Comparing German and Bulgarian Provenances of European Beech (Fagus Sylvatica L.) Regarding Survival, Growth and Ecodistance

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Abstract

As a response to global warming-related increase of temperature and drought, tree species react with reduction of growth and vitality. This is also valid for the drought-sensitive European beech, a major broadleaf species in Europe. One way of studying the possibilities of adaptation of this species to the expected changes is transferring beech reproductive material from wetter and colder to drier and warmer areas. Within this transfer experiment five German and three Bulgarian beech provenances with mean annual precipitation (MAP) amounts of 700 – 1004 mm at origin were planted at three trial sites in Bulgaria (MAP 573 – 811 mm). The study was conducted during the first three years after the provenance trials (PT) were established. At the most xeric site, massive mortality rates for beech of both German and Bulgarian provenances were observed. Hence, MAP < ~580 mm or an Ellenberg quotient (EQ) by ~38 leads to high losses of European beech rejuvenation. Furthermore, it is likely that in lower-altitude regions in Bulgaria beech will face a high extinction risk at the end of the century. In the 3-year study period the trees of Bulgarian provenances were taller than the German ones, which is a sign of a better adaptation.

Key words: climate change, distribution, transfer experiment, Ellenberg quotient.

Introduction

Global warming will most likely increase the frequency of heat waves and decrease precipitation during growing season in large parts of Europe (Schär et al., 2004; Rowell, Jones, 2006; IPCC, 2013). The European beech, a major European tree species, is affected by climate change, which consequentially leads to a reduction in growth and vitality (Eilmann et al., 2014). Notably, beech has a wide distribution and great economic importance (Ellenberg, Leuschner, 2010). With increasing climate-warming effects, the question arises whether provenances from wetter and cooler climates will be able to adapt to drier and warmer climates. Besides occurrences of frosts and summer warmth, drought is the most important factor influencing vigour and survival of Fagus sylvatica (Ellenberg, Strutt, 2009). Growth reductions were observed in the year following the drought (Granier et al., 2007) and as a consequence there was a long-term decrease in precipitation (Knutzen et al., 2017). Also decreasing tree-height growth (Braun, Flückiger, 1987) and even mortality due to drought periods (Jump et al., 2006) could be detected. Together with water availability,
growing-season warmth was most important for beech distribution (Fang, Lechowicz, 2006). Both climatic variables are used for the calculation of the Ellenberg climate quotient (EQ), which has been first introduced for the European beech (Ellenberg, 1988). The EQ is believed to be the most influential predictor describing the distribution limit of the Fagus sylvatica (Horváth, 2014), the distinguishing predictor substantiating its drought-sensitivity (Czúcz et al., 2011) and the major factor regarding its xeric limits (Mátyás et al., 2010).

Vulnerability to drought is reflected by the southern and eastern limits of the distribution of the European beech (Aranda et al., 1996). Its distribution area ranges from Italy to the south, Spain to the south-west, Sweden to the north, Poland and Ukraine to the east and Bulgaria and Greece to the south-east (Bohn, 2004). Not too distant from that area, within the Eastern Alps-Slovenia-Istria, as well as in parts of Moravia and Bohemia, bulk of refuge areas have been identified from which the European beech started its post-glacial recolonisation (Magri, 2006; Magri, 2008; Gömöry, Paule, 2010). Not surprisingly, the highest allelic richness was found in that part of the species distribution (Comps et al., 2001). The high genetic diversity increases the adaptability and mitigates mortality risks under changing environmental conditions (Agrawal, 2001).

The evolution of the European beech has mainly occurred through natural rejuvenation and adaptation to local climate regimes (Müller-Stark, 1996). Consequently, the properties differ within each provenance (Knutzen et al., 2015; Müller, Finkeldey, 2017). Studies of rear-edge European beech populations have revealed that Polish provenances from the more arid eastern margin show better drought adaptation than populations originating from the more humid centre (Czajkowski, Bolte, 2006; Rose et al., 2009). Surprisingly, beech provenances originating from South-Eastern Europe are underrepresented in European studies (e.g. Jump et al., 2009; Lindner et al., 2010; Wortemann et al., 2011). In order to understand the adaptation processes and to find appropriate seed and plant material, investigations of marginal populations with common garden or transfer experiments are crucial (e.g. Hampe, Petit, 2005).

In Bulgaria, the first provenance test with European beech was established in 1974 with three local provenances, using three variants of planting density (Botev, 1995). Different growth indicators, as well as the properties of stems and crown branches were explored. The study showed that the density affected more height growth rather than the diameter of the stem base. Of the three tested provenances with the highest growth rates and as most promising was identified the provenance Petrohan.

The same provenance Petrohan (Barzia) was explored also in a common beech provenance test with 49 provenances from eight European countries, including Germany and Bulgaria (Alexandrov et al., 2006). The trial site was located in the Eastern Balkan Range. In the first and the fifth years of the investigation, an increased mean survival rate was recorded. In the following years, massive damages caused by herbivores were observed. On the basis of measurements of heights and stem-base diameter of 1-, 5- and 12-year-old trees, the German provenances Herrenberg, Zwiesel and Eisenach were identified as the most promising for these conditions while the worst results were determined for the Danish provenance Grasten.
Transfer experiments examine the phenotypic response of various characteristics. These traits are strongly impacted by microclimatic conditions of the respective environment, where these provenances originate from and / or are relocated to. Furthermore, the extent and the direction of the transfer between the original and relocated positions play an important role (Matyas, Yeatman, 1992; Mátyás et al., 2009a). The concept of transfer analysis and ecological distance (ecodistance) is based on the assumption that all other factors are negligible or remain unchanged. Accordingly, this measure of environmental change between origin and test site represents a valid scenario for exploring the response of populations to predicted future climates and projected environmental conditions. Local populations always take the value zero, while shifts northwards result in negative values and shifts southwards – in positive values, depending on the direction and distance of the transfer. The calculation of the ecodistance through the use of the Ellenberg climate quotient incorporates the climate characteristics, such as its humidity and it being continental (Ellenberg, 1988).

Growth rates of the tree height can be used as an indicator of the adaptability of a tree species to the environment. Higher growth rates are likely to increase competitive ability, survival and long-term success of a tree species. Especially during the seedling stage, higher growth rates are a decisive trait for survival (Vitasse et al., 2009). Tree growth can also be used as a first estimate for the selection for drought- adapted species and genotypes (Zang et al., 2014), while growth decline in response to drought is generally used as a measure of the vitality loss (Dobbertin, 2005). At the same time, higher drought tolerance in trees could be associated with lower relative growth rates (Rose et al., 2009; Taeger et al., 2013). This is supported by the generally lower growth rates at the warm and dry margins of the distribution area (Loehle, 1998).

Beech of Balkan provenances would be important for forestry management under an increasing warmer and drier climate. This study aims to compare the survival and height growth of provenances originating from more central regions with the ones of marginal provenances from South-Eastern Europe. Furthermore, the influence of the Ellenberg climate quotient and the ecodistance were examined. For this purpose, a transfer experiment was conducted. Five German and three Bulgarian beech provenances with 700-1004 mm mean annual precipitation (MAP) at origin, were transferred and planted at three trial sites in Bulgaria (573-811 mm MAP) and investigated during the important three years after establishment.

We tested the following hypotheses:
(1) Beech provenances from the south-eastern Range margin show lower mortality and better tree growth than provenances from more central regions.
(2) Height growth decreases with increasing Ellenberg quotient (EQ) and with increasing ecological distance ($\Delta E$).

**MATERIAL AND METHODS**

The investigated three provenance trials (573-811 mm MAP) were established in North-Western Bulgaria in Vidin (Vidin Regional forest service) and in North-Eastern Bulgaria – Kipilovo (Kipilovo Regional forest service) and Varbitza (Varbitza Regional forest service; Figure 1, Table 1). The soil type in Vidin was chernozems, in Varbitza and Kipilovo gray luvisols were detected (Soil classification after FAO, 2006). The provenance trial in
Vidin was established in autumn 2009, those in Varbitza and Kipilovo – in spring 2010. The experiment was established by the Bavarian Institute for Forest Seeding and Planting in Teisendorf (Germany) in collaboration with the University of Forestry in Sofia (Bulgaria).

In Vidin and Varbitza all eight (five German and three Bulgarian) beech provenances (700-1004 mm MAP) were included. Due to the limited number of seedlings of the Elchingen and Peschtera provenances the number of replicates in Varbitza was reduced to one (Elchingen) and two (Peschtera), respectively. In Kipilovo, beeches of four provenances (two German and two Bulgarian) were planted. The main focus of this study was devoted to the Silberbach, Ebersdorf, Berkovitza and Petrohan provenances, since they were included in all three provenance trials.

All seeds were harvested in autumn 2007. Seeds originating from Silberbach and Ebersdorf in Germany were allocated to the provenance region ‘81011/12 – Thuringian forest, Fichtelgebirge and Vogtland’. Seeds from Mindelzell and Elchingen originated from provenance region ‘81024 – Alpine foreland’, whereas those from Ebrach originated from provenance region ‘81017 – Württemberg and Franconian hill country’. Both seeds from Berkovitza and Petrohan derived from the provenance region ‘150124 – low-mountain sub-belt’ in Northern Bulgaria. Seeds collected in Peschtera were allocated to provenance region ‘150825 – middle-mountain sub-belt’ in the south. Seedlings originating from

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**Fig. 1.** Distribution of European beech in Central and South-Eastern Europe (green), shapes of Germany and Bulgaria (dark grey), locations of provenances (blue): Elchingen (Elch), Silberbach (S), Ebersdorf (E), Mindelzell (M), Ebrach (Ebr), Peschtera (Psht), Berkovitza (B), Petrohan (P) and study sites (red): Vidin (Vid), Varbitza (Var) and Kipilovo (Kip). Map data: EC.Europa.EU/Eurostat; species distribution map: www.EUFORGEN.org/species.
Elchingen, Silberbach, Ebersdorf, Mindelzell, Peschtera, Berkovitza and Petrohan were produced in the nursery Berkovitza. Only seedlings of the provenance Ebrach were produced in a German nursery. The cultivation took two growing seasons (2008 and 2009). The ensuing planting was conducted using a 2 x 1 m scheme. In general, three replicates per provenance were planted, with 50 seedlings each. The afforestation in the provenance trial in Vidin was carried out through digging holes and in Varbitza and Kipilovo – in slits. During each growing season in the study period two cultivations of the soil were conducted in all provenance trials.

Table 1. Location, mean annual precipitation (MAP), mean July temperature (T$_{07}$) and the current as well as projected Ellenberg quotient (EQ) of the 3 provenance trials.

<table>
<thead>
<tr>
<th>Country</th>
<th>Site</th>
<th>Site code</th>
<th>Latitude (N)</th>
<th>Longitude (E)</th>
<th>Altitude (m a.s.l.)</th>
<th>MAP (mm)</th>
<th>T$_{07}$ (°C)</th>
<th>EQ (°C mm$^{-1}$)</th>
<th>MAP (mm)</th>
<th>T$_{07}$ (°C)</th>
<th>EQ (°C mm$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bulgaria</td>
<td>Vidin</td>
<td>Vid</td>
<td>43°53'24&quot;</td>
<td>22°43´48&quot;</td>
<td>200</td>
<td>573</td>
<td>21.9</td>
<td>38.2</td>
<td>521</td>
<td>25.4</td>
<td>48.6</td>
</tr>
<tr>
<td>Bulgaria</td>
<td>Varbitza</td>
<td>Var</td>
<td>42°57'27&quot;</td>
<td>26°37´42&quot;</td>
<td>350</td>
<td>708</td>
<td>22.0</td>
<td>31.1</td>
<td>600</td>
<td>23.4</td>
<td>38.9</td>
</tr>
<tr>
<td>Bulgaria</td>
<td>Kipilovo</td>
<td>Kip</td>
<td>42°51'29&quot;</td>
<td>26°14´42&quot;</td>
<td>500</td>
<td>811</td>
<td>17.0</td>
<td>21.0</td>
<td>697</td>
<td>22.4</td>
<td>32.1</td>
</tr>
</tbody>
</table>

Note: Climatic data are mean temperatures from the period 1931 – 1970 (Kyuchukova et al., 1983) and mean precipitation of the period 1931-1985 (Koleva and Peneva, 1990). Projected data derives from EURO-CORDEX and was dynamically downscaled to a 1 x 1 km resolution (SUSTREE, 2018).

Table 2. Location, mean annual precipitation (MAP), mean July temperature (T$_{07}$) and the current as well as projected Ellenberg quotient (EQ) at the eight sites, where the seed was collected. For information of climate data cf Table 1. The provenances used in every trial are depicted in bold letters.

<table>
<thead>
<tr>
<th>Country of origin</th>
<th>Provenance</th>
<th>Prov-</th>
<th>Latitude (N)</th>
<th>Longitude (E)</th>
<th>Altitude (m a.s.l.)</th>
<th>MAP (mm)</th>
<th>T$_{07}$ (°C)</th>
<th>EQ (°C mm$^{-1}$)</th>
<th>MAP (mm)</th>
<th>T$_{07}$ (°C)</th>
<th>EQ (°C mm$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Germany</td>
<td>Elchingen</td>
<td>Elch</td>
<td>48.456</td>
<td>10.063</td>
<td>560</td>
<td>705</td>
<td>17.4</td>
<td>24.7</td>
<td>804</td>
<td>21.2</td>
<td>26.3</td>
</tr>
<tr>
<td>Germany</td>
<td>Silberbach</td>
<td>S</td>
<td>50.133</td>
<td>12.183</td>
<td>611</td>
<td>700</td>
<td>16.8</td>
<td>24</td>
<td>699</td>
<td>19.9</td>
<td>28.4</td>
</tr>
<tr>
<td>Germany</td>
<td>Ebersdorf</td>
<td>E</td>
<td>50.504</td>
<td>11.328</td>
<td>650</td>
<td>900</td>
<td>15.3</td>
<td>17</td>
<td>940</td>
<td>18.5</td>
<td>19.7</td>
</tr>
<tr>
<td>Germany</td>
<td>Mindelzell</td>
<td>M</td>
<td>48.218</td>
<td>10.423</td>
<td>565</td>
<td>800</td>
<td>17.1</td>
<td>21.4</td>
<td>1030</td>
<td>21.1</td>
<td>20.5</td>
</tr>
<tr>
<td>Germany</td>
<td>Ebrach</td>
<td>Ebr</td>
<td>49.952</td>
<td>10.488</td>
<td>344</td>
<td>800</td>
<td>17.7</td>
<td>22.1</td>
<td>760</td>
<td>20.9</td>
<td>27.4</td>
</tr>
<tr>
<td>Bulgaria</td>
<td>Peschtera</td>
<td>Psht</td>
<td>41.974</td>
<td>24.377</td>
<td>1300</td>
<td>960</td>
<td>16.2</td>
<td>16.9</td>
<td>836</td>
<td>16</td>
<td>19.1</td>
</tr>
<tr>
<td>Bulgaria</td>
<td>Berkovitza</td>
<td>B</td>
<td>43.210</td>
<td>23.089</td>
<td>850</td>
<td>825</td>
<td>21.2</td>
<td>25.7</td>
<td>681</td>
<td>25.2</td>
<td>37</td>
</tr>
<tr>
<td>Bulgaria</td>
<td>Petrohan</td>
<td>P</td>
<td>43.152</td>
<td>23.141</td>
<td>800</td>
<td>1004</td>
<td>21.2</td>
<td>21.1</td>
<td>815</td>
<td>22.7</td>
<td>27.9</td>
</tr>
</tbody>
</table>

Note: The provenances used in every trial are depicted in bold letters.

Elchingen, Silberbach, Ebersdorf, Mindelzell, Peschtera, Berkovitza and Petrohan were produced in the nursery Berkovitza. Only seedlings of the provenance Ebrach were produced in a German nursery. The cultivation took two growing seasons (2008 and 2009). The ensuing planting was conducted using a 2 x 1 m scheme. In general, three replicates per provenance were planted, with 50 seedlings each. The afforestation in the provenance trial in Vidin was carried out through digging holes and in Varbitza and Kipilovo – in slits. During each growing season in the study period two cultivations of the soil were conducted in all provenance trials,
In all trials, an inventory of surviving plants was done during the first three years after their establishment. The heights of all surviving plants of each provenance and its replicates were measured with an accuracy of 1 cm. Measurements were conducted at the end of the respective growing season but before leaf fall, at the end of the first (H₁, 2010), second (H₂, 2011) and third (H₃, 2012) year after establishment.

A two-factor analysis of variance (ANOVA) was applied to determine the individual and interacting effects of provenance and habitat conditions on height. Measured the average heights at the third year after planting of beeches of different provenances were corrected with the site effect, to make them directly comparable (corrected heights are denoted further as $H'$). The site effect was calculated using the standard model of the two-factor ANOVA as the difference between the average heights of the four provenances (Silberbach, Ebersdorf, Berkovitza and Petrohan) included in the three provenance trials and the mean height of the same provenances for each trial (Table 3). A regression analysis was applied to establish the existence of a linear relationship between the Ellenberg quotient and the ecodistance and the height of the provenances.

For each trial and each provenance Ellenberg’s climate quotient EQ (Ellenberg, 1988) was calculated as:

$$\text{EQ} = 1000 \times \left( \frac{T_{07}}{P_{\text{ann}}} \right), \quad (1)$$

where $T_{07}$ was the mean annual temperature of the warmest month (July) and $P_{\text{ann}}$ was the mean annual precipitation.

The mean ecological distance $\Delta E$ was used to express the overall effect of climate conditions in provenance trials as experiments of differently adapted provenances and was calculated using the formula:

$$\Delta E = X' - X_o, \quad (2)$$

where $X'$ was the average value of the EQ of the respective provenance trial and $X_o$ was the EQ of the respective beech provenance (Mátyás et al., 2009b).

The data were processed statistically with statistical and graphical functions using environment libraries in R programming language (Wickham, 2009; R Core Team, 2017).

**Table 3.** Mean tree height at the three provenance trials (PT) of the four beech provenances (S, E, B and P) after three years, site effect (calculated as difference between total mean and resp. PT), slope of a regression analysis (relationship between corrected height and $\Delta EQ$), results of a two-factorial ANOVA for differences between provenances.

<table>
<thead>
<tr>
<th>PT</th>
<th>Mean Height [cm]</th>
<th>Site effect [cm]</th>
<th>f(x) of $H'$ vs. $\Delta EQ$ of provenances</th>
<th>Differences between provenances</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>F</td>
</tr>
<tr>
<td>Vidin</td>
<td>31.8 ± 4.5</td>
<td>-10.6</td>
<td>-0.019</td>
<td>11.31 ***</td>
</tr>
<tr>
<td>Varbitza</td>
<td>55.3 ± 5.5</td>
<td>12.9</td>
<td>-0.35</td>
<td>4.58 **</td>
</tr>
<tr>
<td>Kipilovo</td>
<td>40.1 ± 5.6</td>
<td>-2.3</td>
<td>0.157</td>
<td>10.39 ***</td>
</tr>
<tr>
<td>Total</td>
<td>42.4 n.a.</td>
<td>n.a.</td>
<td>n.a.</td>
<td>n.a. n.a.</td>
</tr>
</tbody>
</table>

Note: Significance level: ** – $p < 0.01$; *** – $p < 0.001$. 

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RESULTS

Survival

At the driest test site in Vidin (573 mm MAP), tree survival was remarkably low (Figure 2a). After the first growing season, it reached 75.2% for the whole trial and kept on declining until after the second (47.0%) and the third year (31.3%).

The specimens from the driest site provenance Silberbach (MAP 700 mm) perpetuated the highest survival over the three years (88.7, 59.3 and 40.0%), followed by the specimens of the Bulgarian provenance Petrohan (74.7, 53.3 and 37.3%). The survival rates of Berkovitza (68.0, 40.7 and 27.3%) and Ebersdorf (69.3, 34.7 and 20.7%) were even lower.

The survival of the investigated trees during the first three years after establishment at the more humid test sites V arbitza (MAP 708 mm) and Kipilovo (MAP 801 mm) was relatively high with 95.5% and 96.7%, respectively after the first year (Figures 2 b, c). Over the next two years, survival rates declined progressively and reached 74.3% in Varbitza and 76.3% in Kipilovo after the third year. Differences between provenances were negligible after the first growing season in Varbitza and Kipilovo, since the survival rates of beech from all provenances was between 94% and 98%.

After the second year of the field trial in Varbitza, the two German provenances showed slightly lower survival rates (Silberbach 85.3%, Ebersdorf 85.5%) than the two Bulgarian ones (Berkovitza 92.0%, Petrohan 88.0%). After the third study year, the provenances Ebersdorf and Berkovitza retained survival of over 80%, while the provenances of Silberbach (66.0%) and Petrohan (63.3%) had larger losses.

After the second year of the transfer experiment in Kipilovo, the provenance Ebersdorf showed the highest survival rate (96.7%), followed by the two Bulgarian provenances (about 93% each), while the provenance from Silberbach exhibited the lowest survival rate (85.3%). After the last year of the experiment, the provenances Petrohan and Ebersdorf exhibited survival rates of about 80%, while those of Silberbach (73.3%) and Berkovitza (70 %) were considerably lower. A grouping in the survival of German and Bulgarian provenances was not observed.

Projected climate data for the period 2080-2100 (Tables 1 and 2) demonstrated that EQ values would increase at every location from which the German plants originated. Solely in Mindelzell the predicted increasing MAP amounts lead to a slightly decreasing EQ from 21.9 to 20.5. In Ebersdorf (EQ = 19.7) conditions would be appropriate for vital beech growth. In Elchingen (EQ = 26.3) and in Ebrach (EQ = 27.4), the climate would mainly prevent beech from distributing naturally. In Silberbach (EQ = 28.4), the threshold might be exceeded where beech loses its competitiveness (Jahn, 1991).

Also in Bulgaria, the forecasted climate could severely threaten young trees of F. sylvatica. In fact, beech would be stressed in Petrohan (EQ = 27.9). However, in Berkovitza (EQ = 37.0) no survival will be possible at the long term. In Kipilovo (EQ = 32.1), no favourable conditions for F. sylvatica could be expected. In Varbitza, limit values would be achieved (EQ = 38.9), while Vidin would be far beyond tolerable conditions for any survival of European beech (EQ = 48.6).
Height growth

In the first year only the beech originating from Petrohan had a mean height of 28.2 cm and were taller than the average of all provenances with a mean height of 25.5 cm (Figure 3). In the second year, specimens of Petrohan (36.8 cm) and Berkovitza (33.4 cm) were above the average (31.9 cm), as well as trees of Berkovitza and Petrohan in the third year. After the first growing season, the trees of the four provenances exhibited a mean height of 22.6 cm in Varbitza and 24.7 cm in Kipilovo. In Vidin, an average height of 29.0 cm was detected.

However, there was a decrease of mean height in Vidin after the second year for the three better growing provenances: Ebersdorf from 27.4 to 23.4 cm, Berkovitza from 31.8 to
31.0 cm and Petrohan from 34.9 to 30.8 cm (Figure 4). This was due to the high mortality rates in Vidin (Figure 2), indicating that at the driest site especially the taller trees were more threatened.

After the third growing season, the highest growth rates were determined in Varbitza with an average height at the third year of 55.4 cm. In Kipilovo, the mean height was clearly lower with 39.8 cm, whereas in Vidin a mean of only 31.8 cm was calculated.

Effects of potential trial-site differences were detectable in Varbitza and to a lesser extent in Kipilovo (Table 3). Due to harsh conditions, the site effect at Vidin was negative and, hence, exhibited the lowest potential. The slope of the regression analysis revealed that heights were slightly decreasing with decreasing ecological distance, while in Kipilovo height increased. The differentiation between provenances was more pronounced in Kipilovo and Vidin, while it was less distinct in Varbitza.

Height was significantly different between the provenances, as well as between the provenance trials in all three years (Table 4). The cross effect of provenance and PT was significantly detectable for the first year of investigation.

A more detailed exploration of the individual provenances confirmed the detected significant differences (Figure 4). In Vidin, the differences in mean height were not significant between the provenances after the first growing season. After the second year, specimens from provenances Berkovitza and Petrohan were significantly taller than these from Silberbach and Ebersdorf. This trend was not so pronounced after the third growing season.

In Varbitza, there were no significant differences between the provenances after the first year. After the second year, the beech originating from Silberbach was significantly shorter than the others. After the third growing season, trees from Petrohan were significantly higher than those from Ebersdorf and Silberbach, while there are no differences of Berkovitza to both groups. In Kipilovo, there were only small but significant differences

![Fig. 3. Mean heights (H at the end of the respective growing season) by provenance (S – Silberbach, E – Ebersdorf, B – Berkovitza, P – Petrohan) and provenance trial (PT; Vid – Vidin, MAP 573 mm; Var – Varbitza, MAP 708 mm and Kip – Kipilovo, MAP 801 mm).](image-url)
between the provenances after the first growing season, whereas trees from Petrohan were significantly higher in growth than the beech from other provenances after the second as well as the third growing season.

A closer view on height growth of beech trees after the important first year after establishment showed that the provenances reacted differently to the changes of environmental conditions (Figure 5). Mean height of seedlings originating from Petrohan (1004 mm MAP) was comparable to mean height of the provenances Ebersdorf (900 mm MAP) and Silberbach (700 mm MAP) in Varbitza and Kipilovo but reached the largest height in Vidin. Young trees from Berkovitza (825 mm MAP) had the smallest height in Varbitza but were the second largest provenance in Vidin.

After the first growing season investigated in this experiment, the average heights of beech trees from all provenances were very similar at the two more humid trial sites in Varbitza (708 mm MAP) and Kipilovo (811 mm MAP). However, at the driest trial site in Vidin (573 mm MAP) there were significant differences among the mean heights of the provenances. At the two more humid locations, growth rates of the four provenances were generally comparable. In Kipilovo, the mean height of the studied trees was between 23.4 and 26.6 cm, in Varbitza it ranked between 20.5 and 23.3 cm. Hence, growth was comparable but a bit more pronounced on the more humid location with a slight increase at the provenances originating from moister climates.

At the driest location, Vidin the pattern was different and showed a greater spread within mean tree heights between 21.9 and 34.9 cm. At this trial site, mean height of the trees from the driest provenance Silberbach had a low growth, whereas provenances originating from moister climates on average exhibited greater heights than on the two more humid trial sites.

**DEPENDENCE OF HEIGHT GROWTH ON THE ELENBERG QUOTIENT AND ECODISTANCE**

The ecodistance $\Delta E$ between the EQ of provenance trial locality and EQ of beech provenance expresses the change of climate, where positive values indicate transfer to warmer and drier, while negative values imply a transfer in direction of cooler and more humid conditions (Mátyás et al., 2010).

The ecodistance of the provenances has shown that their transfer to the provenance trials in Varbitza and Vidin was directed to drier and warmer conditions (Table 5). At the
provenance trial in Kipilovo, where only two of eight provenances were included, solely the value of Ebersdorf was positive. The negative values of the other three provenances (Silberbach from Germany and the Bulgarian Berkovitza and Petrohan) indicated that the transfer was directed to slightly cooler and wetter conditions.

Corrected heights of the different provenances showed diverse reactions to an increasing Ellenberg quotient of the four provenances (Figure 6). The best growing provenance was Petrohan with values > 47.5 cm. The second best growth rate could be detected for trees originating from Berkovitza with values > 42 cm. The provenance
Ebersdorf lied at about 40 cm of corrected mean height, while the provenance Silberbach lied at about only 37.5 cm.

The more humid Bulgarian provenance Petrohan (EQ = 21.1) showed decreasing height growth with increasing EQ. Contrastingly, the corrected height of trees originating from the drier location Berkovitza (EQ = 25.7), increased with an increasing EQ. Corrected heights of the two German provenances Ebersdorf (EQ = 17) and Silberbach (EQ = 24.0) showed only a negligible height growth with an increasing EQ.

Height of seedlings of *F. sylvatica* decreased with increasing ecological distance (ΔE) at both the more humid trial site in Varbitza as well as the more arid trial site in Vidin (Figure 7). A statistically significant correlation between corrected heights of beech originating from the eight provenances with the average ecological distance could not be detected at both provenance trials. However, the distribution of provenances was similar in both provenance trials. The values of the corrected heights of provenances originating from more arid climates (Elch, S, Ebr, B and M: MAP 700 – 800 mm) were grouped at a ΔE ≤ 10 in Varbitza and at ΔE ≤ 16.8 in Vidin and have overall exhibited larger heights at both trial sites. The beech trees originating from more humid locations (E, Psht and P: MAP 900-1004 mm) were grouped at ΔE ≥ 17.1 in Varbitza and at ΔE ≥ 20 in Vidin and have overall developed lesser heights at both trial sites.

Ecological distance for the provenance trial Kipilovo is not depicted, since the transfer to cooler and wetter conditions (Table 3) is not of priority interest against the background of global warming.
Table 5. Ellenberg quotient (EQ) of the studied beech provenances, as well as ecodistance ($\Delta E$) of the provenances at the provenance trials Vidin (EQ = 38.2), Varbitza (EQ = 31.1) and Kipilovo (EQ = 21.0).

<table>
<thead>
<tr>
<th>Country</th>
<th>Provenance</th>
<th>Code</th>
<th>EQ [°C mm-1]</th>
<th>$\Delta E$</th>
<th>$\Delta E$</th>
<th>$\Delta E$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Germany</td>
<td>Elchingen</td>
<td>Elch</td>
<td>24.7</td>
<td>13.5</td>
<td>6.4</td>
<td></td>
</tr>
<tr>
<td>Germany</td>
<td>Silberbach</td>
<td>S</td>
<td>24.0</td>
<td>14.2</td>
<td>7.1</td>
<td>-3.0</td>
</tr>
<tr>
<td>Germany</td>
<td>Ebersdorf</td>
<td>E</td>
<td>17.0</td>
<td>21.2</td>
<td>14.2</td>
<td>4.0</td>
</tr>
<tr>
<td>Germany</td>
<td>Mindelzell</td>
<td>M</td>
<td>21.4</td>
<td>16.8</td>
<td>9.7</td>
<td></td>
</tr>
<tr>
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<td>Ebrach</td>
<td>Ebr</td>
<td>22.1</td>
<td>16.1</td>
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<td></td>
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<tr>
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<td>16.9</td>
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</tr>
<tr>
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<td>12.5</td>
<td>5.4</td>
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<tr>
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<td>Petrohan</td>
<td>P</td>
<td>21.1</td>
<td>17.1</td>
<td>10.0</td>
<td>-0.1</td>
</tr>
</tbody>
</table>

Note: The provenances used in every trial are depicted in bold letters.

Fig. 6. Reaction norm of the corrected heights $H_3'$ of four provenances (Prov) of European beech (S – Silberbach, EQ = 24.0; B – Berkovitza, EQ = 25.7; E – Ebersdorf, EQ = 17.0; and P – Petrohan, EQ = 21.1), displaying individual differences in response to EQ values of provenance trials (PT) Kip – Kipilovo, Var – Varbitza and Vid – Vidin.
DISCUSSION

Massive mortality rates for both the German and Bulgarian beech provenances at xeric site (MAP < 600 mm).

Survival rates of the transferred beech of different provenances were dramatically low at the driest field site in Vidin (573 mm MAP). After three years, about 60% of the trees originating from Silberbach and Petrohan and more than 70% of the trees from Berkovitza died. Trees from the provenance Ebersdorf even died by almost 80%. All provenances, regardless if they originated from Bulgaria or Germany, showed extremely high mortality rates at this trial site. At the more humid trial site in Varbitza (708 mm MAP) from less than 20% to not even 40% of the trees died. At the humid trial site in Kipilovo (811 mm MAP) only 20% to 30% of the trees died during the first three years.

This offers evidence for survival difficulties due to genetically set drought-tolerance limits of European beech. A mean annual precipitation of 573 mm seems to go below a critical minimum of water supply for young trees of *F. sylvatica*. Of course, the edaphic conditions play a major role. However, soil types on our trial sites were luvisols and chernozemes with high base saturation and a sufficient water-holding capacity (FAO, 2006). Results from dendroecological studies on mature beech trees in Germany show growth decline on sandy-loamy soils at a MAP < 660 mm (Knutzen et al., 2017), loamy to clayey soils at 600 – 640 mm MAP (Zimmermann et al., 2015) and on sandy soils of a MAP < 595 mm (Scharnweber et al., 2011).
The critical value for vital beech growth lies at about 600 mm MAP and the mean temperature of the warmest month within the range of 18 to 20°C (Ellenberg, Leuschner, 2010). Both values are included in the calculation of the Ellenberg climate quotient (EQ). The EQ indicates favourable climatic conditions for beech if the value is at about 26 (Mátyás et al., 2009a). If the EQ is above 30, European beech loses its competitiveness (Jahn, 1991). Close to the limit value of 40, the beech is threatened with dying (Mátyás et al., 2010). Dry and warm climatic conditions in the region of Vidin lead to an EQ of 38.2. With the EQ of the trial site in Varbitza (31.1) and that in Kipilovo (21.0), the increasing survival rates with decreasing EQ, confirm the trend of declining performance with increasing change of climate the populations were adapted to, which was also observed by Horvat, Mátyás (2016).

Accordingly to the results of this study, it is very likely that MAP < ~580 mm or an EQ by ~38 lead to high losses of European beech especially during the rejuvenation state.

Episodic drought periods and mean surface temperatures will significantly increase during the 21st century in many parts of Central Europe (IPCC, 2014). A bioclimatic distribution modelling for beech conducted in more central regions of its distribution in Hungary predicts that 56–99% of the current beach populations might be outside their present bioclimatic zone by 2050 (Czúcz et al., 2011). Regarding the fact that precipitation amounts will decrease especially during summer in many Central European parts (Jacob et al., 2014), harsh negative impacts on the vigour of _F. sylvatica_ can be expected, especially against the background of cultivation periods of 100 to 120 years. However, numerous populations of _F. sylvatica_ at the southern and eastern margin of the species distribution are currently located in areas with existing climatic conditions close to those thresholds that have been defined here. Hence, the results of this transfer experiment call out for more studies on eastern and southern beech populations for provenance selection in order to improve the opportunity of provenance choice for forest management activities in Central Europe. Otherwise, populations of European beech might decline in large parts of its present distribution in managed and natural forests.

Additionally to the climatic impacts on trees vigour, other abiotic and biotic factors may also have contributed to the mortality rates. The winter in 2009/2010 led to a heavy and severe snow cover which may have impaired the young trees negatively. Furthermore, the thick snow cover may have helped roe deer to cross the fencing of the trial sites where it bit the shoots mainly of the bigger plants, which top part protruded above the snow cover. The average of damaged plants in the studied provenances varied from 45.7 to 78.0%. Additionally, attacks of cicadas (order _Hemiptera_, superfamily _Cicadoidea_) have been detected. Depositing eggs through female cicadas can injure bark or twigs of the plants, which can lead to extinction of top or side shoots or even intensify processes leading to mortality. Generally, factors impairing vigour of plants mount up. Trees under harsh environmental conditions have more difficulties to cope with attacks by insects or herbivores.

**Beech is likely to become extinct in lower regions in Bulgaria**

Projected climate data for the period 2080–2100 demonstrate tremendous increases of the EQ at practically all explored provenances and at all trial sites within this study (Tables 1 and 2). That leads to unfavourable climatic conditions for European beech in
central regions. However, it is likely that survival will be possible during the current century. In the marginal regions of the species distribution in Bulgaria, beech will solely be able to survive in higher regions e.g. the Rhodope Mountains, predicting its disappearance of the lowest habitats (Raev et al., 2011).

**Bulgarian provenances exhibit larger heights than German provenances**

We can determine that the provenance Petrohan and, with some limitations, Berkovitza can be seen as the best-growing of the studied provenances (Figure 3). From the first- to the third-year trees, originating from Petrohan, exhibited the largest height at all trial sites. Trees from Berkovitza were above the average after the second and third year of the experiment, while the two provenances originating from Germany remained below average. In Kipilovo, trees from Petrohan were significantly higher than those of the other provenances, while in Varbitza and Vidin there were no significant differences to Berkovitza (Figure 4). Hence, we can conclude that the two Bulgarian provenances showed a more pronounced growth than the two German provenances. One reason can be due to the fact that the investigated here Bulgarian provenances flush earlier in comparison to the German provenances (Petkova et al., 2017), which is also consistent with other studies (Muhs, 1985; Madsen, 1995; Stener, 2002). *Fagus sylvatica* shows an ecocline in bud break: eastern populations flush earlier (Matyas et al., 2010). A wood structural study on northern (Sweden, Netherlands) and southern (France, Bulgaria) beech provenances also showed the best values concerning height and radial growth, as well as drought resistance of the provenance from Bulgaria (Eilmann et al., 2014).

Trees originating from the driest site Silberbach (700 mm MAP) exhibited the slowest growth in the first year after establishment at the driest field site in Vidin only (Figure 5), which could be seen as an adaptation process of the provenance used to dry conditions, since slower growth is accompanied with a smaller vessel size (Hacke et al., 2001). Even though the efficiency of the hydraulic system is lowered, the capacity to cope with low sap pressure without being embolised is improved (Hacke et al., 2001). A link between drought vulnerability and growth could be documented for *Pinus sylvestris* (Martínez-Vilalta et al., 2012) Morán-López et al., (2014) observed lower water-use efficiency at fast-growing pines.

Significant differences in height development of the young beech trees not only could not be detected between the particular provenances but also between the specific provenance trials (Table 4). Climate conditions of the field sites reflect growth performance of the trees: on account of the harsh local environmental conditions on the driest trial site Vidin (573 mm MAP), the lowest mean height was exhibited (Figure 3). Accordingly, height growth was more pronounced at the two more humid sites Varbitza (708 mm MAP) and Kipilovo (801 mm MAP).

The presented results have shown growth tendencies of particular beech provenances for the important first time after establishment. Still, there are open questions concerning the development over a longer period. The growth potential of trees can be estimated reliably at mature age, in case of beech at the earliest of the age of 40, which is one third of its rotation period (Gwaze et al., 2001; Ballian, Zukić, 2011). Another remaining question,
which comes along with studies on height growth at range limits in temperate regions, is
cold hardiness. Genetic correlation of early bud burst and frost damage could be detected
on Norway spruce (Hannerz et al., 1999). Loehle (1998) even assumed the existence of a
genetically based trade-off between frost tolerance and height growth of trees.

Therefore, a long- term monitoring of height growth of beech provenances which
also focuses on frost hardiness would be desirable.

**Beech trees originating from Bulgaria seem to be better adapted to expected future
cclimate than German ones**

Between the climatic optimum for European beech (EQ values around 20) up
till the limit where survival of beech is threatened (EQ values > 38), trees of Bulgarian
provenances were taller than those originating from Germany (Figure 6). Hence, within
this decisive part of the climatic range of *F. sylvatica*, the Bulgarian provenances showed a
better adaption.

However, the different provenances responded differently to the changing
environmental conditions regarding their phenotypic plasticity. The height of trees
originating from Petrohan (EQ = 21.1) decreased under warmer and drier surroundings.
This respond could be expected, since harsher environmental conditions impair tree
vigour and, hence, its ability to build up biomass. On the other hand, trees originating
from Berkovitza (EQ = 25.7) increased their heights with increasing summer warmth and
humidity and exhibited the best growing rate at an EQ value of about 30. This could be
due to the fact that these trees have already adapted to a more humid environment and,
thus, show the best growth performance at drier and more xeric conditions than the trees
originating from the moister and colder Petrohan locality. Conversely, the beech from two
German provenances seem to be unaffected by the changing environmental conditions.
This could be due to a lower phenotypic plasticity, which is a crucial element of plants
response to changing climatic conditions (Jump, Peñuelas, 2005).

The results indicate that the studied beech provenances indeed have adapted to local
environmental conditions and exhibit a notable climatic adaptation potential. Furthermore,
we can state that drier and more xeric conditions lead to losses in vigour and growth and in
conjunction with herbivorous or insect attacks – to high mortality rates. Therefore, forests
of *F. sylvatica* are likely to lose major areas of its current distribution during the coming
decades, especially in the lowland zones where aridity and summer warmth increases (with
EQ values above 30). In addition, it seems that European beech originating from the south-
eastern margin of the distribution of the species are better adapted to drought than its
conspecifics from more central regions.

**Provenance traits are more decisive than distance of transfer**

Regarding the climate response and the adaptation potential of beech to
macroclimatic challenges, the concept of ecological distance can be seen as a 'space- for- time
substitution' (Mátyás et al., 2009a). Hence, it was not surprising that in this study growth
suppression was detectable with increasing ecodistance, even though the relationship was
not significant (Figure 7). Interestingly, the pattern of decreasing heights with increasing
summer warmth and aridity was recorded for both the trial site with more distant transfers (Vidin) and the one with less distant transfers (Varbitza). Together with the fact that the particular provenances exhibited comparable heights at both sites, we could state that the characteristics of the particular provenances were more decisive than the magnitude of the ecological distance. The existence of a genetic adaptation potential in beech has been previously demonstrated for provenances from Slovenia and Hungary (Mátyás et al., 2009a, 2010). As demonstrated by our results, this could be also confirmed for provenances from Bulgaria. Accordingly, selection effects could be detected in South-Eastern Europe for *F. sylvatica*.

Furthermore, the effect of ecological distance on the response of European beech trees was substantiated by its linear regression slope related to the respective tree heights. Tree height decreased with increasing ecological distance at the trial site in Kipilovo but not in Vidin and Varbitza (Table 3). Accordingly, European beech was not impaired in Kipilovo under a milder climate regime (EQ = 21).

**CONCLUSIONS**

Our first hypothesis that 'beech provenances from the south-eastern range margin show less mortality and higher tree growth than provenances from more central regions', can be partly accepted. At the most xeric site with mean annual precipitation amount of 573 mm, the environmental conditions were critical for all provenances, no matter where they originated from. However, Bulgarian trees exhibited larger height values than the German trees.

Our second hypothesis that 'height growth decreases with increasing Ellenberg quotient (EQ) and with increasing ecological distance (∆E)' could partly be accepted. In fact, a relationship between decreasing height growth and increasing Ellenberg quotient could be detected. However, a relationship between decreasing heights and the ecological distance, i.e. the magnitude of transfer, could not be discovered.

At the end of the current century harsher climate conditions will threaten beech in large parts of Bulgaria with lower elevation. From this areas may originate various provenances which are likely to reveal better adaptation and, hence, larger growth under a projected future drier climate in various central parts of the distribution of *F. sylvatica*. Therefore, it is of urgent need to explore beech provenances from the Balkans in the near term, since they are likely to represent a valuable genetic reservoir for a sustainable and global- warming adapted forest management for large parts of Central Europe.

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