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ORIGINAL ARTICLE

Xylem hydraulic safety and efficiency in relation to leaf and wood traits in three temperate *Acer* species differing in habitat preferences

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Abstract

Key message **For three widespread European *Acer* species with different climate envelopes, hydraulic traits, but not wood anatomical or leaf morphological traits, were good indicators for habitat preferences.**

Abstract Prediction of drought impacts on trees requires knowledge about species differences in hydraulic traits and how the hydraulic constitution changes along water availability gradients. We studied co-occurring mature trees of three widespread European *Acer* species with different climate envelopes and habitat preferences for branch hydraulic (embolism resistance, hydraulic conductivity), wood anatomical (vessel diameter, vessel density, wood density) and leaf functional traits (specific leaf area, sapwood-to-leaf area ratio, foliar $\delta^{13}C$), and branch growth rate. Study objectives were to examine the relation between hydraulic traits and the species' habitat preferences and to confirm several commonly anticipated trade-offs in hydraulic traits at the genus level. The species' habitat preferences were reflected in the hydraulic traits, but not in the studied wood anatomical or leaf traits. Embolism resistance (P_{12}, P_{50} and P_{88} values) decreased and pit conductivity (potential minus measured conductivity) increased in the sequence *A. campestre*–*A. platanoides*–*A. pseudoplatanus* in parallel with the species' putative drought tolerance. As expected, a trade-off was found between branch hydraulic efficiency and safety. Wood density was related to hydraulic safety, but neither to hydraulic efficiency nor other wood anatomical traits including vessel diameter. Branch growth rate was unrelated to wood density, but linked to vessel diameter and hydraulic conductivity. The findings from the three maple species suggest that hydraulic traits may be under stronger genetic control than leaf and wood anatomical traits that exhibited a more plastic response to the environment. The former are thus better indicators of habitat preferences.

Keywords Embolism resistance · Huber value · Hydraulic conductivity · Specific leaf area · Xylem anatomy · Wood density

Introduction

Climate change scenarios predict a decrease in summer precipitation and a rise in the frequency and severity of heat waves in the twenty-first century for parts of Central Europe and other temperate regions (Fischer and Schär 2008; IPCC 2013; Dai 2013). Trees as long-lived organisms should be particularly sensitive to a long-term increase in water deficits, which explains the recently growing interest in the study of tree hydraulics. Motivated by the recent observation of climate warming-related forest dieback in various regions of the temperate zone (Allen et al. 2015; Neumann et al. 2017), forest ecologists are studying the drought sensitivity of trees and forest stands in order to understand the causal link between climate warming, tree vitality decrease and tree death. Key mechanisms discussed are drought-induced xylem embolism and carbon starvation due to partial

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stomatal closure (McDowell et al. 2008), but a growing body of evidence supports the hydraulic failure hypothesis (e.g., Anderegg et al. 2012; Hartmann et al. 2013; Rowland et al. 2015) although both processes might be ultimately linked (e.g., Salmon et al. 2015; Yoshimura et al. 2016; Trifilò et al. 2017). Many tree species seem to operate relatively close to their hydraulic safety margins, risking embolism formation and thus hydraulic failure during drought events (Choat et al. 2012). Prediction of drought impacts on different species requires information on interspecific differences in hydraulic traits, and whether this variation is determined by the genome or arises from phenotypic plasticity (Anderegg and Meinzer 2015).

An important hydraulic trait is the xylem water potential causing 50% loss of hydraulic conductivity (P_{50} value). This trait provides an indicator of the resistance of xylem to embolism and varies largely among tree species (Maherali et al. 2004; Choat et al. 2012). It appears that the majority of gymnosperm trees are experiencing lethal hydraulic failure at 50% loss of conductivity, while angiosperms typically reach this point later (88 or 90% loss of conductivity, P_{88}) (Brodribb and Cochard 2009; Urli et al. 2013; Li et al. 2016). The relation of P_{50} to other plant traits is intensively debated. For example, various studies were unable to confirm the generally assumed and often reported higher susceptibility of large-diameter conduits to drought-induced embolism (e.g., Fichot et al. 2010; Lens et al. 2011; Hajek et al. 2016). It has further been questioned whether the assumed trade-off between hydraulic efficiency and safety is universally valid (e.g., Gleason et al. 2016). Finally, mixed results do exist with respect to the physiological importance of embolism resistance, i.e. the relation between P_{50} and growth rate. Several studies were unable to confirm this relationship (e.g., Sterck et al. 2012; Hajek et al. 2014; Guet et al. 2015; Schuldt et al. 2016), while others did (Cochard et al. 2007). These and other relationships between embolism resistance and leaf or wood properties await further clarification.

P_{50} studies along climatic and hydrologic gradients have revealed considerable adaptive variation in the embolism resistance of different tree species (Maherali et al. 2004) but also among co-occurring species in the same environment (e.g., Dietrich et al. 2018; Dulamsuren et al. 2019). P_{50} has therefore been used to predict the risk of drought-induced mortality in angiosperm trees (Skelton et al. 2015; Anderegg et al. 2016). This trait could also be used to indicate a species' susceptibility to drought-induced vitality loss prior to death, which may manifest in leaf loss and continued growth decline. However, there are relatively few studies that measured P_{50} in co-occurring temperate tree species in mixed forests where environmental gradients are absent. Such studies can help to determine the relative influence of genetic adaptation versus plasticity on embolism resistance. We also need a better understanding of how P_{50} and other hydraulic traits vary in dependence on the habitat preferences of the species, and how they are related to wood density, foliar traits and growth rate.

Plant water status and water turnover are further influenced by several leaf morphological traits, notably specific leaf area (SLA) and the Huber value (HV), i.e. the sapwood-to-leaf-area ratio, which influence the hydraulic pathway through their effects on canopy water loss and leaf water potential fluctuation. For reducing the embolism risk, plants may alter SLA and HV along water availability gradients as an adaptive response (Poyatos et al. 2007; Gleason et al. 2012; Togashi et al. 2015). The relation between leaf characteristics (SLA and HV) and traits characterizing hydraulic efficiency and safety is, however, not well understood as contradicting results have been reported (Maherali et al. 2006; Willson et al. 2008; Markesteijn et al. 2011; Fan et al. 2012; Sterck et al. 2012; Schreiber et al. 2016).

This study investigates the three European *Acer* species *A. pseudoplatanus* L. (sycamore maple), *A. platanoides* L. (Norway maple) and *A. campestre* L. (field maple). The three taxa are widespread in Central Europe and beyond. *A. campestre* has probably the broadest ecological niche and the largest natural range of the three species, extending far into the semi-humid to semi-arid regions of continental eastern Europe and northern Africa. *A. platanoides* is also widely distributed in large parts of Europe including the continental East, but the species seems to prefer somewhat moister sites than *A. campestre*. Finally, *A. pseudoplatanus* occurs mostly in regions with higher precipitation and air humidity as in the montane belt of the higher mountains, and the species is absent from the more continental East of Europe including parts of Hungary and the Ukraine. From their distribution range and occurrence in certain forest communities, it is assumed that *A. campestre* is the most drought-tolerant taxon, followed by *A. platanoides*, while *A. pseudoplatanus* is generally considered as the most drought-susceptible of the three species (San-Miguel-Ayanz et al. 2016; Leuschner and Ellenberg 2017). We expect that the species' assumed niche differences in terms of moisture requirements and drought tolerance are reflected in a number of plant functional traits. A first investigation on this topic was conducted by Tissier et al. (2004) who compared young trees of the three maple species with respect to P_{50} using the air injection method. They found a P_{50} decrease toward the putatively more drought-tolerant species. However, these authors investigated young trees (10-15 yrs) at a groundwater-influenced site, which meets the habitat requirements of *A. pseudoplatanus*, but not those of the other species.

This study was conducted in a natural drought-influenced broad-leaf mixed forest stand on limestone where the three maple species are growing in direct vicinity to each other, enabling us to study the species' hydraulics under similar environmental conditions. We explored species differences in hydraulic properties under conditions of water shortage, as are expected to increase in importance in a future warmer climate, by investigating the xylem anatomical and hydraulic properties of sun canopy branches together with relevant leaf traits including the carbon isotope signature, wood density and branch growth rate. We further attempted to clarify, what relationships do exist between branch hydraulic properties, leaf and wood properties and productivity and how these traits are varying across the species sample. With reference to the partly controversial evidence available on the relationships between embolism resistance and xylem anatomy, hydraulic efficiency, growth rate and leaf and wood traits, we asked whether (1) the species' habitat preferences are reflected in the branch embolism resistance and hydraulic efficiency, (2) a trade-off exists between hydraulic efficiency and safety, (3) branch growth rate is positively associated with hydraulic efficiency but negatively to xylem safety, and (4) whether embolism resistance is related to leaf traits in these species.

Material and Methods

Study site

The study was conducted in a naturally established broad-leaved mixed forest on Triassic limestone (Muschelkalk formation) near the city of Göttingen (central Germany) at 171 m a.s.l. (51°33′15.4″N, 9°57′20.9″E). The stand has a height of ca. 18 m and an age of 40-45 years. The three *Acer* species co-occur with *Carpinus betulus, Fraxinus excelsior, Prunus avium, Quercus robur, Robinia pseudoacacia*, and *Tilia cordata* on Leptosols (rendzina, terra fusca) of low to medium profile depth, which expose the trees to periods of water shortage in dry summers. Mean annual temperature is 8.7 °C, mean annual precipitation is 645 mm. The terrain is slightly sloping to the north (5°–10° inclination). The 80-m long Göttingen Canopy Walkway in this forest allows sun canopy access to a large number of trees at 16 m height. We chose each five mature trees of comparable size per species in a forest patch of about 50 m^2 north of the walkway (mean diameter at breast height ± SD: 32.6 ± 5.3 cm; mean tree height ± SD: 21.9 ± 3.9 m; for details see Table S1). Within this patch, *A. campestre* grows mainly on the upper slope with shallower soil, while *A. platanoides* and *A. pseudoplatanus* prefer the mid- and lower slope with somewhat deeper profiles. Thus, the three species co-exist under the same climatic conditions but may have access to somewhat different soil water reserves due to preference of different edaphic microhabitats along the slope.

Sample collection

For every tree, at least 3 branches from the uppermost sun-exposed crown were collected in August and September 2015. Only branches not exceeding 10 mm in diameter were sampled. From the branches, a segment of 50–60 cm length, preferably of straight shape, was cut in air and immediately transferred to polyethylene tubes filled with distilled water and a sodium-silver-chloride complex (16 $\mu g\ L^{-1}$ Ag and 8 $mg\ L^{-1}$ NaCl; Micropur katadyn, Wallisellen, Switzerland) to prevent microbial activity and stored at 4 °C until further processing within 6 weeks, a storage time which has been shown not to affect hydraulic measurements (cf. Herbette et al. 2010). In addition, all leaves distal to the branch segment used for hydraulic measurements were collected in a plastic bag and stored at 4 °C. For the hydraulic measurements, branches were shortened to ~30 cm length. From the basipetal left-overs, segments of 3 cm length were taken in proximate distance to the cut and stored in 70% ethanol for subsequent xylem anatomical analyses. For wood density determination, another basipetal segment of comparable length was subsequently cut-off from the 30 cm branch segment after completion of the hydraulic measurements. A list of all traits measured, the corresponding acronyms and units is given in Table 1.

Leaf traits

All leaves of a branch were scanned (V11 Epson Perfection, Epson, Nagano, Japan) and analyzed for the mean lamina size of single leaves (A_{leaf}, cm^2), and total leaf area of the branch distal to the segment investigated using the software WinFolia (version 2014, Régent Instruments, Quebec City, QC, Canada). The Huber value, i.e. the sapwood-to-leaf-area ratio (HV; $10^4\ m^2\ m^{-2}$), was also calculated by dividing sapwood area (see below) by the total leaf area.

Subsequently, leaves were oven-dried at 70 °C for 72 h and specific leaf area (SLA, $cm^2\ g^{-1}$) calculated for the leaves of each branch. Furthermore, the total foliar *C* and *N* concentrations as well as the carbon and nitrogen isotope signatures of leaf dry mass were analyzed at the Centre for Stable Isotope Research and Analysis (KOSI) of the University of Göttingen by mass spectroscopy (Deltaplus, ThermoFinnigan, Bremen, Germany), connected to a Conflo III interface (Thermo Electron Corporation, Bremen, Germany) and a NA2500 elemental analyser (CE-Instruments, Rodano, Milano, Italy). The isotope signatures of *C* and *N* were expressed in standard δ notion:

$$\delta = \left(R_{\mathrm{sample}}/R_{\mathrm{standard}} - 1\right) \times 1000\,(‰).$$

Table 1 List of variables included in the study with definitions and units

Abbreviation	Units	Definition
Hydraulic traits		
P_{12}	MPa	Xylem pressure at 12% loss of hydraulic conductance
P_{50}	MPa	Xylem pressure at 50% loss of hydraulic conductance
P_{88}	MPa	Xylem pressure at 88% loss of hydraulic conductance
K_S	kg m^{-1} MPa^{-1} s	Specific conductivity
K_L	10^{-4} kg m^{-1} MPa^{-1} s^{-1}	Leaf-specific conductivity
K_P	kg m^{-1} MPa^{-1} s	Potential conductivity
K_{pit}	kg m^{-1} MPa^{-1} s	Pit conductivity
Foliar traits		
HV	10^{-4} m^2 m^{-2}	Huber value, i.e. the sapwood-to-leaf-area ratio
A_{leaf}	cm^2	Mean leaf size
SLA	cm^2 g^{-1}	Specific leaf area
C_{mass}	g kg^{-1}	Mass-specific carbon content
N_{mass}	g kg^{-1}	Mass-specific nitrogen content
CN		Carbon to nitrogen ratio, i.e. the C:N ratio
$\delta^{13}C$	‰	Carbon isotopic signature
Wood properties		
BA	year	Branch age
A_{growth}	mm^2 year^1	Annual branch sapwood area increment
A_{xylem}	mm^2	Basipetal maximal sapwood area
A_{lumen}:A_{xylem}	%	Lumen to sapwood area ratio
D	µm	Mean vessel diameter
D_h	µm	Hydraulically weighted vessel diameter
VD	n mm^{-2}	Vessel density
VI	mm m^{-2}	Vulnerability index
WD	g cm^{-3}	Branch wood density

Hydraulic conductivity

The branches were shortened to a length of 300–350 mm, all lateral branches cut off and the generated scars closed with instant glue (Loctite 431, Henkel, Düsseldorf, Germany). The length of the branches and the diameters at the basipetal and distal ends and at four positions along the branch were determined with a caliper prior to hydraulic measurement. Two to three cm of the bark on the basipetal end was then carefully removed. For the measurement of hydraulic conductivity (K_h; kg m MPa^{-1} s^{-1}), the segments were connected to the Xyl'em apparatus (Bronkhorst France, Montigny les Cormeilles, France). Actual hydraulic conductivity (K_h^{act}) was first measured under low pressure (6 kPa). The segment was then repeatedly flushed at high pressure (120 kPa) for 10 min to ensure the removal of potential emboli until maximum hydraulic conductivity (K_h^{max}) was reached. This process was repeated three to four times until no change in K_h values was observed. Distilled and degassed water filtered (0.2 µm) to which 10 mM KCl and 1 mM $CaCl_2$ was added was used for the measurements. The hydraulic conductivity and flow rate data were analyzed with the software XylWin 3.0 (Bronkhorst France, Montigny les Cormeilles, France). Based on the measured maximum hydraulic conductivity and the length of the branch segment, specific hydraulic conductivity (K_S; kg m^{-1} MPa^{-1} s^{-1}) was obtained by deviding K_h^{max} by the basipetal sapwood cross-sectional area without pith and bark (cf. Hajek et al. 2014; Schuldt et al. 2016). Leaf specific conductivity (K_L; kg m^{-1} MPa^{-1} s^{-1}) was obtained by relating K_h^{max} to the associated total leaf area of the branch segment.

Vulnerability to cavitation

The Cavitron technique (Cochard 2002; Cochard et al. 2005) was used to determine the vulnerability to cavitation of the branch segments. We investigated the same flushed branch segments as were used before for hydraulic conductivity measurements, which were either processed directly on the same day, or stored over night at 4° C until the next day. The branches had a mean basipetal diameter of 6.22 ± 0.69 mm (mean ± SD) and a mean acropetal diameter of 5.19 ± 0.59 mm. Because their xylem was relaxed after flushing they were shortened in air to a length of 27.5 cm and the bark removed on the first 4 cm at both ends. Subsequently, the segments were inserted into a custom-made

Cavitron rotor chamber which was attached to a commercially available centrifuge (Sorvall RC-5C; Thermo Fisher Scientific, Waltham, MA, USA). Measurements started with a negative pressure of -0.834 MPa, which was stepwise raised by 0.2–0.3 MPa until the percentage loss of conductivity (PLC, %) reached at least 90%. Conductivity data for each velocity were recorded and analyzed with the software CaviSoft (version 4.0, University of Bordeaux, France). By plotting the PLC-values against xylem pressure, vulnerability curves were generated for each branch. Sigmoidal functions were fitted to the data points following Pammenter and Van der Willigen (1998) to derive the xylem pressure causing 50% loss of conductivity (P_{50}) according to the equation:

$$\mathrm{PLC} = 100/(1 + \exp(s/25 \times (Pi - P50))),$$

with s (% MPa^{-1}) being the negative slope of the curve at the inflexion point and P_i the applied xylem pressure. Subsequently, the xylem pressures causing 12% and 88% loss of conductivity (P_{12} and P_{88}) were calculated following Domec and Gartner (2001).

Xylem anatomy and branch growth rate

A sliding microtome (G.S.L.1, Schenkung Dapples, Zürich, Switzerland) was used to cut transverse sections from all ethanol-stored basipital branch segments, which subsequently were digitalized at x100 magnification using a stereomicroscope equipped with an automatic stage and a digital camera (SteREOV20, Carl Zeiss MicroImaging GmbH, Jena, Germany; Software: AxioVision c4.8.2, Carl Zeiss MicroImaging GmbH). Image processing was conducted with the software Adobe Photoshop CS6 (c.13.0.1; Adobe Systems Inc., San Jose, CA, USA) and ImageJ using the particle analysis function. For all subsequent calculations, the complete xylem cross-section without pith and bark was analyzed. Measured parameters included the lumen to sapwood area ratio (A_lumen:A_xylem, %), vessel density (VD, n mm^{-2}), and vessel diameter (D, µm) from major *(a)* and minor *(b)* vessel radii using the expression $D = ((32 \times (\mathrm{a} \times \mathrm{b})^3)/(\mathrm{a}^2 + \mathrm{b}^2))^{1/4}$ given by White (1991). D was then used to calculate the hydraulically weighted diameter (D_h, µm) according to Sperry et al. (1994) as $D_\mathrm{h} = \Sigma \mathrm{D}^5/\Sigma \mathrm{D}^4$. Furthermore, the vulnerability index (VI) after Carlquist (1977) was calculated by dividing vessel diameter (D) by vessel density (VD) to obtain a rough assessment of the xeromorph or mesomorph character of the branch xylem tissue. Potential conductivity (K_P; kg m^{-1} MPa^{-1} s^{-1}) was calculated according to the Hagen–Poiseuille equation as $K_\mathrm{P} = (((\pi \times \Sigma D^4)/128\ \eta) \times p)/A_\mathrm{xylem}$, where η is the viscosity (1.002×10^{-9} MPa s) and p the density of water (998.2 kg m^{-3}), both at 20°C, and A_xylem (mm^2) is the analyzed sapwood area. Pit conductivity was estimated by subtracting potential conductivity (K_P) from the specific conductivity (K_S) according to Larter et al. (2017) as $K_\mathrm{pit} = ((1/K_\mathrm{S}) - (1/K_\mathrm{P}))^{-1}$. A low K_pit value indicates that a higher resistance to water flow has to be overcome. Branch age was estimated by counting the annual growth rings of each sample. Branch diameter growth rate (A_growth) was calculated by dividing branch sapwood area (A_xylem) by branch age. These data were preferred over data from permanently installed increment tapes on the stem of the trees used to estimate wood production, as the branch data reflect the local growth conditions in the canopy better.

Wood density

To determine branch wood density (WD, g cm^{-3}), branch segments were collected after determining vulnerability to cavitation. A segment of about 3 cm length was cut from each branch and the fresh volume was gravimetrically determined according to Archimedes' principle through water displacement. Afterwards, the samples were oven-dried at 105 °C for 72 h to obtain dry weight, and wood density was calculated by dividing dry mass by the fresh volume of the segment.

Statistical analyses

The statistical analyses were carried out with SAS 9.13 software (SAS Institute Inc., Cary, North Carolina, USA), except for linear regression analyses which were performed with the software XACT 8.03 (SciLab, Hamburg, Germany). Prior to analysis, subsamples from the same tree individuals were averaged to obtain replicates on the tree level. These data were then tested for normal distribution with a Shapiro-Wilk normality test and log-transformed if necessary. To test for significant differences between the species, general linear models (GLM) were calculated for normally distributed data. Non-normally distributed data were tested with the Kruskall–Wallis test. A significance level of $P \leq 0.05$ was used throughout the paper. To test for inter-relationships between traits, Pearson correlation analyses were conducted for all possible trait combinations. Some of the more meaningful relationships are shown in graphs. All graphs were generated with the software XACT 8.03.

Results

Traits related to hydraulic efficiency and safety

The resistance to embolism, expressed by the P_{12}, P_{50} and P_{88} values, differed significantly between the three *Acer* species (Fig. 1). *A. campestre* was the least sensitive species with lowest air-entry point (P_{12}) (-4.9 MPa), P_{50}-value (-5.4 MPa) and point of no return (P_{88}-value, -6.0 MPa) of the three species (difference to other species significant),

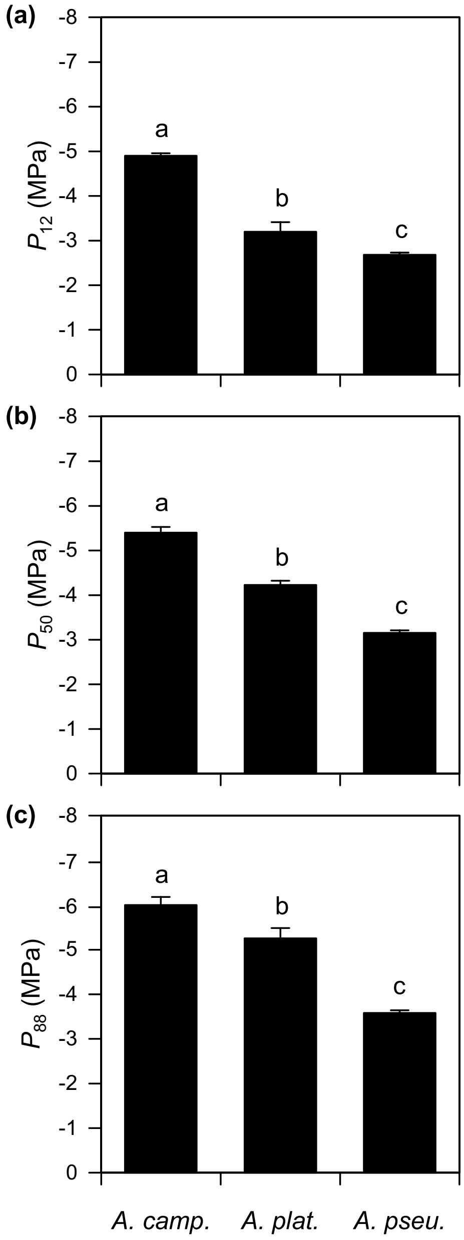


Fig. 1 Traits related to hydraulic safety of *Acer campestre* (*A. camp.*), *Acer platanoides* (*A. plat.*) and *Acer pseudoplatanus* (*A. pseu.*). **a** Xylem pressure at 12%, **b** 50%, and **c** 88% loss of conductivity. Values are means ± SE on the species level. Different letters indicate significant differences at $P \leq 0.05$

followed by *A. platanoides* (P_{50} −4.2 MPa) and *A. pseudoplatoides* as the most sensitive species (P_{50} −3.1 MPa). The same species sequence was found for specific (K_S) and pit conductivity (K_{pit}), but in opposite direction. K_S and K_{pit} were lowest in *A. campestre* and increased toward *A. pseudoplatanus* from 0.9 to 1.4 and 1.1 to 3.0 kg m^{-1} MPa^{-1} s^{-1}, respectively (difference between *A. campestre* and *A. pseudoplatanus* significant, Fig. 2a, d). This species sequence was not reflected in leaf-specific conductivity (K_L) and potential conductivity (K_P), which tended to be lower in *A. platanoides* than in the other two species (Fig. 2b, c). A summary of all major variables explored is given in Table S2.

Leaf traits

The sun leaves of *A. platanoides* were in our stand of larger mean size and had a higher SLA than those of *A. pseudoplatanus* and also exceeded the typically small-leaved *A. campestre* (Fig. 3a, b). Only minor species differences existed for Huber value, i.e. the sapwood-to-leaf-area ratio (not significant), and the carbon isotope signature ($\delta^{13}C$) of leaf dry mass (Fig. 3c, d); the latter was slightly, but significantly, higher in *A. platanoides* than in the other species. The foliar C/N ratio was significantly higher in *A. campestre* than in the two other species.

Wood anatomy

Similar to the leaf traits, the wood anatomical traits did not show the anticipated trends across the three species (Fig. 4). Only branch wood density (WD) decreased significantly from *A. campestre* to *A. platanoides* and *A. pseudoplatanus* in accordance with expectations. The lumen-to-sapwood-area ratio (A_{lumen}:A_{xylem}) also tended to decrease from *A. campestre* to *A. platanoides* and further to *A. pseudoplatanus*, but the differences were not significant.

Vessel density (VD) did not differ significantly between the species, even though mean vessel diameter (*D*) was significantly higher in *A. campestre* than in *A. platanoides* (but not in comparison to *A. pseudoplatanus*). The vulnerability index (VI) was similar in *A. campestre* and *A. pseudoplatanus,* but significantly lower in *A. platanoides*.

Determinants of hydraulic safety

The Pearson correlation analysis yielded some highly significant inter-relationships between xylem safety and efficiency (Table 2, Fig. 5). As expected, a positive correlation existed between specific conductivity (K_S) and P_{50} across the sampled species (Figure 5a), indicating that a higher conductivity is associated with a higher (less negative) P_{50}. Moreover, the P_{50} value was also strongly influenced by pit conductivity, explaining almost 60% of the variation. The lower the pit conductivity, the lower (more negative) the P_{50} value (Fig. 5b). While mean vessel diameter and vessel density were unrelated to P_{50} (Fig. 5c, e), wood density influenced P_{50} highly significantly (Fig. 5d). The denser the wood, the higher the embolism resistance as expressed by the P_{50} value. Furthermore, a close, positive relationship between the foliar C/N ratio and P_{50} was observed.

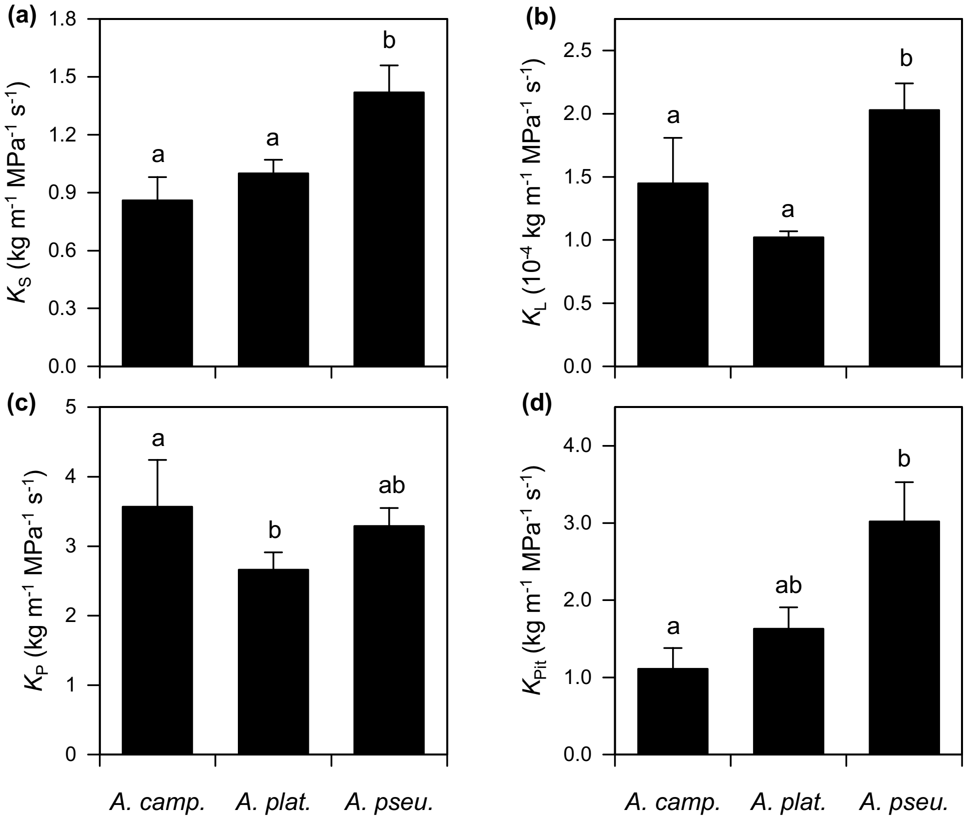


Fig. 2 Traits related to hydraulic conductivity of *Acer campestre* (*A. camp.*), *Acer platanoides* (*A. plat.*) and *Acer pseudoplatanus* (*A. pseu.*). **a** Specific conductivity, **b** leaf-specific conductivity, **c** potential conductivity, **d** pit conductivity. Values are means ± SE on the species level. Different letters indicate significant differences at $P \leq 0.05$

Determinants of wood anatomy and hydraulic conductivity

The wood anatomical traits mean vessel diameter (D) and hydraulically-weighted vessel diameter (D_h) correlated closely with specific conductivity (K_S) and leaf-specific conductivity (K_L) (Fig. 6); VD was negatively related to K_L. Interestingly, wood density was not related to hydraulic conductivity (K_S or K_L; Fig. 6d). Pit conductivity was positively related to K_S and K_L (Table 2). Furthermore, the branch growth rate (A_{growth}) was highly significantly related to the three hydraulic efficiency traits (K_S, K_L and K_P), and also to the wood anatomical traits (D, D_h and VI) (Table 2, Fig. 7).

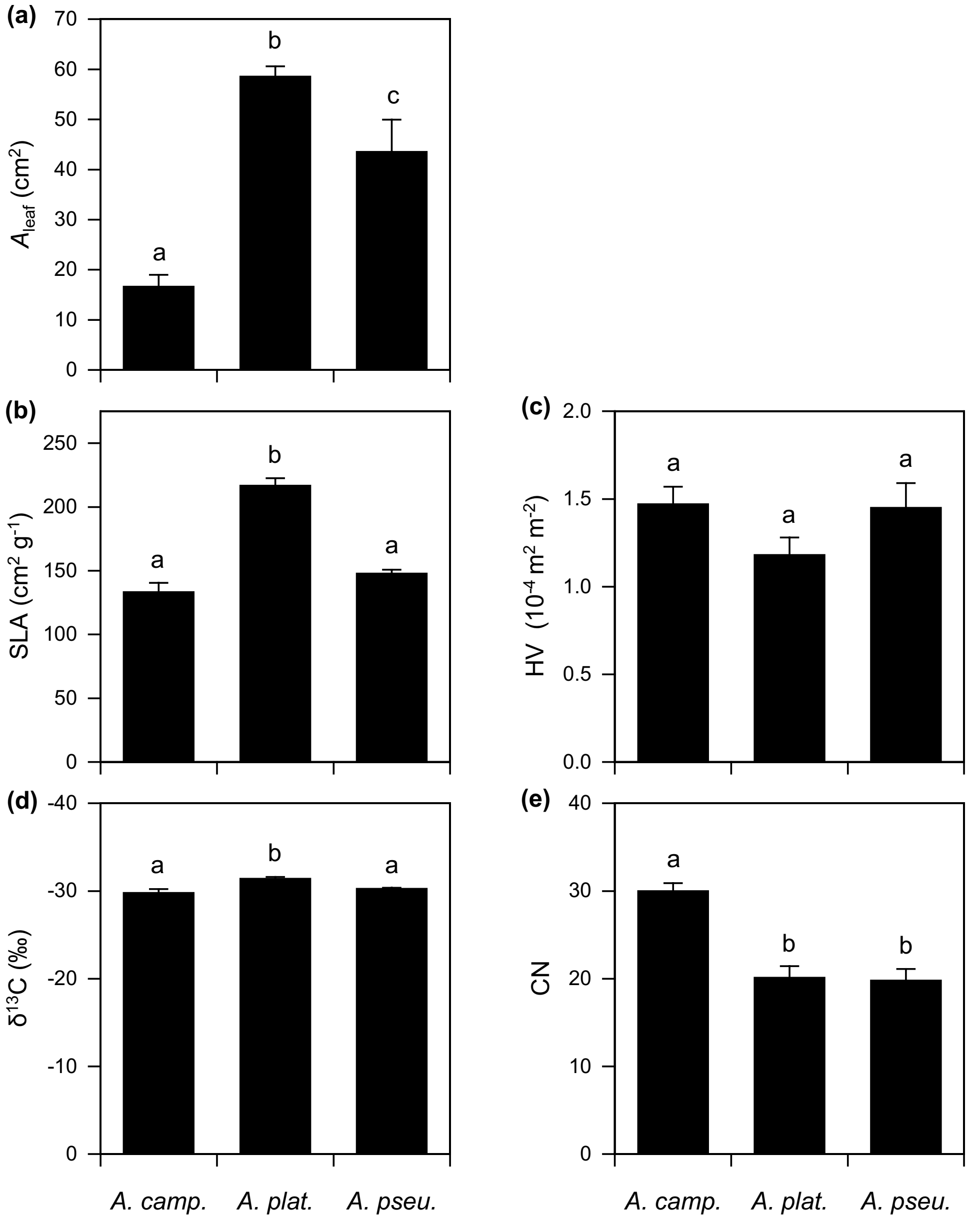
Discussion

Xylem safety and efficiency reflect the species' habitat preferences

In support of our first hypothesis, branch embolism resistance differed markedly between the three species, confirming that *A. campestre* is the most embolism-resistant taxon, followed by *A. platanoides* and finally by *A. pseudoplatanus* as the most vulnerable species. The species differences were similar for the xylem pressures at 12, 50 or 88% loss of hydraulic conductance (P_{12}, P_{50} and P_{88} values, respectively). Our species ranking in embolism resistance matches the results of Tissier et al. (2004) who studied 10 m-tall individuals of the three species in eastern France, although the absolute xylem pressure threshold values are much lower in our study. For example, Tissier et al. (2004) reported a mean P_{50} value of − 1.8 MPa for 1 year-old sun-exposed branches of *A. campestre*, which is about 3.5 MPa higher than our corresponding value (–5.4 MPa). The contrasting results may be caused by both differences in site conditions and in methodology. Our study site is much more xeric than that in France with a high groundwater table. Further, Tissier et al. (2004) used the air-injection method, while we applied the Cavitron technique.

In contrast to embolism resistance, hydraulic efficiency, i.e. empirically measured specific conductivity (K_S), increased from *A. campestre* to *A. pseudoplatanus*. This was, however, not mirrored in any xylem anatomical (e.g., vessel diameter and density) or derived hydraulic trait (potential conductivity, K_P), which were all surprisingly similar across the three *Acer* species. The increase in hydraulic efficiency must therefore be caused by differences in pit properties, which are estimated to account for half of the total xylem resistance along the hydraulic pathway (Choat et al. 2006; Hacke et al. 2006). Accordingly, pit conductivity (K_{pit}), which is estimated as the

Fig. 3 Leaf traits of *Acer campestre* (*A. camp.*), *Acer platanoides* (*A. plat.*) and *Acer pseudoplatanus* (*A. pseu.*). **a** Mean leaf area of single leaves, **b** specific leaf area, **c** Huber value, **d** carbon isotope signature, **e** carbon-to-nitrogen ratio. Values are means ± SE on the species level. Different letters indicate significant differences at $P \leq 0.05$



difference between empirically measured and theoretically calculated hydraulic conductivity, likewise increased from *A. campestre* to *A. pseudoplatanus*.

Relation between xylem hydraulic safety and efficiency

A principal hypothesis of plant hydraulics postulates a trade-off between hydraulic safety and efficiency. In support of this hypothesis, we found significant positive relationships between the P_{12}, P_{50} and P_{88} values of the three *Acer* species and specific conductivity (K_S), which matches results of earlier studies on various European and North American maple species (Tissier et al. 2004; Lens et al. 2011). Safety-efficiency trade-offs have been confirmed for other tree species samples as well (e.g., Markesteijn et al. 2011), but the majority of recent studies could find only weak or no relations between P_{50} and K_S in tree species samples (Maherali et al. 2006; Gleason et al. 2016). It has been suggested that the visibility of a hydraulic safety-efficiency trade-off may depend on the range of variation in wood anatomical properties encountered (Schuldt et al. 2016). Accordingly, positive hydraulic safety-efficiency relationships are more likely to appear in interspecific studies with species from different habitats than in samples of co-occurring, phylogenetically related taxa or in intraspecific studies (Hajek et al. 2016; Schuldt et al. 2016). We assume that our three *Acer* species may

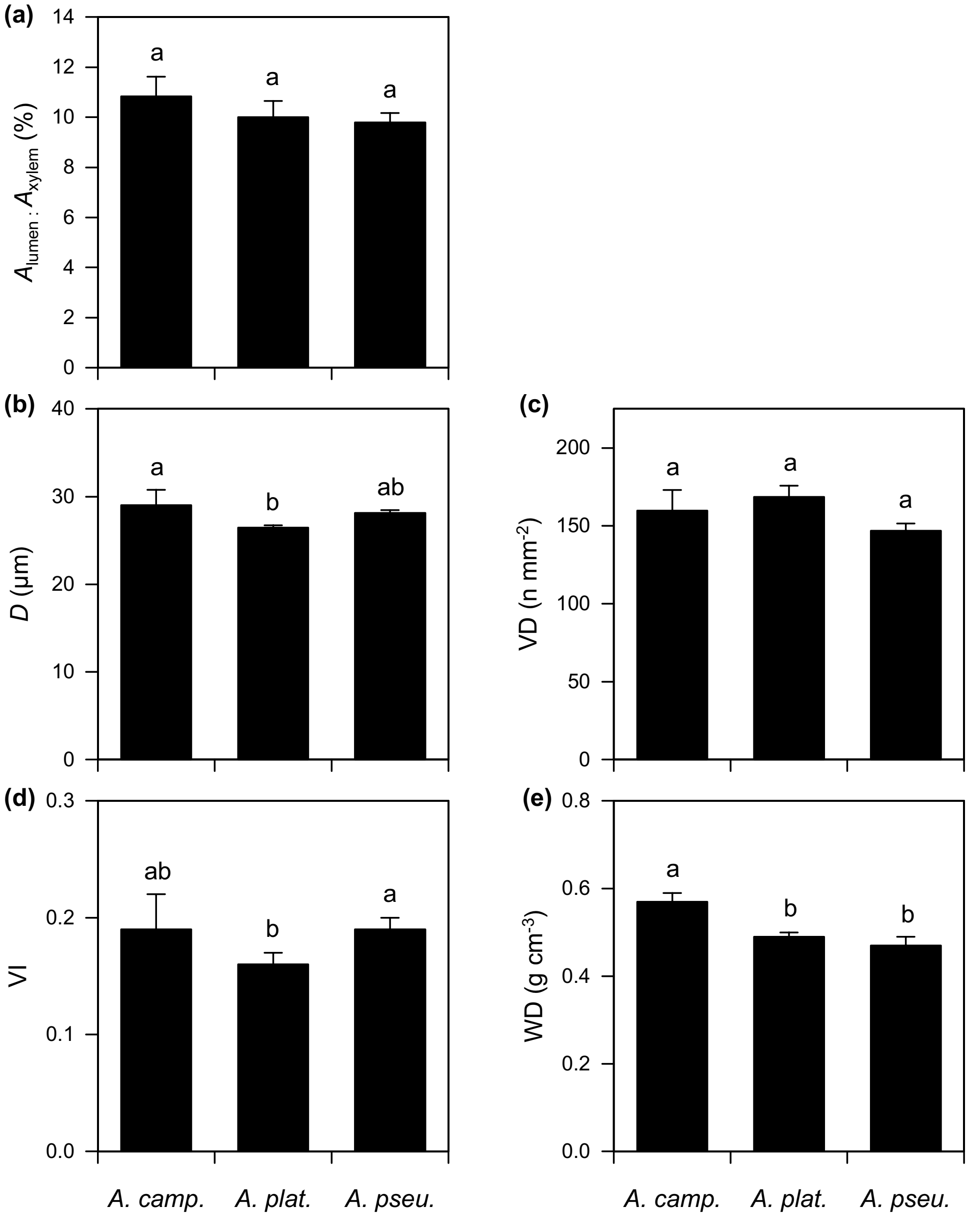


Fig. 4 Wood anatomical traits of *Acer campestre* (*A. camp.*), *Acer platanoides* (*A. plat.*) and *Acer pseudoplatanus* (*A. pseu.*). **a** Lumen-to-sapwood-area ratio, **b** mean vessel diameter, **c** vessel density, **d** vulnerability index, **e** branch wood density. Values are means ± SE on the species level. Different letters indicate significant differences at $P \leq 0.05$

represent tree functional types, which are sufficiently different to reveal a safety-efficiency trade-off in the branch xylem. Nevertheless, a trade-off has also been detected for certain intraspecific samples (Corcuera et al. 2011; Guet et al. 2015) or at the genus level (Torres-Ruiz et al. 2017).

Dependence of hydraulic safety and efficiency on wood anatomy

Since hydraulic conductivity increases with conduit diameter by the fourth power, it was initially assumed that the safety-efficiency trade-off results from vessel diameter itself, as wider, more conductive vessels are simultaneously assumed to be more vulnerable to embolism formation (Zimmermann 1983). Many studies have since then jointly investigated hydraulic and wood anatomical traits to understand how they interact with hydraulic safety. The assumption remains that vulnerability to embolism formation and hydraulic conductivity are determined by vessel properties, but the focus has shifted from conduit diameter to inter-vessel transport. Most likely, pit membrane characteristics are more directly related to embolism resistance than vessel diameter itself (Tyree and Sperry 1989). Nevertheless, as pit membrane characteristics are assumed to depend at least partly on conduit diameter (Hacke et al. 2017), an indirect association between vessel diameter and hydraulic safety may appear in some cases while lacking in others. We found the expected close positive relation between hydraulically-weighted vessel diameter (D_h) and specific and leaf-specific conductivity (K_S and K_L, respectively), and a negative relation between

Table 2 Pearson correlation coefficients for linear relationships between 23 functional trait variables measured in trees of the three Acer species (*A. campestre*, *A. platanoides*, *A. pseudoplatanus*)

	P_{12}*	P_{50}	P_{88}	K_S	K_L	K_P**	K_{pit}**	HV	A_{leaf}	SLA	C_{mass}	N_{mass}	CN	δ^{13}C*	BA	A_{growth}**	A_{xylem}	$A_{lumen}:A_{xylem}$	VD	D	D_h	VI
P_{50}	**-0.93**																					
P_{88}	**-0.77**	**-0.95**																				
K_S	**0.59**	**0.71**	**0.71**																			
K_L	ns	***0.45***	**0.57**	**0.65**																		
K_P**	ns	ns	ns	***0.48***	**0.61**																	
K_{pit}**	**0.75**	**0.77**	***0.68***	**0.92**	**0.67**	ns																
HV	ns	ns	ns	ns	***0.55***	ns	ns															
A_{leaf}	**0.73**	**0.58**	ns	ns	ns	ns	ns	ns														
SLA	ns	ns	ns	ns	ns	ns	ns	**-0.67**	**0.74**													
C_{mass}	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns												
N_{mass}	**0.85**	**0.75**	**0.57**	ns	ns	ns	**0.58**	ns	**0.68**	***0.61***	ns											
CN	**-0.88**	**-0.80**	**-0.63**	ns	ns	ns	**-0.62**	ns	**-0.70**	**-0.63**	ns	**-0.99**										
δ^{13}C*	ns	ns	ns	ns	ns	ns	ns	***0.54***	**-0.63**	**-0.81**	ns	***-0.60***	**0.64**									
BA	ns	ns	***-0.44***	**-0.62**	**-0.69**	***-0.55***	***-0.52***	ns	ns	ns	ns	ns	ns	ns								
A_{growth}**	ns	ns	ns	***0.51***	**0.72**	**0.77**	ns	***0.49***	ns	***-0.56***	ns	ns	ns	ns	**-0.84**							
A_{xylem}	**-0.67**	**-0.57**	ns	ns	ns	ns	***-0.47***	ns	**-0.57**	**-0.63**	ns	**-0.66**	**0.72**	***0.51***	ns	ns						
$A_{lumen}:A_{xylem}$	ns	ns	ns	ns	ns	**0.81**	ns	ns	ns	ns	***0.44***	ns	ns	ns	ns	***0.54***	***0.45***					
VD	ns	ns	ns	***-0.44***	**-0.68**	ns	**-0.64**	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns				
D	ns	ns	ns	ns	**0.67**	**0.90**	ns	ns	ns	ns	ns	ns	ns	ns	***-0.56***	**0.81**	ns	**0.59**	***0.49***			
D_h	ns	ns	***0.51***	**0.61**	**0.77**	**0.85**	***0.55***	ns	ns	***-0.50***	ns	ns	ns	ns	**-0.69**	**0.80**	ns	***0.44***	***-0.52***	**0.85**		
VI	ns	ns	ns	ns	**0.75**	**0.61**	***0.57***	ns	ns	ns	ns	ns	ns	ns	***-0.51***	**0.67**	ns	ns	**-0.85**	**0.85**	**0.74**	
WD	**-0.82**	**-0.81**	***-0.70***	ns	ns	ns	***0.49***	ns	**-0.79**	ns	ns	**-0.80**	**0.83**	***0.49***	ns	ns	**0.69**	ns	ns	ns	ns	ns

ns non significant; bold and italic text, $P < 0.05$; bold text, $P < 0.01$; bold underlined text, $P < 0.001$, *not normally distributed, **not normally distributed and log transformed. See Table 1 for definitions of abbreviations

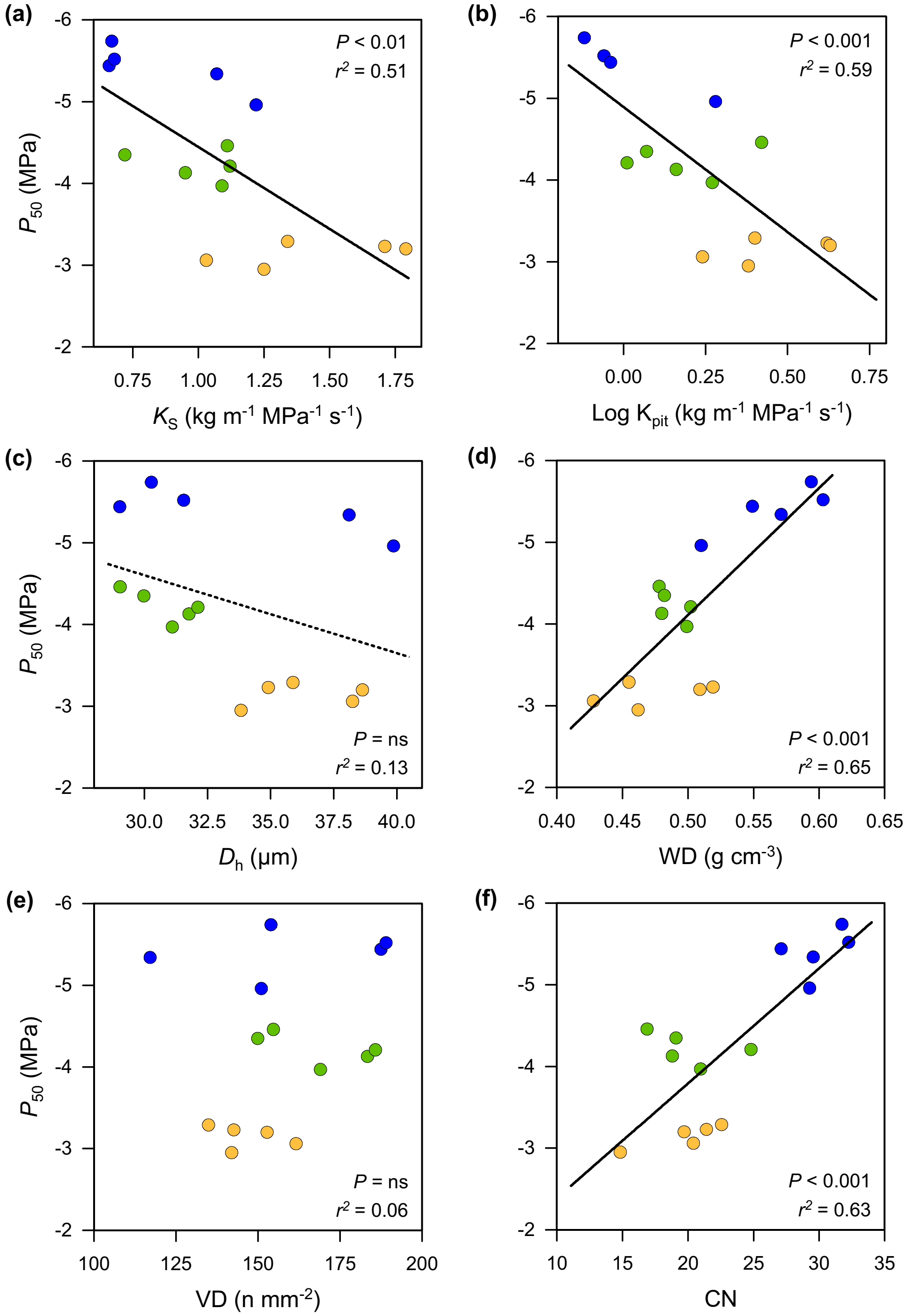


Fig. 5 Various traits in their relation to P_{50}. **a** Specific conductivity, **b** pit conductivity, **c** hydraulically weighted vessel diameter, **d** branch wood density, **e** vessel density, **f** carbon to nitrogen ratio. Blue filled circles, *A. campestre*, green filled circles *A. platanoides*, orange filled circles *A. pseudoplatanus*. Values are means on the tree level. *ns* non-significant relationships

vessel density and K_S and K_L, but no correlation between vessel diameter and P_{50}.

In fact, the published evidence for a relation between vessel diameter and embolism resistance is mixed, with several studies reporting such a dependence within or across species (e.g., Hargrave et al. 1994; Maherali and DeLucia 2000; Maherali et al. 2006; Jacobsen et al. 2007; Awad et al. 2010; Sterck et al. 2012; Hajek et al. 2014), while others do not (e.g., Alder et al. 1996; Choat et al. 2007; Fichot et al. 2010; Lens et al. 2011; Hajek et al. 2016; Schuldt et al. 2016). Yet, it is unclear which pit membrane property is the decisive one. There is strong evidence for pit membrane thickness and porosity to be closely related to hydraulic safety (Li et al. 2016; Schuldt

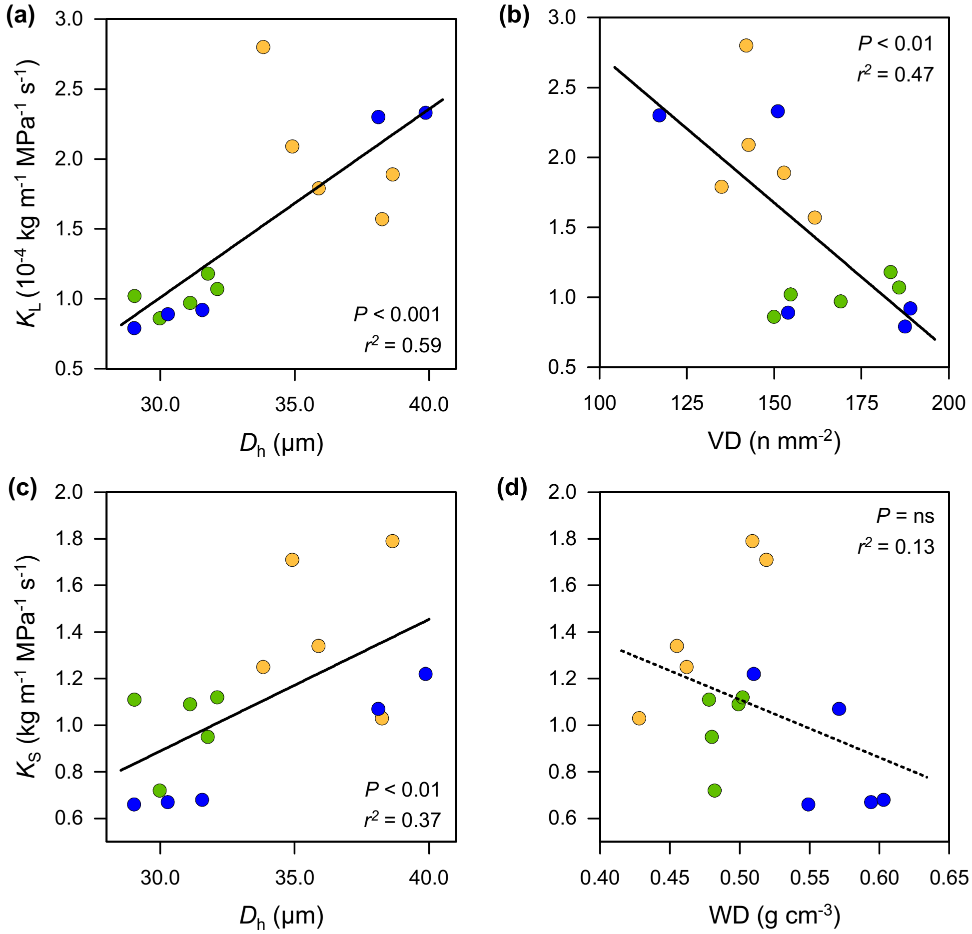


Fig. 6 Various traits in their relation to leaf-specific conductivity (K_L) and specific conductivity (K_S). **a**, **c** Hydraulically weighted vessel diameter, **b** vessel density, **d** branch wood density. Blue filled circles, *A. campestre*, green filled circles *A. platanoides*, orange filled circles *A. pseudoplatanus*. Values are means on the tree level. *ns* non-significant relationships

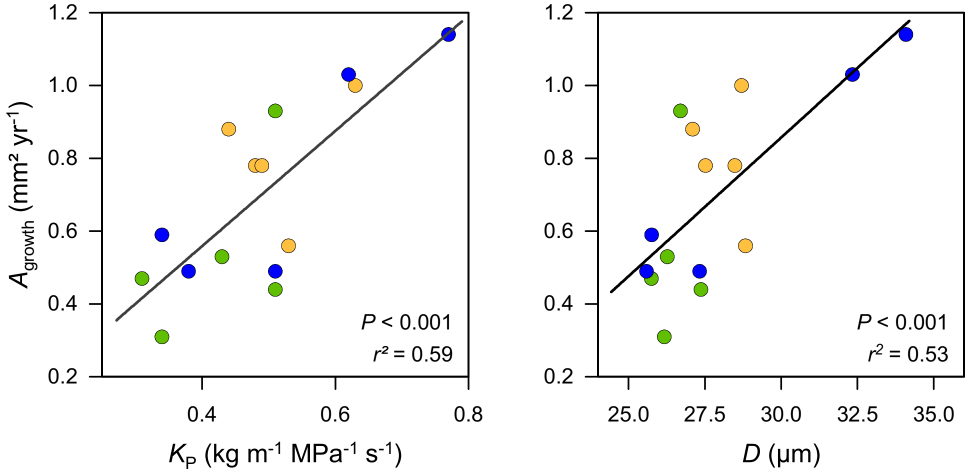


Fig. 7 Potential conductivity (K_P) and vessel diameter (D) in relation to branch growth rate (A_{growth}). Blue filled circles, *A. campestre*, green filled circles *A. platanoides*, orange filled circles *A. pseudoplatanus*. Values are means on the tree level

et al. 2016), as well as for a role of pit chamber depth and width (Hacke et al. 2004; Lens et al. 2011). The current study is support for the assumption of a key role for pit membrane properties in that it shows a large decrease in calculated pit membrane conductivity from *A. pseudoplatanus* to *A. campestre,* in parallel to the lowering of the P_{50} value.

Influence of wood density on xylem safety and efficiency

Wood density is another trait, which may in theory affect hydraulic safety and efficiency, as high wood density generally should be associated with narrower vessels that are less vulnerable to embolism and have a lower conductivity.

However, the evidence for this relation is mixed. There are studies reporting wood density to correlate with P_{50} in angiosperms (Jacobsen et al. 2007; Markesteijn et al. 2011; Ogasa et al. 2013), but other studies show contradicting results (Willson and Jackson 2006; Cochard et al. 2007; Schuldt et al. 2016).

This study revealed a highly significant negative relationship between wood density and P_{50}, but on the other hand, wood density was neither related to hydraulic conductivity nor to any other wood anatomical trait including vessel diameter. As lumen-to-sapwood-area ratio showed also no relation to wood density in the three *Acer* species, other properties unrelated to water conduction (such as fiber wall thickness) must have a larger influence (Poorter et al. 2010; Martínez-Cabrera et al. 2011; Ziemińska et al. 2013).

The relation between branch hydraulics and leaf traits

The correlation between branch hydraulic properties and leaf morphological and chemical traits was remarkably weak. None of the studied leaf parameters showed a systematic relation to the decline in xylem safety and the increase in hydraulic efficiency from *A. campestre* to *A. platanoides* and further to *A. pseudoplatanus*. Huber value, i.e. the ratio of branch sapwood area to dependent leaf area, varied only little among the species and the specific leaf area (SLA) was significantly smaller in the apparently more vulnerable *A. pseudoplatanus* than *A. platanoides*. This contradicts the general finding in meta-analyses of leaf trait data that SLA decreases with increasing aridity (Wright et al. 2004). Similarly, HV has often been found to be responsive to gradients of water availability when different populations of a species are compared (e.g., Maherali et al. 2002; Willson et al. 2008; Martínez-Vilalta et al. 2009; Gleason et al. 2012). Also, the foliar carbon isotope signature (δ^{13}C) was remarkably similar among the species, probably reflecting the uniform microclimate of the stand, while inherent differences in stomatal conductance apparently are less important.

Our results suggest that these foliar traits are more plastic than the hydraulic traits, reflecting foliar acclimation of the three species in the mixed stand to rather similar environmental conditions. The weak association between leaf traits and hydraulic traits in our sample could thus be a consequence of different degrees of phenotypic plasticity in these trait groups. In their study of different tropical tree species, Markesteijn et al. (2011) similarly found no relation between SLA and xylem safety, even though they investigated a hydrological gradient. In contrast, Maherali et al. (2006) found a relatedness between leaf and hydraulic traits, but they referred mostly to the root level and not to stem or branch hydraulics.

The largest species differences existed for leaf size. The much smaller lamina of *A. campestre* may well reflect the species' assumed greater drought tolerance and occurrence in more drought-prone environments, but leaf size in the two other maple species does not relate to the different habitat preferences and hydraulic properties. Interestingly, the foliar C/N ratio of *A. campestre* was significantly larger than in the other two species and closely related to the P_{50} value.

Hydraulic properties in their relation to branch growth rate

If greater hydraulic safety is associated with reduced pit membrane conductivity, it should in general also be related to a xylem with thicker conduit cell walls. This requires higher carbohydrate investment into the conducting system, which must reduce growth (Enquist et al. 1999). Therefore, growth rate should decrease with increasing hydraulic safety, as it typically does with increasing wood density. Although there is substantial support for a negative relation between wood density and growth rate (King et al. 2006; Poorter et al. 2010; Hietz et al. 2013; Hoeber et al. 2014), wood density cannot serve as a good predictor of growth rate, as many other factors are acting on wood density as well. Correspondingly, many authors have found a much tighter relation of growth rate to hydraulic conductivity and vessel diameter than to wood density (Hajek et al. 2014; Hoeber et al. 2014; Kotowska et al. 2015). This is supported by the current study, where branch growth rate was significantly positively related to the three measures of hydraulic efficiency (K_S, K_L and K_P) as well as to vessel diameter, the key determinant of hydraulic conductivity. However, in line with other studies (Sterck et al. 2012; Hajek et al. 2014; Guet et al. 2015; Schuldt et al. 2016), we did not detect a relation between branch growth rate and embolism resistance suggesting that measures to increase safety are less resource-consuming than adaptations to increase hydraulic efficiency.

Conclusions

Our comparative study in a natural mixed forest with mature trees of three maple species differing in habitat preferences revealed a plausible decrease in embolism resistance and concomitant increase in hydraulic efficiency from *A. campestre* to *A. platanoides* and finally to *A. pseudoplatanus*, which reflects the species' assumed drought tolerance according to their habitat preferences in Central Europe and the distribution ranges (Leuschner and Ellenberg 2017). As in several other studies with trees, we found a trade-off between hydraulic safety and efficiency at the branch level, and a positive relation between branch growth rate and hydraulic conductivity. Even though wood density is reflecting the decreasing drought exposure of the species in the distribution ranges of the three species, wood density was unrelated to hydraulic efficiency and associated xylem anatomical traits. However, wood density was closely positively related to embolism resistance, possibly indicating effects of xylem cell wall thickness and related pit membrane properties. The fact that all three species grew in mixture suggests that the hydraulic properties of these species may be largely under genetic control, displaying the adaptation of the species to different climatic and hydrologic conditions in the past. The observed species differences in hydraulic efficiency and safety might therefore serve as valuable indicators of the overall drought exposure of *Acer* species in their distribution ranges. In contrast, most leaf morphological and chemical traits differed only weakly among the species and are likely more plastic in their response to the environment.

Author contribution statement BS designed the study, KS collected the field samples, performed the hydraulic measurements, the wood anatomical and statistical analyses, and wrote together with CL a first version of the manuscript, which was intensively discussed and revised by all authors.

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Compliance with ethical standards

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

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