

# Hydraulic variability of three temperate broadleaf tree species along a water availability gradient in central Europe

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Received: 12 October 2020  
Accepted: 1 May 2021

New Phytologist (2021) 231: 1387–1400  
doi: 10.1111/nph.17448

**Key words:** embolism resistance, Huber value, hydraulic conductivity, hydraulic plasticity, hydraulic safety margin, leaf turgor loss point, precipitation gradient, xylem safety.

## Summary

- Plant hydraulic traits are key for understanding and predicting tree drought responses. Information about the degree of the traits' intra-specific variability may guide the selection of drought-resistant genotypes and is crucial for trait-based modelling approaches.
- For the three temperate minor broadleaf tree species *Acer platanoides*, *Carpinus betulus* and *Tilia cordata*, we measured xylem embolism resistance ( $P_{50}$ ), leaf turgor loss point ( $P_{TLP}$ ), specific hydraulic conductivity ( $K_s$ ), Huber values (HVs), and hydraulic safety margins in adult trees across a precipitation gradient. We further quantified trait variability on different organizational levels (inter-specific to within-canopy variation), and analysed its relationship to climatic and soil water availability.
- Although we observed a certain intra-specific trait variability (ITV) in safety-related traits ( $P_{50}$ ,  $P_{TLP}$ ) with higher within-tree and between-tree than between populations variability, the magnitude was small compared to inter-specific differences, which explained 78.4% and 58.3% of the variance in  $P_{50}$  and  $P_{TLP}$ , respectively. In contrast, efficiency-related traits ( $K_s$ , HV) showed a high ITV both within populations and within the crowns of single trees. Surprisingly, the observed ITV of all traits was neither driven by climatic nor soil water availability.
- In conclusion, the high degree of conservatism in safety-related traits highlights their potential for trait-based modelling approaches.

## Introduction

In many regions of central Europe, important primary timber species such as European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* [L.] H. Karst.) are approaching their drought limit (van der Maaten-Theunissen *et al.*, 2013; Lévesque *et al.*, 2014; Leuschner, 2020). Since 1980, this region has experienced a continuous increase in temperature and concomitantly in atmospheric vapour pressure deficit (Schuldt *et al.*, 2020), which culminated in a massive tree dieback of these two primary timber species in many central European forests during the exceptional 2018/2019 drought (Braun *et al.*, 2020; Schuldt *et al.*, 2020; Senf *et al.*, 2020). At least in the drier regions of central Europe, there is an urgent need to identify native timber species suited for production forests that better withstand drought and heat.

The survival and therefore overall fitness of trees under drought are intimately linked to their ability to supply water to the canopy by avoiding excessive formation of embolism in their hydraulic system in order to maintain a sufficiently high carbon gain (McDowell, 2011; Sapes *et al.*, 2019). Two interconnected physiological mechanisms that explain reduced tree productivity and increased mortality following severe drought exposure, namely carbon starvation and hydraulic failure, have widely been

discussed in the past since their introduction by McDowell *et al.* (2008). Recent results, however, indicate that hydraulic failure is the proximate cause of drought-induced tree mortality in various biomes (Rowland *et al.*, 2015; Anderegg *et al.*, 2016; Adams *et al.*, 2017; Correia *et al.*, 2019; Hajek *et al.*, 2020; Powers *et al.*, 2020; Arend *et al.*, 2021; Nolan *et al.*, 2021).

Hydraulic traits have widely been used to characterize plants in their disposition to suffer from hydraulic failure (Choat, 2013; Skelton *et al.*, 2015; Choat *et al.*, 2018), and to predict the effects of increased drought exposure on the productivity and mortality of woody plants (Choat *et al.*, 2012; Anderegg, 2015; Anderegg *et al.*, 2016). The link between productivity and mortality under drought is mirrored by the proposed trade-off between hydraulic efficiency and safety (Tyree *et al.*, 1994; Sperry *et al.*, 2008). According to said trade-off, plants are not able to simultaneously maximize the conductivity of their water transport system and minimize the risk of embolism formation. Studies across species and biomes provide moderate support for this hypothesis (Maherali *et al.*, 2004; Lens *et al.*, 2011; Gleason *et al.*, 2016; Schumann *et al.*, 2019), although opposite results exist (Torres-Ruiz *et al.*, 2017). Within species, evidence for this trade-off seems to be even weaker (Burgess *et al.*, 2006; Schuldt *et al.*, 2016; but see Liang *et al.*, 2019).

Two traits commonly used to describe a plant's hydraulic safety are the xylem water potential at 50% loss of hydraulic conductance ( $P_{50}$ ; Sperry & Tyree, 1988) and the water potential at the leaf turgor loss point ( $P_{TLP}$ ; Oppenheimer, 1963). Furthermore,  $P_{50}$  is directly related to the resistance of the xylem against embolism formation, while the  $P_{TLP}$  describes the capacity of a leaf to maintain its turgor during dehydration. Hydraulic efficiency, however, has often been associated with the xylem area-specific conductivity ( $K_S$ ; Farmer, 1918) or the Huber value (HV; Huber, 1928), i.e. the sapwood-to-leaf area ratio. Both parameters are major determinants of the ratio of a tree's assimilation rate to its xylem construction costs. These four traits are crucial for understanding the hydraulic variability of tree species and their potential to cope with drought. Adaptive modifications in these traits to different levels of water availability have been demonstrated across various species and biomes. Several studies observed higher hydraulic safety (Maherali *et al.*, 2004; Schuldt *et al.*, 2016; Larter *et al.*, 2017; Zhu *et al.*, 2018; Rosas *et al.*, 2019) and lower hydraulic efficiency in drier environments (Maherali *et al.*, 2004; Rosas *et al.*, 2019). Intra-specific variability of  $P_{50}$  and  $P_{TLP}$ , however, has been much less studied in the past (Anderegg & Meinzer, 2015), and the few available studies on the response of hydraulic traits to water availability in mature trees of the same species produced contradictory results. For example, while some intra-specific studies indeed observed an increase in embolism resistance with declining water availability (Schuldt *et al.*, 2016; Stojnic *et al.*, 2018), others observed either the opposite (Herbette *et al.*, 2010) or no relationship across climatic gradients (Martínez-Vilalta *et al.*, 2009; Martin-StPaul *et al.*, 2013; González-Muñoz *et al.*, 2018; Rosas *et al.*, 2019). In contrast,  $P_{TLP}$  has been found to decrease rather consistently with increasing aridity across (Lenz *et al.*, 2006; Bartlett *et al.*, 2012b; Mitchell & O'Grady, 2015; Zhu *et al.*, 2018) and within species (Liang *et al.*, 2019; Rosas *et al.*, 2019; Pritzkow *et al.*, 2020). One reason for the difference is that  $P_{50}$  depends on wood properties that are strongly conserved, while  $P_{TLP}$  is not static and can be adjusted actively by the plant to match the current environmental conditions.

Another explanation for the often missing relationship between xylem safety and climatic variables might be that most field studies on plant hydraulics neglect the role of soil hydrology, and only use climatic drought indices like the climatic aridity index. In order to characterize the aridity of a stand, however, variation in soil texture and soil hydraulic properties should likewise be acknowledged, as both properties can strongly affect tree hydraulics (Sperry & Hacke, 2002; Hultine *et al.*, 2006; Waite *et al.*, 2019). Congruently, several recent studies observed a close relationship between soil hydraulic properties (as the soil capacity for plant-available water, AWC) and drought-induced tree mortality (Peterman *et al.*, 2013; Hember *et al.*, 2017; Rehschuh *et al.*, 2017; Breshears *et al.*, 2018).

The vulnerability of the hydraulic system to drought does not solely depend on the xylem resistance to embolism, but on the interaction of several physiological processes which includes the stomatal control strategy (e.g. Mencuccini, 2003; Choat *et al.*, 2018). Hydraulic safety margins (HSMs) relate resistance on the xylem level to stomatal control (Meinzer *et al.*, 2009), and trees

with small safety margins operate closer to the threshold of runaway embolism formation and are therefore more prone to hydraulic failure (Choat *et al.*, 2012). HSMs are usually defined as the difference between minimum leaf water potential ( $P_{min}$ ) and a measure of xylem embolism resistance (e.g.  $P_{50}$ ), representing a measure of the conservatism in a tree's hydraulic strategy (Choat *et al.*, 2012). Recently, the point of stomatal closure ( $P_{gs90}$ , 90% reduction of stomatal conductance) or  $P_{TLP}$  have been used instead of  $P_{min}$  (Martin-StPaul *et al.*, 2017; Ziegler *et al.*, 2019; Powers *et al.*, 2020), as measurements of the latter are labour-intensive and often unreliable.

While most central European studies investigating plant hydraulic traits and their variability under altered water availability focused on the four economically most important tree genera, *Picea*, *Pinus*, *Fagus*, and *Quercus*, only little is known about minor timber species. Yet, small-leaved lime (*Tilia cordata* Mill., Malvaceae), Norway maple (*Acer platanoides* L., Sapindaceae) and European hornbeam (*Carpinus betulus* L., Betulaceae) may be more drought-resistant than European beech and Norway spruce, the most important broadleaf and coniferous timber species in Germany. Under the prospect of climate warming, the importance of minor tree species might increase if they prove to be better adapted to a future warmer and drier climate and their wood is suited for the timber industry. In the absence of physiological data, the drought tolerance assessment of minor timber trees is mainly based on analyses of the climate envelope of the distribution ranges and comparative expert assessment based on habitat preferences in natural forests (Ellenberg *et al.*, 2001; Niinemets & Valladares, 2006; Leuschner & Meier, 2018). Hence, there is an urgent need for more precise empirical data on the drought response of these minor timber species. In particular, information on traits associated with hydraulic safety and efficiency and their variability in response to shifts in water availability is largely missing.

To close this knowledge gap, we examined the variability of the four major hydraulic traits related to hydraulic efficiency and safety at the wood and leaf level ( $P_{50}$ ,  $P_{TLP}$ , HV and  $K_S$ , respectively) in three broadleaf, diffuse-porous tree species along a precipitation gradient in central Germany, and compared the species' drought tolerance in terms of their hydraulic safety margins. For doing so, we partitioned the variance in the four studied traits into the relative contributions of different hierarchical levels of variability, and computed the fraction of variance explained by species differences, by differences between populations, by individual differences within populations, and by random within-individual variability. Subsequently, we tested the hypothesis that within each species, the differences in hydraulic traits between populations are driven by climatic and edaphic water availability. We hereby assumed that traits related to hydraulic efficiency are more closely associated to water availability than traits related to hydraulic safety.

## Materials and Methods

### Study sites and tree species

The nine study sites are situated along a precipitation gradient in west-east orientation in central Germany between Göttingen and

Halle/S. at planar to colline elevation (110–440 m above sea level (asl)). The climate is cool temperate with mean annual temperatures (MATs) of 7.9 to 9.9°C. Mean annual precipitation (MAP) ranges between 528 and 918 mm and mean growing season precipitation (MGSP, April–September) between 291 and 412 mm, with a general decrease from west to east (Fig. 1). This represents a gradient from hydrologically optimal conditions to values close to the assumed drought limit of the species (Leuschner & Ellenberg, 2017).

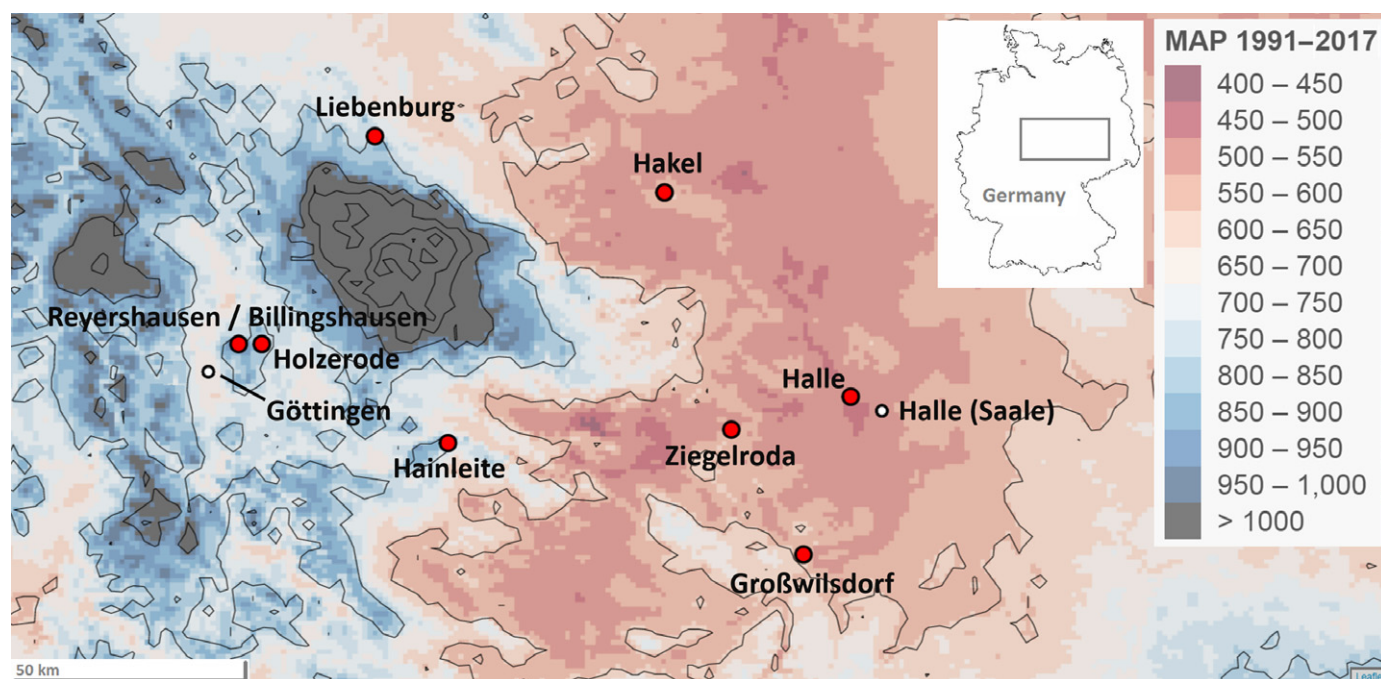
The three investigated tree species (*A. platanoides*, *T. cordata*, *C. betulus*) are naturally widespread in various types of central European broadleaf mixed forest communities of the phytosociological alliances Carpinion betuli (oak-hornbeam forests) and Tilio-Acerion (mixed maple slope forests) (Supporting Information Fig. S1), where the dominant species of central Europe's natural forest vegetation (*F. sylvatica* L.) is rare or absent (Leuschner & Ellenberg, 2017). The three species are more demanding in terms of soil base saturation than *F. sylvatica*, but they also occur in more continental climates in eastern Europe and thus are thought to be more drought tolerant (Roloff & Grundmann, 2008; Roloff *et al.*, 2010). While *F. sylvatica* is the most important broadleaf timber species in central European forestry, the three investigated species are only minor timbers. Therefore, mixed stands of comparable age, soil, and structure with presences of all three species are uncommon. Consequently, not all species were present at all nine study sites, but every species occurred in five stands along the precipitation gradient. Each site was composed of several mixed forest stands of variable species composition. The target species grew at a given site in a maximum

distance of several hundred metres to a few kilometres to each other under comparable edaphic and climatic conditions. To take small-scale variation within a site into account, the edaphic and climatic conditions in the different stands were recorded separately for each species. All stands were located on level terrain (maximum inclination 5°) without groundwater influence.

### Climatic conditions

Precipitation, air temperature, and potential evapotranspiration (PET) data were calculated from gridded data of 1 km mesh width retrieved from the German Weather Service (Deutscher Wetterdienst (DWD), Offenbach, Germany) database. The PET data of the DWD were calculated with the Penman–Monteith equation (Penman, 1948; Monteith, 1965; Löpmeier, 1994), the climatic water balance (CWB) was computed for the whole year as the difference of precipitation and PET.

Long-term annual means of climatic variables were calculated for the period 1991–2017, because PET data are available from DWD only since 1991. We tested our models with a variety of climatic parameters including long-term (27 yr) and short-term (2–5 yr) data of precipitation and evapotranspiration of whole year-periods and growing season-periods only. Because the ratio of summer precipitation to annual precipitation is almost constant, temperature is inversely proportional to precipitation along the transect, and short-term and long-term climate data did not differ notably in the 27-yr period, we obtained very similar results for precipitation and CWB data and decided to report results for CWB only.



**Fig. 1** Map of the study area between Göttingen and Halle/S. in central Germany with the precipitation gradient from west to east. The study sites are marked with red dots, the background colours indicate the mean annual precipitation (MAP 1991–2017). The area with MAP over 1000 mm northeast of Göttingen is the Harz mountain range.



## Edaphic conditions

The capability of soils to store water, which is available for plant uptake, is characterized by the AWC. We employed pedo-transfer functions according to Schaap *et al.* (2001), using the module 'ROSETTA LIGHT' implemented in the software RETC (v.6.02; van Genuchten *et al.*, 1991), to estimate soil hydraulic properties (the so-called van Genuchten (1980) parameters) from local data on soil texture class and bulk density. The modelled water retention curves were used to retrieve the soil water content (in vol.%) at field capacity (soil matric potential of  $-0.03$  MPa, pF 2.5) and at the conventional permanent wilting point ( $-1.5$  MPa, pF 4.2). AWC was then calculated as the difference between these two water contents. Soil texture classes and soil bulk density were determined in samples taken in soil pits at 0–10 cm, 10–30 cm and 30–60 cm depth. Sand fractions were obtained by sieving, silt and clay fractions by gravitational sedimentation according to the international standard ISO 11277 with an integral suspension pressure method (Durner *et al.*, 2017), using the Pario device (Metergroup, Munich, Germany). The profile total of AWC (in millimetres) of a given stand was obtained by adding the AWC values of the three measured layers for the 0–60 cm profile, and extrapolating AWC to 120 cm depth by assuming constant soil texture below 60 cm depth. The data of three pits per stand were averaged. In case of shallower soils, we used the measured average bedrock depth for AWC extrapolation.

## Tree selection and sampling

Five mature trees of comparable size per species and site were selected. All trees belonged to the upper canopy (dominant or co-dominant individuals). Tree height ( $H$ ) was comparable across the gradient except for *T. cordata*, where  $H$  decreased notably towards the drier sites (Table 1). In June and July 2017/2018, branches were collected from the uppermost sun-exposed canopy with tree-climbing equipment. Sampling took place in a rotating scheme so that sites and species were spread evenly across the sampled season and the studied years. Seasonal or year effects on the traits of interest were not detected. To decide for an appropriate sample length, we performed preliminary measurements with the air-injection method that suggested the maximum vessel length of all studied species was well below 20 cm. Per tree, six branches of 100 cm length were air-cut, re-cut to 50 cm under water, immediately transferred to plastic tubes filled with de-ionized water, and stored at 4°C. Within five days, three of these branches were used to construct xylem vulnerability curves, and the remaining three used for hydraulic conductivity measurements and quantification of the total leaf area distal to the reference measuring point (basipetal end of the sample, 50–100 cm from the apex). Additionally, three distal twigs per tree with c. 5–10 mature and fully intact leaves were harvested from the uppermost canopy to determine turgor loss point. Twigs were recut under water and transported to the laboratory with the cut surface submerged in water bottles to enable rehydration over-night at 10°C and 100% air humidity. For all four measured variables

( $P_{50}$ ,  $P_{TLP}$ ,  $K_S$ , HV), each 75 samples per species were investigated (three branches  $\times$  five trees  $\times$  five sites), yielding 225 in total.

## Hydraulic efficiency

For calculating HV, i.e. the sapwood-to-leaf area ratio, all leaves distal to the reference measuring point of a branch were scanned (Expression 11000XL; Epson Deutschland GmbH, Meerbusch, Germany) and analysed with WINFOLIA 2014 software (Régent Instruments, Quebec City, QC, Canada). In order to estimate the cross-sectional xylem area ( $A_{\text{xylem}}$  in  $\text{mm}^2$ ) without pith and bark at the reference measuring point, a linear regression was carried out between total cross-sectional area ( $A_{\text{cross}}$ ) and  $A_{\text{xylem}}$  (cf. Hajek *et al.*, 2014; Schuldt *et al.*, 2016). Per species, 75 digitalized semi-thin transverse sections, taken at 1–3 cm proximal from the reference measuring point, were used. The obtained equations are as follows (Eqns 1–3).

$$\text{Acer: } A_{\text{xylem}} = -5.84755 + 0.70525 A_{\text{cross}} \quad (R^2 = 0.98) \quad \text{Eqn 1}$$

$$\text{Carpinus: } A_{\text{xylem}} = -2.02419 + 0.76517 A_{\text{cross}} \quad (R^2 = 0.98) \quad \text{Eqn 2}$$

$$\text{Tilia: } A_{\text{xylem}} = -4.86760 + 0.56120 A_{\text{cross}} \quad (R^2 = 0.90) \quad \text{Eqn 3}$$

For measuring hydraulic conductivity ( $K_h$ ; in  $\text{kg m MPa}^{-1} \text{ s}^{-1}$ ), branches (mean reference point diameter  $\pm$  SE:  $10.12 \pm 0.08$  mm; mean length  $\pm$  SE:  $298.83 \pm 0.46$  mm;  $n = 225$ ) were recut under water with a razor blade, lateral branches cut off and glued with quick-drying superglue working on wet surfaces in combination with an activator (Loctite 431 and 7452; Henkel, Düsseldorf, Germany). The value of  $K_h$  was measured along a 6 kPa-pressure gradient with the Xylem apparatus (Bronkhorst, Montigny les Corneilles, France) after flushing the segments three times at 120 kPa with filtered, degassed, and demineralized water (10 mM potassium chloride and 1 mM calcium chloride). The value of  $K_S$  (in  $\text{kg m}^{-1} \text{ MPa}^{-1} \text{ s}^{-1}$ ) was calculated by dividing  $K_h$  by  $A_{\text{xylem}}$ .

## Hydraulic safety

Vulnerability curves were constructed with the flow-centrifuge method (Cochard *et al.*, 2005) using a custom-made honeycomb rotor attached to a commercially available centrifuge (Sorvall RC-5C; Thermo Fisher Scientific, Waltham, MA, USA). Non-flushed branches (mean diameter at basipetal end  $\pm$  SE:  $9.14 \pm 0.07$  mm;  $n = 225$ ) were recut to 27.5 cm with a razor blade and exposed to increasingly negative water potentials starting at  $-0.8$  MPa. Xylem water potential was lowered stepwise until the percentage loss of conductivity (PLC) reached at least 90% (Fig. S2). Nonlinear mixed-effects models (R package NLME; Pinheiro *et al.*, 2020) were fitted for each species to estimate the xylem pressure at 50% loss of conductivity ( $P_{50}$ ) and the slope of the

**Table 1** Site and tree characteristics of the studied stands sorted by species and in ascending order of the local climatic water balance (CWB).

Site	Species	Altitude (m asl)	MAP (mm)	MAT (°C)	MGSP (mm)	CWB (mm)	Soil texture	AWC (mm)	Tree age	Tree DBH	Tree height
Halle (HA)	<i>Acer platanoides</i>	135	527.8	9.9	291.1	-116.1	loamy sand	28.4	69.2 ± 2.6	40.85 ± 3.5	24.63 ± 0.9
Hakel (HK)	<i>A. platanoides</i>	239	606.5	9.2	316.7	11.9	silt	153.5	97.2 ± 3.2	40.04 ± 4.2	24.28 ± 1.8
Liebenburg (LB)	<i>A. platanoides</i>	285	831.1	9.0	382.3	266.1	silty loam	62.0	114.2 ± 4.9	44.08 ± 4.2	28.08 ± 1.8
Hainleite (HL)	<i>A. platanoides</i>	442	838.6	7.9	363.9	303.3	silty loam	52.2	130.6 ± 3.2	44.63 ± 1.8	27.57 ± 2.1
Reyershausen (RH)	<i>A. platanoides</i>	398	917.8	8.2	412.1	375.3	silty clay loam	32.7	108.6 ± 9.3	38.3 ± 5.1	28.58 ± 0.7
Halle (HA)	<i>Carpinus betulus</i>	110	532.9	9.9	294.3	-111.2	loam	138.6	80	39.67 ± 2.5	25.65 ± 2.9
Ziegelroda (ZR)	<i>C. betulus</i>	263	583.8	9.1	307.2	-20.7	silt	194.5	116	46.66 ± 5.7	27.79 ± 2.1
Hakel (HK)	<i>C. betulus</i>	239	606.5	9.2	316.7	11.9	silt	153.5	133	45.28 ± 3.5	23.78 ± 1.6
Großwilsdorf (GW)	<i>C. betulus</i>	243	624.6	9.3	327.0	15.2	silty loam	90.6	133	44.55 ± 6.7	22.94 ± 0.9
Holzerode (HR)	<i>C. betulus</i>	268	812.8	8.8	376.1	241.3	sandy loam	140.8	112	40.09 ± 3.5	27.28 ± 2.4
Halle (HA)	<i>Tilia cordata</i>	134	530.8	9.8	293.2	-108.8	loam	122.2	102.4 ± 3.3	44.02 ± 5.9	21.72 ± 1.3
Ziegelroda (ZR)	<i>T. cordata</i>	224	560.5	9.3	299.6	-53.6	silt	203.2	137.8 ± 9.2	49.37 ± 8.4	26.04 ± 1.9
Hakel (HK)	<i>T. cordata</i>	239	606.5	9.2	316.7	11.9	silt	153.5	136.6 ± 5.7	47.91 ± 4.4	27.07 ± 3.3
Großwilsdorf (GW)	<i>T. cordata</i>	243	624.6	9.3	327.0	15.2	silty loam	90.6	122.8 ± 4.2	37.09 ± 6.6	23.30 ± 2.1
Billingshausen (BH)	<i>T. cordata</i>	276	768.9	8.9	359.5	190.4	silty clay loam	44.3	115.0 ± 9.1	49.70 ± 7.2	31.89 ± 2.3

MAP, mean annual precipitation (period 1991–2017); MAT, mean annual temperature; MGSP, mean growing season precipitation (April–September); CWB, climatic water balance; soil texture is defined according to the nomenclature of the FAO (Food and Agriculture Organization of the United Nations); AWC, plant-available water storage capacity of the soil; DBH, stem diameter at breast height. Tree age, DBH, and tree height are given as means ± standard deviation. Tree age of all sampled individuals was determined with dendrochronological analyses for increment cores with the exception of *Carpinus betulus*, which was not part of the dendrochronological study; age information was here derived from forestry inventory data of the local forestry offices.

curve at the inflexion point ( $s$ ) according to the sigmoidal function given by Pammenter & van der Willigen (1998):

$$PLC = 100 / \left( 1 + \exp \left( \frac{s}{25} (\Psi - P_{50}) \right) \right) \quad \text{Eqn 4}$$

where  $\Psi$  is the water potential and PLC the percentage loss of conductivity. Due to repeated measurements on the same sample and three investigated samples per tree, a hierarchical structure of random effects had to be considered in the statistical analysis. We allowed both  $s$  and  $P_{50}$  to vary with a site-specific fixed effect and random effects for trees and samples nested in tree. Further analyses were based on conditional predictions on the branch level. The values for  $P_{12}$  and  $P_{88}$  (xylem pressure at 12% and 88% loss of conductivity) were calculated from branch-level  $P_{50}$  predictions by rearranging Eqn 4 (where  $x$  is the desired percentile loss of conductivity):

$$P_x = \frac{\log_e \left( \frac{100}{x} - 1 \right) 25}{s} + P_{50} \quad \text{Eqn 5}$$

Leaf  $P_{TLP}$  (in MPa) was determined within 48 hours after sampling by the osmometric method (Bartlett *et al.*, 2012a). The leaf osmotic potential ( $\Psi_0$ ) of freeze-thawed (liquid nitrogen) leaf discs from fully expanded, sun-exposed, and rehydrated leaves was measured in a vapour pressure osmometer (VAPRO 5600, Wescor, Logan, UT, USA) following the protocol of Bartlett *et al.* (2012a) and used to predict  $P_{TLP}$  as:

$$P_{TLP} = 0.832 \Psi_0 - 0.631 \quad \text{Eqn 6}$$

The HSM was subsequently calculated on the tree level as the difference between mean  $P_{TLP}$  and mean  $P_{50}$ .

## Statistical analyses

The coefficient of quartile variation ( $CQV = (Q_3 - Q_1) / (Q_1 + Q_3)$ ) was used to assess trait variability, as it provides a more robust measure of dispersion than the coefficient of variation, when data are partly nonnormally distributed or log-transformed (Canchola *et al.*, 2017; Altunkaynak & Gamgam, 2019; Rosas *et al.*, 2019). To decompose the variability of each trait for different levels of organization (species, populations (sites), individuals, within-tree (branches)), log-linear mixed-effects models were fitted for each trait separately using the R package LME4 (Bates *et al.*, 2015). Each of the models contained fixed effects for species, and random tree effects as well as species-wise random site effects (i.e. random effects for each combination of site and species). The total variance in the traits was then decomposed into variance components for the fixed (between-species) and random effects (between-population and between-tree) as well as the residual (within-tree) standard deviation analogous to the definition of conditional and marginal  $R^2$  (cf. Nakagawa & Schielzeth, 2013). The same models were used to investigate pair-wise differences between species across all sites using Tukey-adjusted  $P$ -values with degrees of freedom based on Satterthwaite's approximation (R package EMMEANS; Lenth, 2020).

To assess the effect of water availability on intraspecific trait variation, sets of linear mixed-effects models were fit for each trait ( $P_{50}$ ,  $P_{TLP}$ ,  $K_S$ , HV) and species. Climatic (CWB) and edaphic (AWC) water availability were included as fixed effects (both centred and scaled to simplify the comparison of regression coefficients). As the low number of five sites per species precluded adding random site effects, in these models we could only introduce tree-wise random intercepts, which thus are assumed to account both for between-site and within-site intra-specific variability. The explained variance was calculated according to Nakagawa & Schielzeth (2013). This set of models was not fitted for

**Table 2** Means  $\pm$  SE of measured traits per species pooled over all study sites.

Species	$P_{50}$ (MPa)	$P_{12}$ (MPa)	$P_{88}$ (MPa)	$P_{TLP}$ (MPa)	HSM (MPa)	HV ( $A_{xylem}/A_{leaf}$ )	$K_s$ ( $kg\ m^{-1}\ s^{-1}\ MPa^{-1}$ )
<i>Acer platanoides</i>	$-4.62 \pm 0.03$ (a)	$-3.97 \pm 0.04$ (a)	$-5.27 \pm 0.04$ (a)	$-2.02 \pm 0.02$ (a)	$2.59 \pm 0.07$ (a)	$0.0159 \pm 0.0007$ (a)	$1.73 \pm 0.07$ (a)
<i>Carpinus betulus</i>	$-4.25 \pm 0.05$ (b)	$-3.31 \pm 0.06$ (b)	$-5.19 \pm 0.06$ (a)	$-2.66 \pm 0.02$ (b)	$1.60 \pm 0.10$ (b)	$0.0165 \pm 0.0006$ (a)	$1.75 \pm 0.05$ (a)
<i>Tilia cordata</i>	$-3.06 \pm 0.03$ (c)	$-2.44 \pm 0.03$ (c)	$-3.69 \pm 0.04$ (b)	$-2.23 \pm 0.03$ (c)	$0.84 \pm 0.05$ (c)	$0.0195 \pm 0.0011$ (b)	$2.28 \pm 0.12$ (a)

Different letters denote significantly different means based on Tukey-adjusted  $p$ -values from linear mixed effects models with *post hoc* tests for pairwise species differences with degrees of freedom based on Satterthwaite's approximation.

$P_{50/12/88}$ , xylem water potential at 50/12/88% loss of conductivity;  $P_{TLP}$ , leaf water potential at turgor loss point; HSM, hydraulic safety margin; Huber value (HV) =  $A_{xylem}/A_{leaf}$  – ratio of branches;  $K_s$ , xylem area-specific hydraulic conductivity of branches.

the HSMs, as this variable could only be calculated on the tree level. Likewise, trait interrelations could not be assessed on the branch level because traits were not measured on the same observational units (different branches, leaves, etc.). Therefore, simple linear regressions across species based on means per site and species are reported in order to illustrate tendencies in trait interrelations. We are aware that the small number of species is not sufficient to draw generalizable conclusions for a larger species number.

For all dependent variables, model residuals were checked for normality and natural log-transformed whenever required to meet the assumption of normality. All analyses were carried out with the statistical software R (v.3.6.3; R Core Team, Vienna, Austria).

## Results

### Magnitude of traits and variability on different levels of organization

According to their average  $P_{50}$ -values, the xylem embolism resistance of the three species could be ranked in the sequence *A. platanoides* > *C. betulus* > *T. cordata* (Table 2). Both *A. platanoides* and *C. betulus* showed a fairly resistant xylem with the vast majority of  $P_{50}$ -values in the range of  $-5$  to  $-4$  MPa, but *C. betulus* was markedly less resistant at the driest site with a median  $P_{50}$  of  $-3.8$  MPa (Fig. 2a). By contrast, the estimated  $P_{50}$  of *T. cordata* was generally much less negative (mean of  $-3.06$  MPa; Table 2). This species ranking was, however, not mirrored in the  $P_{TLP}$ -values. The highest  $P_{TLP}$  was found in *A. platanoides* and the lowest in *C. betulus* (Table 2; Fig. 2c). Consequently, the three species showed pronounced differences in HSMs with *A. platanoides* having the largest safety margin (2.59 MPa; Table 2), *C. betulus* showing intermediate values (1.6 MPa), and *T. cordata* operating with a narrow margin of 0.84 MPa.

The species rankings in terms of  $P_{12}$  and  $P_{88}$  were the same as in case of  $P_{50}$ , but the vulnerability curves of *C. betulus* showed less steep slopes (Fig. S2) and thus relatively low  $P_{88}$  values that were very close to the values of *A. platanoides* (Table 2; Fig. 2b).

The values of  $K_s$  and HV barely differed between *A. platanoides* and *C. betulus*, but HV was significantly higher in

*T. cordata* and  $K_s$  was at least tendentially higher and more variable in *T. cordata* (Table 2; Fig. 3).

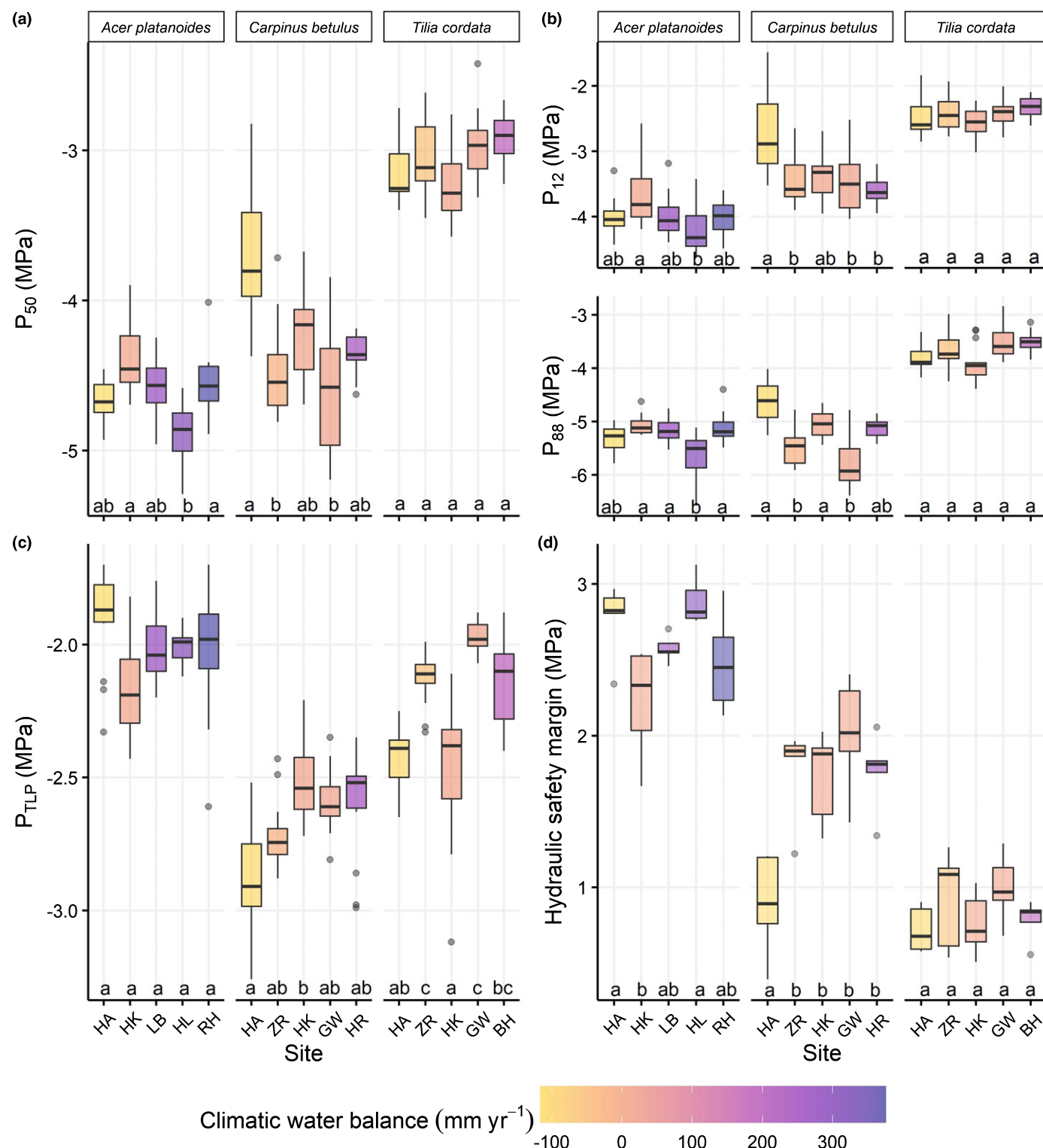
Generally,  $K_s$  and HV were the most variable traits, whereas  $P_{TLP}$  showed the lowest variation (Fig. 4a). For the two hydraulic safety-related traits ( $P_{50}$  and  $P_{TLP}$ ), the by far largest fraction of variance was explained by species differences. The intra-specific trait variability (ITV) between and within populations was small compared to the ITV in efficiency-related traits, especially in case of  $P_{50}$  (22% or 42% of total trait variance for  $P_{50}$  and  $P_{TLP}$ , respectively; Fig. 4b). For  $P_{50}$ , we estimated a between-population standard deviation of 0.20 MPa and between- and within-tree standard deviations of 0.23 MPa and 0.16 MPa, respectively (Fig. 4b; Table S1), while  $P_{TLP}$  varied by  $\pm 0.14$  MPa between populations, by  $\pm 0.14$  MPa between trees within populations and by  $\pm 0.10$  MPa within trees (Fig. 4b; Table S1). Hereby, the range of site averages of  $P_{50}$  spanned 0.84 MPa, 0.52 MPa and 0.31 MPa in case of *C. betulus*, *A. platanoides* and *T. cordata*, respectively (Fig. 2a). The range in site averages of  $P_{TLP}$  was comparable (*T. cordata*: 0.50 MPa, *C. betulus*: 0.36 MPa, *A. platanoides*: 0.26 MPa; Fig. 2c).

In contrast to hydraulic safety, average efficiency-related traits ( $K_s$  and HV) nearly did not differ between species, but varied substantially between populations as well as between and within individuals (Fig. 4b). Particularly the residual variability within individuals was high (44% of total variance in case of HV and 50% of total variance in case of  $K_s$ ).

For all four traits, the variability within populations (intra- and inter-individual) was larger than the variability between populations (Fig. 4b).

### Trait dependence on environmental and stand structural parameters

For most studied traits, significant differences between the study sites were observed for at least one species (Figs 2, 3). However, water availability (as expressed by the combined effect of CWB and AWC) explained only a small fraction of variance in the analysed traits (marginal  $R^2$  0.04–0.19 in nearly all cases; Table 3). The only exception was *T. cordata*, where 37% of the variance in HV was explained by water availability. Conditional  $R^2$  were much larger (0.28–0.88, Table 3), indicating that most of the

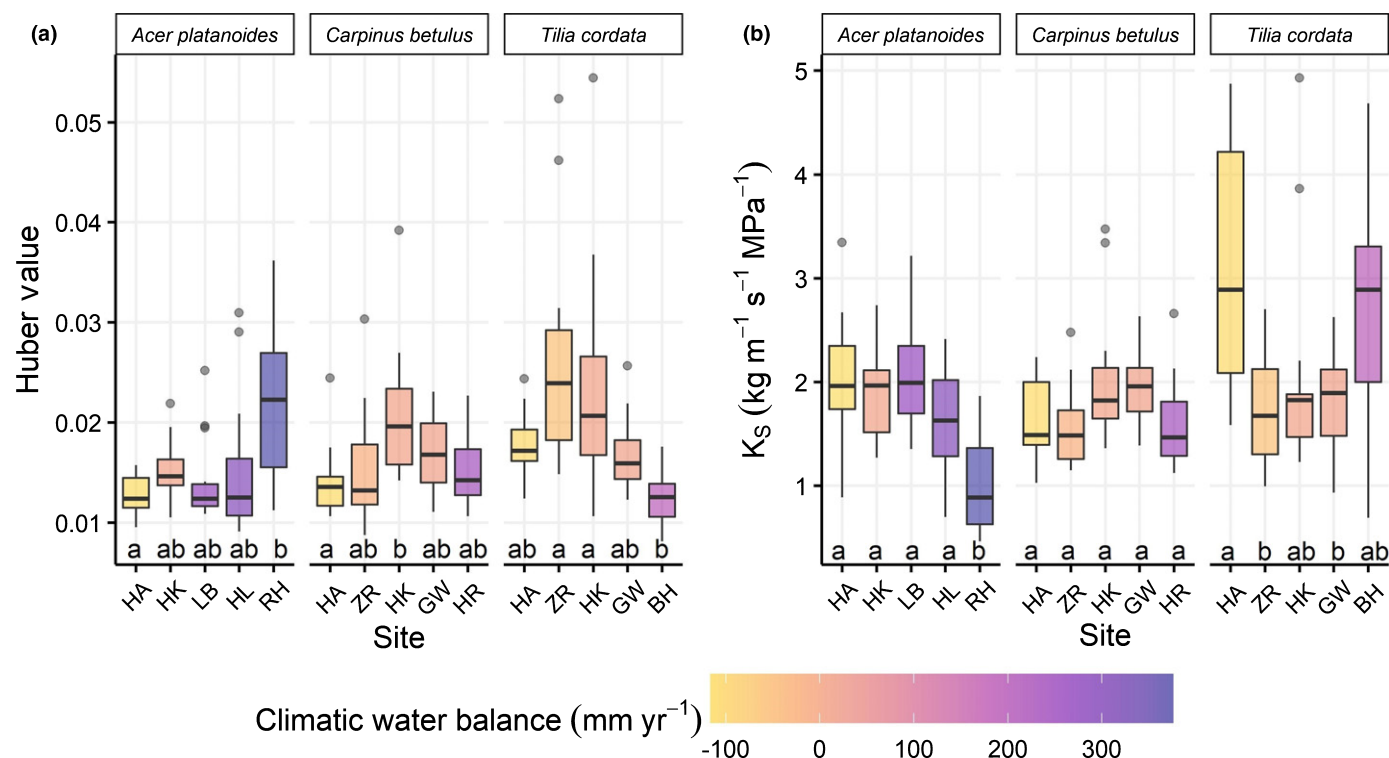


**Fig. 2** Hydraulic safety-related traits: (a) Xylem water potential at 50% loss of conductivity ( $P_{50}$ ), (b) xylem water potential at 12% and 88% loss of conductivity ( $P_{12}$  and  $P_{88}$ ), (c) leaf water potential at turgor loss point ( $P_{TLP}$ ), and (d) hydraulic safety margins of the three tree species at all study sites. Sites are sorted in ascending order according to the climatic water balance. Box-whisker plots include median and interquartile ranges (Q1–Q3); whiskers extend to maximum 1.5 times the interquartile range. Different letters denote significantly different means between sites within a species based on Tukey-adjusted  $p$ -values with degrees of freedom based on Satterthwaite's approximation from linear mixed effects models with *post hoc* tests for pairwise differences.

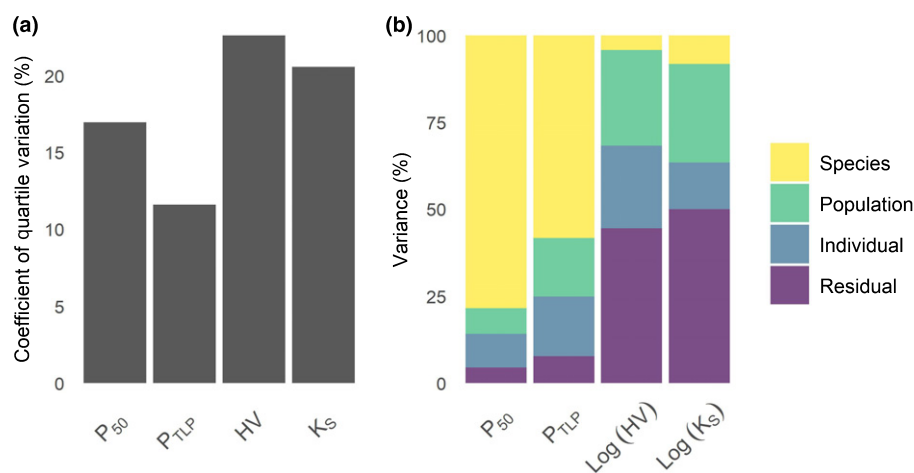
variance in the data resulted from unexplained differences between sites and individual trees.

In general, the observed associations between the studied traits and climatic and soil water availability were weak, the only exceptions being a positive effect of AWC on HV in *T. cordata* (higher





**Fig. 3** Hydraulic efficiency-related traits: (A)  $A_{\text{xylem}}/A_{\text{leaf}}$  – ratio of branches (Huber value), and (B) xylem area-specific hydraulic conductivity of branches ( $K_s$ ) of the three tree species at all study sites. Sites are sorted in ascending order according to the climatic water balance. Box-whisker plots include median and interquartile ranges (Q1–Q3); whiskers extend to maximum 1.5 times the interquartile range. Different letters denote significantly different means between sites within a species based on Tukey-adjusted  $p$ -values with degrees of freedom based on Satterthwaite's approximation from linear mixed effects models with *post hoc* tests for pairwise differences.



**Fig. 4** (a) Coefficient of quartile variation of the studied traits across all species and measurements; (b) variance decomposition between different levels of organization (between species, between populations, and between individuals; see Supporting Information Table S1 for full model output). Given are the xylem water potential at 50% loss of conductivity ( $P_{50}$ ), the leaf water potential at turgor loss point ( $P_{\text{TLp}}$ ),  $A_{\text{xylem}}/A_{\text{leaf}}$  – ratio of branches (Huber value, HV) and xylem area-specific hydraulic conductivity ( $K_s$ ). 'Residual' denotes the unexplained variance of the models (i.e. variability between branches + estimation and measurement uncertainty).

xylem area-to-leaf area ratio on sites with higher soil water storage capacity), a negative effect of AWC on  $P_{\text{TLp}}$  in *A. platanoides* (lower turgor loss point on sites with better soil water storage capacity; Table 3; Fig. S3), and a reduction in  $K_s$  with AWC in *T. cordata* and with CWB in *A. platanoides*. Water availability

had no significant influence on  $P_{50}$ , except for a marginally positive effect of AWC on  $P_{50}$  in *A. platanoides* ( $P < 0.1$ ; Table 3). The value of  $P_{\text{TLp}}$  of *C. betulus* and *T. cordata* was not influenced by AWC, although the leaves of *C. betulus* showed a tendency of a turgor loss point reduction with increasing climatic



**Table 3** Results of the linear mixed effects models examining the relationships between environmental variables and functional traits.

Species	Term	$P_{50}$	$P_{TLP}$	HV	$K_S$
<i>A. platanoides</i>	CWB	-0.054	-0.214	0.343	<b>-0.402*</b>
	AWC	0.374(a)	<b>-0.460*</b>	0.049	0.103
	Tree SD	0.81	0.724	0.708	0.685
	Res. SD	0.529	0.584	0.674	0.629
	Marg. $R^2$	0.141	0.189	0.103	0.184
	Cond. $R^2$	0.743	0.68	0.574	0.627
<i>C. betulus</i>	CWB	-0.278	0.347(a)	0.054	-0.072
	AWC	0.035	-0.074	-0.078	-0.241
	Tree SD	0.854	0.87	0.565	0.548
	Res. SD	0.396	0.445	0.853	0.836
	Marg. $R^2$	0.083	0.121	0.009	0.057
	Cond. $R^2$	0.837	0.818	0.312	0.341
<i>T. cordata</i>	CWB	0.165	0.237	-0.027	-0.315
	AWC	-0.144	-0.04	<b>0.604**</b>	<b>-0.437*</b>
	Tree SD	0.822	0.963	0.511	0.437
	Res. SD	0.559	0.365	0.631	0.867
	Marg. $R^2$	0.076	0.064	0.371	0.094
	Cond. $R^2$	0.708	0.883	0.62	0.277

$P_{50}$ , xylem water potential at 50% loss of conductivity;  $P_{TLP}$ , leaf water potential at turgor loss point; HSM, hydraulic safety margin; Huber value (HV) =  $A_{\text{xylem}}/A_{\text{leaf}}$  – ratio of branches;  $K_S$ , xylem area specific hydraulic conductivity of branches.

Given are the scaled estimates for CWB (climatic water balance) and AWC (plant-available water storage capacity of the soil), as well as the standard deviation for the tree-wise random intercept (Tree SD), the residual standard deviation (Res. SD), and marginal and conditional  $R^2$  of the models (Marg.  $R^2$  and Cond.  $R^2$ ). Bold estimates represent significant effects (\*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ), (a) denotes marginally significant effects ( $P < 0.1$ ). The full output of the models is given in Supporting Information Table S2.

aridity (positive effects of CWB on  $P_{TLP}$  at  $P < 0.1$ ; Table 3; Fig. 2c). Although not part of the regression models, HSMs did not change systematically along the climatic gradient within species, as evident from Fig. 2(d).

Further relationships between site variables and interrelations between traits are presented in the correlation matrix in Fig. S4.

## Discussion

### Variability of efficiency- and safety-related traits on different levels of organization

In our field study on mature trees, the HV, i.e. the sapwood-to-leaf-area ratio, and  $K_S$  showed the highest, and the  $P_{TLP}$  the lowest variability across the three diffuse-porous species. This is in line with recent findings by Rosas *et al.* (2019). The high variability of the efficiency-related hydraulic traits  $K_S$  and HV was driven by large intra- and inter-individual differences. Most likely, this can be attributed to small-scale variability in microclimatic conditions within the canopy of single trees and corresponding morphological and anatomical adjustments (e.g. Lemoine *et al.*, 2002; Sellin & Kupper, 2004; Schuldt *et al.*, 2011; Sellin *et al.*, 2011). In agreement hereon, both branch age and branch growth rate were found to vary considerably within the crown, and both are closely related to hydraulic efficiency (Schuldt *et al.*, 2016). In dependence on

the position in the canopy and associated differences in flow-path length, light exposure and evaporative demand, the xylem architecture is adjusted in order to meet the water demand of the supported leaf area. Still, the covered range in both efficiency-related variables was relatively low compared to other studies (cf. Rosas *et al.*, 2019). We focused on co-occurring diffuse-porous angiosperms only, and did not include conifers or ring-porous angiosperms. This might explain why the efficiency-related traits were more or less comparable across species despite pronounced differences in xylem safety. All three species have co-evolved and are widespread in central and eastern Europe in various types of broadleaved mixed forest communities in which European beech (*F. sylvatica*), the dominant species of central Europe's natural forest vegetation, is rare or absent (Leuschner & Ellenberg, 2017).

The low variability in  $P_{TLP}$  compared to other hydraulic traits has likewise been observed in other studies (Mencuccini *et al.*, 2015; Bartlett *et al.*, 2016; Farrell *et al.*, 2017; Zhu *et al.*, 2018). When excluding plants with sclerophyllous leaves or from perhumid ecosystems, the range of  $P_{TLP}$ -variation based on differences in osmolality seems to be restricted to 2 MPa (Bartlett *et al.*, 2012b). In our study, most of the variability in  $P_{TLP}$  could be attributed to species differences, although there still was a considerable amount of ITV between populations and individuals.

In contrast to the two efficiency-related traits, the xylem pressure at  $P_{50}$  differed distinctly between species. Although ITV in xylem safety was not completely negligible as we observed intra-specific ranges of 0.3 to 0.8 MPa across sites, 78% of the total variance in  $P_{50}$  could be attributed to species differences. The highest ITV was observed between trees at given sites, which explained 14% of the total variance in  $P_{50}$ . This pattern of higher variability within than between populations has been confirmed for  $P_{50}$  (Herbette *et al.*, 2010; Wortemann *et al.*, 2011; Hajek *et al.*, 2016; Schuldt *et al.*, 2016) and a wide range of other anatomical, foliar and hydraulic traits (Hajek *et al.*, 2016; Rosas *et al.*, 2019).

The low ITV in  $P_{50}$  reinforces the assessment of xylem embolism resistance as an evolutionarily canalized trait (cf. Flatt, 2005; Lamy *et al.*, 2014; Rosas *et al.*, 2019; Sanchez-Martinez *et al.*, 2020). Accordingly, neither environment nor genotype seems to have strong control over the phenotypic expression of  $P_{50}$ . For trait-based models of tree mortality (cf. Adams *et al.*, 2013; Choat *et al.*, 2018), this is an important finding as these models implicitly rely on trait conservation within species and do not account for ITV.

### Effects of water availability on hydraulic traits

Given the relatively small intra-specific variation in hydraulic safety-related traits, we expected to trace this ITV back to local climatic or edaphic conditions that define the water availability of the stands. However, none of the two measures of water availability had a consistent influence on  $P_{50}$ ,  $P_{TLP}$ , or HSMs. For  $P_{50}$ , a majority of intra-specific studies on a wide range of tree species failed to identify environmental variables that drive ITV (Van der Willigen & Pammenter, 1998; Cornwell *et al.*, 2007; Martínez-Vilalta *et al.*, 2009; Herbette *et al.*, 2010; Wortemann *et al.*, 2011; Martin-StPaul *et al.*, 2013; González-Muñoz *et al.*, 2018; Li *et al.*,

2019; Rosas *et al.*, 2019; but see Schuldt *et al.*, 2016; Stojnic *et al.*, 2018). It is therefore reasonable to conclude that the limited environmental control over  $P_{50}$  is relatively complex, as assumed by Wortemann *et al.* (2011). In our study, only less than 10% of total variability occurred between populations, indicating that the effects of different drivers may often be difficult to disentangle in field studies on mature trees. For example, most of the aforementioned studies disregarded that various site-specific factors might, in addition to atmospheric climatic aridity, affect embolism resistance. To our knowledge, only Rosas *et al.* (2019) also included a wide range of stand, soil, and climatic factors as potential drivers of  $P_{50}$ , but the authors were likewise not able to identify the sources of the ITV in  $P_{50}$  in adult field-grown trees.

In contrast to  $P_{50}$ , reports on an intra-specific decline in  $P_{TLP}$  with increasing aridity are rather consistent (e.g. Liang *et al.*, 2019; Rosas *et al.*, 2019; Pritzkow *et al.*, 2020). In our study, *C. betulus* indeed showed a marginally significant negative relationship between  $P_{TLP}$  and aridity. Leaf traits might thus be under a stronger environmental control than wood traits, and one of the main acclimative responses of the broadleaf tree species of our sample to local climatic gradients might be osmotic adjustment (cf. Hartmann *et al.*, 2021).

We did not find the expected increase in HV on drier sites, even though a high variability of HV across climatic gradients has been reported both within (Martínez-Vilalta *et al.*, 2009; Rosas *et al.*, 2019; Pritzkow *et al.*, 2020) and across species (Gleason *et al.*, 2013; Mencuccini *et al.*, 2019). However, intra-specific variability in HV in response to climatic aridity has mainly been observed in different ecosystems or in conifers that showed limited variability in xylem traits (Martínez-Vilalta *et al.*, 2009; Lamy *et al.*, 2014).

While intra-specific adaptation of hydraulic efficiency in terms of xylem anatomical adjustments has been demonstrated (e.g. Schreiber *et al.*, 2015; Liang *et al.*, 2019), studies quantifying actual conductivities often failed to report such adaptive modifications (Martínez-Vilalta *et al.*, 2009; Schuldt *et al.*, 2016; Rosas *et al.*, 2019). This is in line with our findings that  $K_S$  was not under environmental control, despite its very high ITV. One explanation for the missing relationship might be that empirically measured conductivity, in contrast to theoretical values, additionally includes the flow resistance of inter-vessel pits and conduit irregularities along the flow path, which are estimated to account for 50% of the total xylem resistance (Sperry *et al.*, 2005).

We found a general inter-specific safety-efficiency trade-off as observed by others (Maherali *et al.*, 2004; Gleason *et al.*, 2016; Schumann *et al.*, 2019). Across the three species of our sample,  $P_{50}$  and  $K_S$  were correlated ( $P < 0.05$ ,  $R^2 = 0.23$ ; Fig. S5), but this observed safety-efficiency relationship did not hold within any of the species. We are aware that this finding may not be transferable to more general between-species pattern due to the small number of species in our sample.

### Hydraulic safety in comparison to major timbers

In our study, *A. platanoides* and *C. betulus* showed both an embolism resistant xylem ( $P_{50}$ :  $-4.62$  MPa and  $-4.25$  MPa,

respectively) and large HSMs (2.59 MPa and 1.6 MPa, respectively). In contrast to these two species that have been of minor silvicultural interest so far, the major broadleaf timber species in the study region, *F. sylvatica*, is less drought-resistant in terms of hydraulic safety ( $P_{50}$ :  $-3.8$  MPa to  $-3.5$  MPa; HSM: 0.2 MPa to 1.5 MPa;  $P_{50}$  and  $P_{min}$  data obtained from Schuldt *et al.*, 2016; Dietrich *et al.*, 2018; Schuldt *et al.*, 2020). These two species even turned out to be a match—in terms of hydraulic safety—for another major timber species of the region, namely sessile oak (*Quercus petraea*), which is known to be more drought-resistant than European beech ( $P_{50}$ :  $-5.0$  MPa to  $-4.6$  MPa, HSM: 1.8 MPa to 2.3 MPa; based on  $P_{50}$  and  $P_{min}$  data from Dietrich *et al.*, 2018; Lobo *et al.*, 2018). Especially *F. sylvatica* is currently widely affected by drought-induced defoliation and tree mortality following the extreme 2018/2019 drought (Braun *et al.*, 2020; Schuldt *et al.*, 2020). According to dendroecological analyses, this species is more drought-sensitive than *A. platanoides* even in the core area of its distribution range (Zimmermann *et al.*, 2015; Leuschner, 2020). Thus, *A. platanoides* and, from a plant hydraulic perspective, also *C. betulus* seem to be better suited than *F. sylvatica* for a future drier climate.

However, HSMs alone are not sufficient to capture drought tolerance on the whole-tree level, because stem and leaf water capacitance act as additional buffers against desiccation (Choat *et al.*, 2018). *Tilia cordata* has a relatively high stem water storage due to its low wood density (Köcher *et al.*, 2013) and a high leaf water capacitance linked to a highly elastic leaf tissue (Leuschner *et al.*, 2019), which might partly compensate for the species' relatively high xylem vulnerability and small HSM. Consequently, more holistic and integrated studies on whole-tree drought responses are needed to fully understand tolerance strategies and compare different species.

### Conclusions

The three investigated minor timber species showed a considerable amount of intra-specific variability in efficiency-related traits, which were highly variable between and within individuals. In contrast, ITV was low in xylem safety-related traits despite pronounced differences between species. This implies that xylem safety-related traits at the wood ( $P_{50}$ ) and leaf ( $P_{TLP}$ ) levels are more strongly conserved traits, which—given their high mechanistic importance for plant drought responses—underlines their value for trait-based modelling approaches in dynamic vegetation and land surface models.

Environmental control over hydraulic traits in mature stands seems to involve complex interactions with abiotic drivers. In our study, it was not possible to clearly disentangle their influence from other factors, even though both climate and soil water capacity were taken into account. Most likely, local properties of the stand and soil, including small-scale variability in moisture availability, belowground and aboveground competition with direct neighbours, as well as a high within-crown variability in branch hydraulic properties hamper the identification of the environmental drivers of xylem safety and efficiency for given species.

Despite these uncertainties, our study provides valuable information on hydraulic traits and their variability for three promising minor timber species that may help to assess their suitability for broader inclusion in silvicultural concepts in central Europe in a future warmer and drier climate. In the light of large-scale vitality losses and dieback in some of the primary timber species in central Europe, minor timber species such as *A. platanoides* or *T. cordata* emerge as well-suited potential components of future more drought-tolerant production forests.


## Acknowledgements

The authors gratefully acknowledge the financial support granted by the Bundesministerium für Ernährung und Landwirtschaft (Germany), Bundesministerium für Umwelt, Naturschutz und nukleare Sicherheit (Germany) and the Fachagentur Nachwachsende Rohstoffe eV (Germany) within the frame of the 'Waldklimafonds' (project DIVforCLIM). Additionally, the authors thank the local forestry authorities of Lower Saxony and Saxony-Anhalt and the DBU-Naturerbe GmbH for permissions to conduct the study, and the Nordwestdeutsche Forstliche Versuchsanstalt for kindly providing forest inventory data for the identification of suitable study sites. Special thanks go to Hannah Korp, Ana Sapoznikowa, Greta Weithmann and Leonhard Klinck for their skilful support in laboratory and fieldwork.

## Author contributions

CL and BS developed the original research questions and designed the study, SF collected the field samples, performed all physiological measurements and, in close collaboration with RML, the statistical analyses. SF and BS wrote the first version of the manuscript, which was intensively discussed and revised by all authors.

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## Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

**Fig. S1** Distribution ranges of the three minor timber species.

**Fig. S2** Xylem vulnerability curves illustrating percentage loss of conductivity vs xylem water potential.

**Fig. S3** Xylem water potential at 50% loss of conductivity, leaf water potential at turgor loss point, Huber value, and specific conductivity of the three tree species on all study sites.

**Fig. S4** Pearson correlation matrix of environmental and tree-specific predictors and functional traits.

**Fig. S5** Tendency of a hydraulic safety-efficiency trade-off across species.

**Table S1** Full output table of the linear mixed effects models for the variance decomposition.

**Table S2** Full output table of the linear mixed effects models examining the relationships between environmental variables and functional traits.

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