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ORIGINAL ARTICLE

Different patterns of inter-annual variability in mean vessel area and tree-ring widths of beech from provenance trials in Slovenia and Hungary

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Abstract

Key message **Studied beech provenances showed different patterns of inter-annual variability in mean vessel area and ring widths, indicating influence of intraspecific variability and diverse environment on hydraulic conductivity and carbon storage potential.**

Abstract International provenance trials of ecologically and economically important tree species are crucial to deciphering the influence of environmental factors and intraspecific variability on tree growth and performance under climate change to guide assisted gene flow and assisted migration of tree provenances and species. In this context, we compared inter-annual trends in tree-ring widths (carbon sequestration potential) and vessel characteristics (conductivity optimisation) of four beech provenances in two international provenance trials, one in Slovenia (Kamenski hrib, a core beech growing site) and one in Hungary (Bucsuta, a marginal beech site) in 2009–2019. We found different patterns of inter-annual variability in mean vessel area and tree-ring widths among provenances and sites, pointing to diverse genetic background and environmental influence on these two wood-anatomical traits. The average values of the vessel area varied less between provenances at Kamenski hrib than at Bucsuta. Weather conditions differently affected tree-ring width and mean vessel area. Furthermore, the length of the period of response of vessel area to the analysed weather conditions differed in summer and winter periods. The differences in the mean vessel area within the tree ring were more pronounced in the weather-wise extreme years, regardless of the provenance. Consistent with previous studies, we confirmed that site conditions affect the climate sensitivity of trees, which is more pronounced at marginal sites or in extreme years. The findings on how different environmental conditions affect the radial growth of young beech trees of different origin are very important for future forest management.

Keywords *Fagus sylvatica* · Quantitative wood anatomy · Common gardens · Intraspecific variation · Juvenile period · Weather conditions

Introduction

Various tree-ring proxies (i.e., quantitative wood anatomy and stable carbon isotopes) permanently store past tree response to climate variability and extremes, as well as forest carbon and water dynamics; long-lived trees have therefore become a globally important high-resolution archive of environmental information (Reichstein et al. 2013; Wilmking et al. 2020). Since climate change and climate-associated severe events will clearly influence tree growth and competitive performance (Allen et al. 2010; Keenan 2015), tree response to these changes is particularly relevant for ecologically and economically important European tree species,

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such as common beech (*Fagus sylvatica* L.) (Pretzsch et al. 2015).

Due to substantial genetic diversity and phenotypic plasticity, beech has successfully adapted to various growing conditions by adjusting different phenological traits and growth patterns within its wide distribution range (Stojnić et al. 2016; Vitasse et al. 2011). Compared to natural environments, fairly homogeneous within-trial growing conditions are better suited for provenance tests in attempt to disentangle environmental from genetic controls on functional traits and ultimately on adaptability of trees to climate change (Alberto et al. 2013; Sáenz-Romero et al. 2019; von Wühlisch 2004). Like other growth patterns in the tree, radial growth also responds to different environmental conditions, which is reflected in year-to-year variations in tree-ring widths and wood anatomy (Eilmann et al. 2014; Stojnic et al. 2013). However, environmental and genetic influences on tree-ring widths and vessel features may differ and are not yet fully explained. While several studies found a significant influence of the environment on tree-ring widths in beech (Eilmann et al. 2014; Krajnc et al. 2022; Stojnic et al. 2013), other studies reported that they are primarily controlled by genetic factors (Ježík et al. 2016; Klisz et al. 2020). Furthermore, Eilmann et al. (2014) observed that vessel characteristics are more genetically controlled, suggesting a provenance-specific adaptation of water transport. These contradictory results show that further studies are needed to understand the role of different factors in secondary tissue development, especially because environmental and genetic factors may differ between sites with adverse growing conditions. In Norway spruce, for example, it has been shown that the environmental influence on radial growth of trees at marginal sites predominates, regardless of the tree origin (Klisz et al. 2019). The authors concluded that site conditions should be taken into account in the climate sensitivity studies of different provenances in the trials.

The great majority of past investigations of vessel characteristics have been performed on an annual level (e.g., Eilmann et al. 2014; Stojnic et al. 2013), while lately the focus has been on intra- and inter-annual variability of vessel traits (Arnič et al. 2021; Miranda et al. 2022). In combination with cambial phenology, these analyses allow a more detailed insight at the seasonal level into the influence of various factors on wood structure (Prislan et al. 2018). For example, dry weather conditions have been shown to affect beech wood structure, which is reflected in a change from a diffuse-porous to a semi-ring porous structure (Arnič et al. 2021). Furthermore, studies of various beech provenances have revealed that predicted climate change will affect tree-ring widths and wood structure in beech; however, the response is expected to be provenance- and site-specific (Eilmann et al. 2014). In those regions in Europe for which climate scenarios predict an increase in temperature and a change in precipitation amount or/and distribution, planting more drought-tolerant provenances would minimize the effect of drought on the future growth of beech forests (Pachauri et al. 2014). Because of the plastic response of intra-annual vessel characteristics to adverse weather conditions, the same species can show strikingly different survival and growth rates, as demonstrated by the results of provenance trials. However, there are often trade-offs between xylem safety and water-transport efficiency (Gömöry and Paule 2011; O'Brien et al. 2007; Sebastian-Azcona et al. 2019).

In Slovenia, common beech is the dominant tree species in most forest stands, representing one-third of the wood stock (Slovenia Forest Service 2022), while in Hungary it represents only 6.6% of the forest cover (Hungarian National Forest Inventory 2022). Its proportion and distribution are projected to change in the future, so the possible effect of climate change and extreme weather events (late spring frost, summer drought) on the future productivity and survival potential of different beech provenances is of great ecological and economic interest for both countries (Gálos and Führer 2018; Matyas et al. 2009; Poljanec et al. 2010; Prislan et al. 2019). In this study, we compared trends in year-to-year variations in tree-ring widths and vessel characteristics in four beech provenances at two sites of international beech provenance trials: Slovenia and Hungary. Previous studies (Sass and Eckstein 1995; Diaconu et al. 2016; Arnič et al. 2021) showed that mean vessel area is the only vessel trait that shows no relationship with tree-ring width, suggesting different external and internal control on their formation. Consequently, they contain different climatic information. Thus, associations between weather and selected wood-anatomical variables were evaluated. In addition, we assessed the plasticity of radial growth (in terms of tree-ring widths) and vessel formation (in terms of intra-annual trends of vessel area) of the selected four beech provenances under contrasting weather conditions (wet year 2014 and dry year 2017). We set the following hypotheses: (H1) There are differences in inter-annual trends in tree-ring widths and vessel characteristics between the selected beech provenances at Kamenski hrib and Bucsuta; (H2) Extreme weather conditions affect tree-ring widths and mean vessel area regardless of provenance/site; (H3) The response of an individual provenance to weather conditions may be similar in the two provenance trials. However, the strength of the weather signal in tree-ring widths and vessel area may differ at Kamenski hrib (a site optimal for beech growth) and at Bucsuta (a dry site, marginal for beech growth).

Material and methods

Characteristics of study sites, provenance trails and provenances

The research was carried out in two international beech provenance trials, which were established in 1998: Kamenski hrib in Slovenia and Bucsuta in Hungary (von Wuehlisch et al. 1997). The environmental conditions at the two sites differ. In general, Kamenski hrib is relatively well-supplied with precipitation, and provides optimal growth conditions for beech. Bucsuta is drier, with approximately half the amount of precipitation of the Slovene site and is at the extreme edge of where beech occurs naturally. More detailed information on the characteristics of the two sites is provided in Table 1 and Fig. 1.

For the analyses, we selected four provenances; two from Slovenia, which differ in the timing of leaf development, and two provenances from contrasting environments in Europe (i.e., Belgium and the Czech Republic) (Table 2). Namely, in diffuse-porous beech, the timing of leaf development in spring is closely related to stem cambial reactivation and consequently to the timing of initial vessel formation (Marchand et al. 2020a). The weather conditions of the original sites served for characterizing the adaptation of provenances before the collection of seeds for the experiment (Fig. 1).

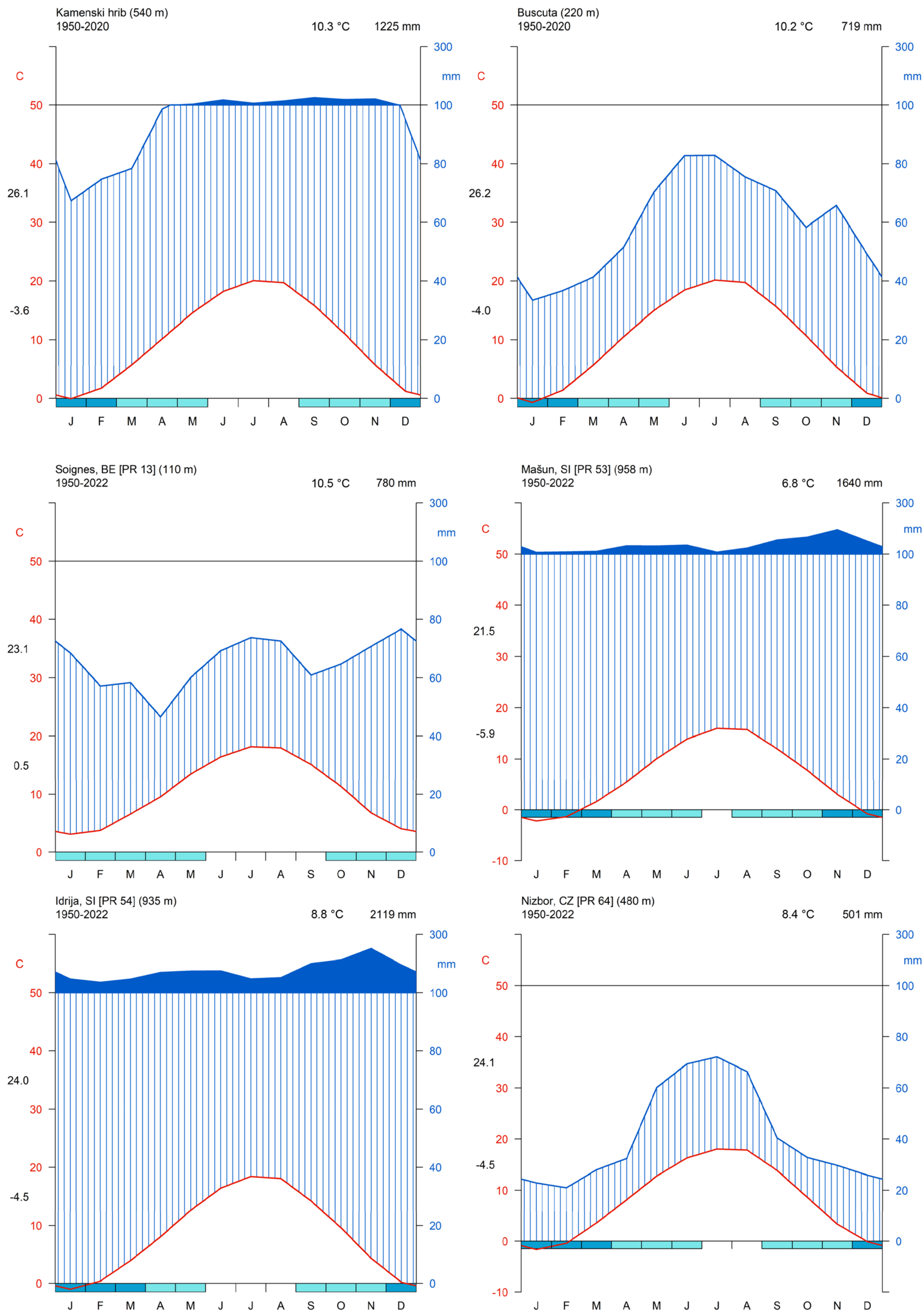
Sampling, tree-ring measurements and vessel analysis

Sampling was done in the fall of 2019 after the cessation of the growing season. For each selected provenance, we chose 13 dominant trees, which were 21 years old at both sites, with a diameter at 1.3 m above the ground (DBH) of 10.5–11.5 cm and a height of 13.5–15.0 m at Kamenski hrib and a DBH of 10.5–12.5 cm and a height of 9.5–11.0 m at Bucsuta (Krajnc et al. 2022). We took one increment core from the stem of each tree 1.3 m above the ground, which was used for measurements of tree-ring width and vessel analyses for the period 2009–2019. The cores for tree-ring width measurements were prepared in the Laboratory for Dendrochronology at the Slovenian Forestry Institute according to standard dendrochronological procedures; the cores were dried, glued into holders, sanded and an image of the core was recorded using the Atrics system (Levanič 2007). The tree-ring widths were measured using CooRecorder software (Cybis Elektronik and Data AB, Saltsjöbaden, Sweden) and further analyzed using robust mean chronologies from the R package dplR (Bunn 2008).

Table 1 Characteristics of both sites

Provenance trial	Country	Latitude	Longitude	Elevation [m]	Mean annual T [°C]	T_{Jan} [°C]	T_{Jul} [°C]	Annual sum of P [mm]	P range [mm]	Soil characteristics
Kamenski hrib	Slovenia	45° 47′ 46″ N	15° 02′ 50″ E	540	11.3	− 3.0	28	1260	869–1636	Deep eutric cambisols on haplic luvisols, limestone bedrock
Bucsuta	Hungary	46° 35′ 00″ N	16° 51′ 00″ E	220	11.7	− 2.3	28	736	476–965	Deep brown forest soil, loess bedrock

Weather data for Kamenski hrib and Bucsuta are for the period 2009–2019: mean monthly temperature (T) (minimum, mean and maximum) and monthly sum of precipitation (P)



Kamenski hrib (540 m)
1950-2020
10.3 °C
1225 mm
26.1
-3.6
Buscuta (220 m)
1950-2020
10.2 °C
719 mm
26.2
-4.0
Soignes, BE [PR 13] (110 m)
1950-2022
10.5 °C
780 mm
23.1
0.5
Mašun, SI [PR 53] (958 m)
1950-2022
6.8 °C
1640 mm
21.5
-5.9
Idrija, SI [PR 54] (935 m)
1950-2022
8.8 °C
2119 mm
24.0
-4.5
Nizbor, CZ [PR 64] (480 m)
1950-2022
8.4 °C
501 mm
24.1
-4.5
C
mm
J F M A M J J A S O N D

◀**Fig. 1** Walter–Lieth climate diagrams for Kamenski hrib and Bucsuta calculated for the period 1950–2020. The values at the top of the diagrams show the long-term annual mean temperature and the total amount of precipitation. The value at the top left of the temperature axis represents the mean value of the average daily maximum temperature of the warmest month; the value at the bottom of the same axis represents the mean value of the average daily minimum temperature of the coldest month. The horizontal black line at 100 mm and 50 °C illustrates the threshold value above which precipitation scales by a factor of 10. The blue line represents the annual cycle of monthly precipitation. The red line shows the annual cycle of the monthly mean temperature. The area with the blue shaded lines illustrates the humid conditions below the threshold. The blue filled area shows the humid conditions above the threshold (excess water)

Quantitative vessel analysis was performed on six cores per provenance and per site. The procedure of core preparation for vessel analysis on cross-sections under a light microscope is described in detail by Arnič et al. (2021). Briefly, cores were split into segments of similar length (3–4 cm) in such a way that the edge two tree rings were cut diagonally so that information about their width and structure was not lost. From the segments, a 15–20 µm thick transverse section was cut from each segment with a WSL sledge microtome using OLFA-80 × 9 mm spare blades. The sections were then treated with bleaching solution (5–15% chlorine content) to remove sawdust from the cell lumina and to improve the staining intensity in the subsequent staining with a safranin/Astra-blue water mixture. High-resolution images (0.514 pixel/1 µm) of the sections were prepared using a Leica DM 4000 B light microscope (Leica Microsystems, Wetzlar, Germany) at 50 × magnification, a Leica DFC 280 digital camera (Leica Microsystems, Wetzlar, Germany), and LAS image analysis software (Leica Application Suite). Image-sequences of the tree rings were captured with at least 25% of the overlapping area and then merged. Panoramic pictures were then processed with Image-Pro Plus 7.1 and ROXAS (v3.0.437) image analysis software to obtain vessel features (von Arx and Carrer 2014). For wood-anatomical analysis, the chronologies of tree-ring widths and mean vessel area were created on an annual scale. Furthermore, to assess the intra-annual variability of vessel area (so-called tracheograms; for details, see Abrantes et al. 2012) its trend was created in a relative scale from 0 to 100% of the tree-ring width (Fig. 2). Tracheograms were then smoothed using the general additive model (GAM), which were then used in the Kolmogorov–Smirnov test to infer statistically significant differences in the intra-annual MVA distribution between provenances.

Weather data and SPEI calculation

Weather data (daily mean, minimum and maximum air temperature and sums of precipitation) data were downloaded as netCDF files from http://surfobs.climate.copernicus.eu/dataaccess/access_eobs.php as described in Jevšenak (2019). We used the E-OBS version 25.0e on a 0.1 degree regular grid that was released in April 2022 and covers the time span from 1 January 1950 to 31 December 2021 (Cornes et al. 2018). Using the knnLookup() function from the SearchTrees Rpackage (Becker 2012); the closest grid point was located in the E-OBS dataset for each individual site, and weather data were extracted. To study weather-growth relationships on daily and monthly scales, mean temperature and sums of precipitation data were used. In addition, downloaded minimum and maximum air temperature data were used to calculate daily SPEI series (Fig. 3) (Vicente-Serrano et al. 2010; Beguería and Vicente-Serrano 2017). An additional methodological explanation can be found in Jevšenak (2019) and Klisz et al (2022).

Correlation analysis

Weather-growth correlations were analyzed using the *daily_response()* function from the dendroTools R package (Jevšenak 2020; Jevšenak and Levanič 2018), whereby day-wise aggregated correlations were calculated using 1000 bootstrap samples considering all windows between 7 and 60 days from the previous June to the current October to assess the temporal effects of the climatic response (e.g., Arnič et al. 2021). Kendall-Tau correlation coefficients were calculated for the 2009–2019 common period and only those with $p < 0.05$ were used to infer the relationship of weather and tree-ring widths and mean vessel area.

Results

Tree-ring width and vessel area

For the period 2009–2019, differences in tree-ring width between provenances were generally small, with average values ranging between 3.0 and 4.0 mm. A greater inter-provenance variability in the tree-ring widths was observed at Bucsuta. However, deviations from the average values of the tree-ring width in the two contrasted years, 2014 and 2017, were visible at both sites (Fig. 4). At Kamenski hrib, in the wet year 2014, we found the largest increase in tree-ring widths in PR13 (Soignes, BE; 4.7 mm) and PR64 (Nizbor, CZ; 4.6 mm), while in the Slovene provenance PR53 (Mašun) the increase was 3.4 mm. At Bucsuta, we observed the largest 2014 increment increase in PR64 (5.4 mm), and the smallest in PR54 of Slovene origin (Idrija, SI; 3.2 mm). In the dry year of 2017, the largest increment decrease was observed at Kamenski hrib in PR13 (2.5 mm), while other provenances had a comparable tree-ring width (1.6–1.7 mm). At Bucsuta, we found the largest annual decrease in PR54

Table 2 Weather conditions at the original sites and flushing time of the selected beech provenances

Code	Provenance	Elevation [m]	Flushing time	Mean annual temperature [°C]	Annual sum of precipitation [mm]
PR13	Soignes, BE	110	Late	9.4	835
PR53	Mašun, SI	958	Intermediate	6.4	1609
PR54	Idrija, SI	935	Late	8.4	2090
PR64	Nizbor, CZ	480	Intermediate	8.5	500

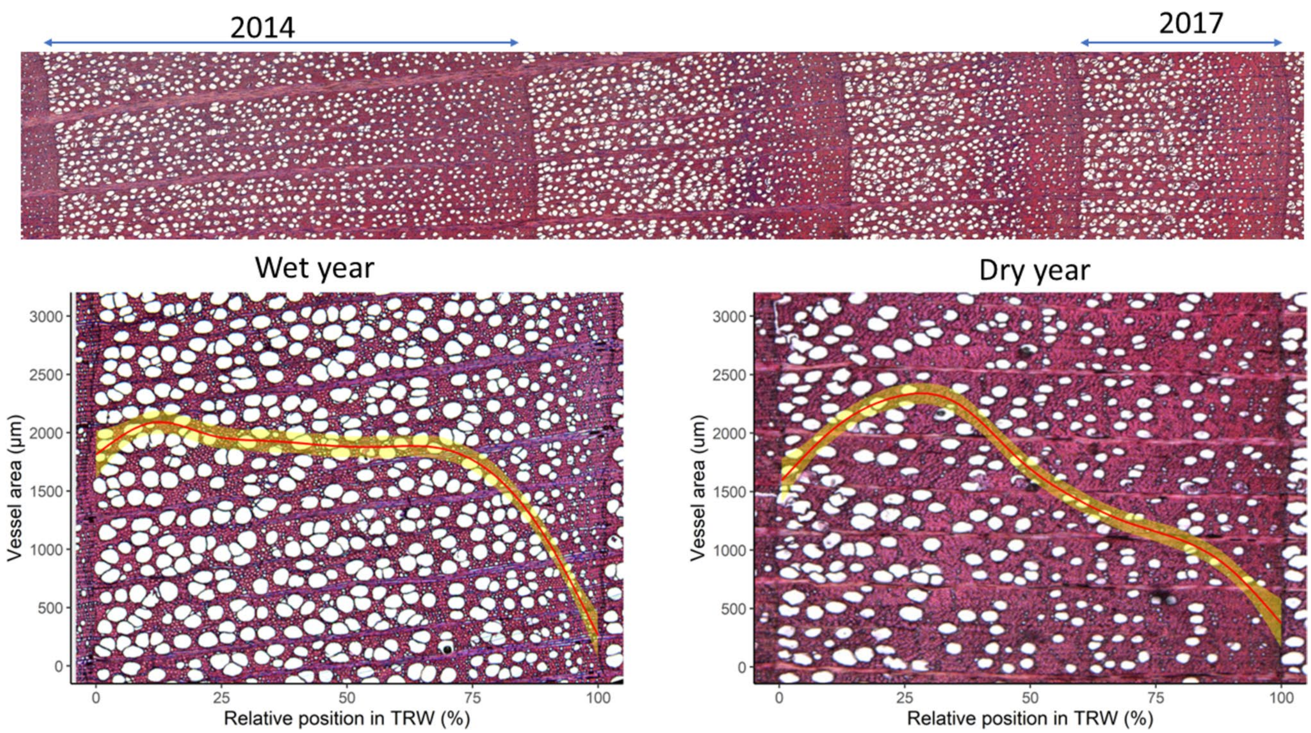


Fig. 2 An example of variability in widths of annual xylem increments and wood structure in beech in years with contrasting weather conditions. *TRW* tree-ring width

(3.0 mm), while the other three provenances had a decrease of from 2.7–2.8 mm.

The inter-annual variability in the mean vessel area showed a different trend than the tree-ring width among provenances and sites (Fig. 4). In the period 2009–2019, the provenance variability in the mean values of vessel area was less expressed at Kamenski hrib than at the Bucsuta site. Similarly, the inter-annual variability in the mean values of vessel area within an individual provenance was smaller at Kamenski hrib. Regardless of provenance, the mean values of vessel area generally increased between 2011 and 2014 at Bucsuta, while at Kamenski hrib the inter-provenance variability in the values was small in the period 2010–2016 but increased after 2016. At Kamenski hrib, the mean values of vessel area were highest at PR13 (1460 µm^2) and lowest at PR54 (1270 µm^2). The values of the extreme years 2014 (wet) and 2017 (dry) that we examined in more detail showed no deviations of 2014 values from the values in the remaining years. In contrast, in 2017, a drop in the values was recorded for all provenances, with the lowest values found for the two Slovene provenances PR53 and PR54 (Fig. 4). At Bucsuta, the mean values of vessel area were the highest in PR64 (1430 µm^2) and the lowest in PR54 (1103 µm^2). In 2014, an increase in the values was detected in all cases, whereby the values of Czech provenance PR64 stood out significantly. In 2017, all provenances showed a decrease in the mean vessel area; however, none of the provenances exceeded the minimum values reached in another dry year, 2011 (Fig. 3). Otherwise, among the selected provenances, the lowest values in 2017 were found for Slovene PR54 (1057 µm^2) and Belgian provenances (1135 µm^2).

The seasonal trend of vessel area within the tree ring for the selected beech provenances is shown in Fig. 5. The vessel-area values within the tree ring were generally

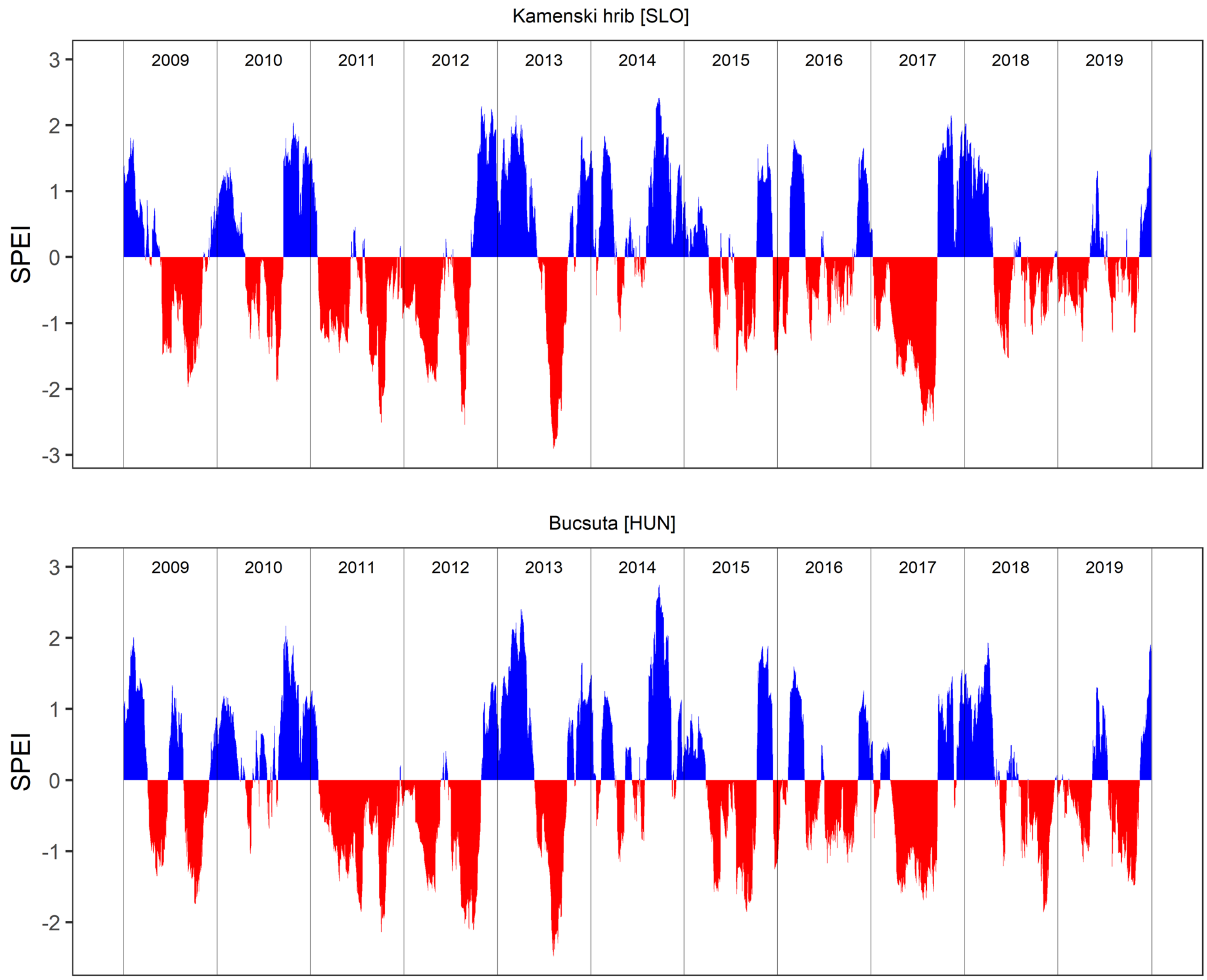


Fig. 3 Daily SPEI series for the two sampling locations, Kamenski hrib and Bucsuta, calculated for the period 2009–2019

higher in the first half of the tree ring than in the second half, whereby the smallest values were found at the growth ring boundary. In the initial part of the tree ring, the maximum values were not reached at the growth ring boundary, but the values increased to 15–25% of the final-ring width, when they reached their maximum; the values then began gradually to decrease. In PR13 and PR54, the intra-annual variation of vessel area was always larger at Kamenski hrib than at Bucsuta. In PR53, this trend was the same in the case of mean values for the entire study period, while in extreme years 2014 and 2017, the mean vessel values within the tree ring were larger at Bucsuta. In PR64 at Bucsuta, however, the intra-annual variation of vessel area was generally larger in the first quarter of the tree ring, including in the two extreme years (Fig. 5). The maximum values of mean vessel area for the period 2009–2019 were recorded at the Bucsuta site for PR64 (around 1850 µm) and at Kamenski hrib for PR13 (around 1800 µm). The latter provenance had the lowest values at the Bucsuta site (around 1450 µm).

In addition, weather conditions greatly affected the vessel dimensions, especially in the extreme years (2014 and 2017), as can be seen from one example of the variability in structure of tree rings in beech (Fig. 2). Regardless of provenance and site, vessel area increased slightly in the initial part of the tree ring in the case of above average rainfall. The vessel area then remained relatively constant, up to 60–80% of the final-ring width, followed by a rapid drop in the terminal part of the tree ring. In the case of the dry year 2017, the diffuse-porous structure of beech wood changed to semi-ring porous; vessel area increased quickly in the initial part of the tree ring and reached the maximum at 25% of the final-ring width, followed by a rapid decline in the vessel area (Figs. 2 and 5).

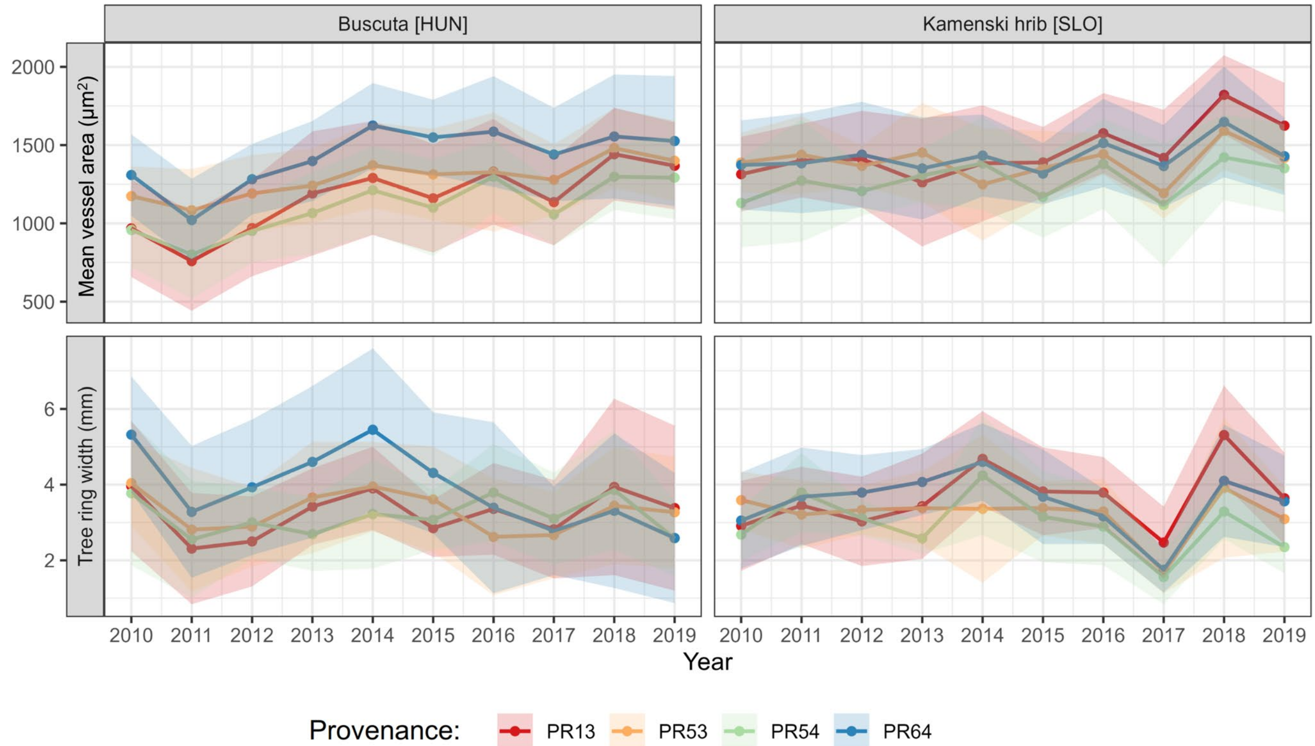


Fig. 4 Tree-ring width and mean vessel area of selected beech provenances (PR13—Soignes, PR53—Mašun, PR54—Idrija, PR64—Nizbor) in the period 2009–2019; *PR* provenance. The vertical lines indicate the mean values, while the dashed vertical lines indicate the standard deviation from the mean value

Relationship between weather variables and tree-ring widths/vessel area

Different weather drivers were found to correlate with the tree-ring widths and/or mean vessel area. Differences were also found between the selected provenances and the two sites (Figs. 6 and 7). At Kamenski hrib, the year-to-year variability of tree-ring width was generally more related to temperature than to precipitation for all provenances. All provenances generally showed a positive response to winter maximum (not PR53) and minimum temperature. A negative response to summer maximum and minimum temperature was the most expressed in PR54, but noticed also in PR53 and PR64 (Fig. 6). In addition, a positive correlation between tree-ring width and minimum temperature in April and May, at the onset of the growing season, was found for PR53, and a negative correlation with maximum temperature in February and March for PR53. Furthermore, a positive correlation between tree-ring width and winter sum of precipitation was observed in PR13, PR53 and PR64, and with the summer sum of precipitation for PR13 and PR54, as reflected also in SPEI. At Bucsuta, less strong response of tree-ring width to weather conditions was found for all provenances. A positive response of tree-ring width to winter maximum temperature was found for PR13 and PR54, and a negative response to June maximum temperature for PR13, PR53 and PR64 (also with minimum temperature). A positive response of tree-ring width with sum of precipitation was found in April in PR53, and in summer in PR13 (also with SPEI) and PR54.

For vessel area, the weather response differed among the provenances at Kamenski hrib while at Bucsuta it was fairly uniform (Fig. 7). At Kamenski hrib, in PR13 maximum and minimum temperature in June affected vessel area. In PR53, a positive correlation between mean vessel area and March–April maximum temperature (at the onset of the growing season) was found. In PR54, winter maximum and minimum temperature positively affected mean vessel area, as well as minimum April temperature. A negative response of mean vessel area to summer maximum temperature was noted. Also, a positive response with summer sum of precipitation/SPEI and mean vessel area was found in PR54. In PR64, a negative correlation of mean vessel area with minimum temperature in the previous autumn and a positive correlation with minimum April temperature was detected. In addition, a positive response of mean vessel area with winter and summer sum of precipitation was found. Thus, at Bucsuta, all provenances exhibited positive correlations with previous autumn and winter temperature as well as with winter and summer sum of precipitation. In addition, they

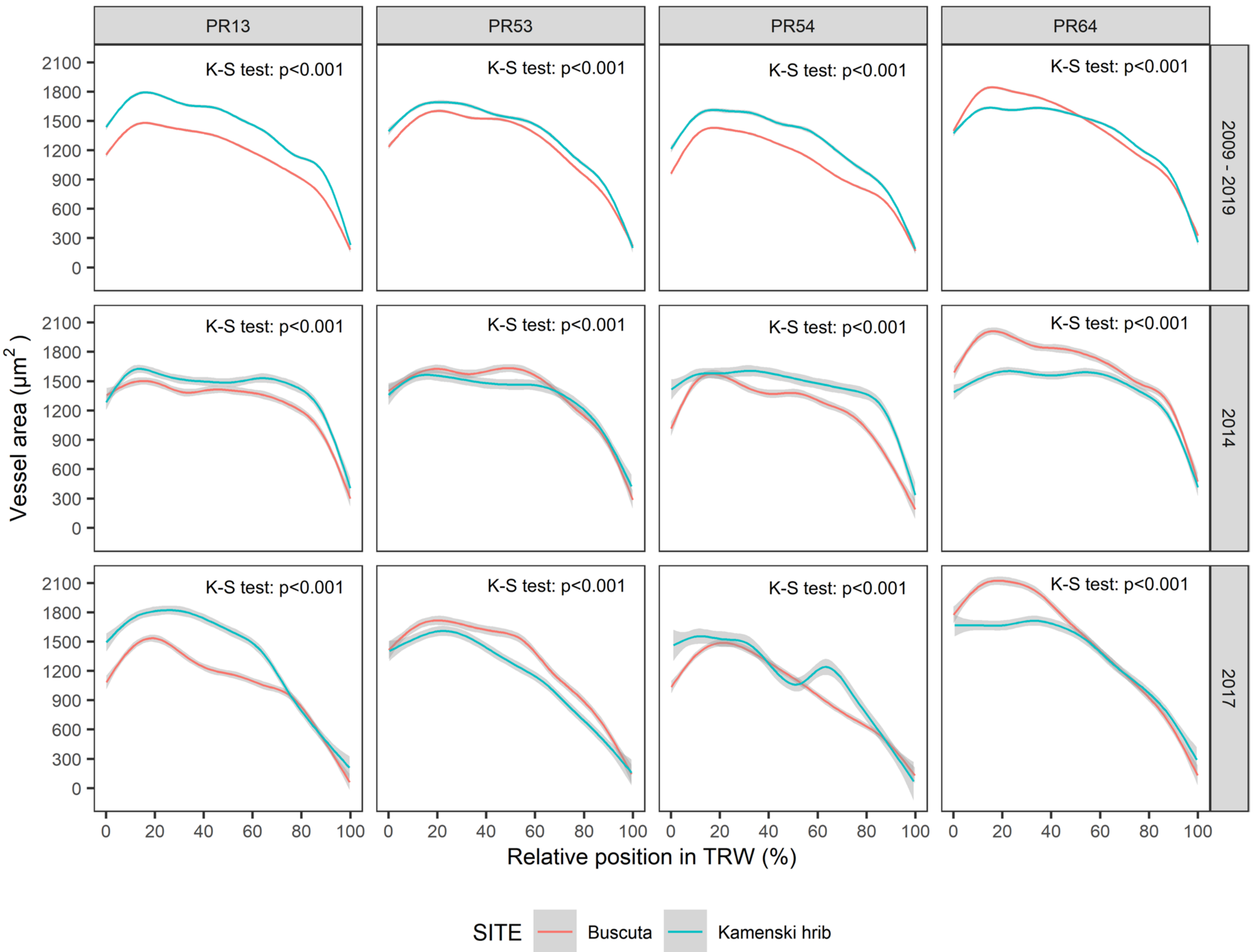


Fig. 5 Seasonal trend of vessel area within the tree ring (tracheograms) in selected beech provenances (PR13—Soignes, PR53—Mašun, PR54—Idrija, PR64—Nizbor) at Kamenski hrib (blue line) and Bucsuta (red line). The trends are shown for the entire period 2009–2019 and separately for the wet year 2014 and the dry year 2017. The lines represent the mean values of the measurements, and the grey shaded area represents the standard error. The differences between general additive model (GAM) trends were tested by the Kolmogorov–Smirnov test. *TRW* tree-ring width

showed a positive and negative response to summer minimum and maximum temperature, respectively.

Discussion

The study confirmed the first two hypotheses, while the third hypothesis was rejected. Differences were thus found in inter-annual trends in tree-ring widths and intra-annual variations of mean vessel area among the four selected beech provenances at Kamenski hrib, a site optimal for beech growth, and Bucsuta, a dry site marginal for beech (H1). The results point to diverse genetic background and environmental influence on these two wood anatomical traits. The average values of the vessel area varied less between provenances at Kamenski hrib than at Bucsuta. Weather conditions differently affected tree-ring width and mean vessel area at both sites. The length of the period of response of vessel area to the analysed weather conditions differed in summer and winter periods. Furthermore, the effects of more pronounced weather conditions, i.e., wet year 2014 and dry year 2017, affected tree-ring widths and mean vessel area regardless of provenance and site (H2). In 2017 (dry year) and 2014 (wet year), the vessel size began to decrease at ca. 25% and 60–80% of the tree-ring width, respectively. Generally, wet conditions promoted tree-ring widths and vessel size, while the dry year negatively affected both wood-anatomical characteristics. Contrary to our expectations (H3), the within-provenance response to weather conditions, in terms of tree-ring width and vessel size, differed at Kamenski hrib and Bucsuta. At Kamenski hrib, a uniform inter-provenance response to

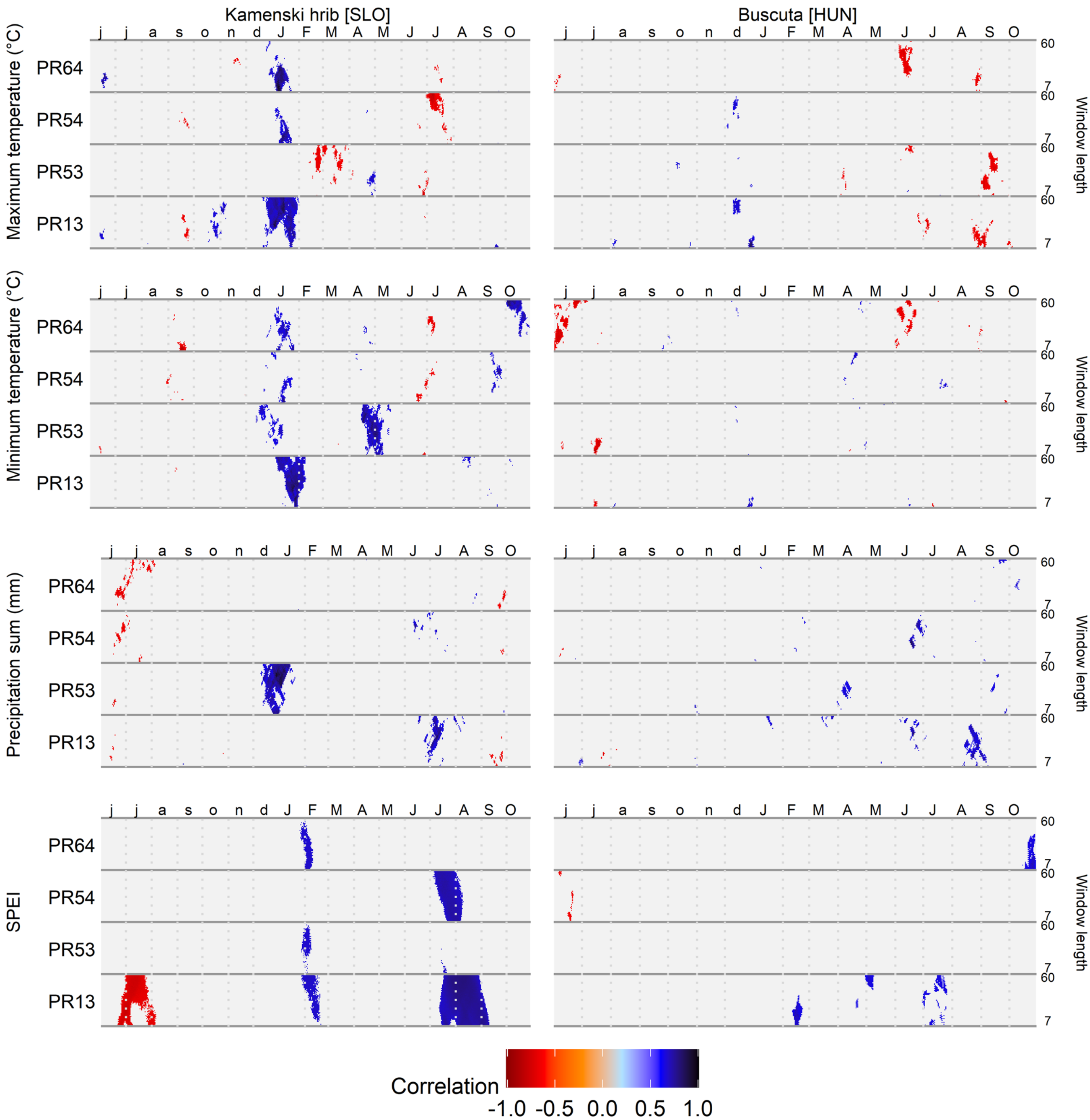


Fig. 6 Correlations between standardized tree-ring width chronologies and maximum and minimum daily temperature, daily precipitation sums of selected beech provenances at Kamenski hrib (left) and Bucsuta (right) in the 2009–2019. We used a time window span of between 7 and 60 days. We show only significant correlations ($p < 0.05$) between the pairs of mean vessel area and aggregated daily weather data. Lowercase letters are abbreviations for the months of the previous year, uppercase letters for the months of the current year. Dashed lines delimit the months

weather conditions was found for tree-ring widths, while at Bucsuta for mean vessel area. We confirmed that site conditions affect the climate sensitivity of trees, which is more pronounced at marginal sites or in extreme years.

Inter-provenance differences in tree-ring width and vessel area

As already reported in our previous paper (Krajnc et al.

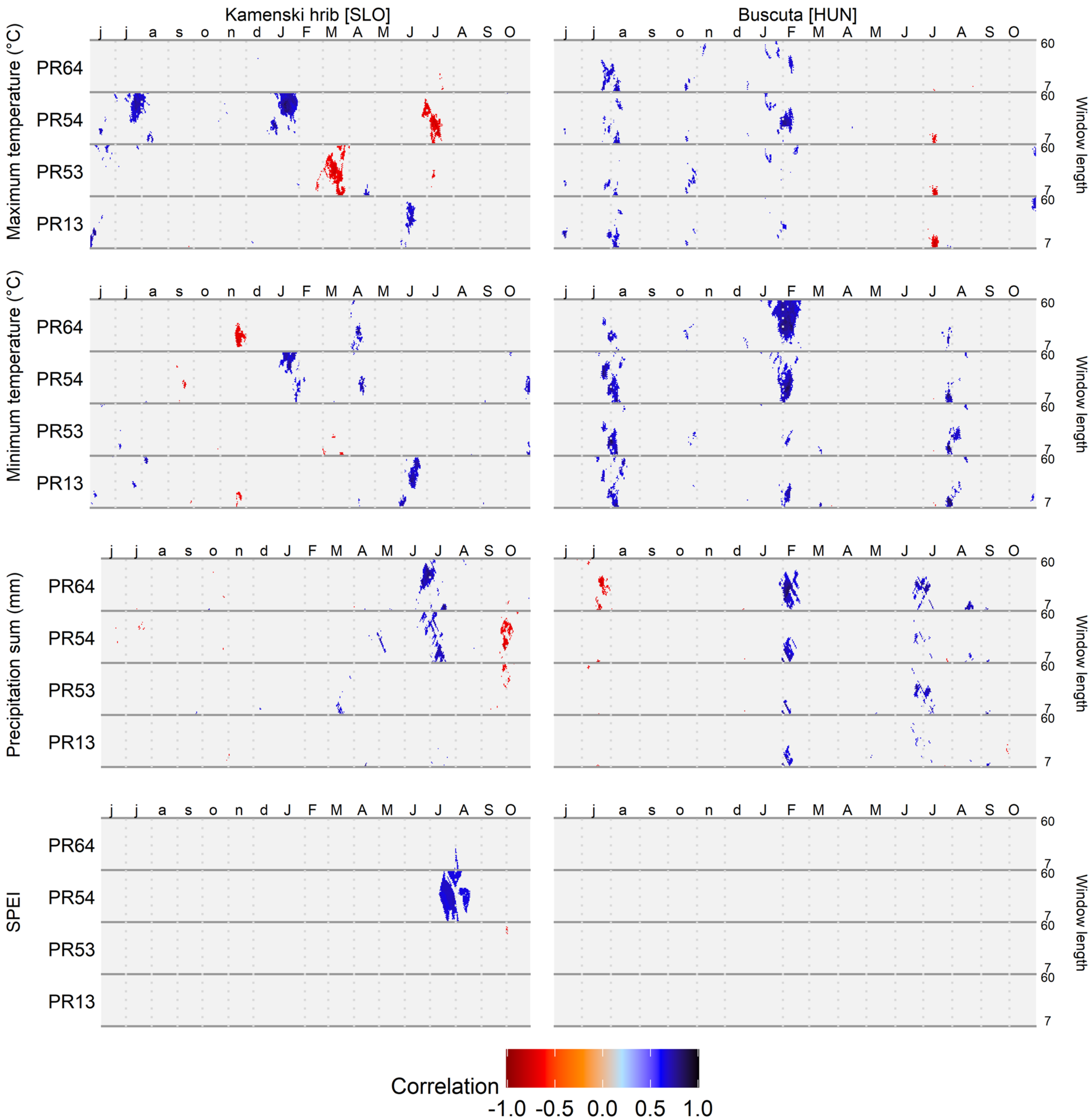


Fig. 7 Correlations between the standardized chronologies of mean vessel area and maximum and minimum daily temperature, daily precipitation sums of selected beech provenances at Kamenski hrib (left) and Bucsuta (right) in the 2009–2019 period. We used a time window span of between 7 and 60 days. We show only significant correlations ($p < 0.05$) between the pairs of mean vessel area and aggregated daily weather data. Lowercase letters are abbreviations for the months of the previous year, uppercase letters for the months of the current year. Dashed lines delimit the months

2022), the widest mean tree-ring width for the period 2009–2019 was found in the Czech provenance Nizbor (PR64), which originated from the warmest and driest climate among the study provenances. In addition, this provenance exhibited the largest mean vessel area at Bucsuta and was the only provenance that showed larger maximum values of mean vessel area within the tree ring at this location, while the other provenances exhibited larger mean vessel area for the entire period 2009–2019 at Kamenski hrib. As previously reported, local adaptation to environmental conditions is expected to be particularly important in marginal populations due to stronger selective pressure of the environment at range margins than in the distribution centre (Muffler et al. 2021). Our results showed provenance-specific adaptation of within-tree-ring vessel characteristics, although high within-provenance variability was also found (Fig. 5). However, the absolute values and the position of the maximum mean vessel area within the tree ring also depended on weather conditions, in particular precipitation, which affected tree-ring width and thus the relative position of the vessel within the tree ring, as well as the final vessel size.

At Kamenski hrib, Belgium provenance PR13 displayed the widest tree rings and mean vessel area after 2014. This provenance is late flushing, meaning that it is more resistant to late spring frost events, which have become more frequent in recent decades, amplifying the consequences of climate change (Zohner et al. 2020). Late leaf development could thus be an important adaptation for spring frost-prone environments. However, early season snowfall (i.e., end of October) in 2012 autumn caused the highest damage to the Belgium provenance, because the trees were still in leaf at that time (Krajnc et al. 2022; Železnik et al. 2019). Understanding the spring and autumn leaf phenology response of trees to climate change is thus crucial for the appropriate selection of the most suitable tree species or provenances to changing environments (Beil et al. 2021; Zhang et al. 2020). Whether this atypical early autumn snow event positively affected tree-ring widths and vessel area formed in the following years in survival trees, as seen from our data, remains open for further studies. Namely, the high mortality rate undoubtedly improved the growing conditions (enhanced radial growth) for the survivors due to reduced competition and newly available growing space. Since updated information on tree mortality and its direct effect on growth of the survivors at the provenance level is lacking for both locations, this aspect needs to be included in the analysis, as already previously demonstrated (Mátyás et al. 2018).

Interestingly, the spring frost event in 2016, which occurred in various regions in Europe (D'Andrea et al. 2020; Nolè et al. 2018; Zohner et al. 2020) did not cause drastic reductions in ring widths of the studied beech provenances at Kamenski hrib and Bucsuta, although it has been shown in previous studies that such events may essentially influence beech foliage and xylem increments in the current year (D'Andrea et al. 2020; Decuyper et al. 2020; Sangüesa-Barreda et al. 2021) or in the wood structure as reported for *Pinus contorta* (Montwé et al. 2018). There are two main reasons that may explain this lack of weather signal in wood-anatomical features in our study: (1) the provenances selected in our study were either intermediate (PR53 and PR64) or late flushing ones (PR13 and PR54) so the event did not substantially affect leaf development due to delayed phenology; (2) frost damage, which is known to be strongly related to site-specific conditions and to the phenological state of the trees (Allevato et al. 2019), did not occur at this elevation at Kamenski hrib and Bucsuta (micro weather conditions).

Inter-provenance specifics

Plasticity in leaf and cambial phenology is an important adaptation of tree species/provenances to changing environmental conditions to avoid stress by adjusting the timing of their growth (Prislan et al. 2013). Adaptation of common beech populations and provenances to extreme weather events, such as drought and frost, varies. The phenotypic plasticity and evolutionary adaptability of common beech seem to be underestimated, since these traits may counteract further range contraction of beech due to climate change (Bolte et al. 2007; Mátyás et al. 2018).

In terms of tree-ring widths and mean vessel area, we found greater differences between Kamenski hrib and Bucsuta in the case of mean vessel area. A provenance-specific response to harsh weather conditions, in terms of radial growth patterns, was evident in 2014 and 2017. The observed inter-provenance differences in tree-ring widths and mean vessel area may also be associated with differences in the timing of leaf and cambial phenology (Marchand et al. 2020a). In diffuse-porous beech, the timing of leaf development in spring is closely related to stem cambial reactivation, which occurs shortly after budbreak (Marchand et al. 2020a; Michelot et al. 2012; Prislan et al. 2013). Early flushing provenances are thus expected to start stem radial growth earlier than intermediate or late flushing ones, reflecting different environmental and internal constraints on tree-ring and vessel development. From this it can be inferred that the timing of initial vessel formation is also provenance-specific and depends on the timing of leaf development. In this sense, early flushing provenances are more susceptible to late spring frosts, which results in diminished radial growth (D'Andrea et al. 2020), as already mentioned in the previous section. Late flushing provenances, such as Slovene Idrija PR54 (special local conditions, which cannot be modelled by large-scale weather models) and Belgium PR13 (Atlantic provenance), are considered to be better adapted to survive long winters and avoid late spring frost events, whereas adaptive traits related to greater tolerance to water limitation and successful recruitment are important for southern provenances (Kramer et al. 2010). Both the Slovenian provenance PR54 and the Belgian provenance PR13 seem to have adaptations to evade late frosts, despite the differences in their climate of origin (moderate continental with sub-Mediterranean precipitation regime vs. Atlantic). More information besides mean weather data of provenance origin climates is therefore needed to support these speculations. The cessation of wood formation is less clearly connected to autumn leaf phenology, although a positive effect of canopy duration on storage reserves is known (Barbaroux et al. 2003). Moreover, leaf and cambial phenology in spring have been shown to be related to the preceding autumn phenology (Marchand et al. 2020a,b). Environmental conditions at the end of the previous growing season may thus influence wood structure in subsequent years. On the one hand, higher temperature in autumn prolongs canopy duration in autumn due to later leaf colouring (Vitasse et al. 2009). On the other hand, this could be detrimental to tree survival if there is a sudden drop in temperature and heavy snowfall in early autumn, which breaks leafy branches, as in the case of Belgium provenance PR13 in October 2012 (see previous section). This phenomenon has also been observed in other Atlantic provenances (Robson et al. 2018).

Vessel characteristics affect water-transport efficiency

Vessel diameter is a crucial parameter that determines the tree-water relation by affecting hydraulic conductivity, vulnerability to freeze/thaw-induced xylem embolism and vulnerability to drought-induced cavitation (e.g., Stojnić et al. 2017). Water transport efficiency and xylem safety in plants is thus regulated through vessel size and density adjustments (Oladi et al. 2014). However, numerous other mechanisms besides conduit dimensions affect xylem efficiency: pit structure (membrane thickness, size, quantity), inter-conduit connectivity and grouping, presence/absence of conductive ground-tissue (i.e., hydraulically functional tracheids or vasicentric tracheids) etc. (Gleason et al. 2016). Finally, water transport in diffuse-porous beech does not rely solely on the youngest xylem increment but on the outer portion of multiple rings; the contribution of an individual ring on the total water-transport capacity is consequently fairly moderate (Gasson 1985).

Our study shows that different weather factors affect tree-ring width and mean vessel area, which is in line with previous findings and confirms the latter as being suitable as an additional bioindicator for environmental changes (Sass and Eckstein 1995; Diaconu et al. 2016; Arnič et al. 2021). Intraspecific variation in the mean vessel area reflected a provenance-specific adaptation of the water transport system to the local environmental conditions. However, adverse growing conditions at Bucsuta and Kamenski hrib affected the pattern of year-to-year variation in this anatomical variable. The fairly synchronous year-to-year intraspecific variation in mean vessel area at a dry site Bucsuta suggest a strong influence of water availability on vessel properties. At Kamenski hrib, well-supplied with precipitation, a more synchronous year-to-year variation in the mean vessel area among the provenances was detected in extraordinary growing conditions, which is in line with the findings of Klisz et al. (2019) that site conditions affect the climate sensitivity of trees, which is more pronounced at marginal sites or in extreme years. The present and previous studies indicate a complex relationship between radial growth patterns and climatic/environmental conditions. Finally, the inclusion of additional site factors, such as soil properties (i.e., soil water availability) which determine vessel size (and consequently water-transport efficiency) by affecting the turgor pressure in the cells (Hölttä et al. 2010), would help to unravel these relationships.

Effect of weather conditions on tree-ring width and vessel features

We used daily response functions to examine the effect of weather conditions on the tree-ring widths and vessel features, including extreme events, such as the 2014 wet year and 2017 dry year. The main methodological limitation of our analysis was the short period time series included in the study, i.e., only 10 years (Figs. 6 and 7). Although traditional dendroclimatological analyses usually rely on longer time series of at least 40 years, the variable response window showed expected and significant results, indicating the potential for applying these functions to shorter intra-annual growth series, as already previously demonstrated in Gričar et al. (2022) on intra-annual radial growth patterns of pubescent oak.

Another important aspect that needs to be emphasized is the juvenile period of our analyzed beech trees (11–21 years), which is generally associated with greater climate sensitivity of trees. Namely, our recent study on four Douglas-fir provenances in sub-Mediterranean Slovenia (Krajnc et al. 2023) showed that the two provenances with the highest annual radial increment in the juvenile phase did not exhibit the same trend in the adult phase. Thus, possible changes in the relative growth rate from the juvenile to the mature phase must be taken into account when selecting the most promising provenance for planting. Nevertheless, the survival of beech trees in the future is strongly dependant on their survival potential in the juvenile phase of growth and, as such, similar studies offer a valuable insight into the future growth of beech. In addition, wood structure is different in young and old trees; in the former age group, annual increments are generally wider and vessel size is smaller (e.g., Colangelo et al. 2017; Rossi et al. 2008) so the results of the two age groups cannot be simply compared.

Weather conditions differently affected tree-ring width and mean vessel area. At Kamenski hrib, common weather signals, in particular temperature, were found in tree-ring widths, while at Bucsuta this was seen in the case of mean vessel area. In addition, the length of the period of response of vessel area to the analysed weather conditions differed in summer and winter periods. At Bucsuta, even short and intense summer drought (7 days) could greatly negatively affect vessel size. In contrast, a positive effect of temperature in late winter was seen in the wood anatomy of beech only if this warm period lasted more than a month.

As already previously mentioned, the fairly uniform response of the analysed vessel size in beech at Bucsuta compared to the very different response on Kamenski hrib indicates that the first location is more limiting for vessel development in the selected juvenile beech provenances. At more water-limited locations, such as Bucsuta, favourable spring and drought summer conditions also strongly determine vessel characteristics. A change from a diffuse-porous to a semi-ring porous structure was also clearly seen in juvenile beech wood. This is in line with previous observations that precipitation affects wood porosity in beech (e.g., Arnič et al. 2022). The drought effect is thus linked to the specific position at the climatic (xeric) limit of the tree species. At Kamenski hrib, there is a provenance-specific adaptation of water conduits to weather conditions, with the PR13 provenance being the least sensitive to them. Unlike Bucsuta, Kamenski hrib is a location in the current optimum range of this tree species. Consequently, the same weather effects have a different influence on the studied anatomical features. The effect of temperature and precipitation on vessel-area values within the tree ring was particularly evident in the weather-wise extreme years, regardless of the provenance. In the dry year of 2017, the vessel size began to decrease at ca. 25% of the tree-ring width, while in the wet year of 2014 the decrease was noticed at 60–80% of the tree-ring width. The predominant influence of environmental factors on the radial growth of trees on marginal sites, regardless of the tree origin, has also been demonstrated for other tree species, such as Norway spruce (Klisz et al. 2019). The provenance trial in Hungary (Bucsuta), which is in the immediate vicinity of Slovenia, is marginal for beech growth due to low amount of precipitation. Given climate scenarios that predict a similar situation in many regions of Slovenia in the coming decades (IPCC 2014), the research findings on how such conditions affect the radial growth of young beech trees of different origin are very important for future Slovenian forest management.

Conclusions

Provenance trials are a key source of information for future management of individual tree species. However, they must be monitored continuously and long-term, since the growth responses of different provenances can change over the years as demonstrated in the study by Krajnc et al. (2023) on four Douglas-fir provenances. Our study showed that the studied provenances have different growth and wood anatomy formation responses to weather stress. Thus, within the same species, different provenances of the same tree species may react differently to changes in the environment (i.e., climate change). Local adaptation to environmental conditions is expected to be particularly important in marginal populations, as environmental selective pressures are stronger at the edges of their range than at the centre of distribution (Muffler et al. 2021). In agreement with previous studies, we confirmed that site conditions influence the climate sensitivity of trees, which is more pronounced at marginal sites or in extreme years. In addition, weather conditions affected intra-annual trends in tree-ring width and mean vessel area differently. Moreover, also intra-annual trends of mean vessel area significantly affected in dry (2017) and wet year (2014), which resulted in different hydraulic efficiency. It is therefore worthwhile to consider not only species response but, primarily, provenance response in the face of climate change. On sites where water supply is projected to be limited, drought-tolerant provenances could be planted to minimize the effect of drought on the growth of beech forests. Since climate change models show that the climate of Slovenia in the future will be more similar to that in more southern Balkan countries (Buras and Menzel 2019), such as Bosnia and Herzegovina, these countries are one of the prime candidates for sourcing forest reproductive material that could thrive in Slovenia under climate change (Broadmeadow et al. 2005). In Hungary, beech decline has already been observed in recent years, so decision support systems have already prescribed a switch from beech to oak for climatically endangered sites (e.g., Czimber and Gálos 2016; Matyas 2016).

Author contribution statement JG and DA contributed equally to this work and are to be considered co-first authors. LK, DA and PP conceived and designed the work; LK, DA, PP, GB and CM performed the field work and collected the samples; DA and LK performed analysis of quantitative wood anatomy and statistical analysis, as well as prepared the figures and tables; JG and PP wrote the first draft of the manuscript followed by substantial contribution of all authors; all authors approved the final version of the manuscript to be published; HK and MW funding acquisition.

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Code availability (software application or custom code) Not applicable.

Declarations

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