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A comparison of radial increment and wood density from beech provenance trials in Slovenia and Hungary

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Abstract

Provenance trials are a valuable source of information, especially in species such as European beech (*Fagus sylvatica* L.), which will likely increase its distribution due to global warming. The current study compares radial increment and wood density of beech provenances in the juvenile development stage from contrasting environments in Europe (Belgium, Slovenia, Czech Republic, Italy) planted at a mesic to wet site in Slovenia and a xeric site in Hungary. Existing data (past measurements of diameters and height) was combined with new measurements of tree height, diameter, dendrochronological and resistance drilling density measurements to assess differences in provenance radial growth. The wood density data was evaluated using a Bayesian general linear model. In order to study the differences in radial increment in more detail, two weather-wise contrasting years (2014 and 2017) were selected from the last decade, based on calculations of the 12-month Standardized Precipitation-Evapotranspiration Index. The differences in average tree-ring width among provenances at each sampled site appeared to be relatively small when averaged over a whole decade of data. However, according to year-to-year data, some provenances grew faster than others, especially in favorable weather conditions. In unfavorable conditions, the differences in tree-ring widths among provenances were smaller. For most provenances, variation in tree-ring widths within the same provenance increased in unfavorable conditions. The difference between the provenances with the highest and lowest wood densities at both locations did not exceed 5%. The model results indicate that the Idrija (Slovenia) provenance probably has a higher median wood density than other studied provenances at both sites. Although the current study confirmed some differences in wood density between provenances and trial locations, the differences are negligible in practice due to their low magnitude and the fact that the analyzed trees were still juvenile. As beech has a diffuse-porous wood, negligible differences in wood density would also be expected in adult trees. Beech provenances for planting in relation to changing weather should probably be chosen for their ability to survive more extreme weather events rather than to improve radial increment or wood density, especially as the differences in wood density of juvenile trees is relatively small.

Keywords: Fagus sylvatica, ring width, common garden, resistance drilling

1 Introduction

Climate change encompasses rising average temperature, changes in the rainfall distribution and extreme weather events that are becoming more frequent, more severe and more widespread. The changes will influence the structure, distribution and function of forest ecosystems, as well as forest health (Schär et al, 2004; Pachauri et al, 2014). In turn, this will probably result in decreased forest productivity in some areas and increased tree mortality due to climate-induced physiological stress and other climate-mediated processes, such as insect outbreaks (Allen et al, 2010; Anderegg et al, 2015). Because of the long lifespan of trees, forests are sensitive ecosystems and can only slowly adapt to changing environmental conditions (Lindner et al, 2010). Their ability to withstand such changes depends on phenotypic plasticity, genetic diversity within and between populations, and gene flow (Kramer et al, 2010). How trees may respond to environmental changes is particularly relevant for ecologically and economically important European tree species, such as European beech (*Fagus sylvatica* L.), since future climate conditions will clearly influence its growth and competitive performance, and ultimately forest management practices (Pretzsch et al, 2015).

Beech is known to be a drought-susceptible species with high competitive ability (Houston Durrant et al, 2016). European beech has expanded its distribution range significantly over the last 40 years and has almost doubled its growing stock in Slovenia (Poljanec et al, 2010), while its area remained stable in Hungary (Führer et al, 2010). Its radial increment will probably increase in the future due to longer growing seasons (Prislan et al, 2019), although extreme weather events could disrupt its growth. In Slovenia, it is considered a natural replacement for declining Norway spruce stands. Climatic projections for the next decades indicate a general warming tendency in Slovenia (de Luis et al, 2014) and especially in the summer months in the whole of Hungary, which is critical for beech. At low elevations in Hungary, climatic conditions suitable for beech may completely disappear by 2050 and the long-term existence of beech forests will be limited to higher elevations. This means a reduction of their area by half (Gálos and Führer, 2018). The climate of both countries is is largely continental, but less humid in Hungary than in Slovenia. The lack of humidity also limits the natural distribution range of beech in Hungary (Mátyás et al, 2009).

Because the species is so widespread across Europe, a network of international beech provenance trials was created three decades ago to evaluate its genetic variation and adaptability to climate change by studying different traits (von Wuehlisch et al, 1997; Gárate-Escamilla et al, 2019). Growth of some beech provenances in a subset of trials was recently shown by Horváth and Mátyás (2016) to be directly linked with the change in climate between the trial site and source of the provenance.

Radial increment of trees is determined by a number of factors, such as site fertility, climate, competition, individual growing space, vitality and genetics (Hacket-Pain et al, 2016; Geßler et al, 2006). Because these factors are interrelated, it is difficult to determine the influence of any single factor on tree growth. In this sense, similar environmental conditions within individual provenance trials and dividing the trials into separate blocks to lessen site-specific variation make it possible to assess the genetic variation and adaptive capacity of different populations of the same tree species (Bussotti et al, 2015; Robson et al, 2018). Recent dendrological and wood anatomical studies on beech provenances (Eilmann et al, 2014; Kreyling et al, 2014; Stojnić et al, 2015) have often focused on more drought-tolerant provenances (generally from the southern or other marginal edges of beech natural distribution), which is in line with future climate scenarios for central Europe that generally predict a temperature increase and a change in precipitation amount or/and distribution (Pachauri et al, 2014). These studies have shown that drought tolerant provenances could be planted to minimize the effect of drought on growth of beech forests.

Wood density is related to biomass production and carbon sequestering and is an important physical property for wood usability (Skomarkova et al, 2006; Chave et al, 2009). The anatomical traits that affect wood density are regulated by synergistic effects of internal (genetics, hormones) and external factors (environment) (Downes and Drew, 2008; Downes et al, 2009; Fukatsu and Nakada, 2018). The established provenance experiments are very valuable for investigating these relations (Nabais et al, 2018; Eilmann et al, 2014). Although variations in wood density are less pronounced in diffuse-porous (vessels inside growth rings are of approximately similar diameter) species such as beech compared to ring-porous (vessels are of two different and distinct sizes within a growth ring) species and conifers, it has been shown that semi-ring wood structure can form in beech in very dry years (Arnič et al, 2021). Semi-ring wood structure has a different porosity within individual tree rings and subsequently wood density, meaning that different beech trees could have different wood densities.

Climate change and forest management practices that are focused on biodiversity conservation, as well as the highly competitive timber market, demand quality rather than quantity of harvested timber (Mina et al, 2016; Zhang et al, 2020). Wood quality depends among other things on wood anatomy, such as ring width, earlywood/latewood proportion and density, juvenile/adult stage (Plomion et al, 2001; Huang et al, 2003). Wood density is closely related to the elastic modulus or bending strength (Niklas and Spatz, 2010), all three properties together can be used to assess wood quality. While assessing these properties on wooden boards or logs is possible (Legg and Bradley, 2016), measuring them accurately or predicting them in standing trees for identifying higher-quality trees is considerably harder, especially when measuring the elastic modulus or bending strength in larger-diameter trees (Krajnc et al, 2019). However, accurately measuring wood density is possible in standing trees *in situ* using resistance drilling.

This study compares the radial increment and wood density of beech provenances in the juvenile development stage from contrasting environments in Europe (Belgium, Slovenia, Czech Republic, Italy) planted at a mesic to wet site in Slovenia, which provides optimal conditions for beech growth, and a xeric site in Hungary. We combined existing data from COST-Action E52 (Robson et al, 2018) with new measurements of tree height and diameter together with dendrochronological and resistance drilling density measurements to assess differences in provenance performance. Finally, we evaluated the growth plasticity of different beech provenances to contrasting weather conditions (2014, a wet year vs. 2017, a dry year). We hypothesized a) that native Slovenian provenances would perform better in height and radial increment than others; b) that signiffcant differences in resistance drilling density would be found between the two sites, and c) that differences between provenances in the measured tree characteristics related to productivity would be higher at the Slovenian site due to more favorable growing conditions, which could make any potential differences due to genetic make-up more pronounced. The trees in the Slovenian trial are probably less exposed to climate-induced stress, which might not be the case in the Hungarian trial, as it is located in a more marginal environment.

2 Material and methods

2.1 Provenance trials and sampling description

The sampling was performed in two parallel beech provenance trials, established as part of the international beech provenance trials initiated by the Institute of Forest Genetics and Forest Tree Breeding (Grosshansdorf, Germany) (von Wuehlisch, 2004). Some of the information on both trials is shown in Table 1. The provenances planted in the Slovenian trial were mostly planted in a cooler and wetter climate than at their place of origin (Mátyás et al, 2009) and the overall site conditions are very favorable for beech (Sijacic-Nikolic et al, 2019). The Bucsuta site is warmer with lower annual rainfall and a higher likelihood of drought-induced stress than at the place of origin for most provenances, since the site is located at the low-elevation xeric limit of European beech (Horváth and Mátyás, 2016).

Table 1: Information on the two included provenance trials.

Provenance trial	Location	Elevation a.s.l. [m]	Planting year	Soil and bedrock
Kamenski hrib, SI	N45°47′46″ E15°2′5″	540	1998	deep eutric cambisols and haplic luvisols, limestone bedrock
Bucsuta, HU	N46°35′0″ E16°51′0″	220	1998	deep brown forest soil, loess bedrock

Weather data for both locations was extracted using E-OBS daily climate data version 22e (Cornes et al, 2018), where mean, minimum and maximum daily temperatures, and sum daily precipitation were obtained from the nearest grid point for the last two decades. The climate diagrams for both locations are shown in Figure 1.

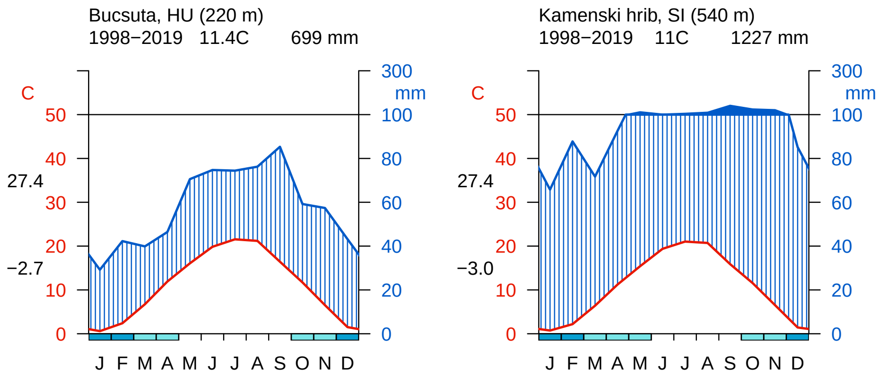

Fig. 1: Walter-Lieth climate diagrams for both sampling locations (Walter and Lieth, 1960). The location name is followed by elevation above sea level (in brackets), displaying the analyzed period, average temperature and precipitation in the second line and maximum temperature of the warmest month with minimum temperature of the coldest month on the left side of the diagrams.

Six different provenances were selected for sampling in the Slovenian trial, three originating from Slovenia (Postojna Mašun, Idrija-II/2 and Postojna Javorniki) and three originating from elsewhere in Europe (Soignes from Belgium, Val di Sella from Italy and Nizbor from the Czech Republic). Idrija and Soignes are late flushing (Robson et al, 2011), Val di Sella is early flushing (Pučko et al, 2005), while the remainder flush around the average flushing date in the Slovenian trial. The original elevation of Slovenian provenances ranges from 875 (Idrija) to around 1000 metres (Postojna Mašun and Javorniki) above sea level with average yearly temperatures of around 5.5 °C and yearly precipitation of 2000-3000 mm. Val di Sella comes from a similar altitude (1150 m) with higher average temperatures (8.4 °C) and less rain (1269 mm), as do Nizbor (480 m, 8.5 °C and 500 mm of rain) and Soignes (110 m, 9.4 °C and 835 mm of rain) (Alía et al, 2010).

Four provenances out of the six sampled in Kamenski hrib were also planted in Bucsuta and were sampled in the same manner as in the Slovenian trial.

The other two provenances (Val di Sella and Javorniki) were not planted in Bucsuta and were therefore not available for sampling. This unequal number of provenances could have important implications on the statistical analysis of the gathered data. As this is an impossible obstacle to overcome or modify when measuring existing provenance trials, appropriate statistical methods should be used and Bayesian approach should be favored over a more frequentist one. The sampling was done in September 2019 in Kamenski hrib and in November 2019 in Bucsuta. The provenance trials were planted in three separate replicates and the sampling was stratified across all three replicates equally. For each selected provenance, 30 trees with the largest diameter at breast height (DBH) based on previous inventory data (Table 2) were sampled. The DBH of the selected trees was remeasured. Tree height was measured on three trees with the highest DBH per provenance per replicate, giving a sample size of nine trees per provenance for height measurements. Neither of the trials were thinned.

Table 2: Historical data (Robson et al, 2011) of chosen provenances on Kamenski hrib: mean values of DBH, tree height of each provenance and mortality as percent of dead trees in a given year from all planted trees. Coefficient of variation in brackets. Data for the Bucsuta trial not available.

		DBH		Height		Mortality	
Provenance	N	2005	2015	2005	2015	2005	2015
Idrija, SI	146	1.7 (34)	7.4 (30)	2.5 (21)	8.4 (19)	53	53
Javorniki, SI	135	1.3 (51)	7.2 (30)	2.1 (27)	7.9 (20)	54	57
Masun, SI	138	1.8 (32)	7.4 (34)	2.4 (20)	7.9 (18)	24	34
Nizbor, CZ	124	1.4 (42)	7.7 (26)	2.2 (23)	8.0 (22)	38	61
Soignes, BE	150	1.2 (46)	7.1 (33)	2.1 (24)	7.4 (25)	10	67
Val di Sella, IT	149	2.2 (32)	7.9 (26)	2.9 (18)	9.1 (16)	43	45

Note: diameter in *cm*, height in *m*, mortality (and CV) in *percent*.

In each of the 30 selected trees per provenance (distributed equally among blocks), wood density was measured at breast height using a resistance drilling device - Resistograph SC-650 (Rinntech, Heidelberg, Germany) with a 500 mm long drilling needle, which is used to drill into standing trees and record the resistance to drilling while moving through the stem. The drilling needles were calibrated by the manufacturer for absolute wood density assessment and, as such, the measurements provide an estimation of wood density in the radial direction (Rinn et al, 1996; Gao et al, 2017). The drilling was done bark-to-bark through the center of the tree and was stopped manually once the needle emerged on the opposite side of the tree. The resistance drilling density measurements (in kg/m^3) were imported into the R statistical environment using the R package *densitr* (Krajnc, 2020) and the bark portion of the measurements was trimmed away, after which the measurements were detrended automatically using a linear regression fit provided by the R package *densitr*.

The wood density values are median values of resistance drilling density profiles for each individual tree. Median values were used instead of mean values to minimize the potential influence of wood density anomalies within individual tree stems (branches, localized instances of rot etc.). The values of resistance drilling density are generally relatively low when drilling into live standing trees and the results have to be corrected for basic wood density. The relationship between basic wood density and resistance drilling density measured in fresh wood was measured using European beech stem disks in a separate study (Krajnc et al, 2020). The reported calibration factor of 1.41 for European beech was used to convert the resistance drilling density values into values of basic wood density (ratio between oven-dry mass and green volume). The values of basic wood density of European beech obtained using resistance drilling with the correction factor are comparable to values obtained by previous studies using more traditional density assessment methods (Dietz, 1975). This is in line with a review of resistance drilling to assess wood density done by Gao et al (2017), which lists a number of similar studies validating the relationship between resistance drilling and wood density.

Following resistance drilling, increment cores were extracted from a subset of 13 trees from each provenance (distributed equally among blocks), with the exception of the Javorniki provenance on Kamenski hrib for which only six trees were available for core extraction. Increment cores were also taken from 13 trees in the Bucsuta trial, distributed equally among the three blocks. The cores were then 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 & Data AB, Saltsjöbaden, Sweden) and further analyzed using robust mean chronologies from the R package *dplR* (Bunn, 2008). The set of trees planted on Kamenski hrib was compared to the set of trees planted in Bucsuta for each provenance.

2.2 Calculations of Standardized Precipitation-Evapotranspiration Index

In order to study the differences in radial increment in more detail, two weather-wise contrasting years were selected from the last decade, based on tree-ring width and calculations of the 12-month Standardised Precipitation-Evapotranspiration Index (Vicente-Serrano et al, 2010, SPEI) on the daily data obtained from E-OBS daily climate data version 22e (Cornes et al, 2018), as described above. SPEI calculation is based on combining precipitation with temperature data and is used for assessing the onset, duration and magnitude of droughts. R package *SPEI* (Beguería and Vicente-Serrano, 2017) was used for the calculations (see Figure 2). The year 2017 was chosen as an example of a year with relatively poor growing conditions and 2014 as a year with good growing conditions. By only looking at SPEI, the year 2012 would be a better representative of relatively poor growing conditions, but early snow in that year damaged some trees in the Slovenian trial and it cannot be assumed that radial increment was unaffected, which is why we chose an alternative year, 2017. SPEI values above 1.5 indicated a wetter summer period in 2014, especially at Kamenski hrib, whereas summer SPEI values around -1 indicated a drier summer in 2017, especially at Bucsuta.

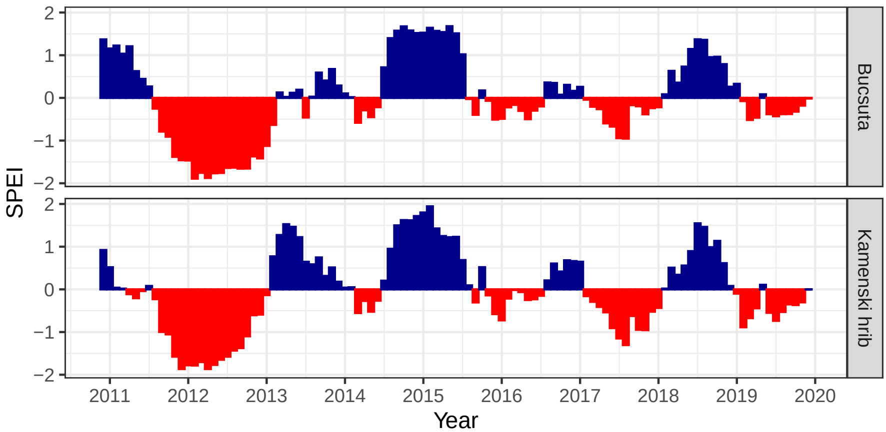

Fig. 2: SPEI for the two sampling locations for the last decade ending with 2020.

2.3 Statistical analysis

Statistical analysis was conducted in the open-source statistical environment R (R Core Team, 2020) by using a Bayesian general linear model to evaluate the differences in wood density among provenances and trial locations. The Bayesian approach was chosen over the more traditional frequentist approach, as it incorporates uncertainty into the model directly and provides a more informative inference (McElreath, 2020). The model was implemented in Stan (Carpenter et al, 2017), with the help of the R package *brms* (Bürkner, 2017). The priors used were weakly informative, the model was specified as follows (see McElreath (2020) for additional information on model specification):

$$
\begin{aligned}
&\rho_b \sim Normal(\mu_i, \sigma)\\
&\mu_i = \alpha + \beta_{dbh[i]} * DBH + \gamma_{provenance[i]} + \delta_{block[i]}\\
&\alpha \sim Normal(600, 50)\\
&\gamma_j, \delta_k \sim Normal(0, 50) \text{ for } j = 1..6 \text{ and } k = 1..3\\
&\beta_{dbh[i]} \sim Normal(0, 5)\\
&\sigma \sim Cauchy(0, 1)
\end{aligned}
$$

Tree median basic wood density was the dependent variable, while the explanatory variables were provenance, replicate and diameter at breast height. Three models were made: 1-2) one for each site (Kamenski hrib, Bucsuta) and 3) one for combined data from both sites using the four provenances found in both trials and with site as additional explanatory variable with the same priors as for block and provenance. All three models were manually checked for convergence and effective numbers of samples, as suggested by McElreath (2020).

3 Results

Mean diameters at breast height and height of the sampled trees are presented in Table 3. The differences in diameter among provenances and between the two sampling locations are smaller than differences in tree height. More variability in diameter and heights can be observed in trees from Bucsuta than from Kamenski hrib. No fruiting was observed, which was expected due to their age.

Table 3: Sample properties, as measured in 2019: displaying number of trees, mean values of DBH and tree height of the nine most dominant trees for each provenance. Coefficient of variation in brackets.

	Bucsuta, HU			Kamenski hrib, SI		
Provenance	N	DBH	Height	N	DBH	Height
Idrija, SI	30	10.4 (31.7)	9.5 (23.9)	30	11.1 (21.6)	13.4 (6.2)
Javorniki, SI				30	10.4 (25.1)	13.4 (7.8)
Masun, SI	31	12.4 (21.7)	10 (19.5)	30	11.3 (22)	14.9 (8.7)
Nizbor, CZ	27	12.4 (28.3)	11.1 (15.6)	30	11.1 (21.6)	13.8 (3.3)
Soignes, BE	27	11.5 (34.8)	10.5 (26.8)	30	10.5 (22.4)	14.5 (10)
Val di Sella, IT				30	11.5 (18.6)	14.6 (6.7)

Note: dbh in cm, height in m, CV in percent.

3.1 Analysis of tree-ring widths

The tree-ring width chronologies of the analyzed beech provenances for Kamenski hrib and Bucsuta are shown in Figure 3, while mean tree-ring widths for the last decade of growth can be seen in Table 4. For the period 2009–2019, the differences in yearly radial increment are generally small; the average tree-ring width is between 3.0 and 4.0 mm for all years. A higher variability in tree-ring widths within individual beech provenances can be observed in Bucsuta.

Table 4: Overall mean tree-ring width in millimeters for the period 2009-2019 (RW) by provenance and location, number of included tree rings (N). Coefficient of variation in brackets.

	Bucsuta, HU		Kamenski hrib, SI	
Provenance	N	RW	N	RW
Idrija, SI	130	3.2 (40.3)	112	3.2 (37.4)
Javorniki, SI			54	3.7 (32.5)
Masun, SI	132	3.2 (39.8)	94	3.1 (35.2)
Nizbor, CZ	130	3.9 (47.2)	132	3.7 (36.1)
Soignes, BE	142	3.2 (47.2)	143	3.5 (38.2)
Val di Sella, IT			132	3.0 (33.3)

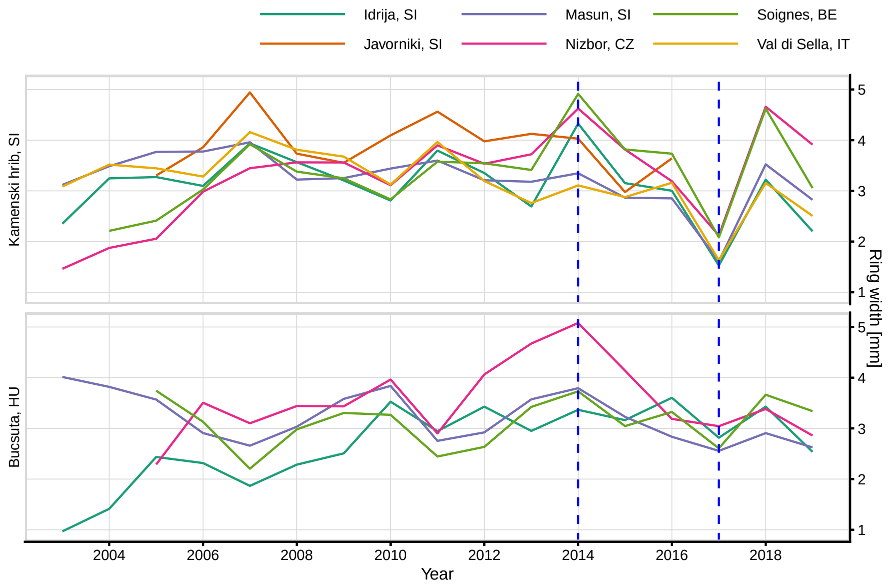

Fig. 3: Provenance chronologies (displaying robust mean values for each provenance), shown separately for each location. Two chosen weather-wise extreme years marked with a blue dashed line.

Deviations from the average tree-ring width values are most pronounced in the two contrasting years (Figure 4, Table A1), since more variation can be observed in the two selected years compared to overall variation over the last decade. In 2014, a year with above average precipitation, the highest radial increment in Kamenski hrib can be found in the Soignes provenance (4.9 mm) and the lowest in trees originating from Val di Sella (3.1 mm). In 2017, a year with below average precipitation, all provenances were similarly affected, and the largest difference in Kamenski hrib was 0.7 mm between Nizbor and Masun/Soignes. In Bucsuta, the largest difference in 2014 was 1.7 mm between Idrija and Nizbor, while in 2017 it was 0.4 mm between Masun/Soignes and Nizbor.

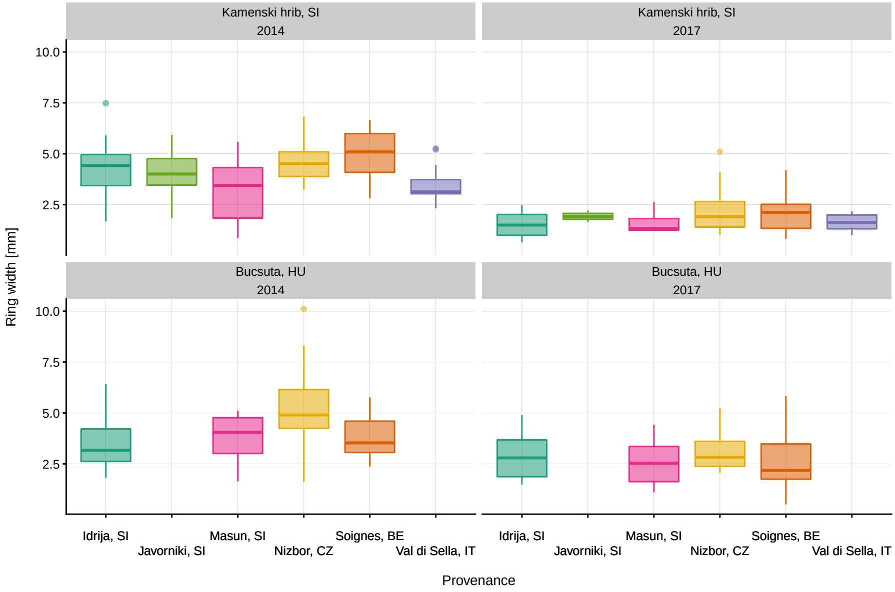

Fig. 4: Boxplots of tree-ring widths between provenances for the two chosen weather-wise extreme years.

3.2 Comparing wood density between provenances and sampling locations

Distributions of median tree wood density by provenance at both locations are shown in Figure 5. The difference between the provenances with the highest and lowest wood densities at both locations does not exceed 5%. At both sites, the Idrija provenance appears to have the highest wood density. In order to quantify the differences between provenances a Bayesian general linear model was used, as described in Section 2.3. The model parameters for the three models (one for Kamenski hrib, one for Bucsuta and one with combined data) and the summaries of their posterior distributions are listed in Table A2. Although trees from the Slovenian trial had a slightly higher wood density than those in Bucsuta, the difference is relatively small in magnitude when compared to the effect of other factors. For example, both provenance and block had a stronger influence on wood density than location.

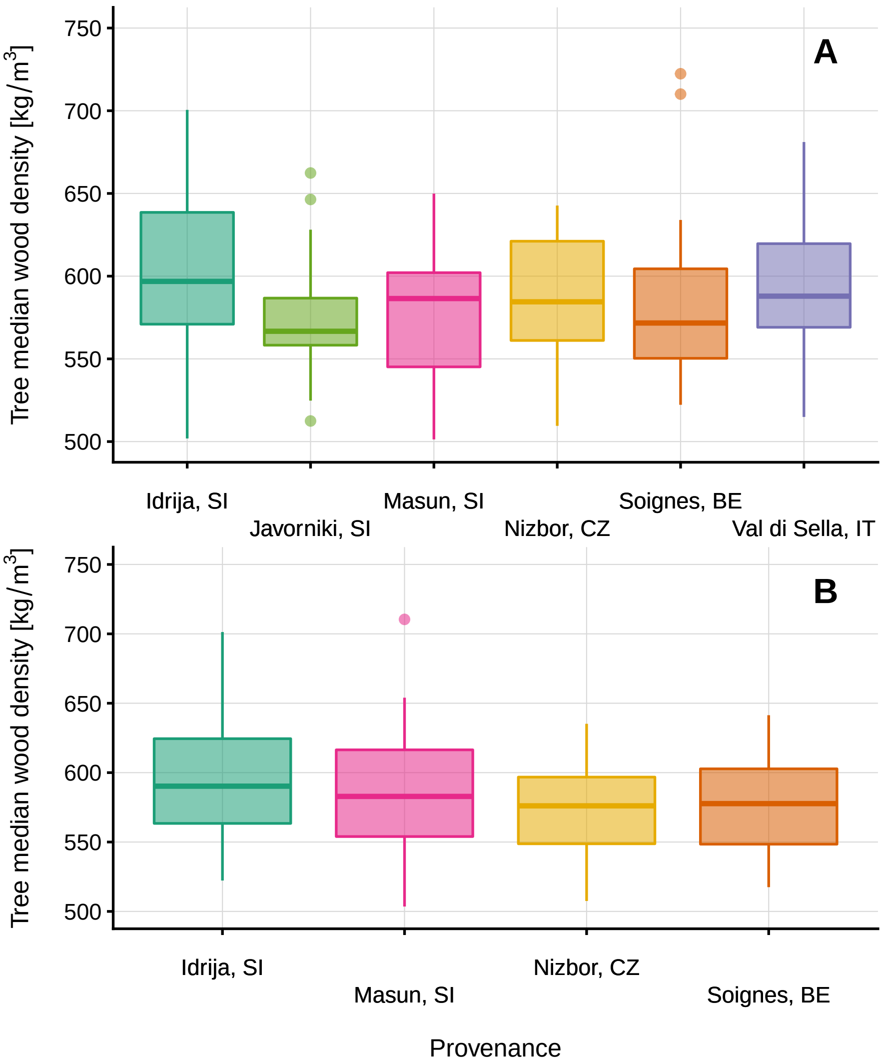

Fig. 5: Boxplots of median wood density of provenances in A) the Kamenski hrib trial and B) the Bucsuta trial.

In order to compare wood density among provenances, posterior distributions of differences are shown in Figure 6, relative to the wood density of the Idrija provenance at each studied site. Based on the formulated model and obtained data, the distributions of posterior differences indicate that the Idrija provenance probably has a higher median wood density than other studied provenances at both sites, although the difference between Idrija and the other two Slovenian provenances is less pronounced.

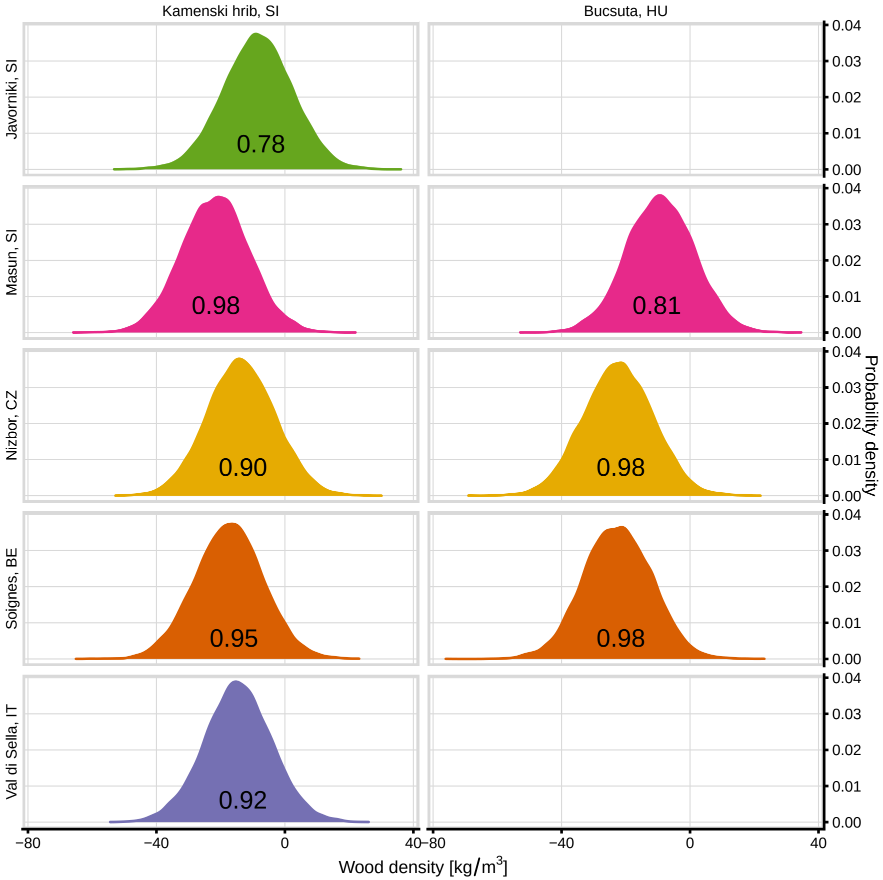

Fig. 6: Comparison of wood density of Idrija to wood density of other provenances across the two provenance trials, displaying posterior distributions of the Bayesian general linear model. In the middle of each posterior distribution: probability (0-1) of lower wood density when compared to Idrija using measured data, formulated model and prior distributions.

The effect of diameter at breast height on wood density was found to be more likely positive, as shown in Figure 7. This relationship was more pronounced in Bucsuta than in Kamenski hrib.

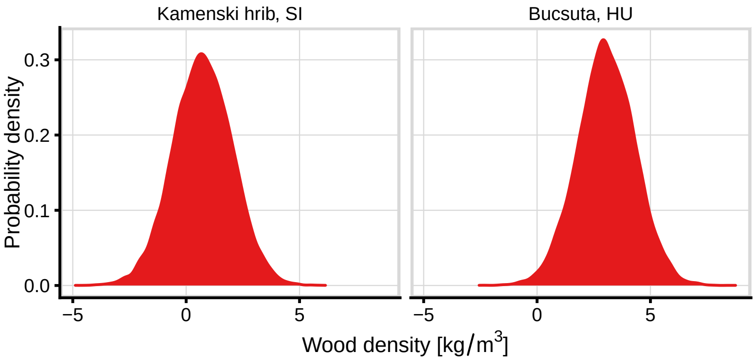

Fig. 7: The effect of diameter at breast height on wood density.

4 Discussion

4.1 Tree-ring widths

The differences in average tree-ring width between provenances at each sampled site appeared to be relatively small when averaged over a whole decade of data. This indicates a high potential of beech trees to adapt radial increment to yearly local environmental conditions, as already previously reported (Prislan et al, 2013). However, when looking at the year-to-year data, all provenances grew faster in favorable weather conditions (*i.e.* 2014) than in a year with unfavorable conditions (*i.e.* 2017). In unfavorable conditions (*i.e.* 2017), the differences in average tree-ring widths were smaller in the Slovenian trial and remained the same in the Hungarian trial. For most provenances, variation in tree-ring widths within the same provenance increased in unfavorable conditions. The results of the current study with regard to to tree-ring widths are in line with those of Stojnic et al (2013), where no differences in tree-ring width were found between four different beech provenances in a provenance trial in Serbia. The same authors also reported that radial growth of beech provenances originating from a climate with more precipitation to a drier site was not affected and resembled the radial growth of a local provenance.

Differences in tree-ring widths of beech are in general influenced by the length of the growing season and the rate of cell production (Prislan et al, 2013). Both parameters may vary among provenances and years, which would explain the observed variability in widths. However, as reported by Stojnic et al (2013), wood-anatomical variables showed similar inter-annual patterns for all provenances and no differences were observed between provenances. Tree-ring widths could also be related to the flushing time of the provenances (Čufar et al, 2008, 2014). This relationship differed between the two locations. In Kamenski hrib, the average tree-ring widths of the late flushing provenances (Soignes and Idrija) were generally wider, whereas the widths of the average-flushing provenances (Masun, Nizbor) were slightly wider in Bucsuta. Spring leaf phenology is considered one of the most important determinants of growth and survival in young stands. The response of trees to the environmental stimuli that determine spring phenology is largely under genetic control. However, inter-populational differences exist within species, suggesting site-specific selection of the trait (Robson et al, 2011). Autumn phenology should be included along with spring leaf phenology, as leaf and cambial phenology in spring have been shown to be related to the preceding autumn phenology (Marchand et al, 2020). Environmental conditions at the end of the previous growing season may thus influence wood structure in subsequent years. While this could be an interesting direction to explore in the future, the relationship between provenances, leaf phenology, tree-ring width and wood-anatomical traits was not examined in this study.

The effect of environmental conditions on tree-ring width probably overrides the effect of genetic variation, as reflected in the synchronous annual variation of the mean ring-width series of the four provenances present in both trials (Figure 3) from the current study, which has already been previously observed (Stojnic et al, 2013; Eilmann et al, 2014). However, the causal relationship between genetic make-up, environment and ring width should be examined in adult trees to avoid any influence of juvenile wood and its different properties.

4.2 Wood density

The relationship between ring width and wood density in beech trees was thoroughly explored by Bouriaud et al (2004), showing that the two variables expressed different sensitivity to different climate-related properties. Wood density reacted more strongly to temperature and late-summer rainfall, while ring width was more governed by soil water deficit. Since the Bucsuta site in the current study is on the xeric limit for European beech, this could explain a higher proportional drop in ring width values between Kamenski hrib and Bucsuta. Although some differences in wood density can be observed in provenances across the two sampled locations and were quantified using the Bayesian model ($\sim 7\ kg/m^3$), they are negligible as bigger differences were found between provenances or blocks within both trials. Mean July temperature on both sites is within half of a degree Celsius (Mátyás et al, 2009) and the differences in late-summer rainfall are less pronounced than in overall precipitation (see Figure 1), which is probably reflected in approximately similar wood densities across the two sites and larger differences in ring width.

The positive association between diameter at breast height and wood density (Figure 7) is interesting and unexpected, since a similar relationship has been reported in several softwood species. In softwoods, this is directly related to the inverse connection between ring width and wood density, but this explanation cannot be used in beech, a diffuse porous species (Dinwoodie, 1981).

4.3 Application of the results in practice

The largest radial increment of the dominant trees in the last decade across both trials was found for the Nizbor provenance. Interestingly, the Nizbor provenance comes from the warmest and driest climate of the provenances considered in this study. Whether it will maintain its growth advantage in the coming years, taking into account the weather conditions in the future and tree physiology at the adult stage, cannot be asserted based on our results. However, when looking at the overall population-level historical data (Table 2), Nizbor is not the best-growing provenance when also considering height growth and mortality. Still, in the face of climate warming and increased droughts and based on the current results, it is an interesting candidate to test for enrichment planting on a smaller scale, which could be extended also to other beech provenances coming from drier and hotter sites than the current local conditions. The Val di Sella provenance appears to be the best overall, looking at combined radial and height growth along with overall mortality.

The apparent jump in mortality rate within the decade on Kamenski hrib (see Table 2) can be explained by the early snow in 2012, which caused the most damage to the Soignes provenance. This provenance was the only one of the sampled provenances still having leaves on the trees when snow fell, which is why the early snow severely damaged it. Prolonged leaf duration, either due to genetics or a higher temperature in autumn that is connected to later leaf coloring (Vitasse et al, 2009), can have important implications in the context of climate change. In combination with extreme events (such as early snow, ice storms...) they could be detrimental to survival and/or growth of beech trees from certain provenances, especially if leaf retention periods increase overall due to warmer autumn weather. For example, atypical early-season snowfall (i.e., end of October) on Kamenski hrib in 2012 caused the highest damage to the Soignes provenance (Železnik et al, 2019), suggesting that it is therefore not the best suited to continental climates. Spring extreme events (especially frost) should also be considered in future research.

International beech provenance trials have shown that not all provenances interact with local climate (Ivankovic et al, 2008; Jastrzebowski et al, 2017), but the decrease in height growth was not significant when provenances were moved to a cooler and wetter environment (Mátyás et al, 2009). However, the effect of ecodistance, which refers to environmental change that each provenance experienced because of translocation to the provenance trial site (Mátyás et al, 2009), was visible in height growth at the Slovenian site (Železnik et al, 2019). The climatic conditions at Kamenski hrib are similar to the original conditions of the Italian (Val di Sella) and Slovenian provenances, which are close to optimal growing conditions for beech. Czech provenance comes from a completely different environment, i.e., xeric and warmer conditions, and experienced higher ecodistance. While the overall drought-induced mortality appears to be dependent on genetic make-up (Bolte et al, 2016), local adaptation appears to occur within short geographical distances (Pluess and Weber, 2012). All three Slovenian provenances originate from higher elevations with more precipitation than at Kamenski hrib, which could explain why Nizbor and Val di Sella outgrew local provenances in some time periods. This experiment should be repeated with a higher number of provenances covering a wider climatic gradient and also when trees have moved pass the juvenile stage.

5 Conclusions

The first hypothesis was not confirmed, as Slovenian provenances did not outperform the other three provenances in radial growth across both sites. The second hypothesis was confirmed, as the differences in wood density between sites are negligible in practice. In terms of height or DBH, Slovenian provenances were inferior to the other provenances in the more xeric climatic conditions in Hungary and approximately similar to others in the Slovenian trial. The third hypothesis was therefore not confirmed. Beech provenances for planting in relation to changing weather should therefor probably be chosen by their ability to survive more extreme weather events rather than to improve radial increment or wood density. Other individual tree properties (such as volume or height growth, competition effect, browsing damage, pests and diseases) should be included in such studies, since they may explain some of the variability of wood density in mature trees. In addition, the effect of age on wood properties in un-even aged trees needs to be accounted for in the analysis, since it could have a sizable effect (Mátyás and Peszlen, 1997; Diaconu et al, 2016) - however, this is not really a problem in provenance trials as trees within provenance trials were planted at the same time and are therefore of the same age.

Although the current study found some differences in tree-ring width and wood density between different provenances and trials, they are small and should have no effect on the quality of wood from such trees, especially as the trees in this study were all juvenile. However, given the importance of wood density and tree ring widths not only on wood value but also on carbon sequestration in standing trees, more such research on adult trees is urgently needed. Trees take decades to grow and climate change mitigation measures are needed today. The best option would be to study wood density in mature provenance trials and, if that is not possible, in adult forest stands (which would require much larger sample sizes to correct for environmental variation). The differences in radial increment and wood density among provenances could change with increasing tree age and the observed changes in variation of tree-ring width between favorable and unfavorable growing conditions indicate that extreme weather events could have a pronounced effect on the overall growth of beech trees. Other characteristics besides radial increment and wood density, such as homogeneous growth, high survival rate and resistance to extreme weather events, appear to be more important for appropriate provenance selection.

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Declarations

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Appendix A Appendices

Table A1: Robust mean tree ring width in millimeters (RW) for the two chosen weather-wise extreme years, N = 13 trees for all provenances except Javorniki (N = 6). Coefficient of variation in brackets.

	Bucsuta, HU		Kamenski hrib, SI	
Provenance	2014	2017	2014	2017
Idrija, SI	3.4 (36)	2.8 (39)	4.3 (36)	1.5 (46)
Javorniki, SI			4 (35)	1.9 (21)
Masun, SI	3.8 (30)	2.6 (42)	3.3 (51)	1.4 (36)
Nizbor, CZ	5.1 (45)	3 (32)	4.6 (24)	2.1 (54)
Soignes, BE	3.7 (26)	2.6 (59)	4.9 (26)	2.1 (46)
Val di Sella, IT			3.1 (27)	1.6 (27)

Table A2: Model parameter values, displaying posterior distributions of the general linear model parameters: mean values and a 0.89 percentile span in brackets.

	Model dataset		
	Kamenski hrib	Bucsuta	Combined
Intercept	628.6 (600.9, 655.7)	546.6 (518.2, 575.3)	602.4 (578.2, 626.6)
σ	42.7 (39.3, 46.6)	41.1 (37.1, 46.1)	46.9 (43.5, 50.7)
dbh	0.7 (-1.3, 2.8)	3 (1, 5.1)	0.4 (-1.3, 2.1)
Location			
Kamenski hrib, SI			7.4 (-2.3, 17.1)
Provenance			
Nizbor, CZ	-13.7 (-30.5, 3.5)	-22.3 (-39.6, -5)	-17.1 (-30.8, -3.3)
Postojna Javorniki, SI	-8.4 (-25.7, 8.8)		
Postojna Mašun, SI	-21.6 (-38.3, -5)	-9.3 (-25.9, 7.7)	-13.9 (-27.4, -0.5)
Soignes, BE	-17.3 (-34.5, -0.4)	-22.6 (-39.3, -5.7)	-20.1 (-33.6, -6.3)
Val di Sella, IT	-14.7 (-31.5, 2.3)		
Block			
Block 2	-53.3 (-66.5, -40)	23.3 (7.2, 38.6)	-19 (-31, -6.4)
Block 3	-51.9 (-65, -38.8)	13.8 (-2.9, 30)	-24 (-36.2, -11.7)

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