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Inter-provenance variability and phenotypic plasticity of wood and leaf traits related to hydraulic safety and efficiency in seven European beech (*Fagus sylvatica* L.) provenances differing in yield

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Abstract

Key message Seven European beech provenances differing largely in growth performance were grown at two common garden sites in Germany and Slovakia. The intra-specific variability of most traits was explained more by phenotypic plasticity than inter-provenance variability, and efficiency-related traits showed a higher phenotypic plasticity than safety-related traits.

Context To maintain climate-resilient future forests, replicated common-garden experiments are suited for developing assisted migration strategies for key tree species.

Aims We analysed the magnitude of inter-provenance variability and phenotypic plasticity for 12 functional traits of European beech (*Fagus sylvatica* L.) and analysed whether the climate at the place of origin left an imprint. Moreover, we asked whether growth is unrelated to xylem safety and to what extent the foliar, xylem and growth-related traits are coordinated.

Methods Terminal branches were collected from 19-year-old and 22-year-old trees of seven European beech provenances planted at two common garden sites in Germany and Slovakia, respectively. Three hydraulic, three wood anatomical and four foliar traits were measured and related to two growth-related variables.

Results At the two sites, the same pair of provenances showed the highest and lowest growth. Nevertheless, a high degree of phenotypic plasticity was observed, as all traits differed significantly between sites after accounting for provenance effects, with hydraulic safety-related traits showing the lowest and efficiency-related traits the highest plasticity. There was no evidence for inter-provenance variability in xylem embolism resistance (P_{50}) or the foliar carbon isotope signature ($\delta^{13}C$), a proxy for intrinsic water use efficiency (iWUE), and both were unrelated to growth. P_{50} was positively correlated with the lumen-to-sapwood area ratio and vessel density.

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Conclusions Because of the lacking trade-off between embolism resistance and growth, highly productive provenances can be selected without reducing the drought tolerance of the branch xylem. However, as xylem safety is only one element of a trees' drought response, it may be beneficial to select provenances with other more conservative drought adaptations such as smaller vessel lumen areas for increasing xylem safety and small supported total leaf areas for reduction of total transpiration.

Keywords Assisted migration, Carbon isotope, Embolism resistance, Hydraulic conductivity, Provenance trial, Wood anatomy

1 Introduction

European beech (*Fagus sylvatica* L.) is a crucial broadleaf tree species in Europe, playing significant roles in both ecological and economic domains (Antonucci et al. 2021). Nevertheless, recent changes in precipitation patterns and increasing frequency of heat waves have resulted in reduced production and stability as well as in elevated drought-induced mortality rates of beech stands (Krupková et al. 2019; Schuldt et al. 2020; Schmied et al. 2023). To mitigate the negative impacts of climate change, the use of assisted migration, which involves artificial transfer of seeds or seedlings, has been proposed as a possible adaptive strategy (Williams & Dumroese 2013; Bolte et al. 2023). Assisted gene flow is a subcategory of assisted migration defined by the movement of genetic material between different populations or provenances. This process aims to enhance the genetic diversity and adaptive potential of tree populations in response to environmental challenges, without species replacement. To assess the benefits and potential risks associated with this measure, common garden experiments have been established across Europe (Liesebach 2015; Robson et al. 2018). The implementation of common garden designs is crucial for evaluating changes attributable to the genetic composition of tree provenances (Robakowski et al. 2022; Balekoglu et al. 2023; Park & Rodgers 2023). Furthermore, evaluating multiple plots with different environmental conditions can provide insights into the short-term acclimation potential (phenotypic plasticity within provenance) of a population to new conditions.

Intraspecific variability allows for the existence of diverse traits among different populations or genotypes of European beech (González de Andrés et al. 2021). This variability can encompass variation at the wood level, i.e. wood anatomical features, embolism vulnerability and hydraulic efficiency, or at the leaf level, i.e. leaf morphology and leaf physiological responses such as carbon and nitrogen isotopic compositions, which all might be interconnected with growth-related patterns. This diversity serves as a reservoir of potential adaptive traits that may confer advantages under altered climatic conditions. A high degree of phenotypic plasticity—the ability of populations to exhibit different phenotypes in response to environmental cues—allows European beech to adjust its physiological, morphological and biochemical traits in the face of changing environmental stressors (Frank et al. 2017). For instance, the plasticity in xylem vulnerability to embolism or water use efficiency could enable some individuals or populations to better withstand drought or heat stress, essential qualities in times of a rapidly changing climate including increases in frequency and intensity of such stressors (Cavallaro et al. 2023; Rowland et al. 2023). As climate change continues to alter environmental conditions unpredictably, the adaptive potential within a species becomes crucial for its persistence (Bussotti et al. 2015). The ability of European beech to exhibit phenotypic plasticity in traits related to water use, growth and resistance to drought-induced embolism allows for higher survival rates as it can potentially acclimate to new climatic regimes or geographical areas (Gárate-Escamilla et al. 2019). By identifying populations or genotypes with superior adaptive potential, conservation efforts can prioritize these variants for maintaining genetic diversity or selectively introducing them into vulnerable or newly established ecosystems, thus aiding in the species' survival and adaptation.

Drought is a major limiting factor of photosynthesis, growth and survival of European beech (Leuschner et al. 2023). Hydraulic failure due to embolism formation occurring during frost exposure (Charra-Vaskou et al. 2023) and under low water potential during drought periods (Arend et al. 2021; Blackman et al. 2023) is one of the main factors behind tree mortality. The water potential at which plants lose 50% (P_{50}) or 88% (P_{88}) of their hydraulic conductance is a key trait describing drought tolerance in trees (Brodribb and Cochard 2009; Petek-Petrik et al. 2023). Embolism formation in xylem vessels commences a cascade of physiological responses that ultimately lead to tissue mortality (Mantova et al. 2023). While some tree species to a certain degree might be able to repair the damaged tissue (Knüver et al. 2022), this could not be confirmed for European beech after the severe 2018/2019 drought in Central Europe (Arend et al. 2022), highlighting the importance of an embolism-resistant xylem for withstanding drought.

The P_{50} of European beech can be affected by interactions of provenance (genotypic variability) and site (phenotypic plasticity) (cf., Wortemann et al. 2011). Hence, selection of populations with more negative P_{50} can be useful for assisted migration efforts toward greater drought stress resistance as long as this does not trade-off with yield. Such differences in P_{50} are caused by morphological adjustments at the xylem ultra-structure level (Isasa et al. 2023), which might likewise affect hydraulic efficiency and thus tree growth (e.g. Hajek et al. 2014, 2016). While the diameter of the water-conducting vessels commonly is associated with xylem safety across species, this often-described pattern disappears at the intra-specific level (Isasa et al. 2023). Here, the total number of pits and thus the total vessel wall area seem more influential, which is mirrored by the lumen-to-sapwood area ratio among other traits (Lübbe et al. 2022; Avila et al. 2023; Waite et al. 2023). This wood anatomical variable refers to the total area occupied by vessel per cross-sectional xylem area, where a higher lumen-to-sapwood area ratio indicates either the presence of wider and/or more vessel per cross-sectional xylem area. In European beech, however, two studies observed limited variability in P_{50} across provenances (Wortemann et al. 2011; Hajek et al. 2016), indicating that this safety-related trait might be quite static.

Specific conductivity (K_s) influences a tree's ability to transfer water and nutrients from the roots to the leaves, which are critical for various physiological processes essential for growth and productivity. Adequate water supply due to an efficient water-conducting system supports increased photosynthetic rates, which, in turn, provide the necessary resources for growth, including carbohydrates for structural development and energy. Consequently, different descriptors of hydraulic efficiency at either stem and/or branch level are commonly positively correlated with tree growth, both at the intra-specific (Hajek et al. 2014, 2016; Ramesha et al. 2022) and inter-specific (Hoeber et al. 2014; Kotowska et al. 2015; Kumar et al. 2022) levels. Hence, enhanced growth often demands larger, more efficient conduits for water transport, which facilitates increased nutrient uptake and biomass production. Moreover, tree-level hydraulic conductance is affected not only by vessel size, but also by total sapwood area involved in water transport (Kotowska et al. 2021; Pappas et al. 2022). Because xylem safety is strongly related to the thickness of inter-vessel pit membranes (Li et al. 2016; Isasa et al. 2023) while vessel diameter seems not to trade-off with xylem safety at the intra-specific level for beech (Hajek et al. 2016; Schuldt et al. 2016; Isasa et al. 2023), it might be possible to identify genotypes with high yield and high xylem safety. The lacking trade-off between P_{50} and

growth at the intra-specific level (e.g. Cochard et al. 2007; Fichot et al. 2009; Hajek et al. 2014, 2016) highlights the potential of this important drought-tolerance trait (e.g. Blackmann et al. 2023) for selecting suitable provenances for assisted migration efforts.

Another key trait for identifying provenances that are potentially better drought-adapted is water use efficiency (WUE), i.e. the amount of carbon gained per unit of water loss. An efficient use of water enables trees to maintain physiological functioning and sustain growth and survival during periods of water scarcity (Olano et al. 2023). Therefore, WUE is a crucial characteristic of forest ecosystems (Petrík et al. 2023). This is confirmed by studies reporting a negative relationship between tree growth and intrinsic water use efficiency (iWUE), i.e. the ratio of net photosynthetic assimilation to stomatal conductance (Wang et al. 2013; Dixit et al. 2022; Johnson and Brodribb 2023). Using leaf ^{13}C isotopes (δ^{13}C) as a proxy of iWUE is particularly advantageous as it captures the long-term carbon–water balance of plants (Condon et al. 2004; Frank et al. 2015; Brendel 2021; Rabarijaona et al. 2022).

The efficiency of photosynthesis and the water content in plant tissues are significantly linked to N availability. A higher leaf N concentration can potentially counterbalance the adverse effects of water scarcity and increased evaporative demand, enabling trees to maintain high WUE (Song et al. 2019). Higher soil N availability is often reflected in a lower foliar C:N ratio (Sardans et al. 2012; Sheng et al. 2021), while a lower foliar nitrogen isotopic composition (δ^{15}N) can be indicative for a rich mycorrhizal fungal network (Hobbie & Högberg 2012; Clemmensen et al. 2021).

We selected seven European beech (*Fagus sylvatica* L.) provenances differing in growth performance from two common garden sites in Slovakia and Germany differing in climatic and edaphic conditions. The provenances originate from the Pyrenees in Spain up to the Carpathian Mountains in Slovakia, covering a steep climatic gradient at their places of origin. We investigated two growth-related and ten functional wood and leaf traits of which most are related to hydraulic safety and efficiency (Table 1) in order to quantify the magnitude of inter-provenance and/or phenotypic plasticity. Here, we consider the specific hydraulic conductivity, average vessel diameter, vessel density and the lumen-to-sapwood area ratio as traits related to hydraulic efficiency while the xylem pressures at 50% and 88% loss of hydraulic conductivity and the carbon isotope signature are considered as traits related to hydraulic safety. We tested whether (i) traits related to hydraulic safety display less variability (inter-provenance variability and/or phenotypic plasticity) than traits related to hydraulic efficiency, while (ii) yield is unrelated to hydraulic safety.

Table 1 List of variables included, with units and definitions

Acronym	Unit	Variable
Environmental conditions		
MAT	°C	Mean annual temperature
MMT	°C	Mean minimal temperature in January
MAP	mm	Mean annual precipitation
MSP	mm	Mean early growing season precipitation
EQ		Ellenberg's quotient
FAI		Forest aridity index
Growth-related parameters		
H_{inc}	m year^{-1}	Tree height
AGB_{inc}	kg year^{-1}	Aboveground biomass
Wood properties		
$A_L{:}A_X$	%	Vessel lumen-to-sapwood area ratio
D	μm	Vessel diameter
VD	n mm^{-2}	Vessel density
K_S	kg m^{-1} MPa^{-1} s^{-1}	Empirical specific conductivity
P_{50}	MPa	Xylem pressure at 50% loss of hydraulic conductance
P_{88}	MPa	Xylem pressure at 88% loss of hydraulic conductance
Foliar traits		
$A_S{:}A_L$	10^{-4} m^2 m^{-2}	Sapwood-to-leaf area ratio (Huber value)
C:N		Carbon-to-nitrogen ratio
$\delta^{13}C$	‰	Carbon isotope signature
$\delta^{15}N$	‰	Nitrogen isotope signature

2 Materials and methods

2.1 Plant material, experimental sites and field conditions

Provenance seeds of European beech (*Fagus sylvatica* L.) were collected from 100 natural populations across Europe, the seeds grown in a nursery, and 2-year-old seedlings were distributed to common garden sites within a Europe-wide provenance experiment (von Wühlisch et al. 1998; Liesebach 2015). Two common garden sites established in 1995 were used for this study (Fig. 1a). The German site is located near Kiel (54° 18′ N, 10° 16′ E, 40 m a.s.l.), while the Slovakian site is situated near Hriňová (48° 31′ N, 19° 34′ E, 840 m a.s.l.). The German site was previously used as agricultural land, and the Slovakian site was afforested from 1970 onwards, mostly with Norway spruce. The climatic data for comparison of the provenances and common garden sites were derived from the WorldClim database (Fick and Hijmans 2017). The reference period for the climate at origin of the provenances was 1950–2000, as it characterizes the period of seed collection and the conditions under which the parent trees developed before their seeds were transferred to the common garden sites (Sáenz-Romero et al. 2019). The comparison period for the common garden sites is 2000–2017, the interval during which the trees grew and were sampled. We used two aridity metrics, the Ellenberg quotient (EQ; Ellenberg 1988) and the Forest Aridity Index (FAI; Gavrilov et al. 2019), to compare the two sites

$$\mathrm{EQ} = 1000 \times \frac{T_w}{\mathrm{MAP}},$$

where T_w represents the temperature of the warmest month (°C) and MAP represents the total sum of annual precipitation (mm), and

$$\mathrm{FAI} = 100 \times \frac{T_{7-8}}{P_{5-7} + P_{7-8}},$$

where T_{7-8} represents mean temperature from July to August (°C), P_{5-7} represents the precipitation sum from May to July (mm) and P_{7-8} represents the precipitation sum from July to August (mm).

Even though the North German site has a more oceanic climate and the Slovakian site is more continental, the relatively high altitude of the Slovakian site leads to similar precipitation patterns. This is reflected also in very similar values of EQ and FAI between the common garden sites. However, winter temperature is lower in the Slovak plot and early frost risk is higher in the Slovakian site (Table 2). The two sampling campaigns (leaf and branch samples) were conducted in August of 2014 at the German site and in August of 2017 at the Slovakian site. The vegetation seasons of sampling years were similar in regard to average air temperature and precipitation patterns (Fig. 1e, f).
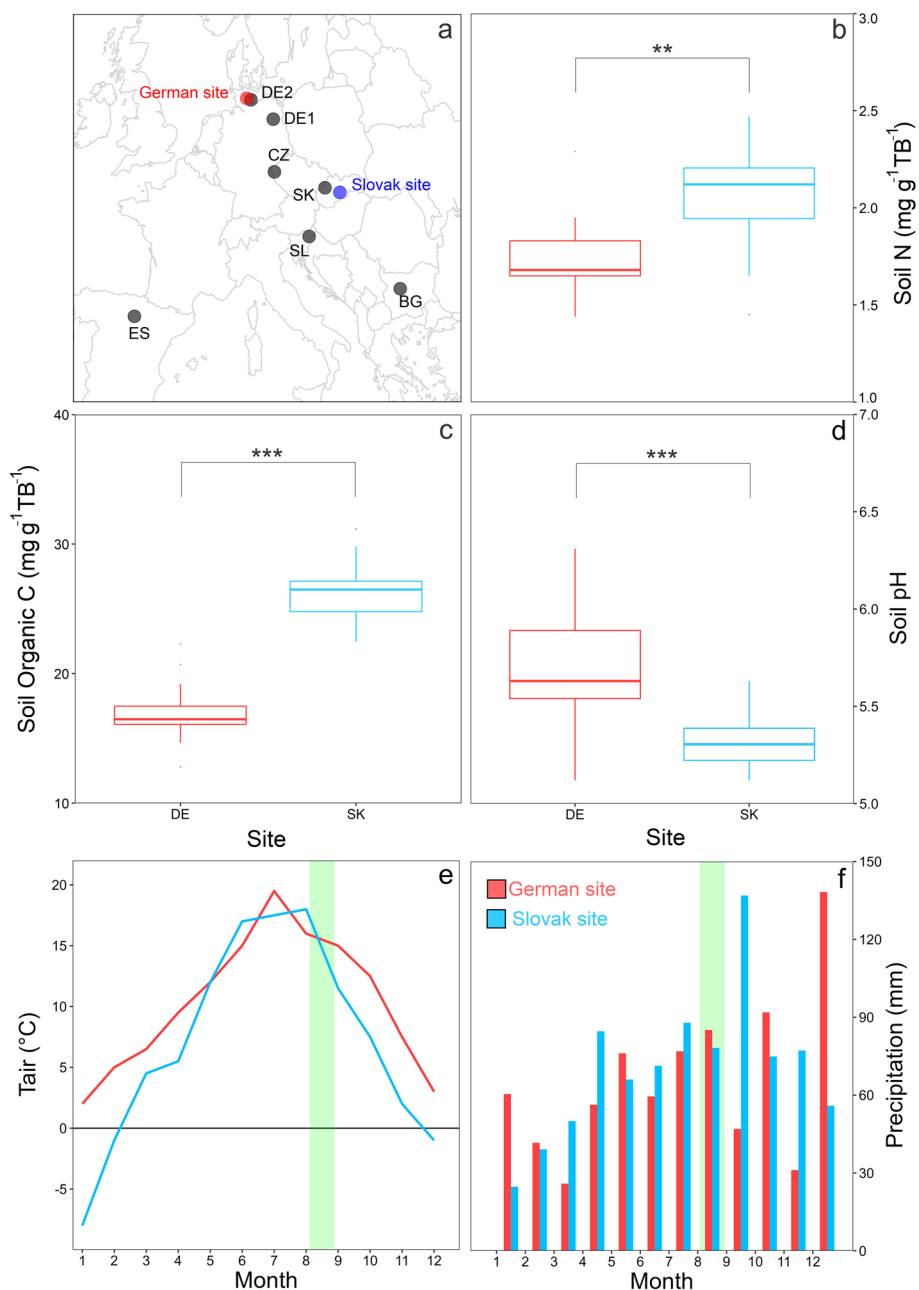
Fig. 1 Map of the locations at origin of the analysed populations (black dots) as well as the location of the experimental common garden sites in Germany (red colour) and Slovakia (blue colour) (**a**), and soil N content (**b**), soil organic C content (**c**) and soil pH (**d**) for both common garden sites. Further given are the monthly mean air temperature (**e**) and monthly precipitation sums (**f**) during the sampling years (DE, 2014; SK, 2017) for both sites; the sampling period has been highlighted with light green stripes. Significance levels: ***$p < 0.001$; **$p < 0.01$

Provenances were planted under a randomised block design, with three blocks at the German site and two blocks at the Slovakian site. The set of seven provenances occurring in both sites was selected to cover a broad climatic gradient at the place of origin (Fig. 1). Thus, we selected provenances from different geographic regions and climates throughout Europe with a wide range of

mean annual temperature (6–15.3 °C) and mean annual precipitation (575–1050 mm). The geographic and climatic data of both common garden sites and provenances are presented in Table 2.

At the German site near Kiel, the soil type varies from loamy sand to sandy loam with good nutrient availability that does not limit tree growth (Müller 2012). At the

Table 2 Location, altitude and climatic characteristics of the place of origin for all tested provenances and common garden sites extracted from WorldClim database (Fick and Hijmans 2017) for the 1950–2000 period for provenances and 2000–2017 period for sites

Provenances	Country	Coordinates	Altitude (m)	MAT (°C)	MMT (mm year^{-1})	MAP (mm year^{-1})	MSP (mm year^{-1})	EQ	FAI
BG	Bulgaria	42° 55′ N, 24° 16′ E	900	15.3	na	945	214	32.12	6.09
CZ	Czech	50° 2′ N, 12° 37′ E	690	6.0	na	750	218	16.30	3.03
DE1	Germany	53° 0′ N, 13° 10′ E	70	8.5	na	575	162	31.23	5.75
DE2	Germany	54° 12′ N, 10° 45′ E	80	8.3	na	700	162	22.41	4.63
ES	Spain	42° 15′ N, 2° 45′ W	950	9.9	na	860	170	33.79	9.16
SK	Slovakia	48° 53′ N, 18° 0′ E	200	9.0	na	670	211	27.99	4.59
SL	Slovenia	46° 18′ N, 15° 36′ E	420	9.0	na	1050	286	19.67	3.68
Common gardens									
DE$_{site}$	Germany	54° 18′ N, 10° 16′ E	40	9.2	−0.8	788	168	22.25	4.67
SK$_{site}$	Slovakia	48° 31′ N, 19° 34′ E	840	7.1	−7.0	822	235	21.36	3.69

MAT mean annual temperature, *MMT* mean minimal temperature during January, *MAP* mean annual precipitation, *MSP* mean early growing season precipitation from April to June, *EQ* Ellenberg's quotient, *FAI* Forest Aridity Index

Slovakian site, soil is a mesotrophic Eutric Cambisol, a sandy loam on granodiorite parent rock (Šály et al. 2011). In addition, soil samples from both sites were collected in 2022 from the 0–30-cm layer using a Puerckhauer sampler. A composite sample from three positions in each subplot (for each provenance and block separately) was used for the analysis. The samples were sent to the laboratory of the Department of Plant Ecology and Ecosystem Research at the University of Göttingen, Germany, for analysis of soil N and organic C (Fig. 1b–d). Soil samples were oven-dried at 70 °C for 48 h and soil C and N concentrations quantified by gas chromatography (Vario EL III; Elementar, Hanau, Germany). The soil organic matter content was determined by the dry ignition method at 600 °C.

2.2 Huber value, leaf carbon and nitrogen analysis

The leaves from 9 to 12 branches from each branch were removed from the basipetal segment upwards to determine cumulative leaf area (A_L, m^2) using a flatbed scanner and the WinFOLIA software (Régent Instruments, Quebec, Canada). The branch-level Huber value, i.e. sapwood-to-leaf area ratio (A_S:A_L, 10^{-4} m^2 m^{-2}), was calculated by dividing the maximal sapwood area of the branch by A_L.

Leaves for the measurement of carbon and nitrogen concentration and isotope partitioning were sampled in August 2014 and August 2017 from the German and Slovakian site, respectively. The leaves were sampled from upper-canopy branches of at least ten random trees per provenance with a long-reaching pruner. Both samplings were conducted during summer to obtain fully mature leaves. In total, leave samples of 145 individuals were analysed at the Centre for Stable Isotope Research

and Analysis (KOSI), University of Göttingen. C and N concentrations as well as carbon and nitrogen isotopic signatures (δ^{13}C and δ^{15}N, respectively) were measured with a Delta Plus isotope mass ratio spectrometer (Finnigan MAT, Bremen, Germany), a ConFlo III interface (Thermo Electron Corporation, Bremen, Germany) and a NA2500 elemental analyser (CE Instruments, Rodano, Milan, Italy) using standard δ notion: $\delta = (R_{sample} / R_{standard} - 1) \times 1000$ (‰).

2.3 Xylem anatomy

Branches for the xylem anatomy measurements were sampled from the sun-exposed upper part of the crown in 2014 and 2017 from the German and Slovakian site, respectively (the same branches used for leaf sampling). Anatomical parameters were assessed on 9–12-branch segments per provenance from the basal end of the branches used for hydraulic measurements. Although the samples from the German site were collected and analysed in August 2014 and those from the Slovakian site in August 2017, branch age of the analysed segments was comparable (2.81 ± 0.07 years, mean ± SE, $n = 148$). The segments were stored in ethanol (70%) until further processing. Transverse sections of 10–20 μm width were then cut with a sliding microtome (G.S.L.1; Schenkung Dapples, Zürich, Switzerland), stained with a safranin solution (1 in 50% ethanol; Merck, Darmstadt, Germany) and embedded in Euparal medium. Microscopic images of the cross-sections were obtained with a stereo-microscope with an automatic stage (SteREO V20; Carl Zeiss MicroImaging GmbH, Jena, Germany) using the AxioVision v4.8.2 software (Carl Zeiss MicroImaging GmbH, Jena, Germany) to digitalise the complete cross-section. Images were analysed using Adobe Photoshop CS2 (version 9.0;

Adobe Systems Incorporated, USA) and the particle analysis function of ImageJ (Schneider et al. 2012). The complete xylem cross-section without pith and bark was used for all subsequent calculations. The parameters were calculated as follows: idealised vessel diameter (D, μm), as obtained from major (a) and minor (b) vessel radii as $D = (32 \times (a \times b)^3 / (a^2 + b^2))^{\frac{1}{4}}$, and vessel density (VD, n mm^{-2}) (Lewis and Boose 1995). The lumen-to-sapwood area ratio ($A_L{:}A_X$, %) was derived by dividing the cumulative vessel lumen area by the corresponding sapwood area. While distance to the branch tip is known to be highly influential for measurements of wood anatomical traits (Lechthaler et al. 2019; Soriano et al. 2020), no measurements are available for the present dataset. To overcome this shortcoming and to test for differences in distance to tip between sites and provenances, we modelled it based on the branch diameter-branch length scaling (cf. Weithmann et al. 2022a, b). According to this analysis, the analysed samples did not differ systematically in distance-to-tip between provenances and/or sites. For the complete analysis of a modelled distance-to-tip effect, please refer to the data repository (Kurjak et al. 2024).

2.4 Hydraulic conductivity

The hydraulic conductivity of ten branch segments per provenance was measured using the Xyl'em apparatus (Bronkhorst, Montigny-les-Cormeilles, France) on branch segments with an average length of 294.4 ± 0.9 mm (mean ± SE, $n = 148$). In the laboratory, all lateral branches were removed, and the resulting scars were sealed using quick-drying superglue (Loctite 431; Henkel, Düsseldorf, Germany) suitable for wet surfaces. To determine the maximum hydraulic conductivity (K_h, kg m^{-1} MPa^{-1} s^{-1}) at 6 kPa, demineralized and degassed water containing 10 mM KCl and 1 mM CaCO$_3$ was used. Prior to the measurements, three 10-min flushes at 120 kPa were conducted to ensure the removal of any potential emboli. The diameter of each segment was measured at both the basipetal and distal ends, as well as at four positions along the segment. The sapwood area without pith and bark for a given beech branch segment diameter was then calculated using the regression coefficients from Schuldt et al. (2016) as $A_{xylem} = -3.715 + 0.770 A_{cross}$. Subsequently, the branch-level, empirically specific conductivity (K_s, kg m^{-1} MPa^{-1} s^{-1}) was determined by dividing K_h by the maximum basipetal sapwood area (cf. Schuldt et al. 2016; Hajek et al. 2016).

2.5 Vulnerability to embolism

Vulnerability to xylem cavitation was measured on 9–12 branch samples (replicated trees) per provenance and site (137 samples in total), using the Cavitron technique (Cochard et al. 2005). Segments with a length of 27.5 cm were inserted into the chamber of a custom-built honeycomb rotor attached to a commercially available centrifuge (Sorvall RC-5C; Thermo Fisher Scientific, Waltham, MA, USA). The software Cavi-Soft (version 4.0.1.3; University of Bordeaux, France) was used to record conductance under increasing rotation speed to create rising tension in vessels. Conductivity measurements started at -1.0 MPa and were repeated while reducing water potential in steps of 0.2 to 0.3 MPa until the percent loss of conductivity (PLC) was 90%. All vulnerability curves were s-shaped, indicating that the curves were not affected by open-vessel artefacts (cf. Martin-StPaul et al. 2014). Consistent with this, a maximum vessel length of 19.3 ± 2.6 cm has been reported in European beech (Lübbe et al. 2022). For each sample, the PLC values were plotted against xylem pressure and fitted to a sigmoidal function using nonlinear least squares (Pammenter and Vander Willigen 1998) as $PLC_i = 100 / (1 + \exp(s/25 \times (P_i - P_{50})))$, where PLC_i is the observed PLC for observation i, P_i is the corresponding water potential, P_{50} (MPa) is the water potential causing 50% loss of hydraulic conductivity and s (% MPa^{-1}) is the slope of the curve at the inflexion point. The water potential at 88% loss of conductivity (P_{88}) was computed from the equation by substituting the corresponding PLC quantile and solving for P. The provenance average PLC curves for each common garden site are plotted in Figure 6 in Appendix.

2.6 Dendrometric measurements

The aboveground growth performance of the respective provenances within the two common gardens was evaluated based on diameter at breast height (DBH, cm) and tree height (H, m), measured with a forestry calliper and a Vertex III device (Haglöf, Inc., Sweden), respectively. The measurements were conducted after the vegetation seasons 2014 (German site) and 2016 (Slovakian site). Aboveground biomass was estimated from an empirical equation given by Wutzler et al. (2008) as aboveground biomass (AGB) $= 0.00523 \times DBH^{2.12} \times H^{0.655}$. To make data of the two sites comparable, we divided the measured values of H and AGB by the number of vegetation seasons from establishment of the trials to measurements to obtain annual increments, height increment (H_{inc}) and aboveground biomass increment (AGB_{inc}).

2.7 Phenotypic plasticity

The phenotypic plasticity for each provenance and trait was calculated from the median differences between the two sites. As most of the traits were not normally distributed (Valladares et al. 2006), we computed the plasticity

Kurjak *et al. Annals of Forest Science*   (2024) 81:11

Page 8 of 21

index, based on maximum and minimum medians (PI_{md}), as follows:

$$PI_{md} = (x_{max} - x_{min})/x_{max},$$

where x_{max} is the maximum median (provenance median from site with higher median) and x_{min} the minimum median (provenance median from site with lower median. Values of PI_{md} closer to 0 represent limited phenotypic plasticity, and values close to 1 represent high phenotypic plasticity.

2.8 Statistical analysis

All statistical analyses were conducted in the R statistical software v4.2.0 (R Core Team 2022). After excluding individuals with missing values, the total sample size is 145 individuals for all traits, 69 individuals from the German site and 76 from the Slovakian site. The homogeneity of variance between populations was first analysed by Bartlett's test. Then, the normal distribution of each trait was tested by the Shapiro–Wilk test. All traits except P_{50}, P_{88}, $\delta^{13}C$ and D were not normally distributed and were further log-transformed for the ANOVA. A three-way ANOVA was used with provenances, common garden sites and blocks as factors with fixed effects. Moreover, differences between provenances were tested separately for each plot by Tukey's HSD post hoc test. Pearson correlation analysis was used to test for inter-relationships between traits based on data pooled across all provenances and both sites, with the corrmorant R package (Link 2020). The significance of Pearson correlations was tested via cor.test function in R. Finally, principal component analysis on scaled and centred data was applied with factoextra library (Kassambara and Mundt 2020) to explore the overall relationship between the traits and examine the site and provenance clustering within this system.

3 Results

3.1 Overall variability across provenances and sites

All tested traits showed significant differences between the two common garden sites (Table 3). Likewise, provenance had a significant impact on 9 of the 12 growth-related, wood and foliar traits, indicative for a high degree of inter-provenance variability; only vessel diameter (D), water potential at 50% loss of hydraulic conductance (P_{50}) and carbon isotope signature ($\delta^{13}C$) did not differ across provenances according to the three-way ANOVA (Table 3). On the other hand, block as a fixed factor did not influence any of the tested traits. The interaction of provenance and site significantly impacted all growth-related traits, the foliar nitrogen isotope ratio ($\delta^{15}N$) and D (Table 3),

Table 3 Results of three-way ANOVA for growth-related, wood anatomical, hydraulic and foliar traits between provenances (PV), across common garden sites (Site), their interactions (PV×Site) and blocks

Factor	df	SumSQ	MeanSQ	F	p
H_{inc}					
PV	6	0.06	0.01	2.64	*0.02*
Site	1	0.08	0.08	19.54	*<0.001*
PV×Site	6	0.19	0.03	7.98	*<0.001*
Block	3	0.01	0.004	1.05	0.37
Residuals	107	0.43	0.004		
P_{50}					
PV	6	0.2	0.03	0.62	0.72
Site	1	0.44	0.44	8.18	*<0.01*
PV×Site	6	0.81	0.14	2.5	*0.03*
Block	3	0.125	0.04	0.76	0.52
Residuals	107	5.853	0.05		
AGB_{inc}					
PV	6	1.6	0.27	7.5	*<0.001*
Site	1	0.34	0.34	9.66	*<0.01*
PV×Site	6	0.72	0.12	3.36	*<0.01*
Block	3	0.06	0.02	0.57	0.64
Residuals	107	72.48	0.66		
P_{88}					
PV	6	0.7	0.28	4	*<0.01*
Site	1	0.45	0.45	6.3	*0.01*
PV×Site	6	0.67	0.11	1.58	0.16
Block	3	0.36	0.12	1.68	0.18
Residuals	107	7.57	0.07		
$A_S{:}A_L$					
PV	6	4.95	0.83	0.76	0.60
Site	1	10.01	10.01	9.25	*<0.01*
PV×Site	6	7.6	1.27	1.17	0.33
Block	3	1.76	0.59	0.54	0.65
Residuals	107	115.72	1.081		
$A_L{:}A_X$					
PV	6	0.105	0.02	2.49	*0.03*
Site	1	0.36	0.36	43.55	*<0.001*
PV×Site	6	0.07	0.01	1.61	0.15
Block	3	0.03	0.01	1.61	0.26
Residuals	107	0.75	0.01		
$\delta^{13}C$					
PV	6	1.05	0.17	0.28	0.95
Site	1	34.06	34.06	54.56	*<0.001*
PV×Site	6	6.04	1.01	1.61	0.15
Block	3	1.39	0.46	0.75	0.53
Residuals	107	66.8	0.62		
D					
PV	6	23.8	3.96	0.97	0.45
Site	1	147.9	147.86	36.28	*<0.001*
PV×Site	6	68.1	11.35	2.79	*0.02*
Block	3	9.7	3.22	0.79	0.5

Table 3 (continued)

Factor	df	SumSQ	MeanSQ	F	p
Residuals	107	436	4.08		
$\delta^{15}N$					
PV	6	4.39	0.73	5.88	*< 0.001*
Site	1	2.81	2.81	22.56	*< 0.001*
PV × Site	6	1.01	0.17	1.35	0.24
Block	3	0.51	0.17	1.36	0.26
Residuals	107	13.31	0.12		
VD					
PV	6	0.13	0.02	4.79	*< 0.001*
Site	1	0.83	0.83	189.7	*< 0.001*
PV × Site	6	0.02	0.004	0.83	0.55
Block	3	0.03	0.01	2.44	0.07
Residuals	107	2.27	0.02		
C:N					
PV	6	0.02	0.003	3.44	*< 0.01*
Site	1	0.4	0.4	414.69	*< 0.001*
PV × Site	6	0.007	0.001	1.15	0.34
Block	3	0.004	0.002	1.51	0.22
Residuals	107	0.1	0.001		
K_s					
PV	6	0.28	0.05	2.84	*0.01*
Site	1	0.9	0.9	54.79	*< 0.001*
PV × Site	6	0.11	0.02	1.12	0.36
Block	3	0.02	0.007	0.43	0.74
Residuals	107	1.78	0.02		

PV, Site, PV × Site and block are evaluated as fixed factors

df is degrees of freedom, SumSQ is the sum of the squares, MeanSQ is the mean square, *F* is the *F*-statistic, *p* is the significance, DBH_{inc} is the diameter at breast height increment, H_{inc} is the tree height increment, AGB_{inc} is the aboveground biomass increment, $\delta^{13}C$ is the carbon isotope ratio, $\delta^{15}N$ is the nitrogen isotope ratio, C:N is the carbon-to-nitrogen ratio, P_{50} is the water potential at 50% loss of hydraulic conductance, P_{88} is the water potential at 88% loss of hydraulic conductance, A_L:A_X is the lumen-to-sapwood area ratio, *D* is the vessel diameter, VD is the vessel density, K_s is the specific conductivity

indicating that provenances differed in their response to the different environments. The partitioning of sums of squares from the ANOVA analysis showed a strong effect of site on the variability of leaf $\delta^{13}C$, $\delta^{15}N$, the carbon-to-nitrogen ratio (C:N) and VD. Provenance had a high contribution to the variance in the increment of the DBH (DBH_{inc}) and AGB_{inc} compared to the other traits. The *Provenance-Site* interaction had the largest influence on H_{inc} (Fig. 2a). The results of the pairwise comparison between the provenances for all traits are given in Tables 4 and 5 in Appendix.

3.2 Growth performance

At the time of sampling, trees at the German site had reached an average AGB between 19.5 kg for the Slovenian (SL) provenance and 75.4 kg for the Slovakian (SK) provenance at an age of 19 years; i.e. growth performance almost differed by a factor of 4 across provenances. At the Slovakian site, a comparable AGB was observed, ranging between 28.0 kg for the SL provenance and 63.8 kg for the SK provenance, although the trees were 3 years older at the time of sampling (Table 4 in Appendix). As a consequence, AGB_{inc} on average was 15% lower at the Slovakian site compared to the German site (1.72 kg year^{-1} versus 2.04 kg year^{-1}, respectively).

Consequently, all studied growth rates differed significantly between sites and provenances, with significant provenance-specific differences in the site effect. Especially, the SL provenance showed lower DBH_{inc} and AGB_{inc} compared to other provenances at both sites, while the SK provenance showed exceptionally high growth rates (Table 4 in Appendix and Fig. 2a, b).

3.3 Embolism vulnerability and hydraulic efficiency

Even though the ANOVA results showed significant site differences in the water potential at 50% loss of hydraulic conductance (P_{50}; Table 3), the absolute difference between the mean P_{50} for the German (mean ± SE, −2.99 ± 0.04 MPa) and Slovakian (mean ± SE, −2.86 ± 0.03 MPa) sites was only 0.13 MPa (Table 5 in Appendix and Fig. 3a). At provenance level, the most remarkable difference between sites was observed for the Czech (CZ) provenance, with a difference of 0.43 MPa. The CZ provenance showed greater vulnerability to xylem embolism at the Slovakian site. The variability observed for P_{88} followed the patterns of P_{50}, with the exception of SL provenance, which differed significantly by 0.45 MPa between sites while no difference was detected in P_{50} (Fig. 3b).

While vulnerability to cavitation was comparable across sites, specific conductivity (K_s) was on average higher at the German site (3.76 ± 0.16 kg m^{-1} MPa^{-1} s^{-1}) than at the Slovakian site (2.64 ± 0.11 kg m^{-1} MPa^{-1} s^{-1}). There were also significant site differences within provenances, with a greater K_s value at the German site for all provenances except the Spanish (ES) and CZ provenances (Fig. 3f). The significant differences between sites for K_s were primarily driven by the CZ provenance, similar to P_{50} (Fig. 3f).

Moreover, provenances from the German site had significantly lower VD in their branch wood with greater vessel diameters (*D*) and lumen-to-sapwood area ratios (A_L:A_X; Fig. 3c–e) although the branches were on average 1 year younger at the German site at the time of sampling (mean branch age ± SE, 2.3 ± 0.1 years) compared to the Slovakian site (3.3 ± 0.1 years). VD differed significantly between sites for all provenances, and *D* differed significantly between sites for all provenances except SK, SL and CZ provenances.
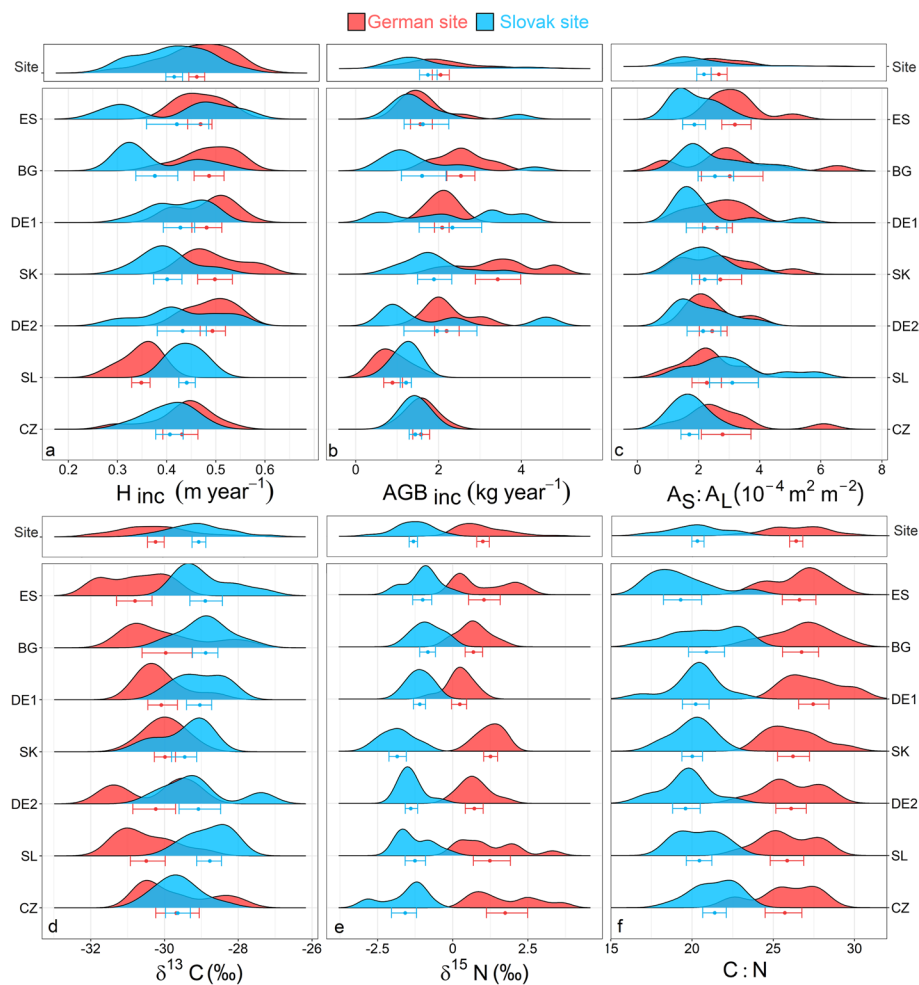
Kurjak *et al. Annals of Forest Science*   (2024) 81:11

Page 10 of 21

Fig. 2 Trait distribution between provenances and common garden sites for tree growth–related variables and leaf nutrient status. Given are the tree height increment (**a**, H_{inc}), aboveground biomass increment (**b**, AGB_{inc}), sapwood-to-leaf area ratio (**c**, A_S:A_L), leaf carbon isotope ratio (**d**, $\delta^{13}C$), leaf nitrogen isotope ratio (**e**, $\delta^{15}N$) and the foliar carbon-to-nitrogen ratio (**f**, C:N). Frequency distributions are supplemented with the provenance average (dots) and 95% confidence intervals. The provenances are sorted from the wettest origin (CZ) to driest origin (ES) based on Forest Aridity Index. Results of the post hoc tests are given in Table 4 in Appendix

3.4 Foliar chemistry

The trees growing at the German site showed significantly lower $\delta^{13}C$ values, higher $\delta^{15}N$ values and a higher C:N ratio of their leaves (Fig. 2d–f). The leaf $\delta^{15}N$ and C:N differed between the sites for all provenances, but the leaf $\delta^{13}C$ differed between sites only for the ES provenance, the two German provenances (DE1, DE2) and the SL provenance.

3.5 Trait relatedness to the climate at origin and phenotypic plasticity index

The phenotypic plasticity index based on medians (PI_{md}) differed between traits and provenances (Fig. 4a, b). The phenotypic plasticity of the safety-related hydraulic

traits, i.e. P_{50}, P_{88} and $\delta^{13}C$, was significantly lower across provenances than that of traits that could be related to hydraulic efficiency, foremost K_s and VD; a high phenotypic plasticity was likewise observed for the foliar chemistry traits ($\delta^{15}N$ and C:N). The provenances from more arid environments (higher EQ, lower MAP/mean season precipitation (MSP)) showed lower PI_{md} for P_{50}, P_{88}, A_L:A_X and $\delta^{13}C$ but higher PI_{md} of leaf C:N according to the correlation analysis (Fig. 4c). Moreover, mean annual temperature (MAT) of provenances' place of origin correlated positively with PI_{md} of H_{inc} and negatively with PI_{md} of A_L:A_X; i.e. provenance originating from a more arid environment developed a xylem with lower lumen-to-sapwood area ratios at the German and Slovakian site.
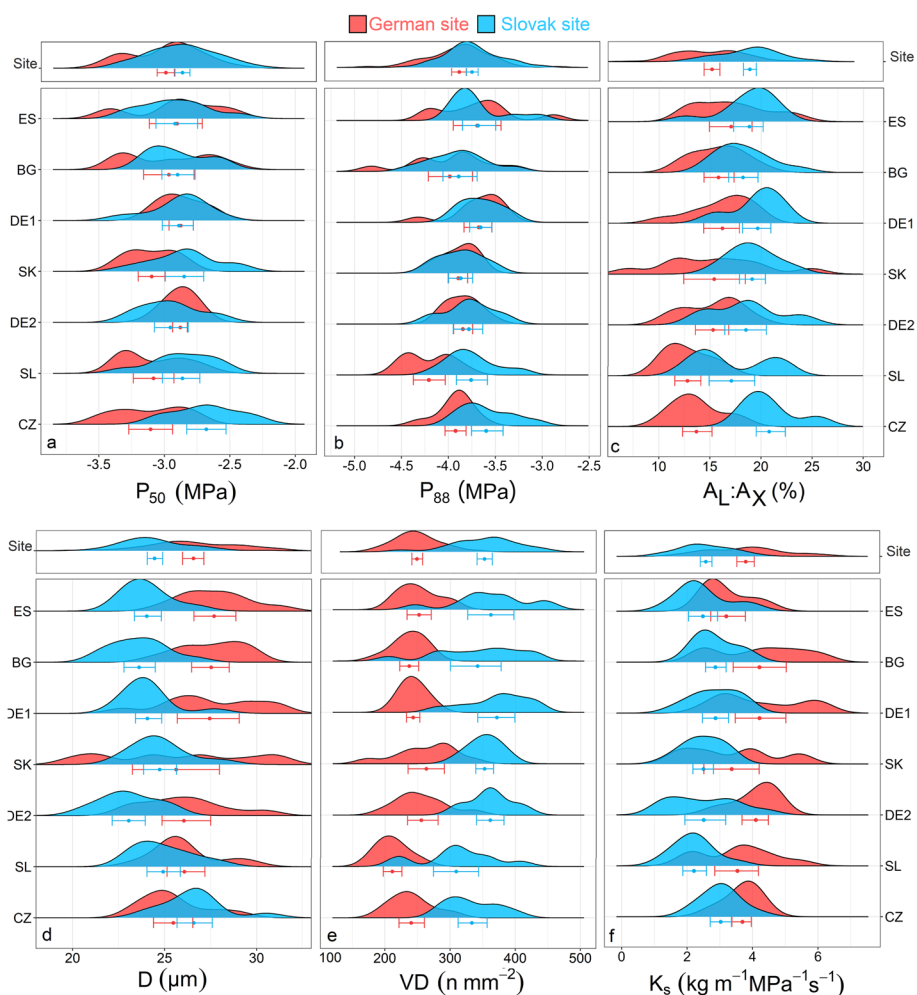
Kurjak *et al. Annals of Forest Science*   (2024) 81:11

Page 11 of 21

Fig. 3 Trait distribution between provenances and common garden sites for xylem hydraulic properties and xylem anatomical traits. Shown are the water potential at 50% loss of conductance (**a**, P_{50}), water potential at 88% loss of conductance (**b**, P_{88}), lumen-to-sapwood area ratio (**c**, $A_L:A_X$), vessel diameter (**d**, D), vessel density (**e**, VD) and specific conductivity (**f**, K_s). Frequency distributions are supplemented with the provenance average (dots) and 95% confidence intervals. The provenances are sorted from the wettest origin (CZ) to driest origin (ES) based on Forest Aridity Index. Results of post hoc tests are given in Table 5 in Appendix

3.6 Interrelationships between growth-related, wood and foliar traits

Across sites, no dependency of growth-related traits with any foliar or hydraulic trait was observed according to the Pearson correlation matrix (Fig. 5). Within sites, however, provenances displaying a high vessel density in their branch wood reached highest growth rates, though again, no trade-off between yield and xylem safety was observed (Figure 7 in Appendix). Across sites, xylem safety (i.e. P_{50}) and hydraulic efficiency (i.e. K_s) were both strongly related with the lumen-to-sapwood area ratio ($A_L:A_X$) and vessel density, two traits that are likewise associated with the

total vessel wall area per cross-section. $\delta^{13}C$ as a proxy for intrinsic water use efficiency was negatively correlated with D and K_s and positively correlated with VD (Fig. 5). Moreover, $\delta^{15}N$ showed a strong positive correlation with C:N and K_s and a strong negative correlation with VD, $A_L:A_X$ and P_{50}. The C:N ratio showed a strong positive correlation with D and K_s.

4 Discussion

4.1 Growth performance across provenances and sites

For European beech, a reduction in water availability, winter temperature, late frost exposure as well as growing season length might result in reduced growth
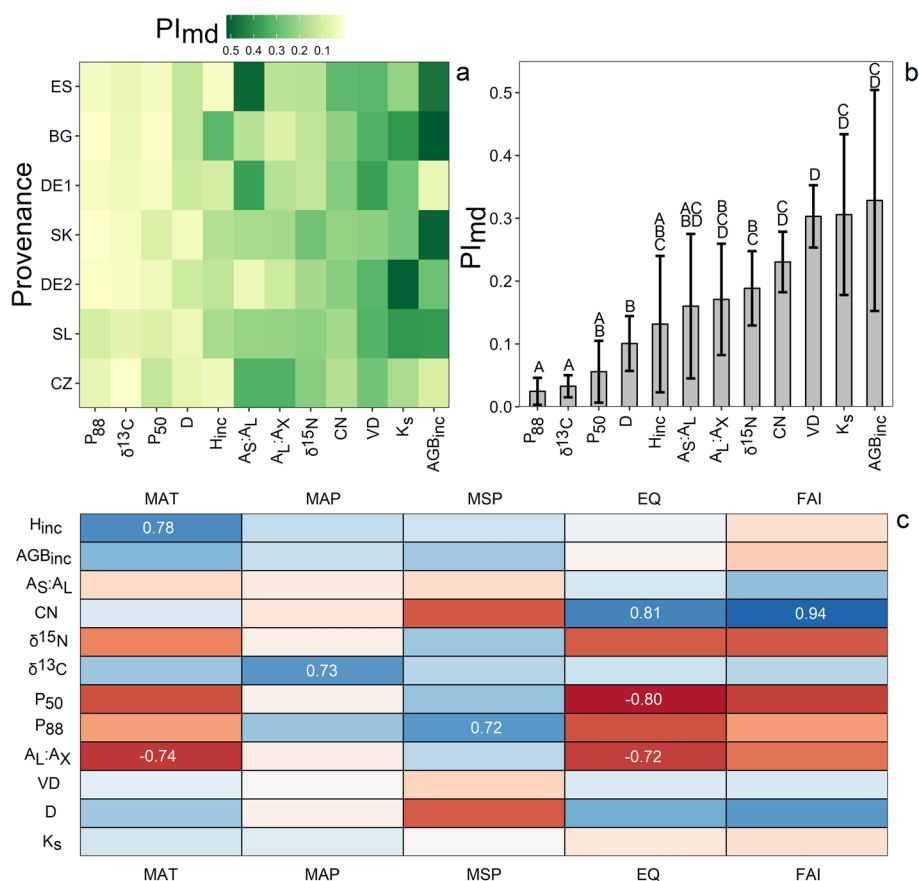
Fig. 4 The phenotypic plasticity indices of each trait and provenance (**a**), where PI_{md} can range between 0 (low plasticity) and 1 (high plasticity). The average PI_{md} of each trait (among provenances) with 95% confidence intervals and capital letters represent significant differences between groups based on Dunn's post hoc test (**b**). The Pearson correlation analysis between the original environment of provenances (MAT, mean annual temperature; MAP, mean annual precipitation; MSP, mean seasonal precipitation during April–June; EQ, Ellenberg quotient; FAI, Forest Aridity Index) and the measured traits (H_{inc}, tree height increment; AGB_{inc}, aboveground biomass increment; A_S:A_L, sapwood-to-leaf area ratio; C:N, leaf carbon-to-nitrogen ratio; δ^{15}N, leaf nitrogen isotope ratio; $\delta.^{13}$C, leaf carbon isotope ratio; VD, vessel density; D, vessel diameter; A_L:A_X, lumen-to-sapwood area ratio; P_{50}, water potential of 50% loss of conductance; P_{88}, water potential of 88% loss of conductance; K_s, specific conductivity) and only the correlations with a numeric value within the heat map were significant at $p < 0.05$ (**c**)

rates (Vitasse et al. 2009; Kreyling et al. 2012; Hofmann et al. 2015; Nord-Larsen & Pretzsch 2017). Here, lower temperatures as well as more frequent and severe frost exposure at the Slovakian site most likely resulted in reduced growth rates by on average 15% despite a more favourable soil nitrogen supply. At both sites, however, the same provenance showed the lowest (Slovenian provenance) and highest (Slovakian provenance) aboveground biomass increment (AGB_{inc}). These two extreme provenances differed by a factor of 2 to 4 in yield. These consistent differences between provenances represent the genetic differentiation of growth in European beech (genetic variability; cf. Hajek et al. 2016).

4.2 Differences in hydraulic safety and efficiency across provenances and sites

Across European beech populations, Stojnic et al. (2018) report a range in P_{50} from -2.8 to -3.5 MPa. In agreement, Weithmann et al. (2022a, b) likewise observed a range in P_{50} from -2.8 to -3.4 MPa across 30 sites in Northern Germany. With an average P_{50} of -3.0 MPa and -2.9 MPa for the German and Slovakian site, respectively, our results fall in this reported range. In European beech, a negative relationship between water availability and xylem safety has been observed, to either variable precipitation (Schuldt et al. 2016) or soil water availability (Weithmann et al.
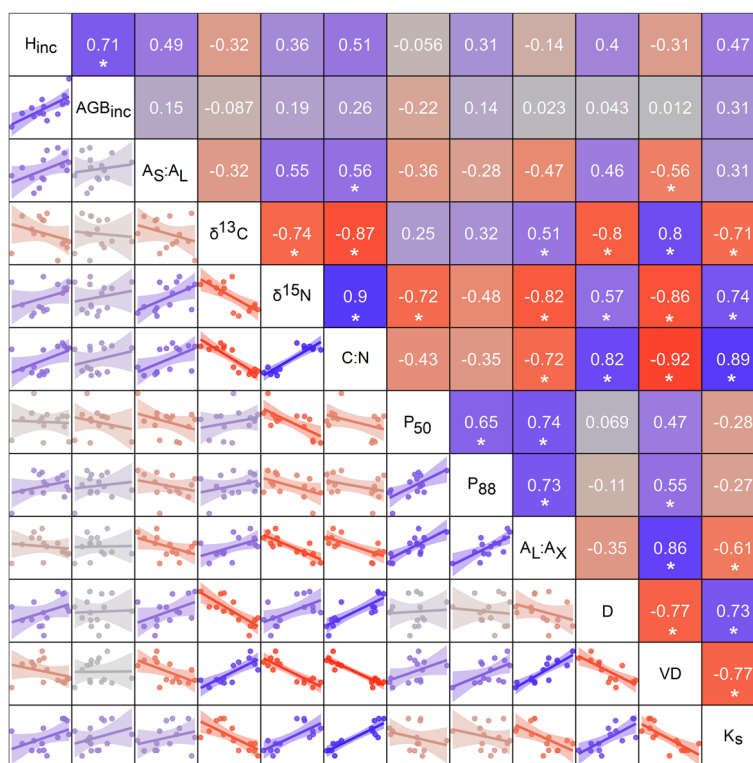
Fig. 5 Pearson correlation matrix with linear trends for all evaluated traits. *$p < 0.05$, significant correlations. Given are tree height increment (H_{inc}), aboveground biomass increment (AGB_{inc}), sapwood-to-leaf area ratio ($A_S:A_L$), leaf carbon isotope ratio ($\delta^{13}C$), leaf nitrogen isotope ratio ($\delta.^{15}N$), leaf carbon-to-nitrogen ratio (C:N), water potential of 50% loss of conductance (P_{50}), water potential of 88% loss of conductance (P_{88}), branch lumen-to-sapwood-area ratio ($A_L:A_X$), branch vessel diameter (D), branch vessel density (VD) and specific conductivity (K_s)

2022a, b). Here, we found a significant site effect in agreement with Wortemann et al. (2011). However, mean P_{50} across provenances differed by only 0.14 MPa between the German and Slovakian site, which we attribute to a fairly comparable precipitation regime throughout the growing season at both sites. Across provenances, however, no significant differences in P_{50} were found, confirming the limited degree of genetic differentiation in P_{50} across populations (Wortemann et al. 2011; Hajek et al. 2016). In combination with field studies along environmental gradients (Schuldt et al. 2016; Stojnic et al. 2018; Weithmann et al. 2022a), our results confirm the high acclimation capacity of xylem vulnerability to cavitation in beech to the prevailing hydroclimatic or soil moisture conditions at the place of growth.

In contrast to these two traits, we observed a high degree of variability in hydraulic efficiency between provenances (inter-provenance variability) and sites (phenotypic plasticity). Specific conductivity (K_s) was on average 30% lower at the Slovakian site compared to the German site and differed significantly between provenances. It is well described that K_s is a highly plastic variable, which differs strongly within (Lübbe et al. 2022) and across (Weithmann et al. 2022a) European beech individuals. We collected terminal branches of comparable diameter and modelled the distance to the tip (Kurjak et al. 2024), which is why we do not attribute our findings to a tree height effect (e.g. Lechthaler et al. 2019). Instead, differences in VD between provenances and sites seem mainly responsible for the high variation in hydraulic efficiency. Across sites, VD was by 30% lower at the German site compared to the Slovakian site, although tree height at the time of sampling was comparable (10.1 m versus 9.6 m at the German and Slovakian site, respectively).

Notably, there was no evidence for differences in distance-to-tip between samples from different sites or provenances, highlighting that the observed patterns are likely to reflect anatomical adjustments rather than artefacts caused by differences in the sampling

protocol (Kurjak et al. 2024). The air temperature and precipitation were similar for the two sites during the sampling years (Fig. 1e, f), but the multi-aged branch anatomy could have been affected by different climatic conditions.

4.3 Phenotypic plasticity and relatedness to the climate at the place of origin

Our findings are in line with various studies that report a high degree of phenotypic plasticity in European beech, which, among other traits, is reflected in stomatal morphology (Petrik et al. 2022), leaf phenology (Kramer et al. 2017), root architecture (Železnik et al. 2019), photochemistry (Pšidová et al. 2018), intrinsic water use efficiency (Dziedek et al. 2017) and seed germination and establishment success (Muffler et al. 2021). The overall high phenotypic plasticity among European beech populations indicates a considerable potential for acclimation or adaptation to the negative effects of climate change, at least to some extent (Leuschner 2020). Consequently, selection of proper seed material can significantly increase both juvenile and long-term survival rates (Andivia et al. 2021). Thereby, selection of provenances with higher iWUE and more negative P_{50} might significantly improve their drought stress survival rates (Stojnic et al. 2018; Mantova et al. 2023; Blackman et al. 2023).

Here, we used the phenotypic plasticity index (PI_{md}) according to Valladares et al. (2006) in order to quantify the degree of intra-population variability between traits. The three safety-related traits (P_{50}, P_{88} and $\delta^{13}C$) showed overall lowest PI_{md} among traits, confirming strong genetic control as concluded above. On the other hand, the two efficiency-related traits (K_s and VD) as well as AGB_{inc} were the most plastic traits. However, the growth-related traits showed a high degree of variability among the provenances, and especially, the SK and Bulgarian (BG) provenances showed high growth phenotypic plasticity. Correlation analysis revealed that provenances from more humid sites (higher MAP/MSP, lower EQ/FAI) showed higher phenotypic plasticity of the three safety-related traits (P_{50}, P_{88} and $\delta^{13}C$) and the lumen-to-sapwood area ratio ($A_L:A_X$). Several recent studies have shown a close relationship between this wood anatomical trait and P_{50}, which will be discussed below. Within a given species like beech, a higher relative lumen area per cross-sectional xylem area is associated with a lower embolism resistance (Lübbe et al. 2022; Weithmann et al. 2022b; Avila et al. 2023; Waite et al. 2023). Interestingly, we

observed that provenances from a warmer climate (MAT) showed a lower phenotypic plasticity of $A_L:A_X$, which might be interpreted as a genetically determined drought-tolerance adaption. In regions with more arid conditions or increased competition at the edges of species distribution, there is likely an elevated selection pressure compared to other areas within the species' range (Michalski et al. 2017). Consequently, populations that evolved under more intense selection may prioritize strong genetic control for safety over extensive phenotypic plasticity within the population (Callahan et al. 2008). This emphasis on genetic control could result in trait canalization, potentially leading to reduced overall phenotypic adaptability (Debat et al. 2001; Klingenberg et al. 2019).

4.4 Interrelationships between growth-related, wood and foliar traits

We expected to find a close dependency of growth performance on hydraulic efficiency as previously reported at the intra-specific level (cf. Hajek et al. 2014; Ramesha et al. 2022), which was not confirmed. In fact, H_{inc} and AGB_{inc} were unrelated to all other wood anatomical, hydraulic and foliar traits. The lack of a clear relationship between growth and P_{50} or iWUE suggests that using more productive provenances would not trade-off with xylem safety in their new environment. We therefore consider the lack of a relationship between growth and P_{50} or iWUE as a major finding for assisted migration strategies of European beech. The measurements of P_{50} included on average two to three years of growth, and for leaf $\delta^{13}C$ we analysed one single year only. On the other hand, the increment data captured 19 or 22 years of growth, which might be one potential explanation for the absence of any correlation.

However, we observed a close relation between xylem embolism resistance (P_{50}) and both VD and the lumen-to-sapwood area ratio ($A_X:A_L$) in agreement with recent studies (cf., Lübbe et al. 2022; Weithmann et al. 2022b; Avila et al. 2023; Waite et al. 2023). At the intra-specific level, not the average diameter of vessels matters but the total vessel wall area, which is mirrored by VD and $A_X:A_L$ and should be related to the total number of inter-vessel pits. While pit membrane thickness (T_{pm}) is directly related to P_{50} (Isasa et al. 2023), increasing the number of pits might trade-off with xylem safety as the probability of encountering large pores in pore constriction sizes will increase, at least within a certain range of T_{pm} (Kaack et al. 2021).

We further found a negative correlation between $\delta^{13}C$ and both D and K_s and a positive correlation between VD and $\delta^{13}C$. This indicates that trees with smaller vessel diameter, greater vessel density and lower specific conductivity have a higher foliar iWUE. Hence, our results suggest that provenances with higher iWUE have lower hydraulic requirements to maintain leaf gas exchange, or the lower K_s leads to greater iWUE by constraining water supply in leaves. The negative correlation between K_s and $\delta^{13}C$/iWUE has been observed for numerous tree species (Fichot et al. 2009; Andrade et al. 2022; Wedegaertner et al. 2022; Liu et al. 2023) although results are mixed as others report either a positive (Jin et al. 2016; Corcuera et al. 2012) or no relationship (Sellin et al. 2013, 2014). Thus, the link between the K_s and iWUE is inconclusive and more extensive analyses are needed.

We did not observe a significant correlation between iWUE and P_{50}. In contrast, Alvarez-Maldini et al. (2022) found that lower P_{50} among almond cultivars corresponded to higher iWUE, suggesting coordination of hydraulic safety and water utilization strategy. Likewise, Yao et al. (2020) observed a close correlation between P_{50} and iWUE in Caragana species under water-deficit treatment, but no significant correlation for the well-watered control treatment. The lack of correlation in our study might therefore be attributed due to humid conditions at both sites.

4.5 Implications for assisted migration

Based on the results of this study, we conclude that the SK provenance showed overall best growth at both the German site and Slovakian site. Moreover, the SK provenance showed above-average $\delta^{13}C$ values, while P_{50} was comparable among provenances. Therefore, it could be seen as a seed source for highly productive forests without a negative trade-off between drought resistance and growth. The SL provenance, on the other hand, showed lowest yield, VD and lumen-to-sapwood area ratio ($A_X:A_L$) as well as the most negative P_{88} value at both sites. Furthermore, this provenance developed the smallest total leaf area per cross-sectional xylem area, i.e. the sapwood-to-leaf area ratio ($A_S:A_L$). During severe drought, the smaller surface area might result in a longer desiccation time (cf. Blackman et al. 2019; Petek-Petrik et al. 2023), which, in the long run, might be more favourable due to the

anticipated increase in severe global change-type drought events (Hari et al. 2020). The SL provenance also showed the highest iWUE ($\delta^{13}C$) at the Slovakian site and above-average iWUE at the German site. Based on these traits, the SL provenance can be categorised as more drought resistant but at the cost of growth performance.

The ES and BG provenances originating from the driest environments (based on FAI) did not show remarkably greater drought resistance based on iWUE and P_{50} than provenances from more humid environments, such as the CZ provenance or the SL provenance. Nevertheless, other important parameters that we did not investigate, such as rooting depth, minimal leaf conductance and capacitance (cf. Choat et al. 2018), might also be critical for the characterisation of drought resistance of these provenances.

5 Conclusion

We observed significant site differences for all traits covered after accounting for provenance effects, suggesting a high degree of phenotypic plasticity in European beech. However, as the sites differed in both soil N availability and winter temperature conditions, we cannot conclude which environmental factor had the prevailing effect on the acclimation response. While $\delta^{13}C$ as a proxy for intrinsic water use efficiency of provenances was associated with hydraulic efficiency, hydraulic efficiency itself was unrelated to xylem safety. Instead, the lumen-to-sapwood area ratio revealed a strong negative relationship with P_{50}. Overall, hydraulic efficiency-related traits had the highest and safety-related traits the lowest plasticity according the phenotypic plasticity index analysis. Tree growth showed no significant correlation with any of the traits measured, confirming no trade-off between growth and xylem safety in European beech. The lack of trade-off suggests that it might be possible to select highly resistance provenances without negatively affecting their growth potential. On the other hand, the provenance with the lowest growth performance developed branches that supported less total leaf area and a xylem with lower total lumen area, which might be considered as drought adaptation. Overall, the observed differences highlight the potential for assisted migration efforts, which should ideally be supported by dry-down experiments.

Kurjak *et al. Annals of Forest Science*   (2024) 81:11

Page 16 of 21

Appendix

Table 4 Provenance-level averages (± 95% confidence interval) of growth characteristics properties and leaf carbon and nitrogen content for both common garden sites

Site	Prov	H_{inc} (m year^{-1})	AGB_{inc} (kg year^{-1})	A_S:A_L (10^{-4} m^2 m^{-2})	δ^{13}C (‰)	δ^{15}N (‰)	C:N
DE	BG	0.49 ± 0.04ab	2.54 ± 0.41ab	3.022 ± 1.19ab	− 29.97 ± 0.83abc	0.69 ± 0.37bc	26.74 ± 1.3a
DE	CZ	0.43 ± 0.06abc	1.54 ± 0.32bcd	2.786 ± 0.98ab	− 29.85 ± 0.84abc	1.81 ± 0.91a	26.18 ± 1.47a
DE	DE1	0.48 ± 0.04ab	2.13 ± 0.22bcd	2.604 ± 0.61ab	− 30.09 ± 0.51abc	0.20 ± 0.33c	27.39 ± 1.36a
DE	DE2	0.49 ± 0.03ab	2.19 ± 0.37abcd	2.445 ± 0.55ab	− 30.24 ± 0.72bc	0.72 ± 0.36bc	26.10 ± 1.25a
DE	ES	0.49 ± 0.05ab	1.48 ± 0.78bcd	3.19 ± 0.57a	− 30.52 ± 1.12c	0.64 ± 1.28bc	26.23 ± 1.73a
DE	SK	0.50 ± 0.04a	3.43 ± 0.69a	2.713 ± 0.87ab	− 29.99 ± 0.36abc	1.26 ± 0.29ab	26.21 ± 1.16a
DE	SL	0.34 ± 0.03c	0.94 ± 0.35d	2.271 ± 0.59ab	− 30.48 ± 0.64c	1.39 ± 0.91ab	25.99 ± 1.19a
SK	BG	0.35 ± 0.04c	1.22 ± 0.43 cd	2.535833 ± 0.71ab	− 29.04 ± 0.47ab	− 0.88 ± 0.28d	21.36 ± 1.62b
SK	CZ	0.41 ± 0.04abc	1.41 ± 0.21bcd	1.696364 ± 0.35b	− 29.58 ± 0.48abc	− 1.72 ± 0.55d	21.31 ± 1.00b
SK	DE1	0.43 ± 0.04abc	2.33 ± 0.91abc	2.194545 ± 0.85ab	− 29.04 ± 0.42ab	− 1.10 ± 0.24d	20.23 ± 0.99b
SK	DE2	0.44 ± 0.07abc	2.02 ± 1.23bcd	2.148 ± 0.65ab	− 28.94 ± 0.72a	− 1.40 ± 0.30d	19.54 ± 1.16b
SK	ES	0.41 ± 0.09abc	1.66 ± 0.73bcd	1.864 ± 0.46b	− 28.81 ± 0.60a	− 1.00 ± 0.43d	19.36 ± 1.61b
SK	SK	0.39 ± 0.04bc	1.99 ± 0.61bcd	2.199167 ± 0.52ab	− 29.23 ± 0.45abc	− 1.88 ± 0.47d	20.11 ± 0.83b
SK	SL	0.45 ± 0.02abc	1.23 ± 0.20bcd	3.104 ± 0.99ab	− 28.90 ± 0.46a	− 1.45 ± 0.35d	20.09 ± 10b

The letters represent grouping according to Tukey's HSD post hoc tests. H_{inc} is the tree height increment, AGB_{inc} is the aboveground biomass increment, A_S:A_L is the sapwood-to-leaf area ratio, δ^{13}C is the leaf carbon isotope ratio, δ^{15}N is the leaf nitrogen isotope ratio and C:N is the leaf carbon-to-nitrogen ratio

Table 5 Provenance-level averages (± 95% CI) of xylem hydraulic and wood anatomy traits for both common garden sites

Site	Prov	P_{50} (MPa)	P_{88} (MPa)	A_L:A_X (%)	D (µm)	VD (n mm^{-2})	K_s (kg m^{-1} MPa^{-1} s^{-1})
DE	BG	− 2.97 ± 0.24ab	− 3.99 ± 0.31ab	15.83 ± 1.79bc	27.53 ± 1.27a	237.00 ± 17.59 fg	4.21 ± 0.98ab
DE	CZ	− 3.12 ± 0.23b	− 3.93 ± 0.16ab	13.27 ± 1.81c	25.50 ± 1.58abc	232.47 ± 20.45 fg	3.71 ± 0.39abc
DE	DE1	− 2.90 ± 0.11ab	− 3.70 ± 0.21a	15.83 ± 2.18bc	27.07 ± 1.94ab	243.66 ± 13.93efg	4.34 ± 1.04a
DE	DE2	− 2.88 ± 0.07ab	− 3.85 ± 0.12ab	15.29 ± 2.03bc	26.05 ± 1.66ab	255.39 ± 28.43defg	4.10 ± 0.47ab
DE	ES	− 2.95 ± 0.33ab	− 3.74 ± 0.35ab	17.85 ± 3.90abc	27.39 ± 2.31ab	270.66 ± 33.87bcdefg	3.25 ± 0.98abcd
DE	SK	− 3.10 ± 0.13b	− 3.89 ± 0.13ab	15.40 ± 3.66bc	25.63 ± 2.88abc	263.21 ± 33.47cdefg	3.36 ± 0.99abcd
DE	SL	− 3.08 ± 0.21ab	− 4.21 ± 0.22b	13.11 ± 1.84c	26.51 ± 1.39ab	209.42 ± 22.56 g	3.57 ± 0.92abcd
SK	BG	− 2.88 ± 0.17ab	− 3.91 ± 0.27ab	17.58 ± 1.57abc	23.85 ± 1.09bc	347.96 ± 40.4abcd	2.87 ± 0.41bcd
SK	CZ	− 2.70 ± 0.20a	− 3.63 ± 0.22a	20.46 ± 1.72ab	26.36 ± 0.85ab	333.70 ± 32.56abcde	3.01 ± 0.46abcd
SK	DE1	− 2.89 ± 0.15ab	− 3.66 ± 0.14a	21.29 ± 3.94a	24.06 ± 0.92bc	413.02 ± 97.63a	2.87 ± 0.48bcd
SK	DE2	− 2.95 ± 0.18ab	− 3.78 ± 0.21ab	17.84 ± 2.30abc	22.83 ± 1.12c	370.99 ± 42.73ab	2.30 ± 0.68 cd
SK	ES	− 2.92 ± 0.2ab	− 3.68 ± 0.24a	19.05 ± 2.09ab	23.99 ± 1.02bc	367.71 ± 46.63ab	2.36 ± 0.57 cd
SK	SK	− 2.90 ± 0.19ab	− 3.92 ± 0.16ab	19.14 ± 1.83ab	24.73 ± 1.33abc	353.62 ± 14.06abc	2.47 ± 0.51 cd
SK	SL	− 2.90 ± 0.19ab	− 3.82 ± 0.17ab	17.06 ± 2.91abc	24.46 ± 1.05abc	320.92 ± 46.32abcdef	2.02 ± 0.36d

The letters represent grouping according to Tukey's HSD post hoc tests. P_{50} is the water potential of 50% loss of conductance, P_{88} is the water potential of 88% loss of conductance, A_L:A_X is the lumen-to-sapwood area ratio, D is the specific vessel diameter, VD is the vessel density and K_s is the hydraulic conductance normalised by max cross-sectional xylem area
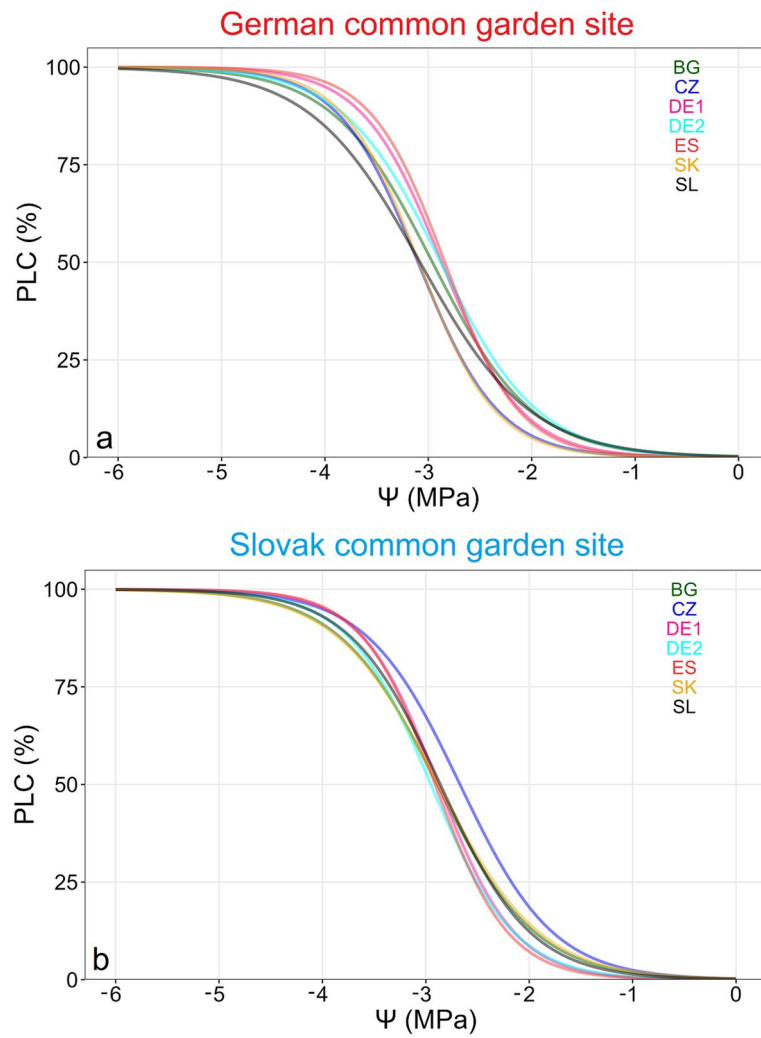
Fig. 6 The provenance average percentage loss of conductance (PLC) curves derived by Cavitron method for German common garden site (**a**) and Slovakian common garden site (**b**)
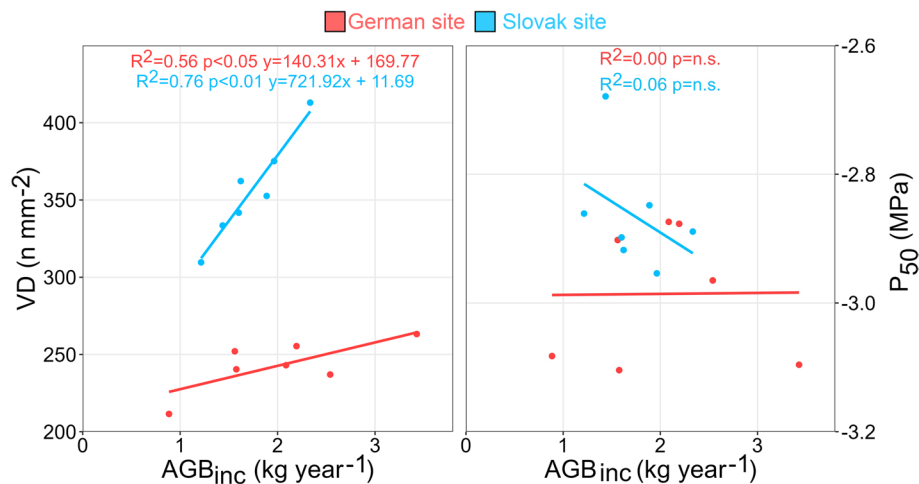
Fig. 7 Linear regressions between provenance-level aboveground biomass increment, vessel diameter (**a**) and water potential of 50% loss of conductance (**b**) for German (red) and Slovakian (blue) sites

Authors' contributions
BS and DK—conceptualization; ASK, BS, DK, DG, ML and PH—methodology, sampling and measurements; PP and RML—data analysis and visualizations; BS, DK, PP and RML—writing of original draft; BS, DK and CL—supervision; all authors contributed to the writing of the final version of the manuscript.

Availability of data and materials
The data generated in the manuscript are freely available under Creative Commons Attribution 4.0 International license at Zenodo depository: https://doi.org/10.5281/zenodo.10560831.

Declarations

Ethics approval and consent to participate
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Competing interests
The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Kurjak *et al. Annals of Forest Science*   (2024) 81:11

Page 20 of 21

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Kurjak *et al. Annals of Forest Science*   (2024) 81:11

Page 21 of 21

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