Morphological Variability of Beech Leaves from Early and Late Flushing Provenances

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Kempf, M., Banach, J. and Skrzyszewska, K. 2018. Morphological Variability of Beech Leaves from Early and Late Flushing Provenances. *Baltic Forestry* 24(2): 210–217.

Abstract

One of the anticipated results of the climate change will be the alteration of the current distribution areas of forest tree species. In light of these processes, it is expected that the role of one of Europe's significant forest forming species –– European beech, *Fagus sylvatica* L. — will be increased, particularly in the north-eastern part of its distribution, the border of which runs through the Polish territory. The study was aimed to determine the morphological characters diversity of beech leaves from 10 provenances, grown on experimental plots, differing in spring flushing. From four years of observation, five provenances with early and late flushing were selected. Seven morphological characters of the leaves were analysed. The study has shown, that beech trees that begin to grow late in spring, develop smaller leaves than those referred to as early flushing. Moreover, morphological distinction of beech leaves from two centres of its distribution in Poland, i.e. northern and southern, has been confirmed. The obtained information on the provenance variability of beech and its adaptive characters are important for breeding and selection tasks. The use of the obtained knowledge will help in the proper implementation of forestry goals, which include the possibility to use forest reproductive material to ensure lasting tree stand stability in the future.

Keywords: *Fagus sylvatica* L., leaf morphological traits, phenology, variability

Introduction

European beech is characterised with highly variable growth and physiological characters, and therefore it is distinctive with high adaptive capability. This is expressed by a wide spectrum of habitats occupied by the species in European forests, where, under favourable climatic and moisture conditions, it forms valuable forest stands. The forecast of the change of distributional areas of forest-forming species, resulting from climatic changes (Hickler et al. 2012), predicts the increasing role of beech on the European continent, particularly at the leading edges in the northeastern part of its distribution (Bussotti et al. 2015), the border of which is located *inter alia* on the Polish territory.

A multiannual study of the survival variability, growth, and phenological characters conducted on the area of the Bk 92–95 experiment (Barzdajn 2002, Sabor and Żuchowska 2002), as well as pollen analyses (Latałowa et al. 2004) and genetic study (Kempf and Konnert 2016), showed two centres of distribution for beech in Poland, northern (Pomeranian) and southern (mountains and highlands). Results of the study on intraspecific variability of beech indicate that one of the more important characters diversifying the provenances is the date of spring flushing initiation. It is a genetically determined character (Bontemps et al. 2016), enabling the possibility to select the provenances that are resistant to late spring frost damage (von Wuehlisch et al 1995, Chmura and Rożkowski 2002). In Poland, beech vegetation starts with a clinal change in the south–north direction as a norm, northern provenances start flushing later than southern provenances (Barzdajn 2006). The character also changes clinally across the entire range, but along with the longitude, i.e., in the west–east direction (Gömöry and Paule 2011).

Morphological characters of assimilation apparatus are susceptible to the effect of environment. The leaves may differ in size, shape, and thickness within the tree canopy. This variability is determined inter alia by the intensity of UV radiation, length of light waves, temperature and water availability (Denk 1999), which influence the level of canopy density and cover (Jack and Long 1991, Frazer et al. 2000, Barna 2004, Hatziskakis et al. 2011). Leaf variability of beech occurs at the inter-population level as a result of environmental factors like e.g. water availability, spring temperature, or possibly nitrogen supply (Meier and Leuschner 2008). For beech, a strong discriminative factor is water stress which causes increases of sclerophylly (Bussotti et al. 1995, 2000, 2005, Gravano et al. 1999). In the light of climatic changes, provenance experiments constitute valuable study objects that enable the determination of character variability (Mátyás 2006). Similar conditions of tree growth on experimental trials, resulting from methodological assumptions (number of repetitions, identical spacing) allow to eliminate the effect of the environment on the variability of characters observed (Bussotti et al. 2015).

The study analysed the progeny obtained from different common beech provenances, grown in uniform environmental conditions of experimental trial. The objective of the study is to determine the interpopulational variability of morphological characters of beech leaves, including the division into late and early flushing provenances. The study also aimed to verify the thesis on the presence of two distributional centres of beech in Poland.

Material and Methods

The study was conducted on the material collected from an experimental plot Bk 92-95 in Krynica (49°24’N, 20°55’E), at the border between the Beskid Sądecki and the Low Beskids, where offspring from 30 seed tree stands of beech from the Polish area of distribution is tested. Mean annual air temperature at the experimental plot is 5.1 °C and annual precipitation is 947.6 mm. The trial was conducted in five repetitions. On each of 150 provenance plots 100 seedlings with 1.5 × 1.3 m spacing were planted, leaving a free row between the plots and repetitions. A more detailed characteristics of the experiment and tested provenances is presented in the publication of Sabor and Żuchowska (2002). Five beech provenances from each of the two-flushing type (late and early) were selected for the analyses of morphological variability of leaves, following the phenological assessment conducted in 1997, 2001, 2007, and 2015. Characteristics of selected beech provenances are presented in Table 1, whereas geographic location of populations including flushing forms is shown in Figure 1. Leaves were collected from the outer, well-illuminated part of the canopy, from its southern side. Leaves were not wrinkled, they were smooth and glossy collected during their 7th phase of spring development following the Mallaisse scale (1964). For each of 10 provenances 500 undamaged and healthy leaves were collected, 10 items from 10 trees and five repetitions of experiment collection was performed.

Leaf morphological evaluation included leaf length (LL, cm), leaf blade width (LW, cm), leaf perimeter (LP, cm), leaf area (LA, cm^2) and petiole length (PL, cm). The first four characters were determined using the digital images of leaves obtained via Epson Expression 1600 scanner, which were subsequently analysed with the aid of WinSeedle program (Regent Instruments 2018). Measurements of petioles were conducted using electronic callipers. Moreover, two indexes based on the leaf parameters

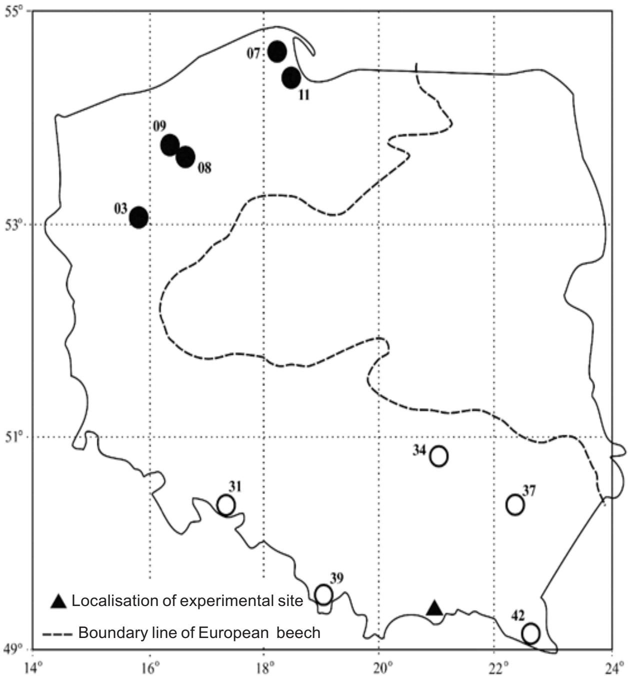

Figure 1. Geographic location of late (full dots) and early (empty dots) flushing provenances of beech. Details of populations are given in Table 1

Table 1. Characteristics of the European beech provenances investigated in the study

Flushing form	No of prov.	Provenance name	Age	Altitude (m)	Longitude	Latitude	Flushing stage (ranking position)			
					(E)	(N)	1997	2001	2007	2015
late	3	Radachowo	107	193	15°54’	53°05’	4.23 (3)	2.39 (2)	3.07 (3)	3.86 (1)
	7	Gniewino	110	115	18°18’	54°37’	4.38 (5)	2.71 (5)	3.35 (5)	4.92 (6)
	8	Jelenino	96	130	16°40’	53°40’	4.43 (8)	2.70 (4)	3.33 (4)	4.32 (3)
	9	Dalęcino	111	130	16°30’	53°45’	4.10 (1)	2.49 (3)	2.81 (1)	3.88 (2)
	11	Marianowo	105	70	18°31’	54°23’	4.21 (2)	2.25 (1)	2.93 (2)	4.35 (4)
early	31	Pokrzywna	130	425	17°20’	50°20’	4.90 (23)	4.03 (28)	5.91 (29)	6.44 (20)
	34	Jeleniów	90	350	20°59’	50°50’	5.31 (30)	4.19 (29)	5.21 (20)	6.67 (27)
	37	Marynin	96	170	22°17’	50°23’	5.13 (29)	4.34 (30)	5.98 (30)	6.81 (30)
	39	Bukowa	122	550	18°54’	49°39’	5,00 (28)	3.79 (24)	5.34 (23)	6.20 (15)
	42	Moczarna	135	700-920	22°29’	49°07’	4.97 (27)	3.70 (20)	5.56 (27)	6.41 (19)

were calculated: leaf index (LI = LL / LW × 100) and petiole index (PI = PL / LL × 100) (Hatziskakis et al. 2011).

The measured characters and calculated indexes were characterised by mean and standard deviation for each provenance and mean for groups of provenances with early and late flushing. The data of morphological features were examined for assumptions of normal distribution (Shapiro-Wilk test, p=0.000) and was not found to confirm to model requirements. For assessment significance of differences in leaf parameters among tested two group of provenances, the nonparametric Mann-Whitney U test was tested. Significance of differences in morphological leaves traits among tested 10 provenances was tested *via* Kruskal-Wallis test. In order to evaluate the grouping factors, a principal component analysis (PCA) was conducted for standardised data. In order to determine the relationship between the tested characters, the Pearson correlation coefficient was used assuming the significance level as $p < 0.01$, $p < 0.05$ and $p < 0.1$. Statistical analysis was performed using Excel 2007 and Statistica 12 (StatSoft 2014) software.

Results

Mean values of the analysed characters for selected provenance groups of beech with early and late spring development are presented in Table 2. Based on nonparametric tests, a high, statistically significant character variability was determined for flushing forms (Table 3) and for provenances (Table 4).

Beech tree stands from the southern part of the distribution, characterised by earlier spring development, also showed higher mean values of analysed leaf characters in comparison to the late-flushing provenances from northern localities. The progeny of the southern 37 Marynin provenance had leaf blades of highest mean length and width (with largest area and perimeter stemming from those). The smallest leaves with the lowest mean values of these characters were found for the late flushing provenance 8 Jelenino from northern Poland. Moreover, beech trees from this provenance developed the shortest mean length of petioles. The longest petioles were found in beech leaves from the southern 39 Bukowa provenance.

Table 2. Mean values and standard deviations of the morphological parameters of European beech leaves

Flushing form	No of prov.	Provenance name	Leaf length	Leaf width	Petiole length	Perimeter	Leaf area	Leaf index	Petiole index
			[cm]	*[cm]*	*[cm]*	*[cm]*	*[cm^2]*		
late	3	Radachowo	7.94 (1.36)	4.45 (0.77)	0.88 (0.18)	20.33 (5.42)	22.16 (8.33)	179.14 (15.80)	11.29 (2.40)
	7	Gniewino	7.83 (1.17)	4.46 (0.78)	0.84 (0.18)	19.90 (5.73)	21.92 (6.58)	177.11 (16.69)	10.88 (2.76)
	8	Jelenino	7.36 (1.29)	4.05 (0.70)	0.81 (0.23)	18.30 (5.56)	18.55 (6.45)	182.50 (17.63)	11.22 (3.30)
	9	Dałęcino	7.97 (1.46)	4.45 (0.89)	0.92 (0.22)	20.07 (5.94)	22.18 (8.88)	180.42 (16.58)	11.74 (2.93)
	11	Marianowo	7.68 (1.16)	4.33 (0.73)	0.94 (0.22)	19.45(5.38)	20.65 (6.11)	178.39 (16.58)	12.43 (3.27)
		Mean	7.75	4.35	0.88	19.61	21.09	179.52	11.51
early	31	Pokrzywna	8.17 (1.47)	4.48 (0.85)	0.98 (0.20)	20.18 (6.73)	22.86 (7.08)	183.35 (18.28)	12.29 (2.98)
	34	Jeleniów	8.18 (1.44)	4.60(0.89)	0.97 (0.25)	19.77 (7.50)	23.70 (9.08)	179.63 (19.73)	12.02 (2.75)
	37	Marynin	8.63 (1.35)	4.83 (0.84)	0.96 (0.22)	21.04 (7.20)	26.09 (9.96)	180.10 (15.59)	11.20 (2.51)
	39	Bukowa	7.90 (1.38)	4.14 (0.72)	0.97 (0.27)	18.49 (9.96)	20.16 (7.31)	191.71 (18.81)	12.60 (4.07)
	42	Moczarna	8.18 (1.63)	4.45 (0.99)	0.94 (0.21)	19.12 (7.82)	22.99 (6.41)	185.71 (19.12)	11.86 (3.02)
		Mean	8.21	4.50	0.96	19.72	23.16	184.10	12.00

Table 3. U Manna-Whitney test for measured morphological features

Analysis	Test	Leaf length	Leaf width	Petiole length	Perimeter	Leaf area	Leaf index	Petiole index
Flushing form	Z	-10.393***	-5.103***	-13.513***	-4.389***	-7.900***	-8.753***	-4.776***

***p<0.001

Table 4. Kruskal-Wallis ANOVA for measured morphological features

Analysis	*df*	Test	Leaf length	Leaf width	Petiole length	Perimeter	Leaf area	Leaf index	Petiole index
Provenance	9	H	235.69***	282.44***	309.41***	131.45***	287.27***	237.78***	140.44***
		χ^2	148.26***	165.63***	255.84***	101.92***	175.39***	155.91***	93.38***

***p<0.001

The principal component analysis (PCA) showed the existence of three factors fulfilling the Kaiser criterion with eigenvalues higher than 1 (Kaiser 1960), which jointly explained 95.78% of variances (Table 5). The first component contributed largely to the explanation of the observed variability, explaining 56.94% of variance and the second one explaining 29.48% of the variance. Figure 2 shows placement of provenances within the space determined by the first two principal components. The first component showed negative correlation to all the analysed characters. This means that provenances located on the right side of the X-axis on the chart were characterised by low mean values of the analysed leaf parameters and they also belonged to provenances with late initiation of vegetation. On the contrary, the provenances on the left side were characterised by large leaves and earlier flushing. The first principal component was primarily affected by the length of the leaf blade, leaf area, and petiole length and the flushing indexes in all four dates of observation. The second principal component was affected by the characters linked to the leaf blade shape and the petiole index.

Table 5. Correlations between tested traits of beech and the tree main principal components eigenvector scores of the principal components and explanation of the percentage of variance

Variable	Factor 1	Factor 2	Factor 3
LL	**-0.916**	0.331	0.062
LW	-0.703	0.701	0.079
PL	**-0.801**	-0.244	0.544
LP	-0.453	**0.834**	0.215
LA	**-0.816**	0.564	0.032
LI	-0.233	**-0.870**	-0.058
PI	-0.248	**-0.679**	0.679
FS_{1997}	**-0.872**	-0.330	-0.280
FS_{2001}	**-0.930**	-0.246	-0.232
FS_{2007}	**-0.914**	-0.317	-0.191
FS_{2015}	**-0.917**	-0.285	-0.209
Eigenvalue	***6.26***	***3.24***	***1.03***
Percentage of variance	***56.94***	***29.48***	***9.36***

LL – leaf length, LW – leaf width, PL – petiole length, LP – leaf perimeter, LA – leaf area, LI – leaf index, PI – petiole index, FS_{1997} FS_{2001} FS_{2007} FS_{2015} – flushing stage of beech from the provenance trial as measured in 1997, 2001, 2007 and 2015

Table 6. Correlation coefficients between leaf morphological parameters of beech age localisation of parent tree stands and values of flushing coefficients. The values shown in bold are statistically significant at the level of $p < 0.01$ (***), $p < 0.05$ (**) and $p < 0.1$ (*)

Parameter	Age	Altitude	Longitude (E)	Latitude (N)	FS_{1997}	FS_{2001}	FS_{2007}	FS_{2015}
LL	0.081	0.325	**0.654****	**-0.647****	**0.637****	**0.737****	**0.720****	**0.704****
LW	-0.194	-0.053	0.516	-0.248	0.368	0.459	0.396	0.435
PL	0.241	0.501	0.504	**-0.718****	**0.636****	**0.680****	**0.698****	**0.689****
LP	-0.171	-0.319	0.119	0.022	0.033	0.174	0.129	0.116
LA	-0.085	0.128	**0.610***	-0.438	0.507	**0.600***	**0.553***	**0.570***
LI	**0.558***	**0.737****	0.163	**-0.689****	0.429	0.416	0.510	0.413
PI	0.362	0.449	0.090	-0.421	0.270	0.247	0.311	0.299

LL – leaf length, LW – leaf width, PL – petiole length, LP – leaf perimeter, LA – leaf area, LI – leaf index, PI – petiole index, FS1997 FS2001 FS2007 FS2015 – flushing stage of beech from the provenance trial as measured in 1997, 2001, 2007 and 2015.

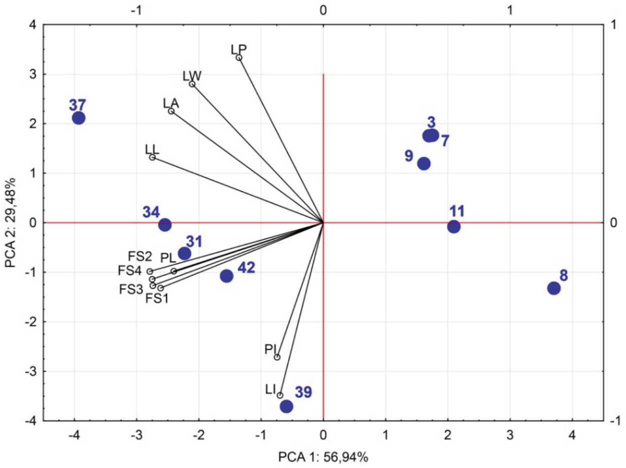

Figure 2. The grouping of provenances tested on the experimental site using principal component analysis. Provenance numbers according to Table 1
LL – leaf length, LW – leaf width, PL – petiole length, LP – leaf perimeter, LA – leaf area, LI – leaf index, PI – petiole index, FS_{1997} FS_{2001} FS_{2007} FS_{2015} – flushing stage of beech from the provenance trial as measured in 1997, 2001, 2007 and 2015

The PCA results were confirmed by the value of correlation (Table 6) of analysed characters with flushing indexes from four observation dates. Leaves from the early flushing provenances were characterised by significantly larger leaves, longer petioles and larger leaf area. The correlation between morphological characters with the location of parent tree stands showed a significant positive relationship between the length of the leaf blade and leaf area and the longitude, and a negative correlation between petiole length, leaf index, and blade length and the latitude. The positive significant correlation between leaf index, age of parent tree stands, and their location above sea level, was indicated (Table 6).

Discussion and Conclusions

The study showed significant diversity of the analysed morphological characters of the beech leaves from provenances, as well as the distinguished flushing forms. High intraspecific diversity of the European beech was corroborated by the studies conducted for the evaluation of variability of assimilation apparatus from European provenances (Denk 1999, Denk et al. 2002, Hatziskakis et al. 2011, Šijačić-Nikolić et al. 2013, Stojnić et al. 2016), including Polish origins (Rzeźnik 1992, Dolnicki and Kraj 2001). High morphological variability was primarily determined by the length of the leaf blade, leaf area, and petiole length. In other studies on the assimilation apparatus of beech, characters that correspond to the axes of the primary component analysis were also mentioned as significant (Denk 2003, Papageorgiou et al. 200, Hatziskakis et al. 2011, Stojnić et al. 2016).

The study determined the occurrence of a clinal trend of variability of morphological characters in the assimilation apparatus of beech from the west to the east and from the south to the north. Provenances in eastern Poland were characterised by their longer leaves and larger area. The variability of beech leaves in the direction from the west to the east was also observed by Denk (1999) and Denk et al. (2002). On the other hand, Hatziskakis et al. (2011) confirmed the increase of the number of 2nd order nerves and a decrease of the petiole length. Following Papageorgiou et al. (2007), leaves of eastern populations are characterised by longer leaf blades, and greater leaf area and perimeter. The variability in the direction from the south to the north determined in our study was characterised by decreasing length of the leaf blades and petioles and decreasing leaf index with increasing latitude. A similar relationship was observed in the study conducted on a provenance trial in Serbia, where lower values of leaf parameters were determined in beech trees originating from Austria, Germany, and Hungary in comparison to populations from Croatia, Serbia, and Bosnia and Herzegovina (Šijačić-Nikolić et al. 2013).

The study did not find any strong relationship between the variability of beech leaves and the location above sea level (a.s.l.) of the parent tree stands, which was confirmed by the results of the study of Pagan (1968) conducted on beech in Slovakia. However, many authors point to the decreasing values of the evaluated beech leaf characters with the increase of the altitude a.s.l. of tree stand localities. Dolnicki and Kraj (2001) showed that the leaf size, independent of the flushing form, decreased with altitude a.s.l. Denk (1999) determined that with the increase of elevation a.s.l, the leaves of *Fagus sylvatica* start to resemble *Fagus orientalis*, whereas Vitasse et al. (2014) showed the decreasing leaf thickness with altitude gradient.

The variability of morphological and physiological characters may have a genetic basis, stemming, inter alia from the history of the species expansion after the most recent glaciation and it may also be caused by the phenotypic plasticity (Bresson et al. 2011). At the level of single genotypes, phenotypic plasticity enables survival in a wide spectrum of environmental conditions (Bruschi 2010) and, as an adaptive mechanism, is subject to inheritance and selection caused by climatic conditions (Mįtyįs 2006). The high level of genetic variability of populations is necessary for the adaptation process, particularly in the case of rapid environmental changes. The study of functional characters variability helps understanding the capability of populations to react to the changing environmental conditions (Körner 2007). The study of Bresson et al. (2011) showed that the variability of functional characters in beech, studied in the altitude gradient, was affected to a greater extent by environmental factors than the genetic ones. Although phenotypic plasticity may explain a greater number of functional than genetic variability, distinguishing the effect of these factors is very difficult (Robson et al. 2012). Analysis of intraspecific variability under the conditions of experimental trials assumes an equal effect of the environment on the formation of the tested characters. The herein showed beech leaf diversity in the late and early flushing provenance and the lack of strong relationship between the variability of beech leaves and the location in the altitude gradient of parent tree stand locations enable to hypothesize that the genetic factor may play an important role in the creation of differences between populations.

Phenological variability, which constituted the criterion for the selection of provenance of the study, a genetically determined character that is also strictly related to the leaf size, is of high adaptive importance. The study showed that beech trees with late spring development produce smaller leaves than those included in the early flushing group. This corroborates the results of the study conducted by Mišić (1957), in which early flushing beech trees had longer leaves than the late flushing ones. Similarly, the leaf size and petiole length were found to be lower in late flushing forms (Dolnicki and Kraj 2001).

The study confirmed the difference of leaf morphology of beech provenances from two centres of occurrence in Poland, i.e. northern and southern ones. The presence of differences at the level of nuclear DNA between northern and southern beech are corroborated by the study of Kempf and Konnert (2016). The usefulness of nuclear DNA in the study of intraspecific variability was showed in the study of Papageorgiou et al. (2007) and Hatziskakis et al. (2011). It is likely that the leaf characters can be controlled by nuclear genes, and the gene flow may obscure geographic and postglacial trends. The study on relationship between leaf characters and postglacial population expansion were conducted in Greece (Hatziskakis et al. 2009) and Spain (Robson et al. 2012). They showed that the refugium locality and later postglacial expansion of the species influenced the variability of leaf characters, but it was seen only in the analysis of populations from a wider distribution range. At a local scale, the leaf variability is affected to a far greater extent by environmental factors.

Results obtained in the present study showed the differences in the size of assimilation apparatus in beech trees are differing in the date of the beginning of spring flushing. Ecophysiological leaf characters (photosynthetic capability, stomatal conductance, size, and thickness of leaves) are strictly related to the capability to accumulate carbon. It is one of the most important components of the life potential of trees (Wright et al. 2004). The interception of photons is largely controlled inter alia by leaf area and is very closely correlated with the accumulation of biomass (Innes et al. 2005). For good and stable productivity of stands, efficiency of the assimilation apparatus is necessary. Leaf morphological structure must guarantee the efficient capture of light and carbon dioxide but, at the same time, ensure adequate heat exchange and transpiration. Jensen and Zwieniecki (2013) indicated that the link between the height of the tree and length of the leaves is associated with the efficiency of flow of energy-rich sugars in the tree's vascular system. Müller et all. (2013) indicated that growth rate was closely associated with morphological traits like the leaf number and total leaf area and was not related to photosynthetic activity. This is of particular practical importance for the forecast changes of species distributions. A beech tree that develops leaves at a later date is less susceptible to spring frosts, but simultaneously it may have lower photosynthetic carbon gain during the growing season, and thus lower growth. This was corroborated by the study of Guzicka and Rożkowski (2010), conducted at similar experimental trial established in the Choczewo Forest District, northern Poland. In conclusion, the authors determined that the leaf size can determine the beech productivity. The carbon assimilation rates and energy budget of trees are closely related to budburst and leaf senescence. Gömöry and Paule (2011) found that height and diameter growth of trees were associated with the length of the vegetative season. The timing of bud burst and leaf number per plant were identified as main determinants of growth rate of *Populus tremula* (Müller et al. 2013). The total leaf size and the phenology were reported to determine growth performance and yield (Müller et al. 2012). The timing of bud burst and duration of leafy period is also important for willow biomass production (Weih 2009) and for height growth of hybrid aspen (Lutter et al. 2016).

The knowledge of the intraspecific variability of characters strongly related to adaptive capabilities (spring frost resistance and fitness) constitutes the significant element of maintaining the stability of forest ecosystems. The variability of functional characters between beech populations confirms the importance of local adaptation (Sánchez-Gómez et al. 2013), which, in the context of climatic change, is particularly important in the provenances at the leading edges of distribution range. Depending on the breeding techniques used, within just a few generations, genetic and phenotypic fragmentation of these populations may occur (Kramer et al. 2010). The obtained information on the local variability of provenances for different environmental conditions of Poland are important in the aspect of the possible use of forest reproductive material and realized breeding and selection tasks. Implementation of the obtained knowledge helps in transfer of planting material to sites with a known frost injury risk. Genotype selection for risk minimising of transplantations within or between provenance regions, should focus on the parameters of leaf phenology and the considerable intraspecific variation of leaf morphology.

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