Intra-annual stem size variations converge across marginal populations of European beech

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Received: 27 May 2019 / Accepted: 24 September 2019 / Published online: 1 October 2019
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Abstract

Key message The intra-annual variability in stem size of marginal beech population from south-eastern distribution range of beech in Poland is higher within than between populations.

Abstract One of the key issues of the distribution of tree species is their ability to track environmental changes. European beech (Fagus sylvatica L.) is a species highly sensitive to extreme climatic events, because of its high phenotypic plasticity. In this study, we aim to determine the variability in stem size between and within marginal beech populations. Marginal populations of beech growing under uniform environmental conditions of provenance trial offer unique opportunity to detect adaptive differentiations driven by natural selection. In this work, we studied stem size variation recorded by automatic band dendrometers in four beech marginal populations growing in a common garden in the south-eastern distribution range of beech in Poland over the period 2016–2018. Strong climatic effects and weak provenance differences in seasonal stem size variation were observed. The provenances exhibited similar climate-related seasonal stem circumference variation. A high within-provenance variation was confirmed. Temperature of spring as well as temperature and precipitation of autumn were detected as key climatic parameters mostly for onset and end of stem size variation. Maximum stem size was mostly affected by the later end of its variation, which positively affected its duration. Climatic distance between beech provenances and provenance trial had a negligible effect on the variability in seasonal stem size variation between provenances. The evidence of weak inter-provenance and high intra-provenance variation in stem size changes observed in the south-eastern distribution range indicates that an individual-based approach could be a suitable strategy, when selecting for phenotypic plasticity.

Keywords European beech · Stem circumference variation · Dendrometers · Marginality · Provenance trial

Introduction

Marginal populations occur at the limit of the ecological tolerance of the species. They are frequently isolated from the core population due to habitat fragmentation, thus manifesting a reduced genetic diversity (Jump and Penuelas 2006; Vilà-Cabrera et al. 2019). The importance of marginal populations in the adaptation of trees to the ongoing climate change seems to be still undervalued (Alberto et al. 2013; Madeira et al. 2018). Phenotypic plasticity is considered to be the change in the expressed phenotype of a given genotype as a function of the environment (Scheiner 1993), and thus is commonly applied to test inter-provenance variation in climate adaptation. However, changes in phenotype could be the result of either genotypic adaptation or phenotypic plasticity. Phenotypic changes may be more or less adaptive, and, in turn, maladaptive or non-adaptive changes might occur as a result of stress (West-Eberhard.
Given the above considerations, studies focusing on the aspect of phenotypic plasticity in climate adaptation require careful and critical evaluation of the proposed conclusions.

The assessment of intraspecies variation in phenotypic plasticity requires experiments that investigate the growth responses of genetically diverse provenances of the same species under the same growth conditions. Common garden experiments of forest tree species are often used in provenance-specific inter-annual climate adaptation studies, although they rarely become a tool for investigations on intra-seasonal variation of growth reaction (Ježík et al. 2016; Suvanto et al. 2016; Klisz et al. 2019b). In the case of marginal populations, the role of the climatic conditions driving onset and the end of activity of growth meristems seems to be of particularly importance, as marginal populations are located at the limits of ecological niches (Rossi et al. 2008; Montwe et al. 2018). Thus, within marginal growth conditions, growth rate can be limited by warming-induced soil moisture deficit (Ren et al. 2019). Indeed, marginal populations’ growth is prone to limiting climatic factors that can change according to their relative position across the distribution area of the species (Hacket-Pain et al. 2016). Common garden experiments collecting different marginal populations undergoing local adaptation to different limiting factors could be the key for understanding if and how the species will adjust to the future climates (Kreyling et al. 2014).

According to recent species distribution models, European beech (Fagus sylvatica L.) could potentially play a dominant role among the other late-successional species, due to its high potential for resilience and level of plasticity in populations (Dyderski et al. 2018; Sáenz-Romero et al. 2019). Nevertheless, the level of adaptation to climate change of marginal beech populations may vary depending on their location within the natural range of this species. Low elevation populations from the southern distribution might be threatened by the forecasting warming (Mátyás et al. 2010), while high elevation population could suffer from late frosts (Allevato et al. 2019). Accordingly, it is evident that marginal populations require special attention. At northern and north-eastern distribution range, the beech populations manifest growth plasticity and high competition ability (Bolte et al. 2007; Farahat and Linderholm 2018; Weigl et al. 2018). Even beech populations introduced outside its natural range seem able to adapt properly at second generation (Matisons et al. 2017) after a period of high sensitivity to unfavorable conditions (Krišāns et al. 2016). In turn, southernmost beech populations, more resistant to xylem embolism, may better cope with frequent droughts (Stojnic et al. 2017; Varsamis et al. 2019). Thus, although the issue of intraspecific variation in phenotypic plasticity of beech was recently widely explored, still little is known on provenances from the south-eastern margin of the distribution range (Rose et al. 2009; Kramer et al. 2017).

Stem size variation is the cumulative result of the reversible elastic changes in phloem and cambium caused by transpiration and the irreversible xylem growth due to expansion of new cells (Deslauriers et al. 2007; Nalevanko et al. 2018). There are evidences that several environmental factors regulate the processes occurring within the stem, manifesting in intra-annual changes in its size (e.g. Köcher et al. 2012; Siegmund et al. 2016; Schäfer et al. 2018). The onset of stem size variation mostly depends on spring temperature and its accumulation over a longer period (Ježík et al. 2011). Moreover, thermal thresholds for the onset and ending of xylogenesis seem to be of importance for xylem production and maturation (Liang and Camarero 2018). However, extremely high temperatures in late spring and early summer cause sharp drop in stem-size curve. Solar radiation influences the hydrological conditions of beech stands, thus eventually causing a shortage of water during summer (Gessler et al. 2001). Furthermore, soil water shortage in late summer along with transpiration due to high temperature may negatively affect leaf water potential (Köcher et al. 2009) and indirectly stem circumference (Betsch et al. 2011). Drought-induced changes in stem circumference result from stem water depletion, when trees are not able to refill elastic tissues, namely phloem, cambium, and subero-phelloderm.

Given the forecasting climate change and resulting shift of ecological niches, the beech is expected to expand not only beyond its current north-eastern, but also south-eastern distribution margin (Saltré et al. 2015; van der Maaten et al. 2017). Moreover, the ongoing changes in environmental conditions could affect more dramatically the populations located at the boundary of the species distribution. Nevertheless, despite reduced genetic diversity (Carsjens et al. 2014), marginal populations may manifest a higher plasticity to adapt to changing conditions (Valladares et al. 2014). However, recent studies carried out at the beech population level revealed relatively high inter-family phenotypic variability in growth and functional traits observed on beech common garden studies (Aranda et al. 2017). In this context, two questions arise (1) if and how climate sensitivity varies between marginal populations belonging to eastern margins of beech distribution range; and (2) whether climate-growth reaction is uniform within a given marginal population.

In this study, we investigated stem circumference variation of marginal populations of European beech growing in a common garden located at the south-eastern distribution of the species in Poland over a three-year period 2016–2018. We expect to detect a higher variability in stem circumference variation within provenances rather than between provenances.
Materials and methods

Study site and provenance selection

This study is based on a beech common garden experiment located in Oleszyce, south-eastern Poland (N 54.0788°, E 13.4787°, 135 m a.s.l.), eastern margin of the European beech distribution range (8.5 °C mean annual temperature and 609 mm annual precipitation, Fig. 1) (NOAA/NCEI/CWC, http://www.noaa.gov/). The experiment was established in 2006 under coordination of State Forests National Forest Holding and composed of 24 provenances covering the south-eastern distribution range of beech in Poland. Marginal environmental conditions refer to climatic properties that represent the climatic margins of a species distributional range (Mellert et al. 2016). Accordingly, we considered our beech population to be marginal due to the fact that the climatic conditions in which they are located are similar to the marginal climatic conditions of beech population from the edge of south-eastern distribution of the species in western Ukraine. Provenance trial was located on leached brown soil in a complete block design with four replications. Each population was represented by 400 planted seedlings (100 per replication) planted in 1.5 × 1.5 m spacing. Four provenances and with each of them, two to four co-dominant trees were selected to monitor stem circumference variation (SCV) from 2016 to 2018 (Fig. 1). Provenance selection aimed at representing highest possible diversity of climatic conditions of their origin in relation to the eastern distribution range (ΔMAT = 1.4 °C, ΔMAP = 160 mm; Fig. S2). The number of trees measured changed in time with two trees per provenance investigated in the first year (2016) and five in the successive year. However, the target trees had to be successively reduced due to technical problems with the sensors, or damages caused by rodents (see Fig. 2).

Dendrometer data

The SCV was recorded from February 2016 to December 2018 using automatic band dendrometers (UMS D6
Due to the low branching, the dendrometers were installed at heights ranging from 1.0 to 1.3 m. The daily means of SCV were calculated from measurements taken at 30-min intervals with 5 μm accuracy and stored in automatic data loggers (Delta-T Devices GP2 Data Logger). To be able to describe SVC between years, a common interval was selected from each annual record corresponding to a general growth period reported in the literature between the day of the year (DOY) 120 and 249 (Prislan et al. 2019). Each dendrometer series was rescaled to start from the beginning of growth in circumference on DOY 120 (van der Maaten et al. 2018).

Weather data

Environmental data was monitored both on-site and nearby climate station on Oleszyce State Forest Nursery (at a distance of 380 m from target trees). On-site weather monitoring covered mean temperature, relative humidity, precipitation, photosynthetically active radiation (“S-THB” air temperature, “S-RGB” precipitation sensor connected to a “HOBO U30-NRC Analog Data Logger”; Onset Computer Corporation, Bourne, USA) at 30-min intervals. Missing data in on-site weather monitoring were filled with the data from climate station on Oleszyce State Forest Nursery. The daily means of air temperature and sum of precipitation were calculated from measurements taken at 30-min intervals.

Climatic and bioclimatic conditions

To characterize contrasting weather conditions during the study period, namely months with water shortage due to above average air temperature and precipitation depletion and monthly anomalies for air temperature and precipitation (recorded on on-site weather station) were determined as relative to mean climate conditions in the period 1985–2018 [National Oceanic and Atmospheric Administration Agency (NOAA/NCEI/CWC1)].

To describe the distance between the climate of provenance origins and the trial site, a principal component analysis (PCA) of four bioclimatic parameters, namely mean annual temperature, temperature seasonality, annual precipitation, and precipitation seasonality was performed. Climatic parameters for Oleszyce provenance trial (OLE) site as well as for the climate of four beech provenances origin were extracted from BIOCLIM 1.4 (Hijmans et al. 2005) at a spatial resolution of 2.5 arcmin for the period 1970–2000. The variables with the strongest impact on the distribution of beech population and OLE trial site on PCA biplot was identified on the basis of Pearson correlation coefficients. Spatial variability of each climatic parameter within study region was visualized on four bioclimatic maps. On each map, location of trial site as well as for the four beech provenances was marked.

Seasonal SCV dynamics

To describe temporal pattern in SCV, the dendrometer series were fitted with Gompertz functions defined by Rossi et al. (2003) as:

\[ y = a \times \exp \left( -\exp \left( \frac{\beta - k \times t}{k} \right) \right), \]

where \( y \) is the re-scaled daily stem circumference, \( t \) is the time in form of DOY, \( a \) is the upper asymptote, \( \beta \) is the x-axis placement parameter, and \( k \) is the growth rate of the curve. The goodness-of-fit for each curve was assessed using the distribution of their studentized residuals. In our study, we adopted the arbitrary 5% and 95% of the upper asymptote as a threshold for the timings of onset and end of SCV (Van der Maaten et al. 2013), as according to Hennhapl et al. (1965) most of the growth of beech trees takes place during this period. The growth duration was calculated as a difference between end and onset of SCV. The estimated variables were used to determine the effect of year, provenance, and tree (nested within the provenance) on the total variance in
stem circumference variation. General linear models (GLM)
were used with F test for type 3 analysis (Liang and Zeger
1986).

\[ G_{ijk} = \mu + Y_i + P_j + T_k(P_j) + e_{ijk}, \]

where \( G_{ijk} \) is the Gompertz model’s parameter in the \( i \)th year
\((i = 1, \ldots, Y)\) for the \( j \)th provenance \((j = 1, \ldots, P)\) and in the
\( k \)th tree \((k = 1, \ldots, T)\), \( \mu \) is the general mean, \( Y_i \) is the effect
of the \( i \)th year, \( P_j \) is the effect of the \( j \)th provenance, \( T_k(P_j) \) is
the effect of the \( k \)th tree in the \( j \)th provenance, and \( e_{ijk} \) is the
effect of experimental error. Multiple pairwise \( t \) tests were
performed to assess the differences between years. To con-
trol the family wise error rate, which may occur in the mul-
tiple comparison approach, a Holm correction was applied
(Holm 1979). Reduced major axis (RMA) regressions were
fitted to assess the relationships between curve’s parameter
values and the duration of the SCV (Smith 2009). PCA analysis
was applied to investigate the effect of monthly climate param-
eters, mean temperature, and precipitation sum of the grow-
ing season (April–September) on the Gompertz parameters.

All analyses were computed in “R” (R Core Team 2017).
General linear models calculations were done with “car”
package (Fox and Weisberg 2011). Gompertz function fitting
and pairwise \( t \) test were performed with “stats” package (R
Core Team 2017). PCA analyses as well as the biplot were
created with “factoMineR” package (Husson et al. 2015).
RMA regressions were performed using the “smatr” package
(Warton et al. 2012).

Results

Seasonal SCV

SCV were characterized by relatively uniform patterns,
mainly in the provenances 453 and 455 in 2017 (Fig. 2).
The good fitting of the Gompertz equation was confirmed
by the symmetrical distribution of their studentized residu-
als and their respective values. The studentized residuals
were indeed located within the – 2 to 2 range in the 97% of
the cases (Fig S1). Overall, SCV increased slowly in spring
between DOY 120 and 140. A quicker increase was observed
during the first part of summer, mainly in the period ranging
between DOY 160 and 200. After which, the growth rate
of SCV reduced until reaching a plateau. The plateau was
attained in summer, on DOY 220–250.

GLM revealed the significant effect of year on SCV for
all the studied variables (Table 1). No significant influence
was confirmed in terms of provenance, and only partially
(namely, the variables \( a \), \( k \) and end) for tree effect. The
majority of the total variability was explained by either year
(onset and end) or tree \((a \text{ and duration of SCV})\). However,
both effects were equally responsible for the overall vari-
ability of \( k \). Linear regression highlighted not only the sta-
ble and similar relationship between the coefficient \( a \), but
also duration and onset with end of SCV (Fig. 3). However,
as the \( R^2 \) values were lower than 0.5, we can only confirm
these relationships as trends. Together with the later end-
ing of SCV, both upper asymptote and duration increases,
although onset of SCV seems to be marginal to these param-
eters. In turn, for \( k \) and onset with end, the opposite pat-
tern can be observed. That is, together with later onset and
earlier ending of SCV, \( k \) increases. For the end parameter
and to a lesser extent for onset (relationship with \( a \)), points
are more dispersed, mainly for higher asymptotic values.
In turn, onset and end points are highly concentrated around
the regression line. In particular, the largest differences be-
 tween years were observed between 2017 and 2018 (Fig. 4).
Onset parameter of 2018 differed significantly from 2016 to 2017,
while no differences were detected between 2016 and 2017.
In turn, end and upper asymptote in 2017 differed from 2016
to 2018.

Climate-shift effect

Climatic conditions of study period were characterized by
shortage of precipitation, except for June 2018 and Septem-
ber 2017. In respect to the long-term average, warmer condi-
tions were observed in September 2016, March 2017, and
April and August 2018 (Fig. 5). Bioclimatic parameters of
provenance origins and trial site reduced to the two dimen-
sions allowed to detect a provenance cluster between 453
and 455, confirming their similarity in terms of climate

Table 1 Results of generalized linear models to test the
differences in upper asymptote \((a)\), growth rate \((k)\), onset, end
and duration of SCV due to year, provenance and tree with F
test for type 3 analysis

| Source of variation | Year | Provenance | Tree (provenance) |
|---------------------|------|------------|------------------|
|                     | Df   | F  | P   | %   | Df   | F  | P   | %   |
| \( a \)             | 2    | 25.24 | <0.001 | 31 | 3    | 3.09 | 0.055 | 4    | 15  | 4.41 | 0.002 | 65  | 10.97 | 0.93 |
| \( k \)             | 2    | 16.70 | <0.001 | 49 | 3    | 2.21 | 0.125 | 1    | 15  | 2.99 | 0.016 | 50  | 5.03  | 0.86 |
| onset               | 2    | 63.84 | <0.001 | 75 | 3    | 1.11 | 0.3734 | 1    | 15  | 1.65 | 0.161 | 24  | 7.97  | 0.90 |
| end                 | 2    | 4.64  | 0.025  | 64 | 3    | 2.55 | 0.090 | 2    | 15  | 3.11 | 0.014 | 35  | 3.57  | 0.81 |
| duration            | 2    | 12.91 | <0.001 | 48 | 3    | 1.59 | 0.229 | 1    | 15  | 2.47 | 0.038 | 51  | 3.80  | 0.82 |

\( Df \) degrees of freedom, \( F \) test statistic, \( P \) p value, \( R^2 \) coefficient of determination, % variance explained
origin (Fig. 6). Provenances 390 and 451 were located on the periphery of the PC biplot, indicating their distinct position in relation to the provenance cluster and OLE trial site. First principal components (PC1) explained 82.64% of the overall variance and positively correlated ($r > 0.98$) with annual precipitation (bio12) and negatively correlated ($-0.92 < r < -1$) with mean annual temperature and precipitation seasonality (bio1, bio15) (Fig. 6, Table 2). Thus, provenances 390 and 451 differ from OLE study site, mainly in temperature and precipitation seasonality (451), but also mean annual temperature (390).

**Climate–SCV relationship**

PCA of main climatic parameters of growing season reveals that duration, end and the upper asymptote $a$ were positively correlated with August temperature and, at a less extent, with August precipitation. The parameter $k$ showed the same relationships, but with negative correlations (Fig. 7, Table S1). Positive correlation was observed between $k$ and June temperature and April precipitation. Onset was strongly and negatively related to spring (April and May) temperature. Clustering highlighted the dominant effect of between-years variation, while the effect of provenance was marginal.

**Fig. 3** The effect of upper asymptote ($a$), duration of growth (dur) and growth rate ($k$) on onset and end of stem radial displacement. Color code assigned for years (red: 2016, green: 2017, blue: 2018)

**Fig. 4** Pairwise comparisons between years 2016 and 2018 for upper asymptote ($a$), growth rate ($k$), onset, end and duration of SCV

**Fig. 5** Anomalies for monthly air temperature (upper panel) and precipitation (lower panel) for the years 2016–2018 as relative to mean climate conditions in the period 1985–2018
Discussion

The study confirms our hypothesis that the variability between beech trees in stem circumference variation (SCV) is higher than that between provenances. Moreover, end of SCV affects positively the duration and amplitude of SCV and affects negatively the growth rate. Spring temperature was the main climatic driver of the onset, while temperature and precipitation of summer months influenced end, duration, and amplitude of SCV. Accordingly, the relatively dry and warm conditions occurring in spring 2018 advanced the onset in SCV.

Table 2 Pearson’s correlation coefficients between climatic variables and the first two major components and contribution of variables in principal components

| Bioclimatic variables | Pearson’s correlation | Contribution in PCs (%) |
|-----------------------|-----------------------|-------------------------|
|                       | PC1       | PC2       | PC1       | PC2       |
| bio1                  | 0.92      | 0.37      | 26.01     | 19.92     |
| bio4                  | 0.69      | 0.73      | 14.32     | 77.1      |
| bio12                 | 0.98      | 0.14      | 29.46     | 2.93      |
| bio15                 | 1         | 0.02      | 30.2      | 0.05      |

Genetic effect in beech populations

Intra-specific gradients of beech are commonly available in the literature (Stojnić et al. 2017; Cocozza et al. 2016; Bolte et al. 2016; Ježík et al. 2016; Buhk et al. 2016; Harter et al. 2015). However, the majority of them focus on the southern, western, and/or northern margins of beech distribution range. Only a few of them have included populations from the northern or eastern distribution range and, when included, only one marginal population was analyzed, thus preventing to assess the phenotypic variability for representative groups (Koláf et al. 2017; Kurjak et al. 2018; Weigel et al. 2018; Rose et al. 2009). Our study covered northern part of the south-eastern boundary of the biogeographic range of beech, revealing that intra-population variability oversteps inter-population variability of seasonal SCV, regardless of dry or wet growing seasons (Table 1). Despite the geographic isolation of a provenance, named 390, it seems likely that gene flow between marginal and central distribution range is able to balance the isolation-by-distance effect in genetic structure (Leonardi et al. 2012). Thus, relatively low differences between population variability in seasonal SCV seem to correspond with the previous studies on beech marginal populations (Aranda et al. 2017; Stojnić et al. 2017). Although Stojnić et al. (2017)
confirmed significant differences between provenances in resistance to embolism, they concerned differences between marginal populations from marginal sites covering a larger geographical and climatical area than the populations analyzed in this study.

**Climate-transfer effect**

Due to the climate-transfer-related constrains in studying provenance adaptability on common garden experiments, resulting from possible maladaptation of populations or diminishing effect of marginal site conditions (Klisz et al. 2018, 2019a), we applied multi-dimensional analysis of bioclimatic parameters. Two-object clusters (provenances 453 and 455), located closest to the provenance trial, would suggest a better adaptation of these two populations to the growing conditions than the provenances 390 and 451, which are climatically more distant. However, results of general linear models (Table 1) provide no basis for such an interpretation. According to Stojnić et al. (2013), beech populations from relatively moist environments are able to cope with drier conditions. Hence, provenance 451 from clearly wetter but also colder conditions (Table 2, Fig. S2) might seem to be predisposed to a plastic reaction in the conditions of OLE site. While provenance 390, from warmer but also similar in terms of annual precipitation conditions, would suffer from late frost due to significantly different temperature seasonality (Table 2; Kramer et al. 2017). Despite the clear provenance differentiation in climate of provenance origin as well as climate transfer (difference in bioclimatic conditions between the provenances and provenance trial), the effect of provenance does not seem to play a role in SCV (Table 1). These results are consistent with previous studies covering a wider group of beech provenance, where the between-provenances variation in stem circumference increase was diminished due to high within-provenance variation (Ježík et al. 2016). Such a high between-individuals variability was widely reported in studies on natural populations and common garden experiments; however, they mainly concerned inter-annual growth variation (Stojnić et al. 2013; Weigel et al. 2018). Indeed, they rarely included more than six trees of a given population; therefore they may not fully represent within-provenance phenotypic variation.

**Inter-annual SCV in relations to climate**

Weather conditions affected the variation in stem size, as reflected in the onset, end and upper asymptote of the Gompertz functions describing seasonal pattern in SCV. Significant differences between years in onset of SCV along with the opposite trends in temperature anomalies of March, April, and May correspond with recent studies on xylem formation in beech (Prislan et al. 2019). The authors observed indeed positive correlations between temperatures of March–May and the spring phenological phases in Slovenia. In our study, strong differences in onset between 2017 and 2018 and between 2017 and 2016 are not reflected in the precipitation anomalies. The above findings are in accordance with recent studies on cambial phenology, confirming that precipitation is not a limiting factor during xylogenesis of beech within its natural distribution (Prislan et al. 2018).

A distinct trend between end of SCV and the upper asymptote, which could be considered as a proxy of the radial expansion of the stem, seems to be consistent with studies on xylem formation in beech (Ćufar et al. 2008; Vavrčík et al. 2013; Semeniuc et al. 2014). Nevertheless, the reversible shrinkage and expansion of the stem related to the changes in water content of outermost tissues should be taken carefully into account, when SCV amplitude is interpreted (Zweifel 2016). According to the above-mentioned studies, maximum cell production takes place between the end of May and July. Therefore, later end of SCV may indicate extension of duration of cell division and cell enlargement. As cell enlargement seems to be related to July precipitation (Ćufar et al. 2008), the differences observed for the end in SCV between 2017 and the other 2 years may be explained by the divergent pattern in summer precipitations. Still, the range of end values in the season 2018 (relationship with a) remains difficult to explain based on the climate parameters.

Duration of SCV is mainly dependent on the end, and not onset, in SCV, which is partly reflected in the period of maximum cell production (Ćufar et al. 2008; Vavrčík et al. 2013; Semeniuc et al. 2014). In contrast, growth rate manifests an opposite, with later onset and earlier end observed with faster growth rate (Fig. 3). These relationships suggest that growth rate increases with shorter durations of SCV, which suggest the opposite to the compensatory mechanism described by Balducci et al. (2016). The relationships between climate anomalies and Gompertz functions parameters are consistent with the multi-dimensional analysis of monthly climate and SCV parameters (Fig. 7, Table S1). The same relationships between climate and SCV parameters were observed in other studies on changes in intra-annual stem diameter of beech, regardless of study period, tree age, and study site locations, (Ježík et al. 2011, 2016; Van der Maaten et al. 2013). However, the high sensitivity to climate anomalies may result from the young age of the trees or/and prolonged vegetation periods reported for young trees (Trouillier et al. 2019). Thus, during our study period 2016–2018, the spring and summer temperatures and to a lesser extent summer precipitation seem to be the common climatic drivers of stem variation for all beech provenances.
Conclusions

Our study investigated the effect of provenance on intra-annual stem circumference variation (SCV) under a beech common garden experiment. It was suggested that the variability in stem circumference variation within provenances masked the variation between provenances. Our study revealed that within marginal beech populations, the intra-annual variability in stem size was higher within than between populations. Spring temperature as well as summer temperature and precipitation are the main climatic drivers of the onset, end, and amplitude of SCV. This suggests that intra-provenance variation in stem size may become more pronounced with the increase in the frequency of climate anomalies expected in the next decades. Considering these conditions, individual-based rather than population-based approach should be applied when breeding marginal beech populations.

Author contribution statement MK and SJ were responsible for data collection; MK, VB, and SR performed all statistical analysis; MK wrote the manuscript; MK, VB, SR, HM, and SJ were involved in text corrections. All the authors read and approved the final manuscript.

Acknowledgements The study was funded by the State Forests National Forest Holding, as part of research project BLP-375. This paper was developed under a granted scholarship within Scholarship Fund of the Forest Research Institute, pursuant to the decision of the Head of the Institute dated 17th October, 2018 (based on an Agreement concluded on 18th October, 2018).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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