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Picea abies provenance test in the Czech Republic after 36 years – Central European provenances

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ABSTRACT: Norway spruce (*Picea abies* [L.] Karst.) provenances from Central Europe (Hercynian-Sudetes area) were evaluated in a long-term experimental project (Germany-Czech Republic) 36 years after the outplanting. The growth characteristics, mortality and qualitative morphological characteristics of 64 spruce provenances were evaluated on the experimental plot Ledeč-Zaháj, in the Czech-Moravian Highland region of the Czech Republic, in typical conditions for Norway spruce cultivation. Results show 15–20% differences in height and radial growth between provenances and insignificant differences in qualitative characteristics e.g. stem shape, branch density and shape and also health state. Environmental variables that significantly influenced production characteristics include longitude, latitude and altitude of the original locations of the provenances, while average annual temperature and average annual precipitation were not significant. Given conditions of the experimental plot, optimal production occurred with those provenances originally from 49–51 N latitude and 13–20 E longitude.

Keywords: Norway spruce; forest tree breeding; spruce production

Intensive research in forest tree breeding started at the beginning of the 20th century and has been supported by the International Union of Forest Research Organizations (IUFRO).The first experimental plots were established in 1907 (Csaba 1996). These research activities also included experiments based on the comparison of open-pollinated progeny populations from different geographic locations.

The most important experiments evaluating the genetic variability of spruce and provenance variability impact on spruce production and some of its features were established in 1938 and in the period 1964–1968 under supervision (and within the recommended methodology) of IUFRO. As part of these experiments, seed samples were collected from 1,100 populations across the spruce natural distribution range from Europe to Siberia and 20 experimental plantings were established in different habitat conditions and altitudes in Europe and Canada (Csaba 1996). Details and particular results of these experiments were published by different authors (Dietrichson et al. 1976; Krutzsch 1992; Oleksyn et al. 1997; Giertych 2001; Chałupka et al. 2008; Gömöry et al. 2012; Romšáková et al. 2012), but mainly in earlier stages of the experiments.

Subsequent provenance experiments were intended to evaluate various provenances from specific areas: the Alpine region in 1978 (Schiessl et al. 2010; Kapeller et al. 2012), the Nordic and Eastern European provenance test in Poland (Chałupka et al. 2008), in southern Sweden (Persson, Persson 1997) and Finland (Repo 1992), the Latvian provenances (Goncharenko et al. 1995), the Slovakian provenances (Gömöry et al. 2010, 2012; Romšáková et al. 2012) and the Beskydy provenances (Chmura 2006). Trees in permanent provenance plots were lat-

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er evaluated for not only production and health-state characteristics, but also for physiological/phenological characteristics of spruce, such as the time of flushing and forming buds (Skrøppa et al. 2009), frost resistance (Repo 1992; Beuker et al. 1998; Johnsen et al. 2005; Gömöry et al. 2010), drought resistance (Modrzyński, Eriksson 2002; Chmura 2006), response to photoperiod (Beuker et al. 1998; Johnsen et al. 2005; Skrøppa et al. 2009), estimation of provenance stability at possible climate change (Beaulieu, Raiville 2005; O'neill et al. 2008; Gömöry et al. 2012), physiological characteristics (Oleksyn et al. 1998) and lately also genetic studies (Goncharenko et al. 1995; Beaulieu, Raiville 2005; Mengl et al. 2009; Tollefsrud et al. 2009; Schiessl et al. 2010; Gömöry et al. 2012; Romšáková et al. 2012).

Originally, it was assumed that the experiment can show not only provenance variability and plasticity of particular populations within the genotype and environment interaction, but also the response and resistance to various environmental conditions – natural (climate) as well as anthropogenic (e.g. pollution load). It was expected that the results of such experiment could point to the appropriate provenance with the highest production, and combining data of production features with adaptability to various climatic changes could also be beneficial in estimation of its stability (Gömöry et al. 2012) in long-term sustainable forestry. From the provenance response to a transfer in the geographical and climatic conditions it should be possible to estimate a reaction to specific climate change.

To estimate the response of a forest tree it is necessary to obtain and process large amounts of data from as many (long-term) experimental plots as possible, and also to gather data from long-term and repeated measurements. Although IUFRO projects 1938 and 1964/68 were generously based, apparently not all experimental plots have been preserved and maintained until today and much of the published results have been measured in relatively young stands, e.g. 15–20 years. Despite many provenance experiments in the past, just a few have been evaluated decades after plantation.

The measurement was aimed to find out growth and vitality differences between almost mature tree groups of different provenances from different locations. We also tried to ascertain whether some important differences in growth and other characteristics could be based on the altitude in the original location of provenances. Another interesting question, especially due to predicted climatic changes, is the survival of spruce provenances from different altitudes and geographic locations.

MATERIAL AND METHODS

Site description. International provenance experimental plot No. 241 Ledeč-Zahájí, CSR-GDR 1972/76-77, was established for evaluation of growth and verification of Norway spruce (*Picea abies* [L.] Karst.) progeny provenances from the Hercynian-Sudeten area close to the town of Ledeč nad Sázavou (Lat. 49.68°N, Long. 15.22°N) in the Bohemian-Moravian Highlands, within the spruce natural distribution area (Hamerník, Musil 2008). The plot is situated in flat terrain at 465 m a.s.l., with the annual average temperature 7.9°C, average temperature of the vegetation period 14.1°C, annual average precipitation 635 mm (Tolasz 2007), the prevailing type of forest stands 4Q6 (oak-fir poor gleyed site), the Cambisol soil type and paragneiss parent rock.

Trial design. The experimental plot was established on an area of 2.56 ha in a uniform experimental double grid design, with trees of each of 64 populations split in 4 randomized blocks (each provenance in 4 replications). Four-year-old trees (2/2 – two years after transplantation in a forest nursery) were outplanted in 1976. Each provenance was planted within a subplot of 10 × 10 m and consisted of 50 plants initially (25 as target ones), planted with spacing 1 × 2 m in 5 rows [recommended standard IUFRO methodology (Šindelář 2004)]. Originally, the site was intended to be monitored for 40–50 years at least. The first (schematic) 30% reduction of individuals with subsequent measurement (Beran et al. 1997) was carried out in the autumn of 1996 (20 years after planting). Individuals damaged by frost or by hailstorm (in 1995) and declined individuals were removed regularly. The second (schematic) thinning followed in 2006 to reduce the number of trees to the target 25 trees per plot (2,500 per ha).

Provenance data. The provenances were originally collected within the area of natural spruce occurrence (Hamerník, Musil 2008) at the altitudes from 80 m a.s.l. (Poland) to 1440 m a.s.l. (Bulgaria), within 12 degrees of Lat. 41.7–53.7°N and 20 degrees of Long. 10.6–30.35°N. The original data are stored by the manager of the evaluated plot, Forest and Game Research Institute, Jíloviště-Strnady, ČR. Since the provenances were collected almost 50 years ago, the coordinates were only roughly recorded at that time. Presented coordinates, listed in (Appendix 1), represent the place of origin to the nearest ± 5 km, and are based on the original data (International Geological Map of Europe, 1:5 000 000, and coordinates with one decimal place) and local name, found on the Google Maps website (https://maps.google.com/2014). The average annual precipitation/temperature were taken from the closest meteorological station (http://www.weatherbase.com/) corrected by altitudinal difference (orographic precipitation interpolation) $y = 0.6022 [xp - xm] + zp$ (Šercl 2008) (where: xm – altitude of meteorological station; xp – altitude of provenance stand; zp, zt – precipitation and temperature, respectively, measured at the meteorological station). The average annual corrected temperature (temperature decreases with altitude) $y = zt - 0.65 [xp - xm]$ (Tolasz 2007). The annual heat-moisture index (AHM) (Wang et al. 2006) – which integrates the mean annual temperature and annual precipitation sum AHM = (–T +10)/(P/1,000). The geological substrate at the place of provenance origin was simplified as a proxy of nutrient availability and sorted on a 6-point scale: 1 – sandstone, 2 – granite and related parent rock, 3 – glacial deposits, 4 – gneiss, mica-schist and related, 5 – limestone, 6 – basic igneous rock.

Although the plot established within the 1972/76 project has been well kept and also measured, previous data are not available in all details necessary for statistical processing. The average H and DBH (Beran et al. 1997) for each provenance are presented in the table in Appendix 1.

Data collection. Dendrometric measurements and morphological characteristics were evaluated in October and November of 2012–2013 and preliminary results were published (Ulbrichová et al. 2013). Dendrometric characteristics were evaluated for each tree (4680 individuals in total). Tree height (H) was measured to the nearest 0.5 m with a digital hypsometer Vertex Laser 400 by Haglöf Langsele, Sweden. Diameter (DBH) was measured at the standard height 1.3 m with a calliper (to the nearest 0.1 cm). Tree morphological characteristics were evaluated on a three-value scale: trunk shape (TS): 1 – straight, 2 – slightly contorted, 3 – contorted or forked; crown characteristics were evaluated within the central section of live crown and included: branch density (BD): 2 – average (2 whorls per 1 m of height), 1 – thin (less than 2), 3 – dense (more than 2); branch inclination (BI): 2 – horizontal (approximately 90° angle with the trunk), 1 – vertical (more than 135° angle with the trunk), 3 – upright (less than 45° angle with the trunk); foliage/density of assimilatory organs (FO): 1 – dense (75–100%), 2 – average (50–75%), 3 – thin (less than 50%). Health state was accordingly evaluated within 3 categories, based on the presence of yellowing or visual symptoms of fungal damage on the trunk (resin exudation): 1 – healthy tree, 2 – slightly damaged tree, 3 – strongly damaged tree. Mortality and/or the number of surviving trees per plot (N) was counted as an average of 4 repetitions, nevertheless it should be considered as a subsidiary criterion, because it is influenced not only by competition and natural mortality, but also by the undertaken management treatment. The data from the last decades and 1996 measurement have been summarized so far mainly in unpublished final reports (VULHM Strnady) and thus are not widely accessible (Beran et al. 1997).

Statistical analysis. Data from the plots were processed using the R (R Core Team 2014) statistical software. Since the data show higher variance differences among provenances, the square root transformation was used to prepare data for subsequent statistical analysis.

ANOVA and Tukey's test for multiple comparisons were used to compare provenance characteristics of variance (the significance level $\alpha = 0.05$) and to determine significant differences between provenances in H, DBH, trunk and crown morphological characteristics, health state and foliage.

Multiple comparisons for parameters of binomial distribution (Anděl 1998) were used to determine significant differences in the rate of survival.

The growth dynamics estimation was based on the comparison of total succession of a particular provenance in H and DBH in comparison with other provenances. Since the time set of 2 measurements is too short, it should be also considered as subsidiary characteristic.

A principal component analysis was performed to display similarity between provenances and interrelations between environmental and geographical parameters and main measured variables. Since there are different scales of variables, we used the calculation from the correlation matrix. A principal component analysis was performed by R statistical software (R Core Team, 2014).

Figs 5 and 6 were modelled to describe the influence of geographical parameters on the growth characteristics. As a basic Equation (1), the linear regression model was used:

$$y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_3^2 + \beta_5 x_4 + \beta_6 x_4^2 + \beta_7 x_5 + \beta_8 x_5^2 \quad (1)$$

where:

β_0 – intercept term,

β_{1-8} – regression model coefficients for independent variables determined in the analysis

y – either height or DBH,

x_1 – precipitation,

x_2 – temperature,

x_3 – altitude,

x_4 – longitude,

x_5 – location latitude.

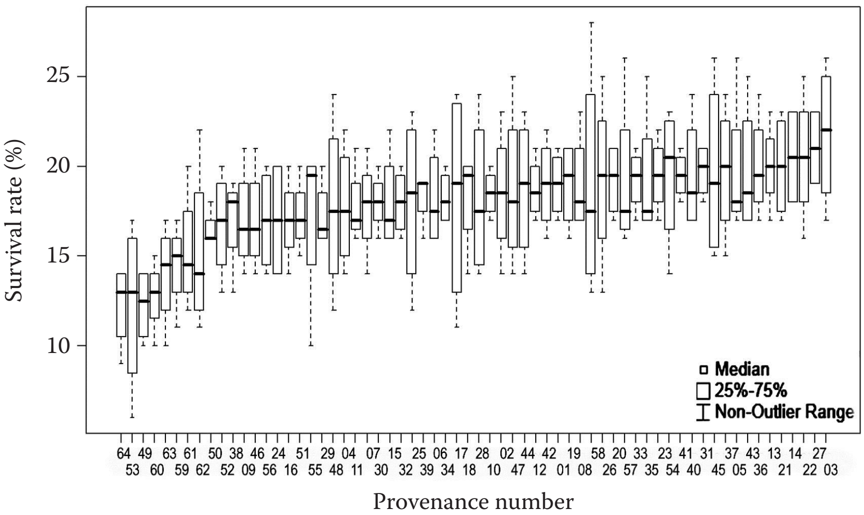

Fig. 1. Survival rate distribution of tested spruce provenances

This equation was used to describe correlations of height and DBH with environmental variables. Figures were constructed using Mathematica 9.0 software (Wolfram Research, Champaign, USA).

RESULTS

Survival rate

The rate of surviving individuals (N) for each provenance (Fig. 1) shows quite a high variability. The number in Fig. 1 is calculated from the number of planted individuals and thus it was influenced not only by natural mortality of individuals, but also by silvicultural measures during the cultivation (50% reduction). Although important for the growth evaluation, it should be considered a subsidiary criterion. Since there are no significant differences in the survival rate (due to the small number of 4 repetitions), Tukey's intervals were not described in the figure. It is possible to conclude that the growth possibilities, given by the number of individuals per plot, are variable, nevertheless, on average, similar for all provenances.

Growth characteristics

The lowest average height of any provenance was 13.6 m (Fig. 2a), the highest avg. *H* was 18.7 m (17.26 ± 1.1 m SD). Differences in *H* between provenances were statistically significant (F =9.926; Df = (63); Pr < $2e^{-16}$) and multiple comparisons (Tukey's method) show 11 partly overlapping groups (Fig. 2a). There is no clear pattern concerning the place of provenance origin.

The minimum average DBH was 13.2 cm and the maximum average DBH was 18 cm (Fig. 2b) (16.07 ± 1.1 m SD) Differences in DBH between provenances were also statistically significant (F = 4.756; Df = 63; Pr < $2e^{-16}$) and Tukey's method of multiple comparisons shows 8 partly overlapping groups.

There is a clear correlation between the height and diameter growth (r = 0.474 at 4608 degrees of freedom, Pr < $2e^{-16}$).

Previous measurements of *H* and DBH (unpublished, accessible just in the form of Project Report, (Beran et al. 1997); *H*, DBH results in Appendix 1) of 20 years old provenances provided the values of mean height 7.89 (± 0.55) m and mean diameter 7.82 (± 0.60) cm that showed relatively low variability. Our comparison of these two characteristics shows that most of the studied provenances had stable growth dynamics within the 15-year time period and a similar position in the ascending sequence with the relation to the other provenances. Provenances with significant differences in the growth dynamics were relatively scarce.

Correlation of growth with environmental variables

The principal component analysis (Fig. 3) of the main environmental explanatory variables and the principal growth characteristics clearly separated provenances originally from Belarus and the eastern part of the source region (Bulgaria and Eastern Austria) and showed similarity of provenances from Central Europe regardless of the country of original location (Germany, Slovakia, Czech Republic). There is a visible correlation between *H* and DBH

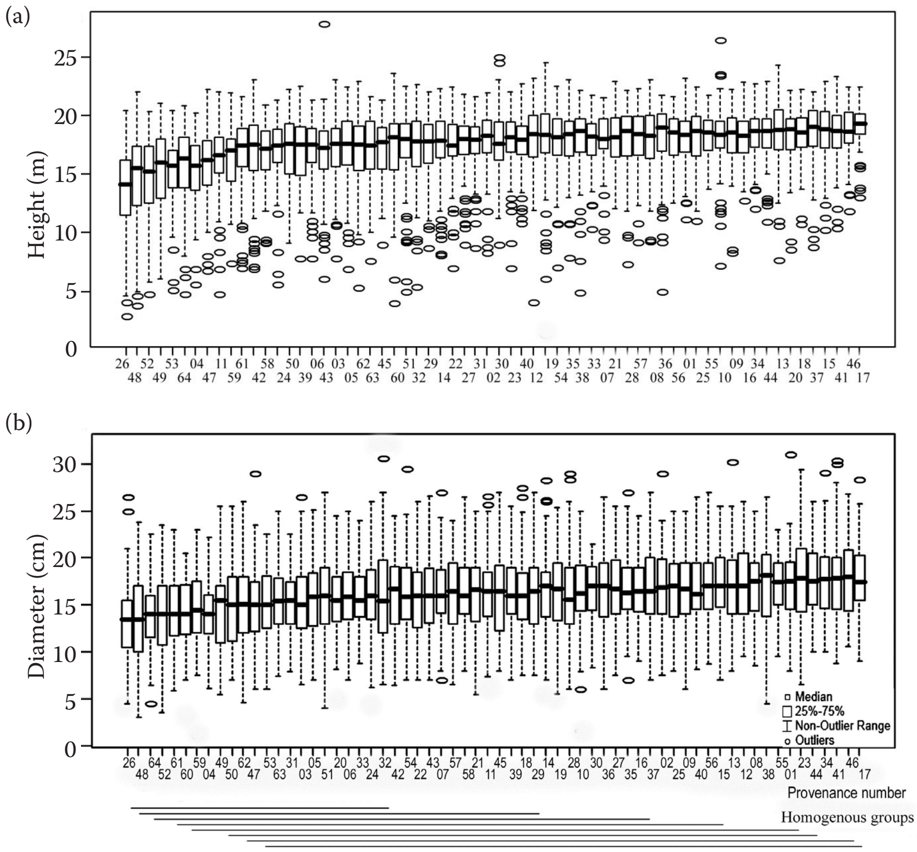

Fig. 2. Height (a), diameter (b) distribution of tested spruce provenances

lines below the figure shows the results of Tukey's multiple comparisons

(mentioned previously) and also with *N* (number of trees per plot). Temperature and precipitation are naturally correlated with the altitude (Tolasz 2007), but the correlation with growth parameters was not significant. The AHM index presenting the combination of precipitation and temperature is (insignificantly) negatively correlated with growth variables. Relations of the growth and altitude or geographical position are not clear at first sight and are further evaluated in Tables 1 and 2 and Fig. 4. Geological characteristics did not generally have any significant influence.

Further evaluation of the provenance distribution in relation to the location of origin is shown in Fig. 4a for the mean height and in Fig. 4b for the mean diameter. These figures show results of a linear regression model (the equation described in the Methods section), related to a specific variable (*H*, DBH) and geographic coordinates. Individual points within the curve stand for actual measurements. These results suggest that provenances from Lat. 49–51° and Long. 13–20° were the best performers. Provenances from southern areas (Dinaric sources) grew more slowly on the study sites, as did provenances from more continental climates (Belarus).

Regression coefficients (Table 1), as a result of the correlation between provenance growth and geographical coordinates plus the main climatic characteristics, suggest that there is no significant

Table 1. Linear regression coefficients for height and diameter growth as a function of location and altitude

Variable	*H* ($R^2 = 0.051$, $P < 2.2 \times 10^{-16}$)			DBH ($R^2 = 0.026$, $P < 2.2 \times 10^{-16}$)		
	Estimate	*T-value*	*P-value*	Estimate	*T-value*	*P-value*
Precipitation (mm)	-1.27×10^{-5}	–0.058	0.950	9.46×10^{-5}	0.31	0.760
Temperature (°C)	-1.09×10^{-3}	–0.017	0.980	-7.39×10^{-2}	–0.81	0.420
Altitude	-8.32×10^{-4}	–1.58	0.110	1.18×10^{-3}	2.63**	0.008
Altitude^2	-7.64×10^{-7}	–2.40*	0.017	-1.94×10^{-6}	–4.88***	1.1e^{-6}
Latitude	4.28	6.00***	2.2×10^{-9}	5.74×10^{-1}	0.56	0.57
Latitude^2	-4.44×10^{-2}	–5.96***	2.8×10^{-9}	-6.02×10^{-3}	–0.57	0.567
Longitude	1.69×10^{-1}	2.22*	0.027	1.82×10^{-1}	1.63	0.103
Longitude^2	-5.10×10^{-3}	–2.49*	0.013	-7.65×10^{-3}	–2.80**	0.006

2 exponential value is used to relativize negative (minus values) differences between localities, *indicates significance of the result

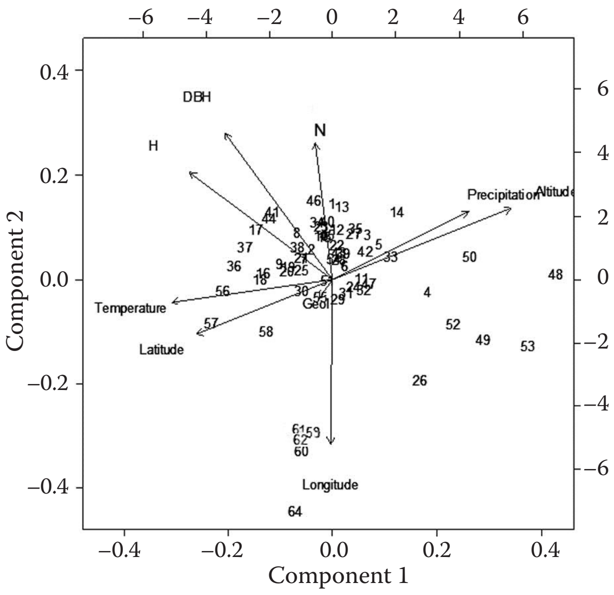

Fig. 3. Principal component analysis of main environmental variables and main growth characteristics

component 1 accounts for 39.2% of the total variability, whereas component 2 accounts for 29.4% (provenance details are listed in Appendix 1)

dependence of the growth on precipitation or temperature; the type of climate, be it oceanic or continental, in our case represented by longitude, and the length of vegetation period, represented by latitude in our case, seem more important. We found correlations between height growth and longitude (Fig. 4a) as well as altitude. Also, there appeared to be a stronger correlation between diameter growth and latitude and a weaker correlation between diameter and longitude and altitude (Table 1, Fig. 4b). Differences in the growth characteristics of provenances originating from different altitudes have been calculated separately for three groups (0–400; 400–1,000, 1,000–1,400 m a.s.l.). Tukey's test separated a group from the highest altitudes from both groups from the lower altitudes (height: $F = -1.804$; Df = 3; Pr < 2e^{-7}); diameter $F = -1.560$; Df = 3; Pr < 2e^{-7}).

Further evaluation of the provenance growth (Table 2), based on the altitude of the original location (0–400 m a.s.l.; 400–800 m a.s.l. and 800 m a.s.l. and more), shows that height differences between altitude classes are statistically significant ($F = 33.6$; Df = 2, 4607; Pr = 3e^{-15}). Multiple comparisons (Tukey's method of multiple comparisons) show two separate groups (Table 2). Diameter differences between altitude classes are also statistically significant ($F = 22.2$; Df = 2, 4609; Pr = 3e^{-10}). The high altitude provenances in the test plot (460 m a.s.l.) had relatively slower growth than provenances from the middle and low altitudes (the best growing).

Morphological characteristics

Evaluation of morphological crown and trunk characteristics, based on subjective selection at a 3-point scale was problematic due to the high stand density and small differences (Appendix 1) between individuals. There are no significant differences between the provenances in characteristics like foliage, branch inclination and density, which is also visible at the altitudinal sorting (Table 2). In the case of stem quality, differences were more pronounced, and poorer stem quality was found in the provenances from Hartz and Belarus and also in provenances from lower altitudes. We found no significant differences in the tree health status and foliage.

DISCUSSION

The Norway spruce area of distribution is fairly large. According to Hamerník and Musil (2008) there are two main areas within the entire range (41–70°N, 5–60°E): Central European-Balkans and North European, separated by the central

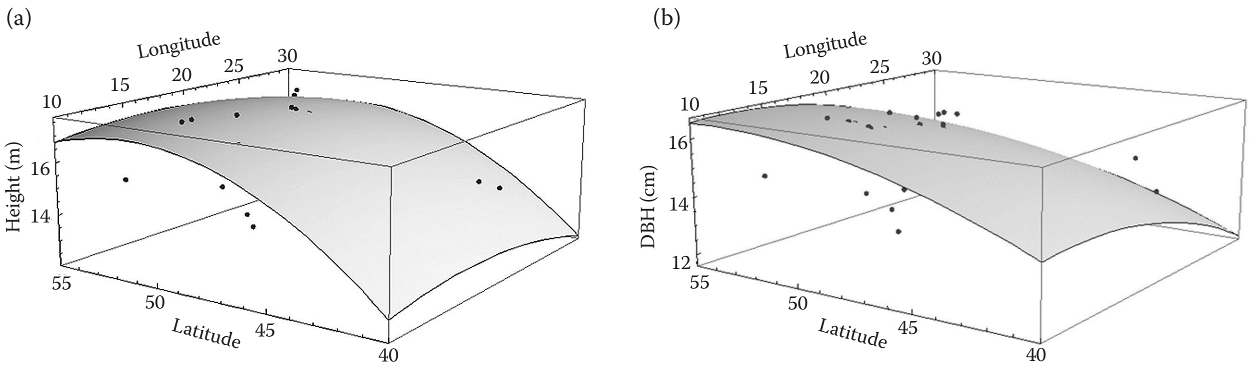

Fig. 4. A model of the dependence of provenance height (a) and diameter (b) distribution on longitude and latitude

Table 2. Differences between provenances from lowlands, highlands and mountain sites

Altitudinal sorting of provenances	Mean		TS	BD	BI	FO	Health
	height (m)	diameter (cm)					
Low altitude group (< 400 m a.s.l.)	17.5^{a}	15.9^{a}	1.23^{a}	2.25^{ab}	2.00^{a}	1.86^{a}	1.91^{a}
Highland group (400–800 m a.s.l.)	17.6^{a}	16.6^{b}	1.19^{ab}	2.22^{a}	2.00^{a}	1.85^{a}	1.89^{a}
Mountain group (> 800 m a.s.l.)	16.8^{b}	15.7^{a}	1.16^{b}	2.29^{b}	2.00^{a}	1.88^{a}	1.92^{a}

same letter – homogeneous groups, TS – trunk shape, BD – branch density, BI – branch inclination, FO – foliage/density of assimilatory organs

Poland disjunction. Temporal genetic studies (Tollefsrud et al. 2009) reflect a hypothesis of two migration routes out of a single Russian refuge; one north-western over Finland to northern Scandinavia, and the other south-western across the Baltic Sea into Scandinavia. The Central European-Balkans species distribution is fragmented, based mainly on the mountain terrain, and consisting of four subregions: Hercynian-Carpathian (Hartz – eastern and southern Carpathians), Alpine, Dinaric, Rhodopian. The northern border of the species range is distinguished by 2–2.5 month length of vegetation period (min. 26 days), 12°C July isotherm for forest, 10°C for individual trees. The southern border is delimitated by 600 mm precipitation (300 mm in the vegetation period) in Europe and by the influence of the continental climate.

The Ledeč experimental plot, used as a growth site for the provenance tests, belongs to the lower part of the altitudinal range of natural spruce habitats, though with sufficient precipitation. The ordination analysis clearly separated provenances originally from Belarus and the eastern part of the species range (Bulgaria and the East Tyrol region in Austria) and showed similarity of provenances from Central Europe (Germany, Slovakia, Czech Republic, even Poland). Although Dering and Lewandowski (2009) considered southern Poland and adjacent countries part of the southern zone of spruce distribution, they regarded the Central Europe a hybrid zone of Norway spruce originating from Carpathian and Russian refuges, with no consistent pattern of reactions of these provenances to the climate. Dering and Lewandowski's (2009) theory may explain features of provenances with quite small differences – e.g. Latvian provenances (Goncharenko et al. 1995), Slovakian provenances (Gömöry et al. 2012; Romšáková et al. 2012), Beskydy provenances (Chmura 2006) and German and Central and Northern Europe provenances (Mäkinen et al. 2002), who did not find any significant differences in comparison even with Norwegian provenances. On the other hand, populations from the Bohemian massive and from the south-eastern fringe of the Alps differ significantly from the Alpine populations (Mengl et al. 2009; Kapeller et al. 2012). High intrapopulation variability (Gömöry et al. 2012) and small differences between populations are likely the result of the undisrupted range of species distribution (Hamrick 2004). On geographically unfragmented areas, the distance between populations with measurable growth differences may exceed 50–100 km along ecological gradients (Kapeller et al. 2012) although a more differentiated territory (e.g. Alpine) has a much stronger effect on the formation of distinct population clusters (Kapeller et al. 2012).

The height and diameter growth of tested provenances confirms moderate conditions of the stand and growth variables measured in 1997 (Beran et al. 1997) are comparable with the results of similar tests, for example Kapeller et al. (2012), who described height differences between provenances of about 10% for a 15 year-old stand (550–600 cm range). Our results show approximately 15–20% oscillation from average values, which suggest a slightly higher variability, probably due to the higher age of stands.

Growth dynamics stability is visible when placing provenances in the ascending order according to growth variables measured at 20 years (Beran et al. 1997) and 36 years of age. In our comparison, there was a small change among provenances with the slowest growth, whereas greater differences were observed in provenances with the highest values. These results were more pronounced for diameter than for height, likely reflecting the strong control that the environment and genetics exert over secondary (diameter) and primary (height) growth, respectively (Gömöry et al. 2012). Differences between provenances in growth, especially diameter increment, can change over time and with the age of the stand (Zubizarreta-Gerendiain et al. 2012). Although according to other provenance tests (Gömöry et al. 2012), the response patterns in volume growth are generally consistent with height, in our case only small differences were found.

There are basically two approaches to estimate the impact of climatic factors upon the provenance productivity and both can be used to infer responses to changing environmental conditions. The transfer function approach, which was used in our study, relates the growth of a provenance to the geographical or climatic distance to the experimental site conditions (represented e.g. by Schmidtling et al. 1994; Persson, Persson 1997; Rehfeldt et al. 2003; Beaulieu, Raiville 2005) and compares the productivity of this transferred provenance to the productivity of a local or other provenance. The second approach describes the growth of a provenance as a function of climate at the test sites. For the evaluation of provenance stability and reaction to the geographical shift and/or climatic change (Beaulieu, Raiville 2005), it is necessary to measure growth parameters of a particular provenance in various site conditions, for which we had no data available, therefore our results are somewhat limited.

The effect of the place of origin on the height or diameter growth of *Picea abies* provenances is a topic which brings diverse results. Csaba (1996) noted that the results of provenance tests often show generally low sensitivity to the change between the original location and experimental site. Other authors found the growth differences significant, especially for provenances from different subregions (O'neill et al. 2008) or for provenances originally from extreme sites (Alpine) (Kapeller et al. 2012). Persson and Persson (1997) described significant differences between Carpathian provenances (highest stem volume) and provenances from North-Eastern Europe (faster-growing types) – and also differences in phenology were documented for these provenances (Skrøppa et al. 2009). In our provenance test we did not find any significant differences between provenances from Germany, Czech Repubelc, Slovakia, but provenances from the eastern and south-eastern part of the region – Belarus and Bulgaria – generally had lower growth characteristics. This result supports the previous recommendation (Šindelář 2004) not to use sources from the south-eastern Dinaric part of the spruce range and from the highest altitudes.

Given the plasticity of spruce populations and variability within one provenance (Dering, Lewandowski 2009; Gömöry et al. 2012), many stand-level factors do not play a very significant role. In our evaluation a significant correlation was confirmed between height growth and latitude plus altitude and between diameter growth and longitude plus altitude. The other characteristics of original locations (average annual temperature and precipitation; parent rock as a proxy of nutrient availability) were not significant.

The role of the average annual temperature at the original location as a factor of correlation with growth on the test site was not significant, not only in our experiment, but also for Sander and Eckstein (2001) Krkonoše Mts. provenances, and also Slovenian provenances (Levanič et al. 2009) where only the diameter increment showed just a weak correlation with temperature in the hottest months of summer. Different results were published by Schmidtling (1994), who found a significant correlation between growth characteristics and temperature. The extremity of the stand is probably quite an important factor (Kapeller et al. 2012) and increment (of European provenances) responds to climatic conditions markedly only on the extreme sites (Mäkinen et al. 2002). It was also confirmed by Savva et al. (2006), who reported for Norway spruce at high altitudes a higher correlation between summer temperatures and radial increment (rather than height increment). Since in our experiment the highest altitude of the provenance location was 1,600 m a.s.l. and only 3 provenances originated from locations above 1,400 m a.s.l., the absence of temperature significance in our study is understandable.

Some authors (Beuker et al. 1998; Kvaalen, Johnsen 2008) also observed that provenance responses to a photoperiod are more pronounced than to temperature. This means a more important relation between growth and latitude than with temperature, which was also confirmed by our results. On the other hand, the plasticity and adaptability of spruce reaction to the combination of temperature and day length was also documented (Johnsen et al. 2005a). His results show that the reaction to a photoperiod is more controlled by the environment than by genetic factors. The increased importance of photoperiod appears especially in severe climatic conditions Csaba (1996), such as high altitudes. In such situations, the effect of precipitation seems to be a minor factor in climatic adaptation.

Probably due to the centrality (in the species range) of the Ledeč site, we found a correlation between provenance growth and precipitation at their original locations insignificant. The precipitation probably has a stronger influence on more extreme sites and/or in more dramatic climatic changes, as was documented for example in the drought years of 1976, 1992, and 2003 in Central

Europe (Boden et al 2014). Although the adaptive capacity of Norway spruce to a high frequency of severe droughts is limited, the trees are able to adapt themselves to average site conditions (Kapeller et al. 2012).

The altitude could be used as a surrogate for combined temperature and precipitation variation and functioning at the same time as environmental selection factors for spruce (Romšáková et al. 2012). It is one of the explanatory characteristics, which appears in our study as a factor of high significance (Table 1) for diameter growth and also (somewhat lower significance) for height increment. According to Savva et al. (2006) results, there is quite a large difference between Norway spruce stands from sites close to the tree line (over 1,440 m a.s.l.) and the other two groups at middle (1,000–1,200) and lower altitudes (800–1,000). Significantly lower growth of provenances originally from the altitude above 800 m a.s.l. was documented on our experimental site (Table 2), which corresponds with other studies (Šindelář 1994; Savva et al. 2006), concerning stem volume (Oleksyn et al. 1997) or biomass (Modrzyński, Eriksson 2002). At the same time Gömöry et al. (2012) documented that (Slovakian) spruce provenances generally responded positively (increased height and volume growth) to transfer to lower altitudes (warmer and drier climates). Also, trees at low elevations usually respond positively to warmer weather in the spring, trees at high elevations respond to higher summer temperatures (Savva et al. 2006) and the diameter growth at high-elevation sites has a higher correlation with temperature and at low-elevation sites with precipitation, at least in mountainous regions of Europe (Mäkinen et al. 2002). Nevertheless, the growth of spruce at the lowland site is much more variable than the growth in the Alpine stands (Levanič et al. 2009).

The survival rate (or mortality) is a characteristic indicator of provenance vitality. In our study, since the initial numbers had been changed by silvicultural measures in 1996 and 2006, this characteristic might be of questionable value to our analysis of the health state of the trees. Some of the most productive provenances had the highest surviving number of individuals per plot (40% of the initial number) at the same time and provenances with the lowest mean height and diameter belonged to the group with a lower number of surviving (and measured) individuals per plot. A similar provenance test (at 15 years of age) reported the survival rate of 77%, with significant differences between sites, not between populations (Kapeller et al. 2012).

Crown and stem characteristics of provenances were not clearly pronounced and did not generally show any significant differences or clearly denoted trends. This result corresponds with Geburek et al. (2008), who assessed the influence of environmental variables on the crown types and characteristics and noted that the basic crown architecture is probably genetically encoded but main crown modifications may be triggered by environmental signals, such as temperature regime and altitude of the original stand (which was responsible for 74% of the crown variability). Similar results were published by Schiessl et al. (2009), who did not find any correlation between the crown form and the original location. Steffenrem et al. (2008) further specified that branch dimension is a factor controlled mainly by environment, while the number of branches is under stronger genetic control.

CONCLUSIONS

Within 64 provenances we found similarities between provenances from the central part of the species range (Czech Republic, Germany, Slovakia). There was a clearly separated group of provenances from Belarus, partly also from Polish lowlands and eastern Austria.

The best growth characteristics at the tested site (in the central part of Czech Republic) were obtained for provenances whose original location was between Lat. 49–51° and Long. 13–20° and at middle altitudes (400–800 m a.s.l.).

The characteristics displaying a strong influence on the height growth were latitude and partly also altitude or longitude of the original location; the diameter growth was influenced by longitude and partly also by altitude.

Tree health characteristics could not be related to individual provenances or their places of origin. There were no significant differences in morphological characteristics of crown, branches and health state, with the exception of stem shape, which is probably more influenced by genetic origin.

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Appendix 1. Overview of tested provenances and characteristics of the site of origin and previous growth results

State of origin	Provenance area	Provenance locality	No.	Latitude	Longitude	Altitude (m a.s.l.)	Precipit. (mm)	Temp. (°C)	AHM index	Geol. substrate	1996				2013				
											H	*H* sequence	DBH	DBH sequence	TS	BD	BI	foliage	health
ČR	Krušné Mts.	Nové Hamry	1	50.35	12.72	870	941.2	4.9	5.4	2	5.7	1	7.0	7	1.08	2.30	1.99	1.80	1.78
		Strádov	2	50.60	13.80	660	791.1	5.8	5.3	4	8.1	42	8.0	34–36	1.19	2.22	2.00	1.89	1.92
	Šumava Mts.	Horní Les	3	48.80	13.99	870	878.3	5.3	5.3	2	8.5	60–61	8.6	58–61	1.09	2.26	2.00	1.83	1.84
		Kvilda	4	49.02	13.57	910	1,331.3	5.4	3.5	2	8.2	46	7.9	25–33	1.03	2.31	2.00	1.78	1.80
		Ježová (PR)	5	48.65	14.40	945	923.4	4.8	5.6	2	6.6	3	6.7	4–5	1.20	2.28	2.00	1.92	1.89
		Černý Kříž	6	48.86	13.86	735	797.0	6.2	4.8	2	7.7	16	7.4	16	1.07	2.30	2.00	1.86	1.97
	Český les	Babylon	7	49.40	12.86	540	731.2	6.9	4.3	2	8.2	45	7.9	25–33	1.17	2.18	2.00	1.89	1.89
		Nová Huť	8	49.46	13.30	610	695.8	6.4	5.2	4	7.8	23	7.7	21–24	1.08	2.24	2.00	1.82	1.90
	Brdy	Kokšín	9	49.60	13.67	540	656.0	7.2	4.3	6	8.0	29	8.1	37–45	1.27	2.27	2.00	1.87	1.88
	Jizerské Mts.	Smědava	10	50.84	15.27	660	1,300.8	7.3	2.1	2	7.6	12	7.9	25–33	1.23	2.25	2.00	1.88	1.93
		Kateřinky	11	50.80	15.80	695	1,094.4	5.2	4.4	2	8.7	64	8.6	58–61	1.30	2.25	2.00	1.90	1.94
	Krkonoše Mts.	Černá hora	12	50.65	15.74	760	1,102.6	5.2	4.4	2	7.7	18	7.3	12–15	1.19	2.25	2.01	1.81	1.88
		Černý důl	13	50.64	15.72	840	1,150.8	4.7	4.6	2	7.9	24	7.9	25–33	1.19	2.23	2.00	1.84	1.89
		Labská	14	50.72	15.57	950	1,497.9	3.2	4.5	4	8.2	48	8.1	37–45	1.16	2.20	2.00	1.89	1.96
		Rezek	15	50.70	15.51	950	798.4	4.8	6.5	4	7.8	20	8.1	37–45	1.04	2.13	2.00	1.86	1.86
	Středočes. highland	Voděrady	16	49.96	14.79	370	604.3	8.0	3.3	2	7.7	15	8.4	50–54	1.15	2.13	2.00	1.87	1.90
		Jedlá	17	49.73	15.24	390	667.2	7.3	4.0	2	8.4	53	8.1	37–45	1.11	2.19	2.09	1.90	1.88
		Želivka	18	49.69	15.11	450	461.3	7.7	4.9	6	8.2	43	8.3	47–49	1.29	2.18	1.99	1.81	1.84
		Zbraslavice	19	49.84	15.18	430	672.9	7.0	4.5	3	8.4	54	7.9	25–33	1.18	2.15	2.00	1.86	1.86
	Českomorav. highland	Svinošice	20	49.34	16.57	410	660.9	7.1	4.4	2	8.2	44	8.4	50–54	1.22	2.26	2.00	1.79	1.90
		Lísek	21	49.65	16.11	545	758.9	6.6	4.5	4	8.1	38–39	8.5	55–57	1.15	2.23	2.00	1.79	1.84
		Herálec	22	49.70	15.96	710	858.2	5.5	5.2	2	8.6	63	8.3	47–49	1.20	2.35	2.00	1.87	2.02
		Městec	23	49.68	15.91	710	858.2	5.5	5.2	2	7.4	10	6.7	4–5	1.14	2.30	2.00	1.85	1.89
		Devět skal	24	49.67	15.91	730	870.3	5.4	5.3	2	8.4	57–58	8.1	37–45	1.24	2.22	2.00	1.85	2.50
	Jeseníky Mts.	Vrbno	25	50.13	17.39	810	454.0	5.3	10.3	4	7.9	25	7.3	12–15	1.08	2.11	2.00	1.82	1.89
		Hubertov	26	50.08	17.30	920	519.9	4.6	10.4	2	8.3	52	8.1	37–45	1.17	2.47	1.99	2.04	2.05
		Vidly	27	50.10	17.27	1,070	610.2	3.6	10.4	2	8.4	60	8.6	58–61	1.13	2.10	2.00	1.86	1.92
	Beskydy Mts.	Řečice	28	49.52	18.48	680	1,238.1	6.4	2.9	4	8.3	50	8.0	34–36	1.15	2.26	2.01	1.86	1.86
SR	Tatry Mts.	Červené skaly	29	48.88	20.78	750	869.8	6.2	4.4	4	8.1	46	8.2	46–47	1.12	2.29	2.01	1.88	2.01
		Lipt. Mikuláš	30	49.00	19.40	800	386.0	6.9	8.1	2	8.3	51	8.3	47–49	1.08	2.26	2.00	1.82	1.85
		Tatr, Lomnica 1	31	49.26	20.26	840	657.9	5.4	7.0	2	8.1	38–39	8.2	46–47	1.29	2.32	2.00	1.86	1.93
		Tatr, Lomnica 2	32	49.26	20.26	970	736.1	4.6	7.4	2	8.1	41	8.4	50–54	1.30	2.32	2.00	1.86	1.93
		Tatr, Lomnica 3	33	49.26	20.26	1200	874.6	3.1	7.9	2	8.1	35	8.5	55–57	1.30	2.32	2.00	1.86	1.93

ČR	Orlické Mts.	Mladkov	34	50.08	16.59	630	1,104.6	5.5	4.1	2	7.9	26	8.1	37–45	1.30	2.21	2.00	1.84	1.88
		Říčky	35	50.21	16.48	780	1,194.9	4.5	4.6	2	8.4	57–58	8.0	34–36	1.13	2.13	2.00	1.84	1.87
D	Lausitzer Park	Kauschwitz	36	51.43	14.60	120	619.7	8.8	1.9	2	8.1	34	8.5	55–57	1.20	2.16	2.00	1.83	1.85
	Älbsandsteingeb.	Reinhardtsdorf	37	50.89	14.17	240	638.1	8.3	2.6	1	8.6	62	8.4	50–54	1.19	2.20	2.00	1.81	1.96
	Erzgebirge-west	Schindelbach	38	50.60	13.12	610	784.7	6.6	4.3	2	8.5	60–61	8.4	50–54	1.16	2.32	2.02	1.88	1.94
		Bütterbächel	39	50.40	12.56	735	817.0	5.1	6.0	2	8.2	47	7.7	21–24	1.15	2.29	2.00	1.89	1.92
	Erzgebirge-mitt	Grosse Mittweida	40	50.49	12.90	830	903.0	5.5	5.0	4	8.0	29	8.1	37–45	1.21	2.15	2.00	1.82	1.86
		Hainsbach	41	50.70	13.20	465	830.0	6.5	4.3	4	8.3	49	8.6	58–61	1.15	2.15	2.00	1.85	1.89
		Tellerhäuser	42	50.43	12.89	920	957.2	4.9	5.4	4	8.0	28	7.5	17	1.22	2.34	2.00	1.93	1.95
	Erzgebirge-ost	Rehefeld	43	50.74	13.69	685	918.3	5.2	5.2	4	8.1	36	7.6	18–20	1.10	2.15	2.01	1.87	1.94
	Thüringer Wald	Älterthal	44	50.60	10.70	410	843.0	7.3	3.2	4	7.8	21	8.7	63–64	1.09	2.19	1.98	1.80	1.79
		Katzhütte	45	50.54	11.40	590	951.3	6.1	4.1	2	7.6	13	7.6	18–20	1.14	2.25	2.00	1.75	1.79
		Gehlberg	46	50.69	10.79	715	843.3	4.0	7.1	2	8.0	32	8.1	37–45	1.09	2.09	2.00	1.78	1.78
	Harz	Scharfenstein	47	51.80	10.60	665	865.9	4.2	6.7	2	7.1	7	6.9	7	1.75	2.19	2.04	1.90	1.92
AUS	Osttirol	Matrei	48	47.00	12.56	1600	1,476.1	0.9	6.1	2	6.8	4	6.5	4	1.14	2.49	2.00	1.93	2.14
		Granitz	49	47.33	15.53	1200	1,388.9	3.4	4.8	5	6.3	2	5.9	1	1.04	2.51	2.00	2.00	2.04
		Fastenberg	50	47.38	13.69	1500	1,044.8	1.8	7.8	2	7.6	14	7.2	10–11	1.18	2.38	2.02	2.00	2.06
		Schneegatten	51	48.04	13.30	500	929.1	7.5	2.7	5	7.8	19	7.1	8–9	1.13	2.29	2.00	1.90	1.90
BU	Rodopi Mts.	Tchepelare	52	41.74	24.71	1000	1,186.6	8.2	1.5	5	7.8	22	7.2	10–11	1.15	2.45	2.00	2.05	2.08
	Rila Mts.	Bistritza	53	42.23	23.60	1440	1,083.4	1.8	7.6	2	7.2	8	6.4	3	1.14	2.45	2.02	1.63	1.61
PL	Salesian Beskyd	Istebna 34	54	49.59	18.86	625	1,106.7	6.5	3.1	1	8.4	55	8.7	63–64	1.18	2.15	2.00	1.85	1.83
		Istebna 66	55	49.59	18.86	600	1,091.6	6.7	3.0	1	7.9	27	7.7	21–24	1.16	2.13	2.00	1.94	1.96
	Zielona Gora	Brody	56	51.77	14.75	80	522.6	8.7	2.4	2	8.4	56	7.9	25–33	1.16	2.15	2.00	1.82	1.77
	Golub-Dobrzyn	Karczewo	57	53.19	19.14	90	422.1	8.9	2.5	3	8.0	33	7.9	25–33	1.22	2.34	2.00	1.78	1.88
	Iłava	Iłava	58	53.58	19.54	116	618.6	6.1	6.3	3	8.1	40	7.9	25–33	1.18	2.13	2.00	1.78	1.80
	Banie Mazurskie	Borki	59	54.01	22.15	155	649.1	6.7	5.1	3	8.0	31	7.9	25–33	1.40	2.88	2.00	1.91	1.97
BL	Hancaviči	Vialikija Kruhovičy	60	52.80	26.61	200	671.2	6.1	5.9	3	7.5	11	7.3	12–15	1.20	2.35	2.00	2.04	2.12
	Bialowieza	Bialowieza	61	52.70	23.80	135	571.0	6.1	6.8	3	7.0	6	7.6	18–20	1.34	2.36	1.98	1.89	2.03
	Bykha	Dousk	62	53.16	30.35	180	661.9	5.3	7.1	3	7.3	9	7.3	12–15	1.49	2.31	2.00	1.89	1.82
	Minsk	Čiervień	63	53.70	28.50	230	701.6	5.5	6.5	3	7.7	17	7.7	21–24	1.21	2.25	2.00	2.04	2.04
	Asipovičy	Bradok	64	53.47	28.51	220	453.4	7.8	4.8	3	7.0	5	7.1	8–9	1.20	2.45	1.98	1.76	2.00

No. – provenance identification number; Precipit.– annual amount of precipitation; Temp. – annual average temperature; AHM index (according to Wang et al 2006); geol. substrate – geology: 1 – sandstone; 2 – granite/gneiss; 3 – glacial deposits; 4 – mica–schist/phyllite/schist; 5 – limestone; 6 – basic igneous rock; H – height (m); DBH – diameter in brest height (cm); *H*, DBH sequence – sequence in ascending order of provenances according to this variable; TS – trunk shape; BD – branch density; BI – branch inclination; ČR – Czech Repulic; SR – Slovak Republic; D – Germany; AUS – Austria; BU – Bulgaria; PL – Poland; BL – Belarus

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