on Rymanów and Nawojowa plot; 452 (SR) – the regional standard

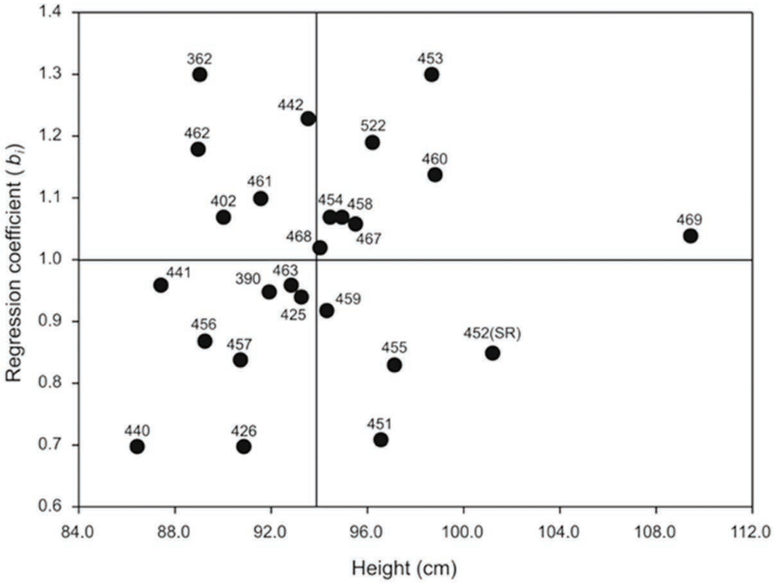

Figure 4. Mean height 5 years after planting and the regression coefficient (b_i) for individual provenances of the European beech tested on Rymanów and Nawojowa plot; (SR) – the regional standard

average results of test plantation and period of measurement, it was found that the progeny of the 452-Lesko provenance (regional standard) achieved the best results of average height, only slightly better than the beeches from stand 459-Strzyżów. The worst height growth was found for the progeny of stand 462-Leżajsk. When analysing the plantations separately, the best provenance in Rymanów was 452-Lesko (the regional standard), while in Nawojowa, it was the 453-Bircza provenance. Large changes were observed in the provenance rankings of this trait between the two measurement periods (a difference of 3 years). The assessment of various beech provenances for growth could change after conducting successive studies planned at 10 years after planting in the test plantations.

Variations in the response of beech to growth conditions depending on location is shown in the studies of Sabor and Stanuch (2009), who found that soil influenced the height of beech to at least the sixth year after planting. Similar relationships were found for beech in test plantations in the south-western region, where the height increment of most of the provenances differed in each site and was due to changes in growth conditions (Sułkowska 2004, Barzdajn 2009).

A similar growth trend was observed in our study. The provenances that grew well in the Rymanów plantation did not always achieve good results in Nawojowa.

It was also shown that local provenances are not always well adapted to local conditions, as suggested, among others, by the research of Sułkowska (2004). The results achieved by local provenances assessed in our study varied. They had the worst results in the Rymanów plantation, but some of the best in Nawojowa.

The results of this study are consistent with those obtained by Kowalkowski (2013) in a plantation established in 1981 in the Strzyżów Forest District, and thus in the south-eastern test region. In Kowalkowski's experiment, beeches from the provenances of Suchedniów, Narol and locally from Strzyżów were the weakest, similar to the trees tested in Nawojowa and Rymanów. Some of the progeny from the south-eastern region were tested by Kowalkowski (2013b) in north-western Poland at a plantation in the Łobez Forest District. At that site, beech progeny from Lagów, Suchedniów and Łosie also poorly adapted, while those from Kańczuga fared slightly better. In turn, provenances planted in Krynica (Sabor, Żuchowska 2002) from the southern range of the species, with the exception of those from the Bieszczady Mountains, did well in their early years of growth, whereas at the Bystrzyca Kłodzka plantation (south-western test region), beeches from northern Poland better adapted than those from the south-eastern range of the species (Matras 2002). Kowalkowski et al. (2012) obtained similar results with one of the oldest national studies of European beech, from 1967, in which a population from Rytro (south-eastern region) was moved a great distance to the south-western region (to a plantation in the Śnieżka Forest Directorate). At 30 and 40 years of age, these trees were found to have the lowest rating in terms of growth traits, and the second generation from this region (Łagów) turned out to have average results.

Height was the only trait to show relatively high heritability by year of measurement (from 0.296 to 0.661). Heritability (h^2) obtained at both test plantations, however, was much lower than that estimated by Galoux (1966, from Giertych 2000) (0.84). The most stable in terms of growth in height was the progeny of stand 469-Nawojowa, which, regardless of test plot, always ranked in the top provenances for this trait. As in the case of survival, the regional standard was also highly rated, achieving relatively better height in Rymanów with more difficult environmental conditions.

A statistically significant linear correlation between height and survival of beech progeny was found only in the Rymanów plantation. Barzdajn (2009) found a similar relationship at the Złotoryja plantation in the south-western region of beech testing. In Rymanów, a significant negative correlation was found between beech height and survival and latitude. A positive correlation was found between these traits and height above sea level of the parent stand, which was not confirmed in the case of the Nawojowa plantation. This suggests the better adaptation of beech trees from higher altitudes growing under the conditions present in Rymanów, where the soil is more compacted and there is more open space. Under these conditions, however, the progeny of stands growing in the same test area, but further to the north, adapted more poorly.

5. Conclusions

1. The analysis of European beech progeny growing in the south-eastern test region of this species exhibited a high degree of variation in adaptive traits (survival and height) during its first year of growth in the test plots.

2. In the early stage of growth, the tested provenances were highly reactive, indicated by the significant interaction of 'provenance × block' and 'provenance × test plantation'.

3. The regional standard selected for the south-eastern test region provides some of the best European beech progeny in this region.

4. The assessment of adaptive traits (survival and height) indicated that it is possible to transfer the reproductive material of forests from some provenances within the same test region. It was also confirmed that the progeny of local tree stands can adapt very well to the site where it is planted, which was not generally exhibited by other authors.

5. The results confirm that natural populations growing in difficult environmental conditions grow better in sites with more demanding conditions (for example, at higher altitudes).

Conflict of interest

None declared.

Acknowledgements and financial support

The research was performed as part of topics BLP-281 and BLP-375 funded by the State Forests National Forest Holding and coordinated by the Forest Research Institute.

References

Barzdajn W. 2006. Proweniencyjna zmienność buka zwyczajnego w Polsce, in: Elementy genetyki i hodowli selekcyjnej drzew leśnych. Eds. J. Sabor, Warszawa, Wyd. CILP 211–222.

Barzdajn W. 2009. Adaptacja i początkowy wzrost potomstwa drzewostanów nasiennych buka zwyczajnego (*Fagus sylvatica* L.) na uprawach porównawczych w nadleśnictwach Złotoryja i Lądek Zdrój [Adaptation and initial growth of

seed stand progeny of European beech (Fagus sylvatica L.) in comparative plantations established in the Złotoryja and Lądek Zdrój Forest Districts]. *Leśne Prace Badawcze*, 70(2): 101–111.
Finlay K. W., Wilkinson G. N. 1963. The analysis of adaptation in a plant-breeding programme. *Australian Journal of Agricultural Research*, 14: 742–752.
Giertych M. 1988. Interakcja genotypu ze środowiskiem oraz z wiekiem polskich proweniencji sosny zwyczajnej (*Pinus sylvestris* L.). *Arboretum Kórnickie*, 33: 159–169.
Giertych M, 1991. Selekcja proweniencyjna, rodowa i indywidualna w doświadczeniach wieloczynnikowych ze świerkiem pospolitym (*Picea abies* (L.) Karst.). *Arboretum Kórnickie*, 36: 27–42.
Giertych M. 2000. Zmienność genetyczna buka, in: Ocena wartości genetycznej oraz problemy zagospodarowania selekcyjnego buczyn karpackich. *Zeszyty Naukowe Akademii Rolniczej im. H. Kołłątaja w Krakowie, Sesja Naukowa*, 68: 35–46.
Kowalkowski W. 2013a. Wyniki badań nad proweniencyjną zmiennością buka zwyczajnego (*Fagus sylvatica* L.) w 30-letnim doświadczeniu w Nadleśnictwie Strzyżów [Results of research into the variability of provenence of the European beech (Fagus sylvatica L.) in a 30 year experiment in Strzyzow Forest District]. *Forestry Letters*, 104: 117–123.
Kowalkowski W. 2013b. Wyniki 18-letniego doświadczenia proweniencyjnego z bukiem zwyczajnym (*Fagus sylvatica* L.) w Nadleśnictwie Łobez [The results of an 18–year old beech trees (Fagus sylvatica L.) provenance trial in the Łobez Forest District]. *Leśne Prace Badawcze*, 74 (3): 197–203.
Kowalkowski W., Kaźmierczak K., Korzeniewicz R. 2012. Analiza cech taksacyjnych buka zwyczajnego (*Fagus sylvatica* L.) w doświadczeniu proweniencyjnym w Nadleśnictwie Śnieżka. *Prace Komisji Nauk Rolniczych i Komisji Nauk Leśnych*, 103: 17–24.
Matras J. 2002. Wzrost i rozwój populacji buka zwyczajnego (*Fagus sylvatica* L.) w okresie pierwszych trzech lat na powierzchni doświadczalnej w Bystrzycy Kłodzkiej . *Sylwan*, 146 (2): 111–127.
Sabor J., Barzdajn W., Blonkowski S., Chałupka W., Fonder W., Giertych M. et al. 2004. Program testowania potomstwa wyłączonych drzewostanów nasiennych, drzew doborowych, plantacji nasiennych i plantacyjnych upraw nasiennych. Dyrekcja Generalna Lasów Państwowych, Warszawa.
Sabor J., Stanuch H. 2009. Genetyczna reaktywność buka zwyczajnego na warunki glebowe [Genetic response of European beech to soil conditions]. *Sylwan*, 153(8): 507–518.
Sabor. J., Żuchowska J. 2002. Wstępne wyniki badań nad proweniencyjną zmiennością buka zwyczajnego (*Fagus sylvatica* L.) na powierzchni porównawczej doświadczenia serii GC 2234 1992–1995 w Krynicy [The initial results of the investigations on the provenance variability of common beech (*Fagus sylvatica* L.) in the experiment of GC 2234 1992-1995 series in Łobez Forest District]. *Sylwan*, 146(2): 43–72.
StatSoft, Inc. 2009. STATISTICA (date analysis software system) version 9. www.statsoft.com.
Sułkowska M. 2004. Zmienność genetyczna wybranych cech biologii buka zwyczajnego (*Fagus sylvatica* L.). Rozprawa doktorska. SGGW Warszawa.
Żuk B. 1989. Biometria stosowana. Wyd. PWN, Warszawa.

Authors' contribution

J.B. – developed the study concept, analysed measurement data, prepared the graphs, and wrote the manuscript. K.S. – verified part of the results and wrote the manuscript. M.S. – performed field research, prepared table sets, and wrote the first version of the section on results. K.K. – performed field research, prepared table sets, and wrote the first version of the section on results.

Translated by: Barbara Przybylska