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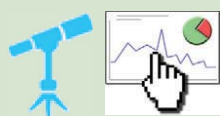Anhui Normal University
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Research paper

Stem hydraulic conductivity and embolism resistance of *Quercus* species are associated with their climatic niche

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The hydraulic traits of a plant species may reflect its climate adaptations. Southwest China is considered as a biodiversity hotpot of the genus *Quercus* (oak). However, the hydraulic adaptations of Asian oaks to their climate niches remain unclear. Ten common garden-grown oak species with distinct natural distributions in eastern Asia were used to determine their stem xylem embolism resistance (water potential at 50% loss of hydraulic conductivity, P_{50}), stem hydraulic efficiency (vessel anatomy and sapwood specific hydraulic conductivity (Ks)) and leaf anatomical traits. We also compiled four key functional traits: wood density, hydraulic-weighted vessel diameter, Ks and P_{50} data for 31 oak species from previous literature. We analyzed the relationship between hydraulic traits and climatic factors over the native ranges of 41 oak species. Our results revealed that the 10 Asian oak species, which are mainly distributed in humid subtropical habitats, possessed a stem xylem with low embolism resistance and moderate hydraulic efficiency. The deciduous and evergreen species of the 10 Asian oaks differed in the stem and leaf traits related to hydraulic efficiency. Ks differed significantly between the two phenological groups (deciduous and evergreens) in the 41-oak dataset. No significant difference in P_{50} between the two groups was found for the 10 Asian oaks or the 41-oak dataset. The oak species that can distribute in arid habitats possessed a stem xylem with high embolism resistance. Ks negatively related to the humidity of the native range of the 10 Asian oaks, but showed no trend when assessing the entire global oak dataset. Our study suggests that stem hydraulic conductivity and embolism resistance in *Quercus* species are shaped by their climate niche. Our findings assist predictions of oak drought resistance with future climate changes for oak forest management.

Keywords: climatic niche, distribution range, embolism resistance, hydraulic conductivity, *Quercus*, vessel anatomy.

Introduction

Climate change is causing more frequent drought events and this trend is predicted to continue, placing sessile and long-lived organisms such as trees at particularly high risks (Pfautsch et al. 2016, Shukla et al. 2019). Although tree mortality due to drought stress involves the injury of multiple tissues, hydraulic failure is a primary factor of tissue dieback and tree death (Anderegg et al. 2016, Cardoso et al. 2020; Chen et al. 2021*b*; Nolan et al. 2021, Powers et al. 2020). Water transport from the roots to leaves in plants is driven by the tensile force created by transpiration. Increased xylem tension during a drought event

can trigger gas propagation from gas-filled to sap-filled vessels when the tension reaches certain thresholds (Tyree and Sperry 1989). Gas bubbles grow into an embolism and further block the xylem hydraulic pathways, impacting leaf water supply and photosynthesis (Martin-StPaul et al. 2017), potentially causing catastropic hydraulic failure and tree mortality.

Many studies have reported functional variations in carbon and water economics between co-occurring deciduous and evergreen tree species. Compared with evergreen species, deciduous species usually have evolved leaves with higher photosynthetic rates to compensate for the relatively shorter

leafy period, which may require a more effective water supply by increasing leaf vein density and the efficiency of the hydraulic network (Zhu et al. 2013, Xiong and Nadal 2020). Leaf shedding by deciduous trees during the dry season can also function as a 'hydraulic fuse' to prevent the occurrence of an extreme negative water potential in the xylem, which can lead to hydraulic failure (Fu et al. 2012, Wolfe et al. 2016). Many studies have reported that deciduous species possess a xylem with lower embolism resistance than evergreen species (Chen et al. 2021b; Meinzer et al. 2008, Méndez-Alonzo et al. 2012, Zhang et al. 2013). However, no difference in the embolism resistance between the two groups has also been identified (Markesteijn et al. 2011). Increased leaf mass per area (LMA) and leaf thickness in arid environments occur in both deciduous and evergreen *Quercus* species, which is associated with an increased leaf density in evergreen oaks but decreased leaf density in deciduous oaks (Sancho-Knapik et al. 2021).

In addition to the phenology, key xylem hydraulic traits are also related to plant geographical distributions (Anderegg et al. 2016, Martin-StPaul et al. 2017, Nolan et al. 2021). For instance, inter-specific variation in embolism resistance may be related to the natural distribution of a species, with those in drier habitats typically possessing a xylem with higher embolism resistance (Bourne et al. 2017, Larter et al. 2017, Li et al. 2018, Oyanoghafo et al. 2021). At the intra-specific level, tree individuals of *Fagus sylvatica* from sites with a lower mean annual precipitation (MAP) had a more embolism-resistant xylem (Schuldt et al. 2015). Relationships have also been reported between habitat/niche climates with vessel diameter (Pfautsch et al. 2016, Larter et al. 2017) and stem hydraulic conductance (Liu et al. 2015). A stem xylem with large vessels often leads to high sapwood hydraulic conductivity (Ks) (Hacke et al. 2006). According to the Hagen–Poiseuille equation, the liquid conductance increases to the fourth power with vessel diameter. Previous research has identified that wider vessels tend to be more prone to cavitation (Hacke et al. 2006, Fu et al. 2012), although vessel ability to resist embolism is more closely related to the thickness of the intervessel pit membranes (Lens et al. 2011, Kaack et al. 2019, Kaack et al. 2021). Hydraulic efficiency and safety showed a weak trade-off across global woody species (Gleason et al. 2016), whereas a positive, negative or lack of significant correlation between xylem hydraulic conductivity (Ks) and embolism resistance (P_{50}) have been reported in smaller scale studies (Wheeler et al. 2005, Larter et al. 2017, Zhu et al. 2017).

The genus *Quercus* consists of ∼450 species, with a wide distribution in the northern hemisphere (Hipp et al. 2020). Many oaks are the dominant species in a wide variety of habitats, and some oaks produce high-quality timber (Nixon, 2006). Many studies have focused on oaks distributed in North American, Europe and the Mediterranean regions (Aguilar-Romero et al. 2017, Robert et al. 2017, Skelton et al. 2018, 2019,

2021, Sancho-Knapik et al. 2021). However, limited research has focused on oaks in southeastern Asia, which is one of the regions with the highest oak species diversity (Xu et al. 2016). The distribution of evergreen species of *Quercus* section *Cyclobalanopsis* is limited to subtropical and tropical areas of Asia (Deng et al. 2018). Our understanding of their hydraulic structural and functional adaptations to climatic niches requires further investigation (Kröber et al. 2014, Wang et al. 2020).

In this paper, we study the anatomical and hydraulic traits of the leaves and branches of 10 *Quercus* species that are mainly distributed in eastern and southeastern Asia. We include different leaf habits and natural distribution ranges. We investigate: (i) whether the 10 Asian oaks from the two phenological groups differ in leaf and stem hydraulic features. The distinct climate niche of the evergreen group suggests these species may possess a different trait syndrome compared with the deciduous group. We also compile a dataset involving key stem functional traits and their niche climates of 41 *Quercus* species to test: (ii) whether evergreen and deciduous oaks adopt different hydraulic strategies. We hypothesize that deciduous oaks possess larger vessel diameters and consequently higher Ks but lower embolism resistance in the stem xylem compared with evergreen oaks. We also test: (iii) whether stem Ks and P_{50} are linked to the climatic niche of oaks, and whether a consistent trend exists within the two phenological groups. We expect that oaks growing in xeric habitats show strong resistance to embolism. Conversely, oaks in humid habitats show low embolism resistance. Species distributed in very humid habitats do not necessarily evolve large vessels with high hydraulic efficiency due to an abundant water supply. Similarly, species distributed in xeric habitats could possess low Ks due to their relatively small vessels conferring resistance to embolism. Thus, significant correlations between Ks and climate niches may not exist.

Materials and methods

Study locations and plant materials

Ten oak species including four deciduous species, namely *Quercus acutissima*, *Q. fabri*, *Q. griffithii* and *Q. variabilis*, and six evergreen species, namely *Q. glauca*, *Q. macrocalyx*, *Q. myrsinifolia*, *Q. pachyloma*, *Q. patelliformis* and *Q. schottkyana*, were included in this study. All individuals were sampled from two arboreta (Qingxiushan and Liangfengjiang) in Nanning City (22°50′ N, 108°21′ E, altitude 82 m a.s.l.), Guangxi, China. Nanning City has a marginal tropical climate which is strongly influenced by the Pacific monsoon, with a mean annual temperature (MAT) of 22.3 °C and MAP of 1500 mm; 80% of the rainfall occurs during February to September. All experiments were conducted between June and September 2017.

Stem hydraulic conductivity

Three to five mature individuals of each species were sampled. Each specimen had grown in the arboreta for over 20 years. Five branches of each species with a length longer than 1.5 m and a basal diameter of 15–20 mm were sampled in the early morning from the sun-exposed canopy at a height of 4–5 m. After excising branches from the trees, the cut ends of the branches were submerged and immediately recut under water. The basipetal ends of the stems were wrapped in wet tissue, and the whole branches were sealed in black plastic bags to eliminate further dehydration. They were transported to the laboratory in Guangxi University within 1 h.

Prior to measuring the stem hydraulic conductivity, the maximum vessel length (MVL) of the stem was determined following the air-injection method (Greenidge 1952). For the hydraulic conductivity measurements, stem segments that were ∼10% longer than the MVL were used and trimmed with a razor blade under water. Stem segments were initially flushed with a filtered and degassed 20 mM KCl solution at a pressure of ∼100 kPa for 20 min to remove embolism. Segments were later connected to a hydraulic apparatus (Sperry et al. 1988), the hydrostatic pressure was generated by a 50 cm water column driving the flow. The flow rate at the downstream end was measured and calculated using the speed of water movement in a pipette. Sapwood specific hydraulic conductivity (Ks, kg m^{-1} s^{-1} MPa^{-1}) was calculated following Eq. (1):

$$K\mathrm{s} = \frac{\mathrm{Jv} \cdot \mathrm{L}}{A_S \cdot \Delta P} \qquad (1)$$

where Jv is the stable recorded flow rate (kg s^{-1}), L is the length of the measured segment (m), ΔP is the pressure drop across the segment (MPa) and A_S is the cross-sectional area of the conducting sapwood (m^2), determined by dye injection.

Stem xylem embolism resistance

Stem vulnerability curves were constructed using the bench dehydration method (Sperry et al. 1988, Wheeler et al. 2013). We followed the same procedures described previously in 'Stem hydraulic conductivity'. We sampled another 20 healthy branches longer than 1.5 m with mature leaves from the same individuals that sampled to determine Ks. Branches were dried with a nearly constant relative humidity of 60% and temperature of 25 °C. It took 1 h to 7 days for the branches to reach the desired different water potentials of the vulnerability curve. Several leaves on the branches were sealed in non-transparent zip-lock bags to allow the equilibration of the water potentials between the leaf and stem. After variable desiccation time, branches were placed in black plastic bags for 2 h, after which water potential of the bagged leaves was measured using a pressure chamber (PMS 1505D, Corvallis, OR, USA). The stem xylem water potential (Ψ, MPa) was determined using

the average of two to three leaf water potentials of each branch. To avoid the potential cutting artifact, the basipetal end of each branch was kept under water and rehydrated for over 2 h to release tension (Wheeler et al. 2013). A 10–20 cm stem segment with a diameter of ∼5 mm at the distal end was cut under the water and connected to the hydraulic apparatus. The initial hydraulic conductivity (K_i) was measured first, and after being flushed with 20 mM KCl solution for 20 min under 100 kPa, the maximum hydraulic conductivity (K_{max}) was measured. The percentage loss of conductivity (PLC) was calculated as:

$$PLC = 100 \times (K_{max} - K_i) / K_{max} \qquad (2)$$

Vulnerability curves were presented with PLCs against stem water potentials (Ψ) and fitted using the following equation (Pammenter and Van der Willigen 1998) in SigmaPlot 12.0 (Systat Software Inc., Erkrath, Germany):

$$PLC = 100/(1 + \exp (S/25) \, (\Psi - P_{50})) \qquad (3)$$

where S is the slope of the fitted curve, and P_{50} (MPa) is the xylem water potential at 50% loss of hydraulic conductivity.

Stem anatomical traits

Stem segments of 5–8 mm in diameter used in constructing the vulnerability curves were cut into ∼1 cm length, and stored in formaldehyde-acetic acid-ethanol solution for further stem anatomical research. Cross-sections with a thickness of 20–30 μm were cut using a microtome (RM2235, Leica Inc., Wetzlar, Germany), then stained with safranin-methylene blue solution. Cross-sections were observed using a light microscope (DM 3000, Leica Inc.) and imaged using a digital camera attached to the microscope. Vessel density (Den_{vessel}, no. mm^{-2}) was calculated as the average number of vessels per mm^2 based on a minimum of 10 cross-sections for each species. The hydraulically weighted vessel diameter (D_h, mm) was calculated as $D_h = \Sigma D^5 / \Sigma D^4$, where D is the equivalent circle vessel diameter measured from over 100 vessels of each species. The vessel fraction (VF, %) was calculated as the ratio of the vessel area to the sapwood area. All measurements and analyses were performed in ImageJ (freely available from the website https://imagej.nih.gov/ij/). Wood density (WD, g cm^{-3}) was determined using the ratio of the dry mass to the fresh volume of the sapwood, and the dry mass was weighted after it was oven-dried for 72 h at 65 °C. The fresh sapwood volume was measured using the water-displacement method after removing the bark and pith.

Leaf midday water potential

Six sun-exposed leaves from three to five individuals of each species were sampled between 13:00 and 14:00 h in September 2017 after three consecutive sunny days. Collected leaves

were enclosed in zip-lock bags, kept in a foam box and trans-ferred to the laboratory within 2 h. The water potential of each leaf was measured using a pressure chamber. The average of the leaf water potential at midday (Ψ_{md}, MPa) was collated for each species, which was considered as the proxy of the water status for the tree individuals during that summer.

Leaf anatomy

Six leaves were sampled from the three to five individuals for each species. Leaf thickness (T_{leaf}, μm) and the ratio of the palisade to spongy tissue ($T_{palisade}$: T_{spongy}) were measured using the transverse sections of the leaves. After treatment with 10% NaOH solution in an 80 °C water bath overnight, leaf fragments from the middle section of each leaf were observed using a light microscope for vein density (Den_{Vein}, mm mm^{-2}), which was calculated as the total length of the veins divided by the observed leaf area. Transparent nail polish was applied to the abaxial surface of the middle section of the leaf. After drying, the nail polished layer was transferred to a slide and observed using a microscope for stomatal density ($Den_{Stomata}$, no. mm^{-2}), which was determined using the number of stomata divided by the observed area. In addition, intact leaves were placed in a 65 °C oven for 48 h, and LMA (g cm^{-2}) was determined using the leaf dry mass divided by the leaf area.

Species distributions and climate niches

To obtain general information on the occurrence of the *Quercus* species, we collected distribution data from the Global Biodiversity Information Facility (http://www.gbif.org/) and the Chinese Virtual Herbarium (http://www.cvh.ac.cn/). For specimens with only descriptive sample information, the geographic coordinates were manually identified using Google Earth (https://earth.google.com/web/). Outliers, incorrect or introduced location records were manually removed after assessing with the native distribution records in Plants of the World Online (https://powo.science.kew.org/). Climatic information (i.e., MAT and MAP) of each geo-referenced occurrence point was extracted from the climatic layers which were downloaded from Worldclim2 (Fick and Hijmans 2017). The aridity index (the ratio of the MAP to annual potential evaporation; AI) was obtained from the CGIAR-CSI database (Trabucco and Zomer 2018). Mean values for MAT, MAP and AI were calculated and represented the general climatic conditions of the distribution range for each species.

Dataset of key hydraulic traits for 41 Quercus species

We compiled a dataset which included LMA, stem Ks, P_{50} and D_h based on the 10 oak species measured in this study and an additional 31 *Quercus* species collected from the literature (Tables S1 and S2 available as Supplementary data at *Tree Physiology* Online). The values of Ks and P_{50} were obtained directly from the literature or extracted from vulnerability curves. Vulnerability curves from the literature were constructed using

the bench dehydration method, air-injection method, centrifugal method or the optical method. As *Quercus* species are frequently reported to have long vessels (Skelton et al. 2018, Pratt et al. 2020), we focused on identifying the shapes of the vulnerability curves in the published literature. We removed any data with vulnerability curves with a typical exponential increase that often suggests an open vessel artifact. A total of 108 cases from 41 *Quercus* species were collected, including the 10-oak species investigated this study (Table S1 available as Supplementary data at *Tree Physiology* Online). Climatic information of each site and the species distribution range of the 41 oaks were used in our analyses. The mean values of each trait were calculated for each species if several measurements were available (Table S2 available as Supplementary data at *Tree Physiology* Online). The data were also used to calculate the phylogenetic signals and investigate the relationships with climatic niches.

Phylogeny reconstruction

The phylogenetic tree was constructed by pruning 40 species out of the 41 *Quercus* species collected from the global phylogeny of *Quercus* (Hipp et al. 2020). The exception was *Q. glauca*, which was not included in the global oak phylogenetic tree.

Data analyses

Differences in traits between the deciduous and evergreen groups were examined with species means using the independent sample *t*-test. Relationships between key hydraulic traits and species climate niche/site climatic conditions for the 41 oak species were tested using Pearson correlation coefficients across all species and groups (i.e., between evergreen and deciduous species). To evaluate how hydraulic traits vary across the phylogeny clades, the phylogenetic signals (Pagel's λ; Pagel 1999) of the hydraulic traits, and the phylogenetic independent contrast (PIC) between the hydraulic traits and climatic niches were calculated using the packages *phylotools* and *ape* in R (version 4.1.2, https://www.r-project.org/). A principal component analysis (PCA) based on the 12 hydraulic structural and functional traits measured was applied to test the coordination among traits in the 10 oak species. The species loading based on the principal components (PCs) were plotted using the package *factoextra* in R. In all analyses, a probability value <0.05 was considered statistically significant ($P < 0.05$).

Results

Comparison of key functional traits between evergreen and deciduous species

There was limited P_{50} variation among the 10 Asian oak species (mean $\pm$ SD = -1.86 ± 0.27 MPa), ranging from -1.54 MPa (*Q. pachyloma*) and -1.55 MPa (*Q. patelliformis*) to -2.26 MPa (*Q. schottkyana*, Table 1, Figure 1). No clear significant

Table 1. Stem anatomical and hydraulic traits and climate of the natural distribution ranges for 10 *Quercus* species grown in the common garden (mean ± SD).

Species	Phenology	Maximum tree height	WD	Den_{vessel}	D_h	VF	Ks	P_{50}	Ψ_{md}	AI	MAT	MAP
Quercus glauca	Evergreen	20	0.57 ± 0.07	29.66 ± 7.37	42.81 ± 12.72	0.20 ± 0.05	3.22 ± 1.24	−1.63	−1.12 ± 0.36	1.44 ± 0.79	15.84 ± 3.27	1551 ± 757
Q. macrocalyx	Evergreen	25	0.62 ± 0.07	41.91 ± 12.02	36.32 ± 14.71	0.29 ± 0.05	1.44 ± 0.72	−1.84	−0.84 ± 0.38	1.46 ± 0.25	19.62 ± 3.33	1770 ± 369
Q. myrsinifolia	Evergreen	20	0.71 ± 0.05	33.09 ± 8.84	26.96 ± 2.21	0.22 ± 0.05	3.00 ± 1.27	−1.63	−0.43 ± 0.09	1.36 ± 0.35	22.25 ± 1.95	1762 ± 249
Q. pachyloma	Evergreen	17	0.54 ± 0.04	28.05 ± 6.63	29.22 ± 10.90	0.17 ± 0.05	1.70 ± 1.39	−1.54	−0.34 ± 0.07	1.54 ± 0.79	19.07 ± 3.37	1811 ± 657
Q. patelliformis	Evergreen	25	0.62 ± 0.04	37.62 ± 8.21	21.74 ± 1.66	0.17 ± 0.03	2.89 ± 1.01	−1.55	−1.25 ± 0.07	1.45 ± 0.26	22.86 ± 2.66	1907 ± 255
Q. schottkyana	Evergreen	20	0.58 ± 0.13	26.28 ± 6.26	34.30 ± 4.24	0.27 ± 0.07	4.85 ± 2.38	−2.26	−0.54 ± 0.19	1.11 ± 0.24	14.48 ± 3.49	1234 ± 306
Q. acutissima	Deciduous	30	0.69 ± 0.06	26.83 ± 7.23	39.69 ± 7.26	0.31 ± 0.14	5.17 ± 2.43	−1.93	−1.40 ± 0.17	1.24 ± 0.44	15.72 ± 3.74	1370 ± 407
Q. fabri	Deciduous	20	0.60 ± 0.05	31.68 ± 4.46	34.10 ± 6.09	0.26 ± 0.09	3.97 ± 1.90	−2.16	−0.96 ± 0.16	1.21 ± 0.28	15.43 ± 2.45	1296 ± 274
Q. griffithii	Deciduous	25	0.40 ± 0.03	31.25 ± 7.34	39.14 ± 2.76	0.32 ± 0.11	3.25 ± 1.34	−2.20	−0.67 ± 0.11	1.21 ± 0.55	15.37 ± 3.60	1361 ± 625
Q. variabilis	Deciduous	30	0.70 ± 0.04	30.55 ± 8.63	41.87 ± 8.56	0.35 ± 0.08	5.92 ± 4.07	−1.86	−1.35 ± 0.12	1.23 ± 0.79	14.34 ± 3.35	1291 ± 717

Abbreviations: Maximum tree height, m (retrieved from http://www.efloras.org/); WD, wood density, g cm^{-3}; Den_{vessel}, vessel density, no. mm^{-2}; D_h, hydraulic-weighted vessel diameter, μm; VF, vessel lumen fraction, no unit; Ks, sap wood-specific hydraulic conductivity, kg m^{-1} s^{-1} MPa^{-1}; P_{50}, water potential at 50% loss of hydraulic conductance, MPa; Ψ_{md}, leaf midday water potential; AI, mean aridity index of the distribution range, no unit; MAT, mean annual temperature of the distribution range, °C; MAP, mean annual precipitation of the distribution range, mm

difference (independent *t*-test, $t = -0.24$, $P = 0.095$) in P_{50} existed between the Asian evergreen (-1.74 ± 0.28 MPa; $n = 6$) and deciduous (-2.04 ± 0.17 MPa; $n = 4$) oaks. *K*s varied more than fourfold among the 10 species, ranging from 1.44 (*Q. macrocalyx*) to 5.92 kg m^{-1} s^{-1} MPa^{-1} (*Q. variabilis*). A marginally significant difference in *K*s was found ($P = 0.058$, Table S3 available as Supplementary data at *Tree Physiology* Online) between the evergreen (2.85 ± 1.22 kg m^{-1} s^{-1} MPa^{-1}; $n = 6$) and deciduous Asian oaks (4.58 ± 1.20 kg m^{-1} s^{-1} MPa^{-1}; $n = 4$). The evergreen and deciduous Asian oak species showed no significant difference in most stem and leaf anatomical traits, including vein density, stomata density, leaf thickness, stem vessel density and D_h (Table 2; Table S3 available as Supplementary data at *Tree Physiology* Online). However, evergreen oaks had a significantly lower VF ($t = -3.229$, $P = 0.012$) and $T_{palisade}:T_{spongy}$ ($t = -2.356$, $P = 0.046$) than the deciduous oaks (Table 2; Table S3 available as Supplementary data at *Tree Physiology* Online).

The PCA based on 12 leaf and stem traits for the 10 Asian oak species revealed the first two PCs explained 38.8 and 17.7% of the total variation, respectively (Figure 2a and b). The first PC was mainly explained by the $T_{palisade}:T_{spongy}$ of the leaves (14.05%) and traits related to the efficiency of stem hydraulic transport, such as *K*s (16.10%), D_h (12.23%), VF (11.51%) and vein density (11.02%, Figure 2c). The second PC was contributed mainly by traits related to stem and leaf structural investment, such as WD (29.00%), leaf thickness (16.34%), LMA (13.21%) and $T_{palisade}:T_{spongy}$ (11.38%, Figure 2d). Deciduous and evergreen Asian oak species were partly separated by the first PC. The main exception was the evergreen species *Q. schottkyana*, which had a relatively high embolism resistance, large vessels and high hydraulic efficiency like the deciduous oaks (Figure 2b).

There was no significant difference in the P_{50} and WD between the deciduous and evergreen groups from the 41 *Quercus* species dataset (Figure 3a and d). However, the deciduous-species group in the 41 *Quercus* species dataset had significantly higher *K*s (Figure 3b, $P < 0.05$) and larger D_h (Figure 3c $P < 0.01$) when compared with the evergreen group.

Relationships between hydraulic traits and species climatic niches

*K*s declined with increasing AI (lower aridity), MAT and MAP of the species distribution ranges of the 10 Asian oaks grown in a common garden (Figure 4a–c). The 41 *Quercus* species dataset had no significant correlations between *K*s and species climate niches (i.e., AI, MAT and MAP, Figure 4a–c), which was further supported by the independent analysis of each relationship for the different leaf habit groups. In contrast, P_{50} positively correlated with AI, MAT and MAP of the distribution ranges for the 10 Asian species (Figure 4d–f). Positive correlations of P_{50}
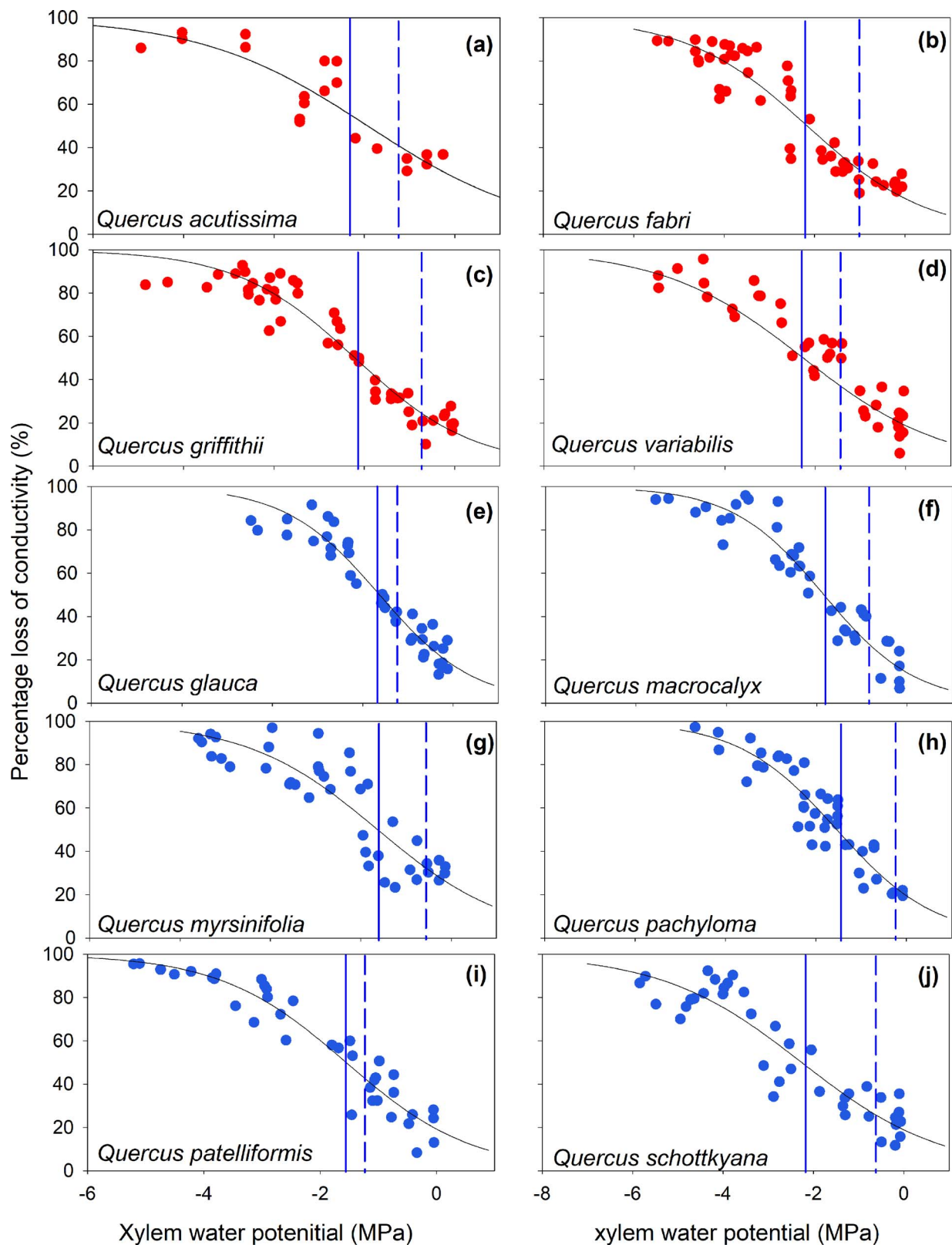
Figure 1. Stem xylem vulnerability curves of the 10 *Quercus* species in the common garden. Evergreen and deciduous species are shown with blue and red dots, respectively. Solid black curves indicate the fitted curves. Xylem water potential at 50% loss of maximum conductivity (P_{50}) and leaf midday water potential (Ψ_{md}) are shown with blue solid lines and dashed lines, respectively.

Table 2. Leaf anatomical traits of 10 *Quercus* species in the common garden.

Species	Phenology	Den_{vein}	$Den_{stomata}$	T_{leaf}	$T_{palisade}$: T_{spongy}	LMA
Quercus glauca	Evergreen	9.32 ± 0.93	391 ± 28	195 ± 9	1.17 ± 0.24	72.2 ± 5.1
Q. macrocalyx	Evergreen	8.57 ± 0.43	377 ± 56	237 ± 21	1.06 ± 0.24	98.2 ± 12.7
Q. myrsinifolia	Evergreen	6.62 ± 0.30	215 ± 35	131 ± 8	0.59 ± 0.25	62.9 ± 12.1
Q. pachyloma	Evergreen	10.97 ± 0.39	369 ± 38	204 ± 8	1.14 ± 0.17	84.0 ± 4.0
Q. patelliformis	Evergreen	6.12 ± 0.42	319 ± 71	165 ± 10	0.68 ± 0.14	97.3 ± 0.4
Q. schottkyana	Evergreen	9.14 ± 0.39	404 ± 35	136 ± 7	1.14 ± 0.20	88.9 ± 9.3
Q. acutissima	Deciduous	12.37 ± 0.79	357 ± 42	143 ± 26	1.25 ± 0.54	61.9 ± 10.8
Q. fabri	Deciduous	9.37 ± 0.77	570 ± 147	152 ± 20	1.21 ± 0.48	60.5 ± 7.6
Q. griffithii	Deciduous	7.24 ± 0.83	209 ± 18	157 ± 15	1.24 ± 0.25	88.1 ± 16.6
Q. variabilis	Deciduous	11.09 ± 0.50	307 ± 39	128 ± 10	1.48 ± 0.20	66.4 ± 5.5

Den_{vein}, leaf vein density, mm mm^{-2}; $Den_{stomata}$: stomatal density, no. mm^{-2}; T_{leaf}: leaf thickness, μm; $T_{palisade}$:T_{spongy}, ratio of the thickness of palisade tissue to spongy tissue, no unit; LMA, leaf mass per area, g cm^{-2}. Data are presented as mean ± standard deviation
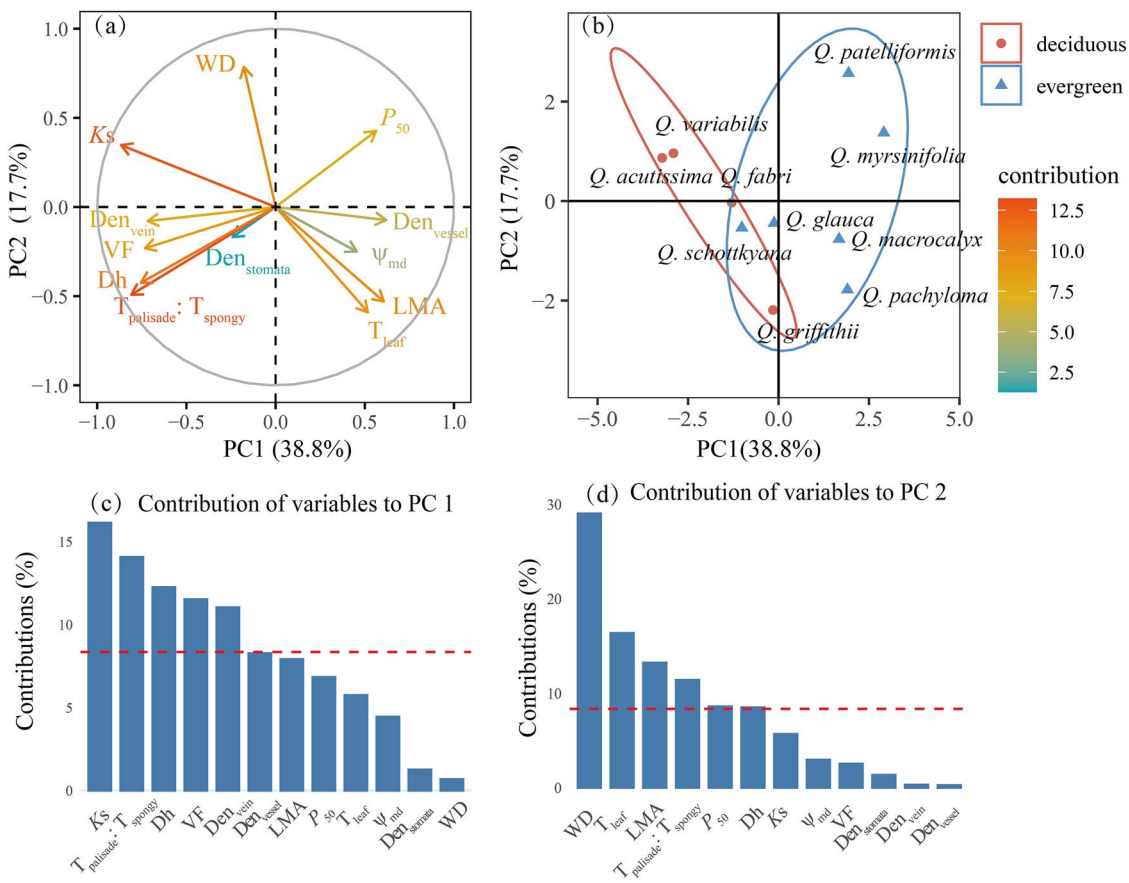

Figure 2. PCA of the 10 *Quercus* species studied based on 12 hydraulic structural and functional traits. (a) The loading of the first two PCs, and (b) scores of each species along PC1 and PC2 for deciduous species (red circles) and evergreen species (blue triangles). (c and d) The first 10 contribution of variables to the first and second PC, respectively. The red dashed lines in (c) and (d) indicate the average contribution of each variable to the corresponding PC. Abbreviations of variables are available in Tables 1 and 2.

with AI and MAP were consistently identified in the 41 *Quercus* species, as well as within the deciduous and evergreen groups of the 41 *Quercus* species (Figure 4d–f).

Ks and P_{50} were positively related to AI, MAP but not MAT of their study sites in the 41 *Quercus* species dataset (Figure S5 available as Supplementary data at

Tree Physiology Online). P_{50} increased with increased site humidity (AI) and MAP for both the deciduous and evergreen groups (Figure S5d and f available as Supplementary data at *Tree Physiology* Online). Conversely, Ks increased with increased site MAT and MAP was only found in evergreen species. In the 10 Asian oaks, T_{leaf} was positively related to AI, but
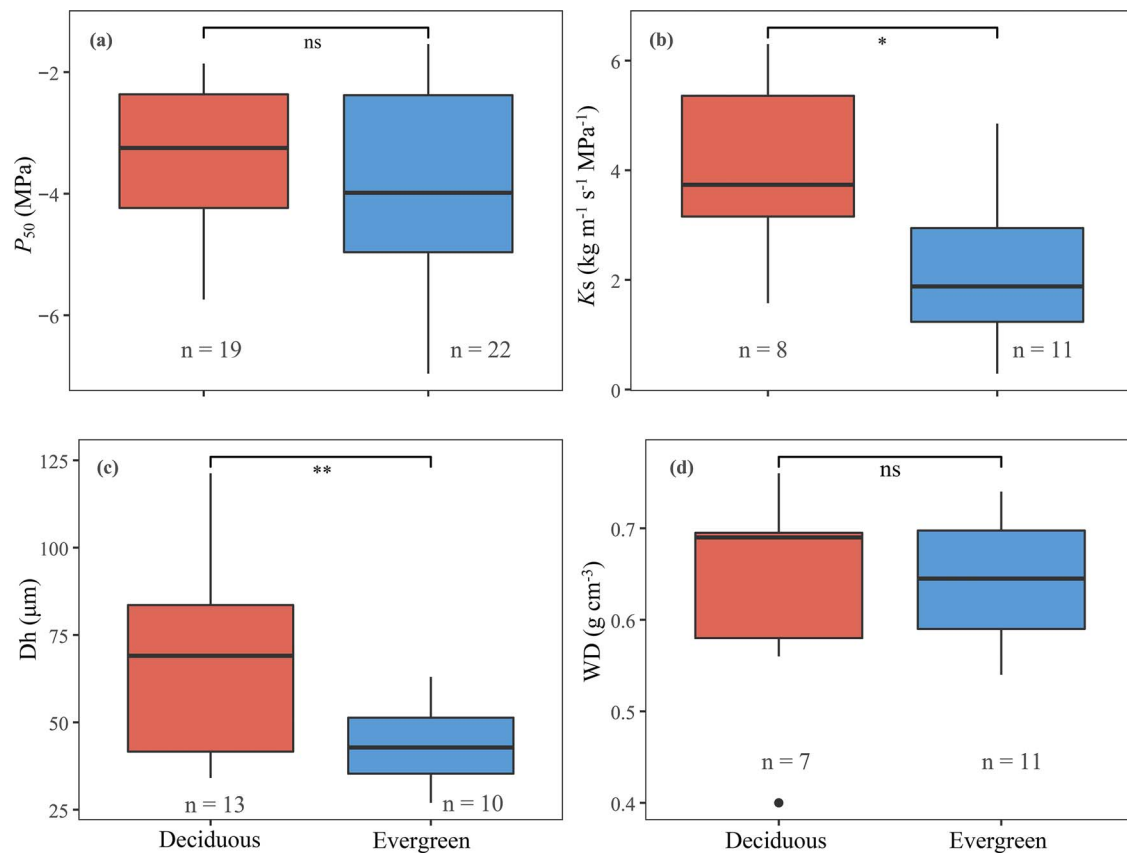
Figure 3. Comparisons of stem xylem functional traits between deciduous and evergreen species based on the dataset of 41 *Quercus* species. Data of deciduous and evergreen groups were compared using an independent-sample *t*-test. Statistical differences are shown as ns ($P > 0.05$), *($P < 0.05$) and **($P < 0.01$). Numbers of species analyzed for each group are also given.

$T_{palisade}$:T_{spongy} had a negative relationship with the MAT and MAP of the species distribution ranges (Figure S2 available as Supplementary data at *Tree Physiology* Online).

For the 40 species with phylogenetic information available, strong phylogenetic signals were found in P_{50} and D_h, but not in *K*s and WD (Figure 5b and c; Table S4 available as Supplementary data at *Tree Physiology* Online). *K*s positively correlated with P_{50}, but there was no significant relationship between PIC P_{50} and PIC *K*s (Figure S4 available as Supplementary data at *Tree Physiology* Online). Phylogenetic independent contrast P_{50} was positively related to PIC AI and PIC MAP. Conversely, PIC *K*s was positively related to PIC AI, and it was negatively related to PIC MAT (Figure S3 available as Supplementary data at *Tree Physiology* Online).

Discussion

In this study, we examined 12 hydraulic traits for 10 Asian *Quercus* species grown in common gardens in a humid climate. The result extends our knowledge of the hydraulic characteristics of *Quercus* species to subtropical areas. We also combined our results with 31 *Quercus* worldwide species to compile an exhaustive dataset. We identified whether evergreen and

deciduous oaks adopt different hydraulic strategies as an adaption to their climate niches. The implications and broad significance of our results are discussed below.

Differences in key functional traits between deciduous and evergreen species

For the 10 Asian oaks, evergreen and deciduous species were partly separated in the first PC axis, which was mainly related to water transport efficiency, such as *K*s, D_h, stem VF and leaf vein density (Figure 2b and c). Similarly, there was a significant difference in *K*s between evergreen and deciduous oak species in the 41 *Quercus* species dataset. These results support our first and second hypotheses (Figure 3b). Previous studies have also identified that deciduous tree species possess a higher hydraulic conductivity when compared with evergreen species in a tropical karst forest and a subtropical broadleaf forest (Fu et al. 2012, Zhang et al. 2013), but not in 17 North American oaks (Cavender-Bares and Holbrook 2001). A high efficiency of water transport is frequently suggested to link with a great photosynthetic capacity (Brodribb et al. 2002, Zhu et al. 2013). Deciduous species may have adopted this strategy to compensate for their relatively short leaf life spans (Escudero et al. 2017).
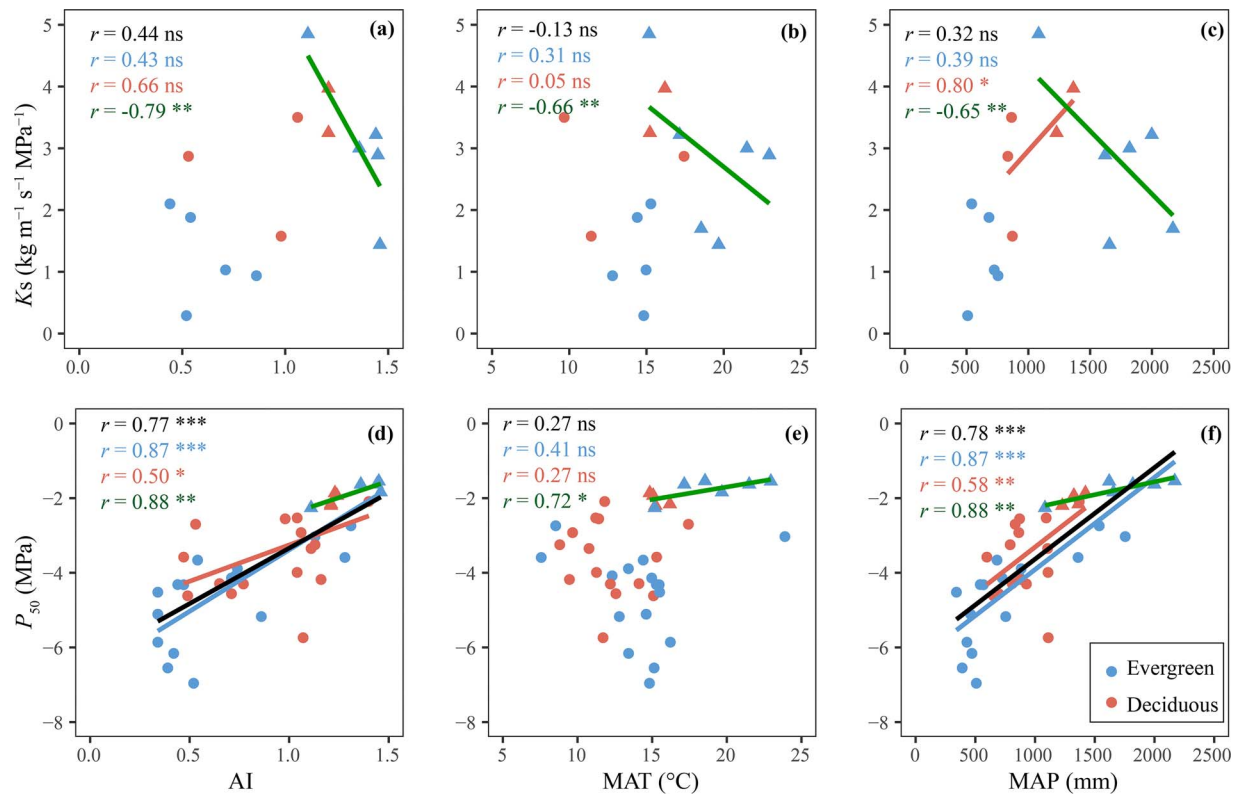
Figure 4. Relationships of stem Ks ($n = 18$ species; a, b, c) and P_{50} ($n = 41$ species; d, e, f) with climatic variables of distribution range (AI, MAT and MAP). Each point represents the mean values of traits and climatic niche for one species. Data measured in this study and collected from literature are shown with triangles and dots, respectively. Data for evergreen and deciduous species are shown in blue and red, respectively. Coefficients of correlation (r) and regression lines are shown in different colors, with black representing the data of 41 *Quercus* species, green the 10 Asian *Quercus* species of this study, blue the evergreen oaks and red the deciduous oaks. Statistical significances are shown as ns ($P > 0.05$), *($P < 0.05$), **($P < 0.01$) and ***($P < 0.001$). Linear regression (solid line) was applied only when the correlation was significant ($P < 0.05$).

There was no significant difference in stem P_{50} between evergreen and deciduous species in the 10 Asian oaks or the 41 *Quercus* species dataset (Figure 3d; Table S3 available as Supplementary data at *Tree Physiology* Online). This result contradicts our first two hypotheses. Plants can largely slow down or even stop the water potential decreasing to a critical point by leaf shedding, thus drought-deciduous species may not necessarily require a xylem with strong embolism resistance (Wolfe et al. 2016). In addition, for the genus *Quercus*, evergreen species typically consist of shrubs with strong embolism resistance that are mainly distributed in arid habitats, as well as tall trees in the section *Cyclobalanopsis* in subtropical and tropical forests that are rather vulnerable to xylem embolism. Therefore, stem embolism resistance in *Quercus* species may not simply differ as a function of phenology, but variations in growth forms may also influence this divergence (Skelton et al. 2021).

Leaf anatomical traits and LMA have been frequently measured to determine how species adapt their leaf morphology to various environments. When compared with deciduous species, evergreen species in the 10 Asian oaks showed a significantly higher $T_{palisade}:T_{spongy}$, which may contribute to their higher

leaf density and chlorophyll concentration, as reported for a neotropical forest in Brazil (De Souza et al. 2020). A previous study based on 85 oak species revealed that evergreen species have significantly thicker and smaller leaves with higher LMA compared with the deciduous oaks (Sancho-Knapik et al. 2021). No significant differences in leaf thickness and LMA were found between the two phenology groups in the 10 Asian oak species, which could be due to the rather small dataset (Table S3 available as Supplementary data at *Tree Physiology* Online).

Stem hydraulic conductivity and embolism resistance are related to the species climatic niche

The stem xylem of the 10 Asian oak species had a mean P_{50} value of -1.86 ± 0.27 MPa, suggesting that these Asian *Quercus* species were vulnerable to xylem embolism when compared with the global oak dataset ($P_{50} = -3.95 \pm 1.44$ MPa, $t = 19.973$, $P < 0.001$). A possible explanation is that these Asian oaks favor rather warm and humid habitats with higher AI, MAT and MAP, when compared with oaks in the global dataset which are mainly distributed in Europe and North America (Figure 4d–f). The Asian oaks had similar stem P_{50} ranges
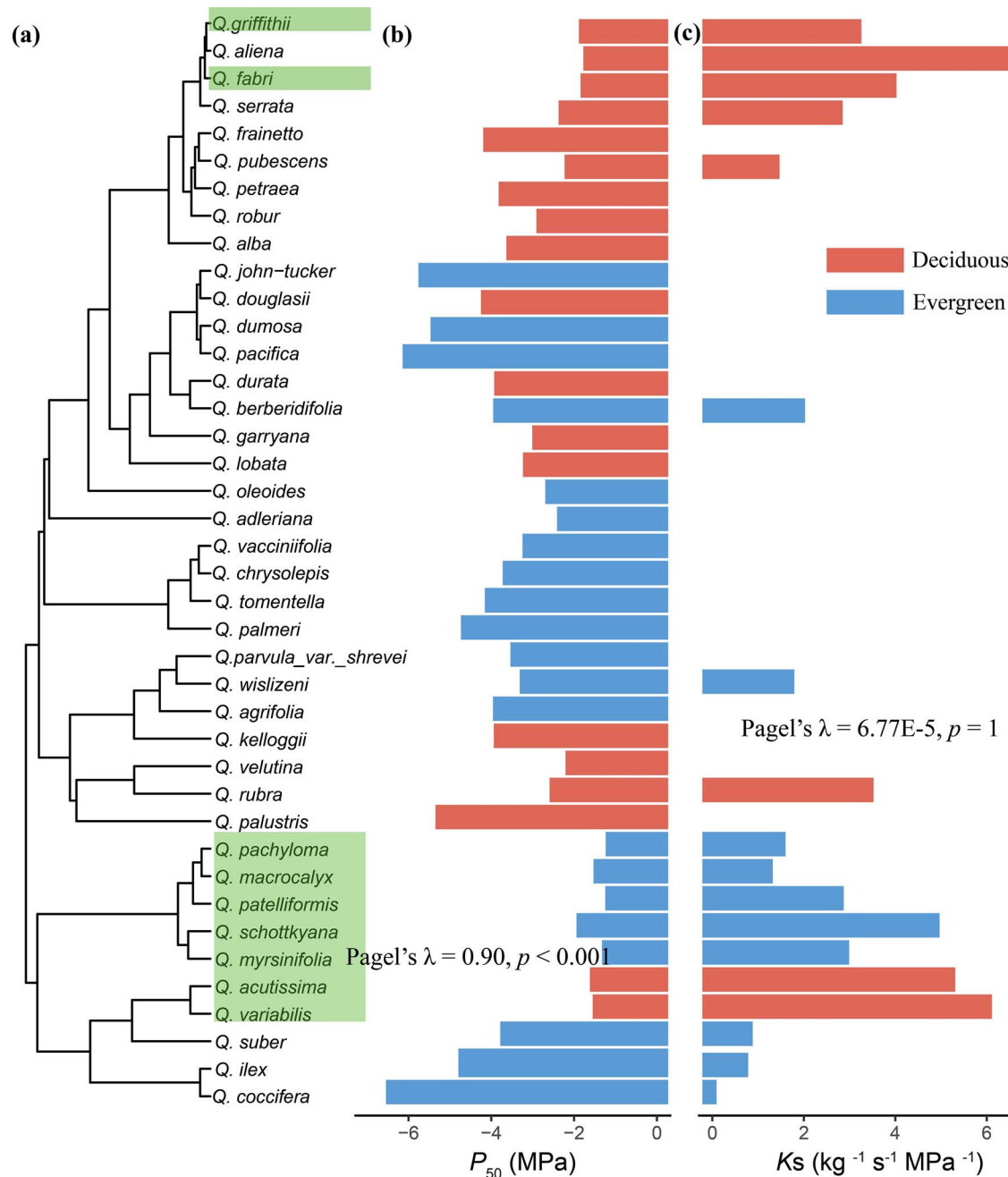
Figure 5. Phylogenetic tree (a) and the variations of stem embolism resistance (P_{50}, b) and stem-specific hydraulic conductivity (Ks, c) based on the 41 *Quercus* species hydraulic dataset. Green boxes indicate the nine species measured in this study, missing *Q. glauca* whose phylogenetic status is not presented in the global phylogeny of *Quercus* (Hipp et al. 2020). Mean values of P_{50} and Ks for each species are presented in (b) and (c). Phylogenetic signals (Pagel's λ) of these traits are shown.

compared with the angiosperm trees growing in subtropical climates (Zhu et al. 2019). Furthermore, all six evergreen Asian oaks belonged to the section *Cyclobalanopsis*, and their distribution ranges are limited to habitats with sufficient water supply, rarely enduring drought stress (i.e., AI > 1, Table 1). The Asian oak species that are able to grow in more arid habitats were all drought-deciduous, which may allow the species to avoid dangerous water potentials by leaf shedding; thus, neither the evergreen nor deciduous Asian oaks were species that

needed to be highly resistant to embolism. In contrast, stem hydraulic conductivity (Ks) in the 10 Asian *Quercus* species was not significantly higher than the mean Ks of the 41 oaks in the dataset ($t = 1.31$, $P = 0.22$, Figure 4a–c), suggesting that *Quercus* species with humid climate niches do not favor stem xylems with high hydraulic conductivity.

Consistent with our third hypothesis, P_{50} positively related to the climatic humidity (AI, MAT and MAP) was found for both the 10 Asian oaks and the 41 global *Quercus* datasets,

suggesting oak species distributed in humid habitats possess lower xylem embolism resistance. This trend was consistent within the evergreen and deciduous groups (Figure 4d–f). Together with the similar embolism resistance of the evergreen and deciduous oaks (Figure 3a; Table S1 available as Supplementary data at *Tree Physiology* Online), the results suggest *Quercus* species with different leaf habits may not adopt different strategies to cope with stem embolism resistance. Besides, more negative P_{50} values were found in species with drier and hotter climatic niches when the relationship was examined using PICs (Figure S3 available as Supplementary data at *Tree Physiology* Online). The results indicate climatic aridity is an important driver of stem xylem embolism resistance in *Quercus* species. This finding is consistent with numerous studies focusing on the variations in stem embolism resistance within a genus, such as North American *Quercus* (Skelton et al. 2021), *Callitris* (Larter et al. 2017), *Eucalyptus* (Bourne et al. 2017, Li et al. 2018) and *Hakea* (Oyanoghafo et al. 2021). In addition, a strong phylogenetic signal was detected in the P_{50} values (Figure 5b), suggesting that stem embolism resistance in oaks is highly phylogenetically conserved. Oak individuals have also been found to possess little intra-specific variation in xylem resistance to embolism even among populations growing along a large aridity gradient (Skelton et al. 2019). A significant difference in P_{50} was identified among the biomes ($F = 21.728$, $P < 0.001$, Table S5 available as Supplementary data at *Tree Physiology* Online). Species of tropical and temperate forests were significantly more vulnerable to embolism than species of woodland and temperate grassland, suggesting oaks adapting their stem xylem to cope with climate niches (Figure S6 available as Supplementary data at *Tree Physiology* Online).

High xylem embolism resistance has been reported in North American *Quercus* species (Skelton et al. 2018, 2021), and previous research has also raised concerns for a potential open vessel artifact in oak species being observed with low embolism resistance. Stem vulnerability curves can be constructed using various methods, including hydraulic-based methods such as bench-dehydration, air-injection and centrifugal method, and non-hydraulic methods such as X-ray, micro-CT, the optical and the pneumatic method. These methods have all been applied to *Quercus* species in previous studies (Robert et al. 2017, Lobo et al. 2018, Pratt et al. 2020, Rosas et al. 2019, Skelton et al. 2018, 2021, Zhang et al. 2018). The air-injection and centrifugal methods may overestimate the vulnerability of species with long vessels (Chen et al. 2021a). After removing the P_{50} data of the R-shape vulnerability curves, we found a marginally significant difference among the P_{50} values obtained using different methods ($F = 2.542$, $P = 0.061$, Table S5 and Figure S6 available as Supplementary data at *Tree Physiology* Online). We took the mean value of P_{50} for each species when multiple P_{50} data were available, to further reduce potential bias

due to the different methodology. Nevertheless, comparisons of P_{50} values across oak species may be problematic, particularly when mixing different methods, and therefore our comparisons across the 41 species dataset should be considered with caution. Estimating P_{50} using the same method can largely eliminate methodology discrepancies which may help us to better understand the relationship between species embolism resistance and their climate niche, especially for long-vessel species like oaks.

The stem Ks negatively correlated with AI, MAT and MAP of the species distribution ranges for the 10 Asian *Quercus* species (Figure 4a–c), indicating that oaks distributed in more humid environments evolved with less VFs and consequently lower hydraulic conductivity (Figure S2 available as Supplementary data at *Tree Physiology* Online). The negative relationships could also be partly explained by the deciduous groups which generally had a greater tree height and higher Ks than the evergreen species of the 10 Asian oaks (Table 1, Liu et al. 2019). A positive relationship between Ks and MAP has also been revealed in previous studies (Gleason et al. 2012, Pfautsch et al. 2016), but this relationship can also be absent (Aguilar-Romero et al. 2017, Hacke et al. 2017, Larter et al. 2017). The study site of the 10 Asian *Quercus* species had sufficient soil water supply due to the abundant precipitation and relatively low transpiration demand (i.e., mean daily vapor pressure deficit < 1 kPa during most days, Liu et al. 2017). Therefore, these plants do not need to evolve wide vessel conduits to meet high hydraulic transportation demand or high xylem embolism resistance against drought. The Ks revealed no significant relationships with species climate niche (Figure 4a–c), but was positively related to AI and MAP of the sampling sites of the 41 species, indicating that Ks could be more strongly influenced by the climate conditions in the growth sites (Figure S5a and c available as Supplementary data at *Tree Physiology* Online). This finding is further supported by a lack of phylogenetic signal in Ks (Figure 5c; Table S4 available as Supplementary data at *Tree Physiology* Online). A higher D_h in species originating from more humid climates was reported for 18 *Quercus* species by Fontes et al. (2021), although highly intraspecific variability in D_h was also observed, which may also occur in Ks. Additional investigations on *Quercus* species from tropical and subtropical forests would enhance our understanding of how these species evolve a suitable xylem network to adapt to their habitat and climates.

In conclusion, the 10 Asian oak species, which were mainly distributed in humid subtropical habits, have evolved a stem xylem that is neither particularly embolism resistant nor hydraulically efficient. Deciduous and evergreen oaks differed in hydraulic efficiency, but not embolism resistance. By compiling the dataset of 41 *Quercus* species, we identified that stem P_{50} is highly phylogenetically conserved; oak species that are distributed in arid habitats have evolved stem xylems with high

embolism resistance, which is consistent across evergreen and deciduous groups. However, *K*s appears to be influenced by the growth-site climate rather than the climate niche. Our findings provide important information on species adaptations to climate in the genus *Quercus*, especially the plant hydraulic network. Our research has implications for the management and conservation of oak forests under current and future climate scenarios.

Supplementary data

Supplementary data for this article are available at *Tree Physiology* Online.

Data availability statement

The data that support the findings of this study are available in the supplementary material of this article.

Authors' contributions

X.G. and K.-F.C. conceived the ideas and designed the experiment; X.G. and Z.C. conducted the measurements; X.G. and Y.W. collected and analyzed the data; X.G. wrote the manuscript, and received revisions from Y.W., Y.Z. and K.-F.C.

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