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Assessment of the height stability in progeny of *Fagus sylvatica* L. populations using the GGE biplot method

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Abstract: Forecasted climate changes demand selection of populations (seed stands) and genotypes (plus trees) best adapted to changing environmental conditions and displaying limited genotype × environment (G×E) interaction. Analysis of multi-environment trials (METs) allows to recognize differences between populations and environments, as well as G×E interaction. To define stability of tree height we used a GGE biplot graphic method based on the results of measurement of 5- and 10-year-old trees originating from 30 European beech populations tested at three experimental sites. Majority of variance was explained in terms of the impact of environment. The studied environments were characterised by a similar discriminating ability and representativeness of growth conditions. Two mega-environments were identified as the studied populations of beech differed in their adaptation to local growth conditions. The analysed set of populations included those growing particularly well under the specific environmental conditions, and others displaying more general adaptability. The GGE biplot method is useful in breeding of forest trees.

Keywords: G×E interaction, GGE biplot, MET, adaptation, European beech

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Introduction

The European beech (*Fagus sylvatica* L.) is a key forest-forming broadleaved tree species in Poland, where it currently covers 530,641.6 ha of forest, i.e. 5.8% of the total forest area managed by the State Forests, and 22.6% of forest area in National Parks (ca 41,769.72 ha). However, data on the presence and structure of forest habitats in Poland suggest further possibilities to increase the role of broadleaved tree species, including beech, in the country's forests (Raport o lasach, 2014). The seed base of beech currently includes 122 selected seed stands (over 2009.3 ha), 604 maternal (plus) trees, 5 clonal seed orchards (35 ha) and 8 seedling seed orchards (43 ha). Fifteen seed regions for the species have been designated in Poland, with 5 of them located in the mountains or uplands (Fonder et al., 2007). The European beech reaches the eastern limit of its natural distribution range in Poland, with two distinguished centres of occurrence – Pomeranian and montane/upland (Boratyńska & Boratyński, 1990), where ecological requirements for growth of beech in natural communities are met (Dzwonko, 1990). However, according to Tarasiuk (1992), the entire country represents a potential territory for European beech to play a more prominent role in managed stands.

In line with the need to make future forest stands more stable, healthy and productive, a detailed study of beech seed stands is being conducted, with the aim of recognizing their genetic value, and ensuring adequate and effective preservation. To better recognize variation among Polish beech populations, many study sites have been established since 1995, with research there seeking best options for beech cultivation under various environmental conditions (Sabor, 1999). Work done elsewhere, especially in Germany and France, points that populations within this species indeed show marked variation in both growth and qualitative traits (Teissier du Cros, 1977; von Wüehlisch, 2004; Ivanković et al., 2008). However, many studies also indicate the presence of strong G×E interaction (Krahl-Urban, 1958; von Wüehlisch et al., 2008), and ecotypic variation. It is therefore clear that transfer of beech seeds over long distances may be not beneficial in terms of commercial results.

Breeding of forest trees needs to encompass not only an effort to improve quantitative and qualitative traits, but also work to assess the stability of those traits, both between different environments and throughout a period of many years (Rodrigues et al., 2008). Predicted climatic change necessitates artificial selection for the populations and genotypes faring best when it comes to adaptation to changing environmental conditions, but at the same time showing a limited G×E interaction. The G×E interaction is of influence where assessments of heritability are concerned, as well as decisions about silvicultural objectives and practices (Yan & Kang, 2002). The G×E interaction is in fact a key parameter for plant-breeders in general (Kang, 1990; Kang & Gauch, 1996; Annicchiarico, 2002). Breeding strategies for forest trees are often based on a search for populations with low values of the G×E interaction, which can thus be described as plastic (Giertych, 1982). With only the results of short-term experiments available, it is hard to to gain at unambiguous recommendations in line with which practical decisions may be taken. However, results obtained after 5 and 10 years of growth do allow to analyse the adaptation and productivity that is represented by tree height. The determination of the stability of this trait in the analysed populations is *inter alia* of key importance to the development of policy on transfers of seeds (Yeiser et al., 2001).

Where work based on multi-environment trials (MET) aims to depict the G×E interaction, as well as its relationship with G (i.e. the effect of genotype) as such, methods based on analysis of variance and regression analysis are found to be less effective than multidimensional methods (Crossa, 1990). A biplot of the GGE type facilitates presentation of relevant relationships in form that is clear and easy to interpret. The GGE effect comprises G – the effect of genotypes, as well as G×E – that is due to the interaction between genotype and the environment (Yan et al., 2000). The GGE biplots are generated by reference to the values of the first two components in the Principal Component Analysis (PCA), i.e. PC1 and PC2. With the aid of GGE biplots it becomes possible to establish correlations between environments, to define the existence of mega-environments, and to estimate the real productivity of genotypes within these mega-enviroments (DeLacy et al., 1996; Ding et al., 2008). From the practical point of view genotypes that can be recommended for growing in given environments are identified (Gauch & Zobel, 1997; Yan et al., 2000; Yan et al., 2001; Ukalski et al., 2010a; Ukalski et al., 2010b; Ukalski & Klisz, 2016; Klisz et al., 2017). One option is to select those genotypes that show favorable and stable values for the traits of interest in the so-called average environment (Ukalski & Klisz, 2016), as identified with the AEC or Average Environment Coordination Method (Yan & Hunt, 2001; Yan, 2002). Yet a further possibility is to seek out genotypes that approximate the theoretical "ideal" genotype, i.e. the one associated with both favorable and stable values for a given trait (or traits) in all of the studied environments (Yan et al., 2000; Yan & Rajcan, 2002).

The "Program of testing the progeny of selected seed stands, plus trees, clonal and seedling seed orchards" in the State Forest aims to determine the genetic value and silvicultural properties of the forest basic material which is used in forestry practice.

It further aims to prepare the recommendations for the rational use of seed base (forest basic material) by determining the directions of possible transfer of forest reproductive material (Program, 2011). Stability of growth traits in various conditions is very important in selection of populations in the case of environmental change. The purpose of this study was to determine stability of tree height growth among progeny of European beech populations originating from southern Poland and growing in montane and upland conditions, using the GGE biplot analysis.

Materials and Methods

Sites and experimental design

The study includes progeny of 30 selected seed stands (populations) of European beech from southern Poland. In 2004 seeds were collected from 50 trees chosen randomly along a transect in each population . Minimal distance between trees in a transect was 20–25 m. Seeds were collected from healthy trees in the year of a good seed crop. All seeds were stored at the Kostrzyca Forest Gene Bank until the time of sowing in a nursery in spring 2005. Seedlings were raised in containers in the Gidle Forest Nursery (50°54’N, 19°37’E), ~ 180 km north of the experimental sites. After one year of growing in the nursery seedlings were transferred directly to the experimental sites in spring 2006.

Three trial plots were estabilished in southern and south-western Poland – in Sucha Beskidzka (SB) (N49°37’40” E19°32’48”, 825 m a.s.l.), Lądek Zdrój (LZ) (N50°19’50” E16°45’03”, 520 m a.s.l.) and Złotoryja (ZL) (N51°56’59” E15°48’53”, 400 m a.s.l.) – Fig. 1. At each site the trial was set up in a complete block design with four replications (blocks). Each tested population was represented by 400 planted seedlings (100 in each replications) planted in 1.5 × 1.5 m spacing.

Habitat conditions associated with these study areas were diverse. According to the Polish forest typology the SB site was a montane broadleaved forest (*LG*); the ZL site was a montane mixed broadleaved forest (*LMG*), and the LZ site was a fresh montane mixed broadleaved forest (*LMGsw*). The first height measurements on these plots were made in 2010, and the second measurements were done five years later, in 2015.

Statistical analysis

Analysis of variance was used to study the differentiation in tree heights among the studied populations, as well as the influence on this differentiation exerted by different environments. The linear mixed model with environment, population and the G×E interaction as class variables (Piepho, 1997) was applied, using the equation:

$$y_{ijk} = \mu+r_k(e_j)+g_i+e_j+ge_{ij}+\varepsilon_{ijk} \qquad (1)$$

where: y_{ijk} is the trait value observed for the i-th genotype (i=1,...,30) in the j-th environment (j=1,...,3) in the k-th block, μ is the overall mean, g_i is the fixed effect of the i-th genotype, e_j is the random effect of the j-th environment, ge_{ij} is the random effect of the genotype × environment interaction, $r_k(e_j)$ is the random effect of the k-th block in the j-th environment (k=1,...,4), and ε_{ijk} is the experimental error. The genotype effect in the model (1) was treated as fixed, due to the fact that the tested genotypes were selected decisively with reference to analyzed traits. The environment effect was treated as random because experimental sites represented the widest possible spectrum of environmental conditions for a given species (Saxton, 2004). The F statistic values for the genotype and environment effects in the model (1) were determined using Hocking’s approach (Hocking & Speed, 1975).

To perform the biplot analysis, the two-dimensional table of means should be factorized using singular value decomposition (SVD) (Golub & Reinsch, 1971), or equivalently, calculations can be performed using PCA (Ukalski & Klisz, 2016). We used PCA on the genotypic means across environments (Table 1). This offered a basis for identifying the most representative environment. The discriminating potential of the environments was determined, and the 30 populations of beech assessed in relation to values of tree height and their stability.

The AEC method was used to determine the similarity of environments depicted on the GGE biplot. The average environment was identified by reference to principal components PC1 and PC2 as related to the three environments. An AE axis was run though the AE point and the centre of the coordinate system. Similarities between all possible pairs of sites were determined using two methods. The first related to α_{ij} angles between vectors OA_i and OB_j (where OA_i and OB_j are the lengths of the vectors between the origin of the coordinate system and sites A and B, respectively). The second method involved Pearson correlation coefficients calculated for all pairs of environments on the basis of PCA values.

Populations mean height-related performance were described by the their position in relation to average environment (AE) axis on the GGE biplots. The zero value for AE denotes the mean value for traits through the environments. Populations with high values for AE are characterised by high values of tree height. The length of the line segment between the population location and its orthogonal projection

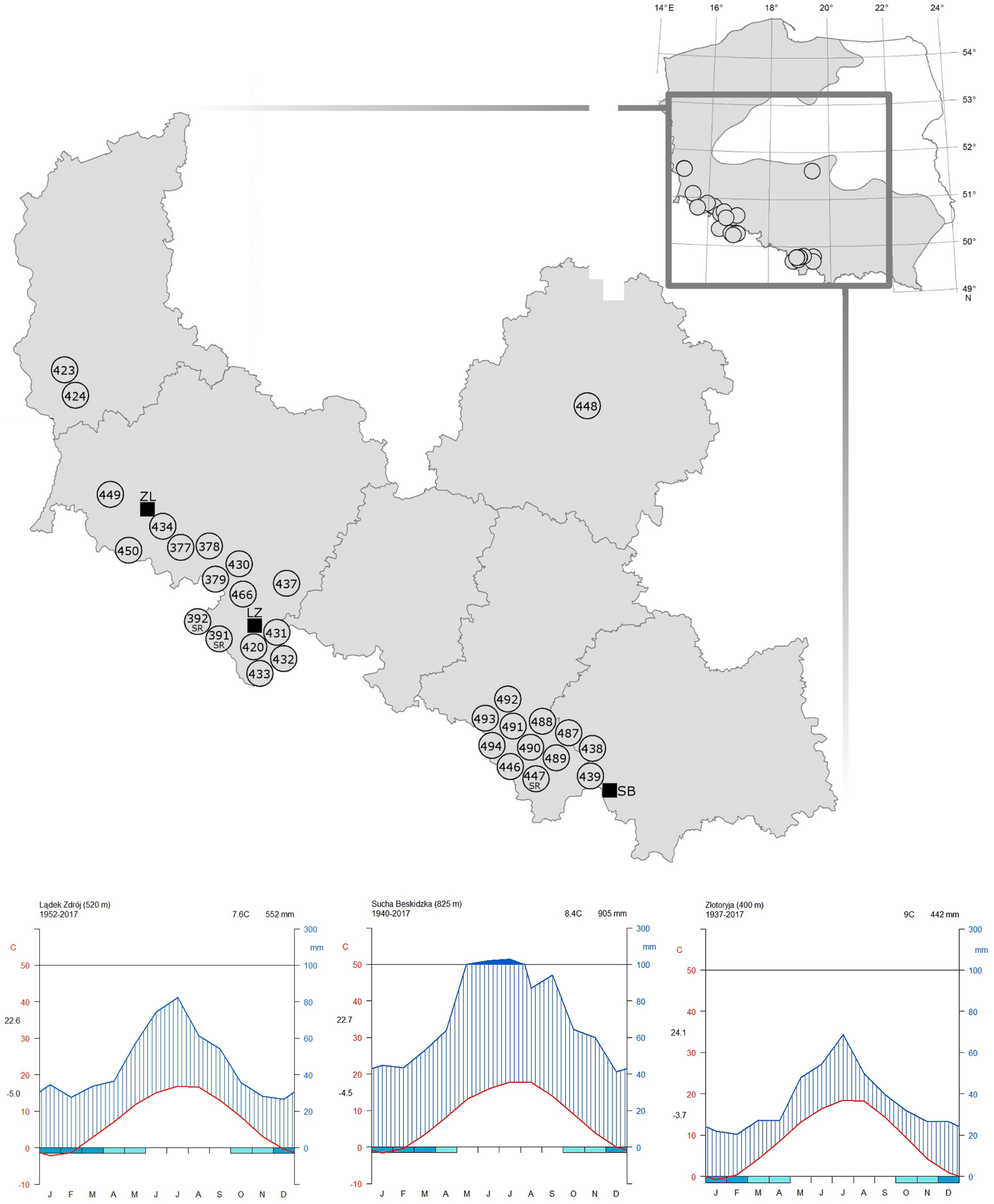

Fig. 1. Location and climatic conditions of study sites. Bottom panel: plots of the precipitation and temperature monthly averages, annual averages of both elements (in the upper part) and monthly averages of the daily maximum and minimum temperatures of the warmest and coldest months respectively (at 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. Upper panel: Squares relate to trial sites (environments); circles with numbers (420, 377 etc.) – tested populations. Grey line – boundaries of Forest Districts

Table 1. Means and variation coefficients of height [cm] and survival [%] of tested populations, 5 and 10 years after planting, SB – Sucha Beskidzka, LZ – Lądek Zdrój, ZL - Złotoryja

Population no.	Population name	Mean height [cm] (CV [%])								Mean survival [%]							
		SB		LZ		ZL		Mean across sites		SB		LZ		ZL		Mean across sites	
		2010	2015	2010	2015	2010	2015	2010	2015	2010	2015	2010	2015	2010	2015	2010	2015
377	Wałbrzych	131 (8)	430 (26)	177 (6)	480 (6)	166 (8)	490^f (21)	160 (13)	455 (22)	54	49	97	89	92	66	81	68
378	Wałbrzych	124 (11)	440^f (15)	179 (4)	510^f (6)	174 (15)	470 (17)	159 (18)	470 (21)	76	67	96	89	94	78	89	78
379	Wałbrzych	114 (13)	400 (29)	169 (8)	480 (10)	143 (25)	400 (21)	142 (21)	427 (25)	67	56	95	90	97	90	86	79
391	Zdroje	121 (10)	400 (12)	156 (8)	450 (9)	146 (15)	430 (16)	141 (14)	427 (15)	86	73	89	79	81	63	85	72
392	Zdroje	121 (10)	430^f (31)	171 (3)	500^f (13)	138 (5)	470^f (19)	143 (13)	467 (27)	62	56	91	89	92	76	82	74
420	Międzylesie	105 (18)	420^f (32)	157 (5)	440 (11)	158 (11)	510^f (16)	140 (19)	440 (27)	58	45	91	84	96	87	82	72
423	Lipinki	125 (7)	400 (30)	152 (7)	430 (14)	158 (17)	470 (20)	145 (15)	433 (24)	65	61	95	86	86	65	82	71
424	Lipinki	126 (20)	410 (13)	158 (3)	500^f (4)	134 (20)	380 (8)	139 (16)	395 (18)	73	65	95	89	90	78	86	77
430	**Świdnica**	112 (12)	340^s (23)	162 (12)	390^s (10)	136 (18)	360^s (16)	137 (19)	363 (18)	65	56	94	89	96	87	85	77
431	Lądek Zdrój	119 (12)	430^f (26)	155 (8)	430 (8)	150 (9)	480^f (16)	141 (14)	430 (22)	69	62	95	85	96	66	87	71
432	Lądek Zdrój	123 (8)	420 (16)	175 (13)	480 (16)	134 (19)	400 (19)	144 (18)	433 (20)	74	69	94	83	90	72	86	75
433	Lądek Zdrój	122 (10)	400 (21)	163 (10)	451 (11)	159 (26)	430 (36)	148 (22)	427 (28)	73	63	93	90	96	91	87	81
434	Jawor	118 (8)	390 (17)	165 (16)	410^s (23)	158 (14)	440 (22)	147 (18)	415 (27)	66	58	94	88	88	66	82	71
437	Henryków	130 (12)	410 (18)	178 (11)	510^f (11)	120 (30)	380 (25)	143 (24)	395 (24)	71	63	94	58	88	61	84	61
438	Sucha	98 (21)	330^s (30)	144 (16)	420^s (6)	97 (15)	320^s (14)	113 (24)	420 (27)	50	35	83	43	96	63	76	47
439	Sucha	126 (8)	430 (33)	178 (8)	500 (19)	154 (9)	480^f (17)	153 (14)	465 (28)	70	64	97	89	91	65	86	73
446	Ustroń	125 (21)	420 (26)	165 (5)	520^f (14)	151 (14)	430 (10)	147 (17)	425 (24)	71	63	95	89	92	77	86	76
447	Ustroń	113 (11)	380 (31)	165 (11)	450 (14)	151 (20)	400 (32)	143 (20)	410 (29)	69	58	93	88	96	91	86	79
448	Kolumna	115 (12)	390 (28)	154 (12)	480 (11)	116 (25)	400 (10)	128 (21)	423 (23)	72	63	94	62	70	59	78	62
449	Lwówek Śląski	107 (17)	350^s (29)	158 (6)	420 (8)	120 (28)	380 (9)	128 (23)	400 (21)	65	56	90	68	86	75	80	66
450	**Śnieżka**	123 (9)	430^f (24)	165 (10)	490 (16)	148 (16)	450 (23)	145 (17)	470 (23)	70	63	95	86	96	86	87	78
466	Jugów	119 (4)	400 (15)	167 (6)	480 (6)	136 (14)	410 (25)	141 (16)	430 (24)	76	71	94	80	91	65	87	72
487	Bielsko	120 (7)	350^s (26)	162 (6)	420^s (7)	105 (14)	330^s (10)	129 (20)	367 (21)	67	60	87	69	85	68	80	65
488	Bielsko	119 (13)	350^s (9)	157 (11)	430 (11)	86 (28)	320^s (12)	121 (30)	430 (19)	76	70	86	40	96	54	86	54
489	Bielsko	131 (7)	390 (25)	163 (10)	420^s (8)	155 (8)	400 (14)	150 (11)	395 (17)	67	62	94	88	92	65	84	72
490	Bielsko	118 (12)	400 (15)	172 (14)	450 (19)	142 (16)	430 (7)	144 (19)	427 (21)	74	63	95	80	89	71	86	71
491	Bielsko	108 (21)	360 (35)	160 (3)	430 (10)	102 (11)	360 (21)	123 (22)	383 (25)	62	54	93	44	96	54	84	50
492	Bielsko	121 (8)	400 (23)	155 (8)	410^s (6)	116 (28)	430 (15)	131 (17)	415 (17)	65	57	89	63	68	62	74	60
493	Bielsko	122 (17)	400 (24)	157 (2)	420 (15)	138 (19)	431 (22)	139 (16)	417 (20)	75	63	94	78	89	79	86	73
494	Bielsko	136 (18)	400 (27)	167 (7)	460 (3)	148 (16)	360^s (13)	150 (14)	430 (19)	73	68	96	92	96	91	88	84
Multi-population mean		120 (13)	397 (23)	164 (10)	455 (13)	138 (23)	415 (22)	141 (19)	422 (23)	69	60	93	78	90	72	84	70

f – fast-growing provenance, *s* – slow-growing provenance.

onto the AE axis describes stability – the higher the absolute value segment length, the lower the level of stability of the population. Therefore the GGE biplot represents the main effects and interactions attributable to the sites, while it cannot be used to determine the statistical significance of these effects.

Statistical analyses and presented biplots were performed with SAS/STAT 13.1 (SAS Institute, 2013) and specifically the GLM, MIXED, PRINCOMP and GPLOT procedures (Littell et al., 1996; Khattree & Naik, 2000).

Results

The mean height of the beech trees across all the analysed environments in 2010 was 141 cm (Table 1). After five years of growth, the highest trees were those at the LZ site (mean 164 cm), while the lowest (mean 120 cm) were at the SB site. The same trend was still visible in 2015, when the mean height across all the environments was 422 cm. Then the tallest trees were still at the LZ site (mean 455 cm), and the shortest were at the SB site (mean 397 cm). In Sucha Beskidzka (SB) the fastest height growth was found for provenances 378, 392, 420, 431 and 450, and the most limited height growth was found for populations 430, 438, 449, 487 and 488. In LZ, the fast-growing trees were from populations 378, 392, 424, 437 and 446, while slow growth was noted for trees from populations 430, 434, 487, 489 and 492. At the ZL site, fast growth on height was noted for the progeny of populations 377, 392, 420, 431 and 439, while the slow-growing trees there were from populations 430, 438, 487, 488 and 494.

Trees of population 392 proved capable of rapid growth on height irrespective of environmental conditions. In turn, the progeny of three populations (378, 420 and 431) showed good growth at two of the three sites, while the weakest growth at all sites characterised offspring of population 430, 438 and 487.

Statistically significant effects of populations, environment and G×E interaction were found for tree height in 2010 and 2015 (Table 2). According to the decomposition of variance (DOV) in 2010, 51.6% of the overall variation in height (G+E+GE) could be accounted for by the effect of environment, while the remaining 48.4% was explained in terms of the impact of genotype, G (25.6%), and G×E interaction (22.9%).

According to DOV in 2015, 63.1% of the overall variation in tree height (G+E+GE) was explicable in terms of the impact of E, leaving 36.9%, of which the effect of G, accounted for 17.9% of the variation, and the effect of the G×E interaction for 18.9%. Throughout the 2010–2015 period between measurements, the effect on height of beech trees attributable to the environment increased by 11.5%, while the influence of genotype and the G×E interaction was lower by 7.6% and 3.9%, respectively.

To determine the changes in tree height in the studied environments, the PCA was carried out separately for 2010 and 2015. In the case of the 2010 data, the division of effects (G+GE) with the aid of the GGE biplot method yielded the result that PC1 explained 82.6% of the variation (G+GE), while the second component PC2 explained a further 12.2%. In the case of the 2015 data, the division of effects (G+GE) with the aid of the GGE biplot yielded the result that PC1 explained 67.9% of the variation (G+GE), while PC2 explained a further 20.9%.

Environmental similarity and production potential

The positioning of the environments in relation to the AE axis shows that both in 2010 and 2015 trees were tallest at the LZ study site (Fig. 2). In turn, the SB site had an environment that was the most similar to the average environment (AE), as was revealed in both tree heights as such, and the stability of their values. The ZL site had trees characterised by the greatest instability of measured heights, thus it contributed more to the G×E interaction in terms of tree heights than the other two sites.

Comparison of the positions of the environments between two ages in Fig. 2 reveals a slowing growth of trees at the SB site during the 2010–2015 period.

Table 2. Results of the analysis of variance for tree height in 2010 and 2015 among 30 populations of beech in three environments

	2010					2015				
Source of variation	Df	MS	F	P	(G+E+GE)	Df	MS	F	P	(G+E+GE)
Genotype (G)	29	1467.83	2.24[1]	0.005	25.58	29	10426	1.90[1]	0.019	17.98
Environment (E)	2	42897	8.5[1]	0.006	51.56	2	530599	7.72[1]	0.010	63.1
Block (Environment)	9	4625.72	19.91	<0.001	–	9	66536	20.27	<0.001	–
Genotype × Environment (G×E)	58	655.99	2.82	<0.001	22.86	58	5488.58	1.67	0.004	18.92
Experimental error	261	232.37	–	–	–	261	3282.51	–	–	–

[1] Hocking's approach.

Df – degree of freedom, MS – mean squares, F – statistic, P – value.

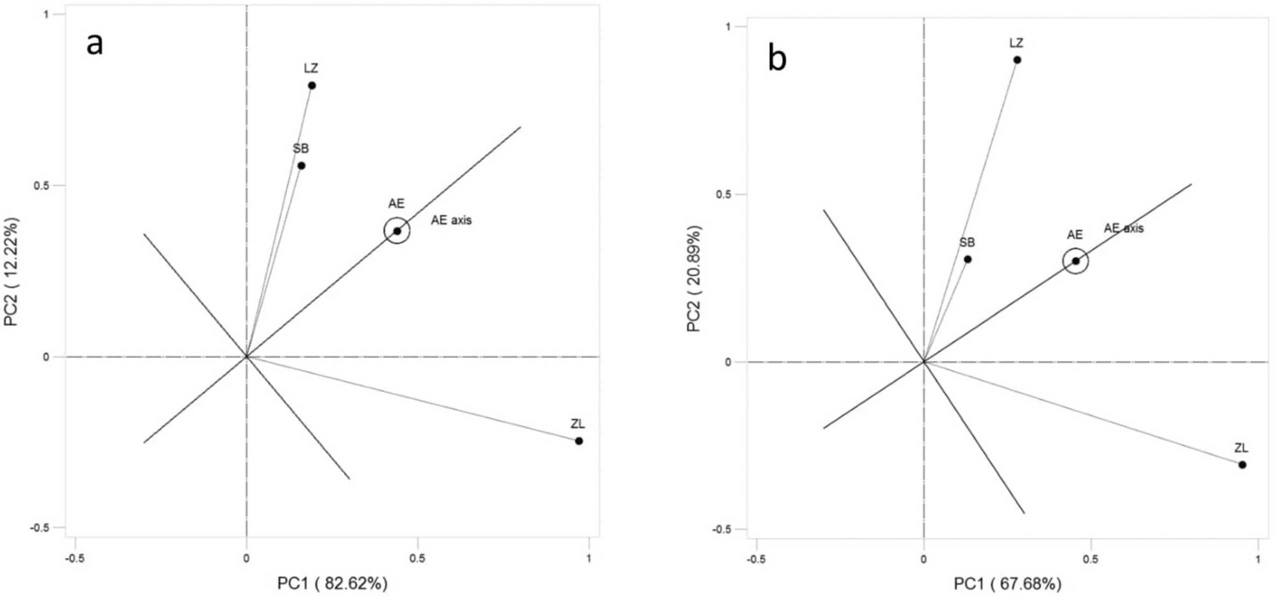

Fig. 2. Production potential and the similarity of studied environments in relation to the average environment (AE) as of 2010 (a) and 2015 (b)

Table 3. Correlation coefficients (above diagonal) and α_{ij} angles (below diagonal) between pairs of environments (upper value in cell – 2010, lower value – 2015; ** significant at the 0.01 probability level, ns – not significant)

Environments	LZ	SB	ZL
LZ	–	0.99** 0.99**	–0.01 ns –0.01 ns
SB	2.38 5.91	–	0.03 ns 0.09 ns
ZL	90.80 90.65	88.42 88.73	–

In contrast, while characterised by unstable increases in the heights of beech trees, the ZL site was found to differ from SB in its greater growth increments over the 2010–2015 period. The increments characterising trees at the LZ site were at an average level.

Analysis of the angles between the vectors for the environments revealed that the LZ and SB sites were most similar to each other both in 2010 and 2015 (Fig. 2). The vector for the ZL site created a near-right angle with the vectors for the two remaining environments, which indicates that correlation coefficients between the ZL and the LZ and SB sites were non-significant (Table 3).

Similarity and stability of populations

The type of biplot as presented at fig. 3 allows to analyse similarity/dissimilarity among the experimental sites and to identify populations adapted to specific environments. The 30 populations of beech and 3 environment (each studied in 2010 and 2015) were distributed across 8 areas (Fig.3). The ZL and LZ sites were very different from each other, while the SB site was similar to the LZ site. This indicated the existence of two mega-environments: LZ+SB (ME1) versus ZL (ME2). Populations specifically adapted to the conditions of ME1 were 446, 432 (good and stable growth) and 437 (good growth but less stable). Specifically adapted to the ME2 (ZL) were populations 420 and 431, for which the height increment was the largest in this area (Fig. 3).

Progeny of populations 378, 439, 392, 377 and 450 grew fastest when averaged across all locations (Fig. 3; Tab. 1). These populations (specifically and widely adapted) should be recommended for future use. On the other hand, progeny of populations 488, 487, 438, 430, 449 and 491 performed poorly in terms of three height at all experimental sites.

The lengths of vectors for the environments are an indication of their discrimination ability of populations (Fig. 3). The environments in 2010 had very short vectors. This is understandable, because tree heights in 2010 did not differ among the populations as much as in 2015. Environment ZL in 2015 was most discriminating as indicated by its long vector.

On the GGE biplot, stability of a population is described by reference to its position along the AE axis (Fig. 4). The closer to AE axis populations are plotted, the more stable they are (i.e. showing small interaction with environments). Among the stable populations the most interesting are those with fast growth in all environments (highest values of AE axis). The populations 378, 439, 392, 377 and 450 emerged as stable and tall (Fig. 4). Populations 446, 437, 432 and 424 were also tall, but less stable.

The GGE biplot based on differences between 2015 and 2010 data was used to describe changes

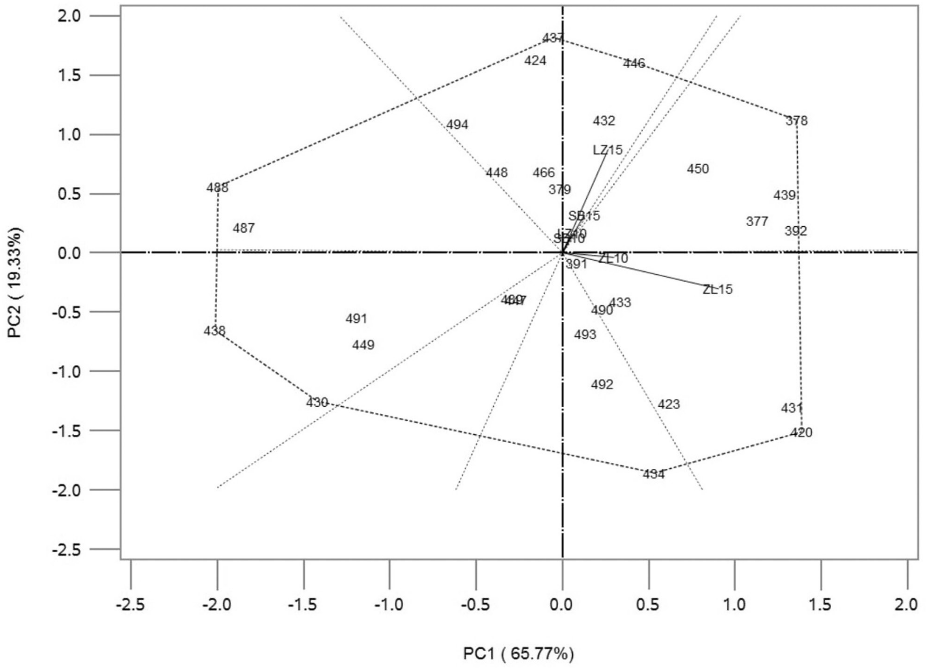

Fig. 3. A polygon superimposed on the GGE biplot on the basis of the first two PCs for 30 beech populations and three environments in the years 2010 and 2015

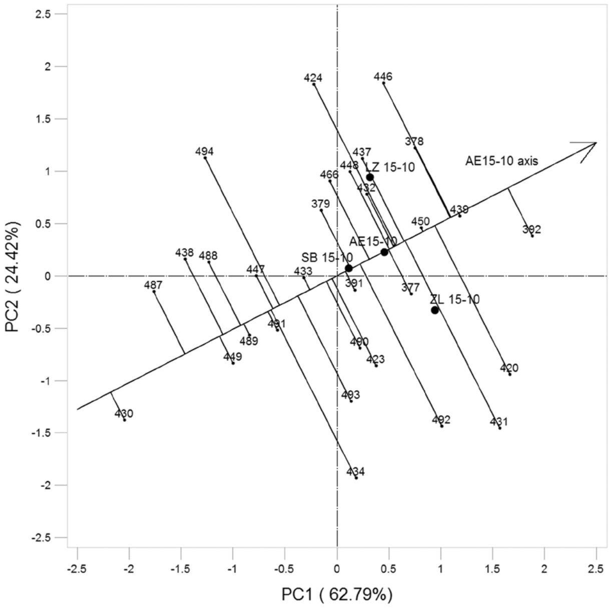

Fig. 4. The GGE biplot of mean height and its stability in relation to the average environment (AE) for 30 European beech populations

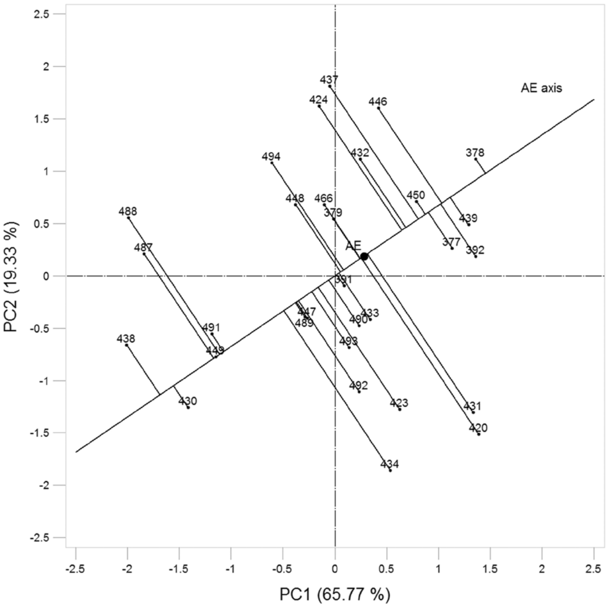

Fig. 5. Changes in the height growth and its stability for the studied beech populations between 2010 and 2015.

in the height growth and its stability across environments and years (Fig.5). Orthogonal projection of population on the AE15-10 axis indicated difference between average height in 2015 in comparison to 2010, and an arrow on the AE15-10 axis indicates direction of these differences. Populations for which tree height differences between 2010 and 2015 were stable across all environments are located closest to the AE15-10 axis (Fig. 5). Populations 392, 439 and 378 grew fastest and stable during analysed growing period across all sites (Fig. 5). Progeny of population 446 was specifically good for the LZ environment while 420 and 431 grew fast in ZL. The fastest growing progenies for the SB site originated form populations 439 and 450.

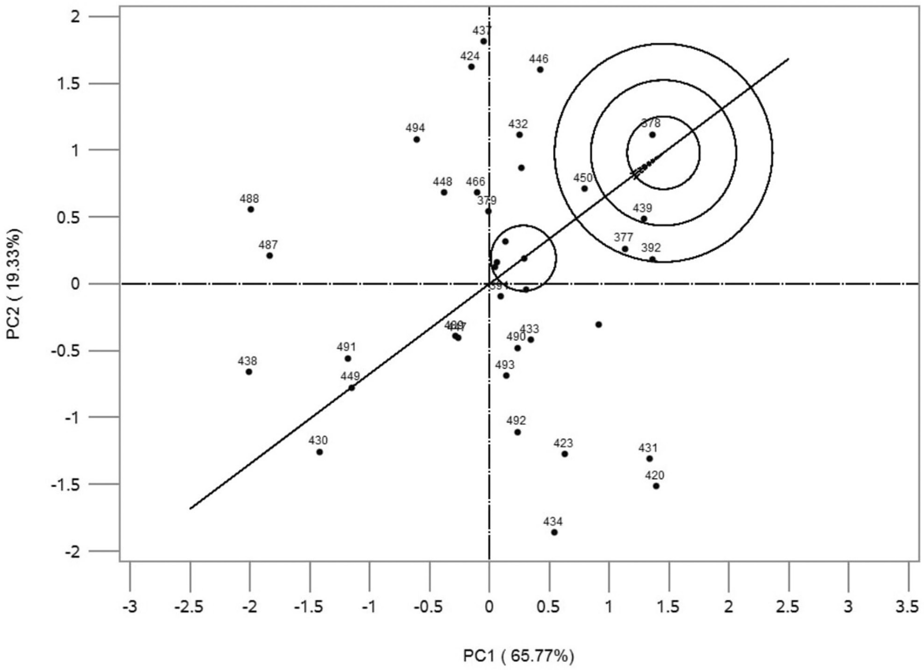

Fig. 6. Comparison between the analysed populations and the theoretical “ideal population”

The “ideal population”

The “ideal population” would be characterised by a high average value for height increments, with values for such trees growing in different environments also displaying a high degree of stability. The “ideal population” is determined by the vector beginning at the center of the coordinate system and ending at the orthogonal projection on the AE axis of the population which has the greatest PC1 value (Fig. 6). Simultaneously the “ideal population” is absolutely stable as as a result of the location on the AE axis (zero value for the G×E interaction in the average environment) (Yan & Kang, 2002).

For easier discovery of objects positioned closest to the end of the vector, the circles centred on that point were drawn. The first such circle includes population 378, which represented the ideal population in the sense that large increments in the heights of beech trees were noted, along with a high degree of stability for these values across environments. The second circle includes the population 439, for which height increments were smaller, but degree of stability was high.

Discussion

The multiannual nature of development of woody plants and the highly dynamic growth with low stability during a juvenile phase likely determine the relatively rare use of the biplot graphic method in breeding experiments with trees. Nevertheless, interest in this method has grown in recent years (Zhao et al., 2016; Klisz et al., 2017). This can be linked to a broad scope of possibilities for interpretation in the case of data obtained from multi-enviroment genetic experiments. An assessment of variability explained by the effects of G×E interaction allows to determine the scale of reduction in genetic gain achievable through selection of genotypes (Murillo, 2001). Furthermore, calculation of the G×E effect offers conclusions regarding allowable transfers of seeds, and the associated designation of seed regions for tested genotypes and populations (Taibi, 2014). The identification of the most favourable origins from the point of view of an analysed trait or group of traits allows to narrow down the selection to genotypes promotable in the plantations grown over short production cycles (Ding et al., 2008; Sixto et al., 2015). The use of biplots in interpreting multi-environment experiments with narrowed selection criteria also allows above-average genotypes to be identified (Zhao et al., 2016). In turn, where genotypes specifically adapted to selected test environments, and stable in the sense of manifesting favorable values for the analysed traits are distinguished, it becomes possible to formulate guideline strategies for afforestation and selective breeding, as well as the protection of gene resources (Correia et al., 2010).

The GGE biplot method used in stability testing for crop yields can also be used successfully in stability analysis concerning breeding of forest trees. To find an environment in which genotypes can be assessed effectively, use is made of a GGE biplot with an AE axis (Fig. 2). The selected environment should be one that both distinguishes effectively between the populations and is representative of the target region (Yan, 2002). In our studies, we identified two mega-environments in which growth conditions were similar to each other in both 2010 and 2015. Environments LZ and SB were more representative than environment ZL, while the latter achieved the most effective discrimination of populations. The biplot (Fig. 3) shows the discrimination power of the environments as indicated by the vector length of the environments. Apparently the differences among populations in 2015 were much larger than those in 2010. Therefore, the 2015 data are more useful than the 2010 data in population evaluation. However, the biplot also shows the 2010 data and the 2015 data were highly correlated within locations (Tab. 3), therefore, the 2010 data are also useful if 2015 data were not available. This means that effective evaluation of populations could be conducted 5 years earlier, although the 2015 data are more reliable.

The results of our research showed that local populations did not prove to be better than others in terms of height growth in any of the analysed environments. Population 438 which is local to the SB site showed the most limited height increments there. Similar behaviour was displayed by the population 431, which is local to the LZ environment (Fig. 3). Earlier results at experimental plots in ZL and LZ point to the need for particular populations, though not necessarily local ones, to be chosen for cultivation at a given site (Barzdajn, 2009). Similar conclusions were reached by Buraczyk et al. (2016), after analysis of various quantitative and qualitative traits among 23 progenies of European beech in southeastern Poland.

Better adaption of the non-local populations seems to be particularly important in the context of the counteracting unfavourable influence of climate change on European beech populations in Poland. Because rate of the climate change is likely to be faster than evolutionary adaptiveness (Aitken et al., 2008; Alberto et al., 2013), the use of assisted migration and seed transfer seems to be promising breeding activity (Bolte et al., 2016).

In our analysis we found a significant effect of genotype on differences in tree height. However, this influence of genotype declined through time. Our results contradict those found for the growth of beech in central Poland (Szeligowski, 2012). In that study analysing the height of beech trees from 47 Polish populations, the percentage input due to genotype was greatest at age 15 years (at 46.3%), while it was most limited in the case of 9-year-old trees (at 32.1%). In our study the overall variability conditioned by a genotype was greater at age of 5 years (a 25.6% input), and went down to 17.9% by the age of 10 years. This shows at the same time a greater influence of the environment on height of trees. This environmental influence grew steadily with increasing age from 51.6% in 2010 to 63.1% in 2015.

Of considerable interest are the results concerning changes in the mean height increments between the years 2010–2015 (Fig. 5). During this period the populations showed varied reactions from the height-increment point of view. For some populations the tree height increment increased (as in the case of 392 and 378) or decreased (430, 487 and 449) between two measurement occasions. There were also those (like 439 and 450) maintaining growth at very stabilised levels across all three environments.

There are two possible approaches to using the obtained results in further silvicultural work with the analysed populations of European beech in this testing region. The first approach, described by Finlay and Wilkinson (1963), assumes a search for stable populations, followed by their wide utilisation in different environments. Looking at our results in line with this approach, we report that populations like 378, 439, 446 and 392 and stand out from the set of studied populations. They do not manifest G×E interactions and reach large height on all three analysed plots through the whole period of investigation. For these reasons the populations in question can be considered worthy of wide introduction into forest management. Their high value is further confirmed by their similarity to the "ideal population" (Fig. 6). In contrast, population 430 shows stability of tree height but is one of the populations manifesting most limited growth. Populations 488 and 438 grow as weakly as 430, but in their case the trait was less stable. These three populations should thus be excluded from further use in the region were testing was conducted.

A second approach, (e.g.McKeand et al., 1990; Baltunis et al., 2010) assumes the delineation of breeding zones in which specifically-adapted populations are used. In our work, we confirmed the presence of such populations, which are suitable for recommendation in breeding in conditions only represented by a defined study plot. The three study sites formed two mega-environments in which the introduction of specifically adapted populations can be advocated. In the case of the ZL site these were populations 420, 431 and 423, whereas for the SB and LZ sites these were populations 437, 424, 432 and 446. Populations adapted to local conditions and stable across the different environments were also indentified in the work of Stojnić et al. (2015), who assessed tree height and survival at 5 and 6 years after planting among 15 beech populations in four areas of Bosnia-Herzegovina, Croatia and Serbia. In our network of progeny testing the tested populations are compared with different types of standards of national, regional or local range. These are most often populations of known genetic value established on the basis of earlier research. In our study these were populations 447, 391 and 392 that were selected for testing as the regional standards for the region III. The obtained results show that only one of those standards was selected effectively (391). On the GGE biplot (Fig. 4) the population 391 was located close to the centre of the coordinate system, denoting that it was characterised by average height and stability of the trait. Furthermore 391 manifested no changes in height increments between 2010 and 2015 (Fig. 5). The other two populations selected as the regional standards showed contrasting growth pattern. According to Giertych (1990; 2000), European beech shows mostly the ecotypic variation, with each population associated with its habitat. This accounts for a lack of economic benefit if seeds from a distant population are utilised. Under these circumstances, the value of a population will depend on the similarity, or the lack thereof, of environmental conditions between deployment zone and the area of the parental population. Within the analysed set of populations it is possible to distinguish (unstable) ones that were characterised by above-average mean heights in given environments only. Equally, there were populations average as regards tree height that were nevertheless stable across different environments representing varied conditions for growth. This same kind of ranking of genotypes in terms of their stability and the mean value for a given trait was presented in studies of *Betula platyphylla* by Zhao et al. (2016).

Progeny testing in the last 10 years has shown that conclusions as regards to specific genotype adaptation may be encumbered with errors. These reflect the negative effect of a potentially discriminatory environment. It must be emphasized that differences in height growth and survival after 5 or 10 years do not fully describe adaptation potential of European beech. On the other hand, early developmental stages of plants are expected to be more sensitive to climate change than adult stages (Walck, 2011). On the basis of our results we cannot determine a geographical pattern for the populations of beech that grow best in terms of height. Populations with the most stable values for height in all three environments can be found in both the mountain and the upland region. It is possible to identify populations that adapt well to local conditions, as well as to growing conditions in the whole testing region. The GGE biplot method used in stability testing for crop yields can also be used successfully in stability studies involving the growth of forest trees.

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