



Growing-season temperature and precipitation are independent drivers of global variation in xylem hydraulic conductivity

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Funding information

National Natural Science Foundation of China, Grant/Award Number: 31570405 and 31825005; Institution of South China Sea Ecology and Environmental Engineering, Chinese Academy of Sciences, Grant/Award Number: ISEE2018YB01

Abstract

Stem xylem-specific hydraulic conductivity (K_s) represents the potential for plant water transport normalized by xylem cross section, length, and driving force. Variation in K_s has implications for plant transpiration and photosynthesis, growth and survival, and also the geographic distribution of species. Clarifying the global-scale patterns of K_s and its major drivers is needed to achieve a better understanding of how plants adapt to different environmental conditions, particularly under climate change scenarios. Here, we compiled a xylem hydraulics dataset with 1,186 species-at-site combinations (975 woody species representing 146 families, from 199 sites worldwide), and investigated how K_s varied with climatic variables, plant functional types, and biomes. Growing-season temperature and growing-season precipitation drove global variation in K_s independently. Both the mean and the variation in K_s were highest in the warm and wet tropical regions, and lower in cold and dry regions,

such as tundra and desert biomes. Our results suggest that future warming and redistribution of seasonal precipitation may have a significant impact on species functional diversity, and is likely to be particularly important in regions becoming warmer or drier, such as high latitudes. This highlights an important role for K_S in predicting shifts in community composition in the face of climate change.

KEYWORDS

biome, climate, functional types, hydraulic diversity, species distribution, water transport

1 | INTRODUCTION

Climate change will likely result in a redistribution of precipitation across the Earth's surface, thus, also affecting the timing and amount of plant available water to plants and ecosystems (Pachauri et al., 2014; Putnam & Broecker, 2017). It is possible that shifts in temperature and rainfall patterns may lead to widespread forest decline in regions where droughts are predicted to increase in duration and severity (Allen et al., 2010; Klein & Hartmann, 2018). Quantifying physiological traits associated with water supply and drought survival (e.g., hydraulic conductivity and water potential at hydraulic dysfunction) has great potential for predicting shifts in community composition (Li et al., 2015), species' distribution (Anderegg, 2015; Fei et al., 2017), and ecosystem functioning (Myers-Smith, Thomas, & Bjorkman, 2019).

Xylem-specific hydraulic conductivity (K_S) represents the water transport potential of the xylem tissue. It is expressed as the rate of water transport through a given area and length of sapwood across a given pressure gradient (Sperry, Donnelly, & Tyree, 1988). Transporting water from soil to the canopy requires an intact water column in the xylem from roots to shoots (Gleason, Butler, Ziemińska, Waryszak, & Westoby, 2012). This process is greatly facilitated by increasing K_S , and as such, K_S plays a critical role in achieving whole-plant water balance and is therefore critically linked with transpiration (Manzoni et al., 2013), photosynthesis (Ávila-Lovera, Zerpa, & Santiago, 2017; Santiago et al., 2004; Zhu, Song, Li, & Ye, 2013), growth (Fan, Zhang, Hao, Ferry Slik, & Cao, 2012; Liu et al., 2019; Poorter et al., 2010), and survival (Anderegg et al., 2012, 2016). The interaction between water availability and hydraulic capacity can also strongly influence the geographic distribution of plant species (Liang et al., 2019; Nardini & Luglió, 2014; Pockman & Sperry, 2000).

A number of studies have examined the covariation among xylem structure, hydraulic vulnerability, xylem hydraulic efficiency, and safety from embolism (Jacobsen, Pratt, Tobin, Hacke, & Ewers, 2012; Méndez-Alonzo, Paz, Zuluaga, Rosell, & Olson, 2012; Zanne et al., 2010), and also the correlations between these hydraulic traits and climatic variables. For instance, Zhang, Cao, Fan, and Zhang (2013) studied 316 angiosperm tree species in southwest China, and found that xylem conduit diameter was positively correlated with mean annual temperature (MAT) and precipitation (MAP). Similarly, at the

global scale, Morris et al. (2018) found that mean vessel diameter was positively correlated with MAT and precipitation across 2,332 woody angiosperm species. Furthermore, xylem safety (P_{50} ; xylem water potential resulting in 50% loss of hydraulic conductance) in stems and leaves has been found to correlate negatively with precipitation (Blackman et al., 2014; Choat et al., 2012; Li et al., 2018). Considering that K_S and its primary component, vessel diameter, are positively correlated with precipitation, and that safety is negatively correlated with precipitation, we might then reasonably expect an inverse correlation between K_S and P_{50} across species and habitats, that is, an efficiency-safety trade-off might exist among vascular plants. Although such a trade-off is often implied (e.g., Choat et al., 2012), the empirical support for it is inconsistent (Gleason et al., 2016; Zhu et al., 2013).

Two conflicting syntheses have been conducted previously to clarify regional patterns of K_S . Maherali, Pockman, and Jackson (2004) investigated K_S among 167 woody species in North Carolina and Texas, United States, and reported that K_S was higher at drier sites (lower MAP). They gave two possible reasons for this result. First, high K_S might facilitate increased transpiration under dry conditions without increasing the water potential gradient, and thus without increasing embolization risk (Maherali & DeLucia, 2001; Mencuccini, 2003). This could be adaptive for plants in arid environments with high evaporative demand. Second, in this study, most species from arid regions were deciduous with short leaf life spans, and thus were able to avoid xylem embolization by dropping their leaves during drought, yet also maintain high K_S during times of sufficient water availability (Reich et al., 1999). More recently, Gleason, Butler, and Waryszak (2013) studied 120 angiosperm species from eight sites across a broad range of climates in eastern Australia. They found that K_S was strongly and positively correlated with summer precipitation. They suggested that natural selection in wet and high radiation habitats should favor the evolution of highly conductive xylem to achieve high levels of water transport and therefore photosynthetic income, whereas natural selection in arid habitats should favor shorter stature and lower leaf surface area to sapwood cross-sectional area ratio (A_L/A_S) to maintain water balance, while at the same time avoiding hydraulic failure.

Despite these regional studies having revealed certain relationship between precipitation and K_S (yet to some extent, the results

are contradictory), our understanding remains limited about how K_S varies across plant functional types (PFTs) and biomes, and which climatic factors drive variation in K_S at the global scale.

K_S is one of the key traits that significantly influences how water and carbon are coupled and the success of different water use strategies in different environments (Anderegg, 2015; Anderegg et al., 2012; Ávila-Lovera et al., 2017; Fan et al., 2012; Manzoni et al., 2013; Poorter et al., 2010; Santiago et al., 2004; Zhu et al., 2013). In areas with warmer temperatures and abundant soil moisture, K_S can be high in part because species must compete, so in order to preemptively use available soil moisture, fast water transport and high water use are likely selected for (Gleason et al., 2013; Morris et al., 2018). In cool, moist habitats, PET (potential evapotranspiration) is rarely high, so there is less selective advantage in having higher K_S , although higher K_S would still allow for either thinner stems or less living sapwood, per unit water delivered to the canopy. In habitats with intermediate or variable temperature and PET, low K_S may be selected for to enhance survival (Anderegg et al., 2016; Petit, Anfodillo, Carraro, Grani, & Carrer, 2011; conceptual relationship shown in Figure 1). Here, we compiled a dataset of published and unpublished K_S measurements for 975 woody species sampled from 199 sites worldwide (1,186 species-at-site combinations, in total; Figure S1a). These species and sites represent a wide range of PFTs and biomes (Figure S1b).

We sought to quantify, at the global scale:

1. Covariation in K_S with climatic variables, and in doing so, identifies key factors underpinning K_S variation. As xylogenesis is often limited by low temperatures and precipitation

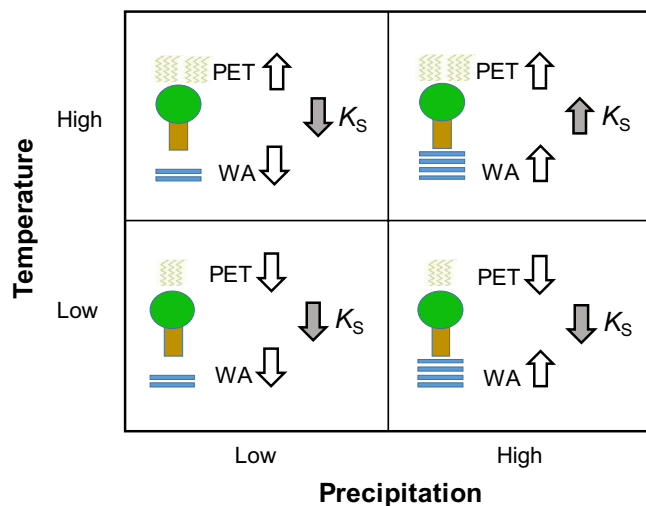


FIGURE 1 Conceptual framework for K_S under different environmental scenarios. K_S , stem xylem-specific hydraulic conductivity. K_S is selected for in wet habitats with high PET to maintain high rates of water delivery (per unit leaf area) and to avoid decreasing xylem water potentials. In habitats with low temperatures and PET, highly conductive xylem is selected against because the driving force for water transport is reduced, and therefore, there is less selective advantage for conductive xylem. In dry habitats, low K_S is selected for to achieve higher survival. PET, potential evapotranspiration; WA, water availability

(Petit et al., 2011; Zhang, Gou, Manzanedo, Zhang, & Pederson, 2018), we hypothesize that growing-season temperature (T_{gs}) and precipitation (P_{gs}) would strongly and positively affect K_S .

2. Variation in K_S across PFTs and biomes. For example, we might expect species differing markedly in xylem anatomy (e.g., angiosperms vs. gymnosperms) or in growth form (e.g., lianas vs. self-supporting angiosperms) to exhibit different values of K_S (Apgaua et al., 2017; Bond, 1989; Chen et al., 2015, 2017; Field & Wilson, 2012; Sperry, Hacke, & Pittermann, 2006; van der Sande, Poorter, Schnitzer, Engelbrecht, Markesteijn, 2019). Similarly, as already discussed, we might also expect regions with marked differences precipitation and evaporative demand (e.g., hot rainforest vs. cold deserts) to favor species with different hydraulic capacities and/or conduit diameter (Anderegg & HilleRisLambers, 2016; Choat et al., 2012; Niu, Meinzer, & Hao, 2017; Yuan et al., 2010).

2 | MATERIALS AND METHODS

2.1 | Data collection

We compiled published and unpublished K_S measurements (Data file S1). Almost half of the data came from the previously published Xylem Functional Traits Database (XFT; Choat et al., 2012; Gleason et al., 2016), which can be accessed from the TRY Plant Traits Database (<https://www.try-db.org/TryWeb/Home.php>; Kattge et al., 2011). We also conducted searches on Web of Science, Google Scholar, and China National Knowledge Infrastructure (<http://www.cnki.net>) using the keywords “xylem hydraulic conductivity,” “branch/stem hydraulic conductivity,” “water conductivity,” and “hydraulic traits.” To minimize ontogenetic and methodological variation, we included data that met the following criteria: (a) wild plants growing in natural ecosystems, excluding greenhouse and common garden experiments; (b) xylem hydraulic conductivity measured on terminal stem or branch segments (commonly 3–10 mm in diameter and 10–30 cm in length), that is, measurements on root or leaf tissues were not included; (c) measurements were made on adult plants or saplings, but not on seedlings; (d) K_S was measured (e.g., Sperry et al., 1988), not estimated from vessel measurements (e.g., Hagen–Poiseuille equation); and (e) only maximum hydraulic conductivity was used, not so-called “native” hydraulic conductivity. Mean K_S values were calculated for each species at the same site (Shao et al., 2019; Wright et al., 2004, 2005).

Based on information in source publications and online floras (e.g., <http://frps.eflora.cn/>), species were coded into the following PFTs: liana, conifer, evergreen angiosperm tree, deciduous angiosperm tree, evergreen angiosperm shrub, and deciduous angiosperm shrub. Sites were assigned to biomes: tropical rainforest, tropical savanna, tropical deciduous forest, subtropical monsoon forest, temperate deciduous forest, semiarid woodland plus shrubland, boreal tundra, and desert.

Climate data were taken from the original reports, where available, otherwise variables such as mean annual and monthly precipitation, temperature, solar radiation, the minimum temperature of coldest month (T_{cm}), and precipitation of driest month (P_{dm}) were

extracted from the WorldClim version 2 (<http://worldclim.org/version2>; Fick & Hijmans, 2017). When elevation data from the WorldClim database did not match elevations from published reports, temperature was scaled to match published elevation using a lapse rate of $6.0^{\circ}\text{C km}^{-1}$ increase in elevation. The data of annual and monthly PET were extracted from the CGIAR-CSI consortium (<http://www.cgiar-csi.org/data>; Zomer, Trabucco, Bossio, & Verchot, 2008). Aridity index (whether monthly or annual) is the ratio of precipitation to PET. Variation of aridity index is calculated using coefficient of variation of the annual aridity index of recent 50 years (1966–2015) extracted from the SPEI data (<http://spei.csic.es/database.html>; Beguería, Vicente-Serrano, Reig, & Latorre, 2014). The data of monthly vapor pressure deficit (VPD) were extracted from the TerraClimate dataset (<http://www.climatologylab.org/terraclimate.html>; Abatzoglou, Dobrowski, Parks, & Hegewisch, 2018). We defined the growing season as being the set of consecutive months that satisfied the conditions: (a) monthly mean temperature $\geq 5^{\circ}\text{C}$, and (b) monthly precipitation/PET ≥ 0.05 (Wright et al., 2017).

2.2 | Data analysis

Data were first \log_{10} -transformed to attain approximate normality (Kerkhoff & Enquist, 2009), except for temperature and solar radiation data. Relationships between K_S and environmental variables were characterized using Pearson correlation and linear regression. One-way analysis of variance (ANOVA) with least significant difference was used to test for differences in mean K_S for species grouped into PFTs and biomes. Multiple regression and stepwise regression analyses were conducted to estimate predictive equations for K_S , and an ANOVA was combined into a linear contrast (regression; Hector et al., 1999). Quadratic regression was used to evaluate the relationship between K_S and latitude. $p < .05$ was used to determine the significant level for all the above models. All analyses were run in R software (version 3.5.0, R Core Team, 2018).

3 | RESULTS

Our synthesis of K_S from 199 sites around the world showed that T_{gs} (Figure 2a) and P_{gs} (Figure 2b) explained 21.3% and 12.3% of the global variation in K_S , respectively, for example, higher K_S at warmer and/or wetter sites (Figures S1c and S2). T_{cm} explained 11.7% of the variation in K_S (Table S1). Several other climatic variables such as solar radiation, aridity index, VPD, and P_{dm} explained relatively smaller portions of variation in K_S than T_{gs} or P_{gs} (Table S1).

K_S increased independently with both T_{gs} and P_{gs} ($R^2 = .22$; Figure 3; the interaction between T_{gs} and P_{gs} was clearly nonsignificant, $p = .756$). Regression models using all climate variables explained up to 32% variation in K_S , and a subset identified in a stepwise process explained 28% variation in K_S . Regression models using

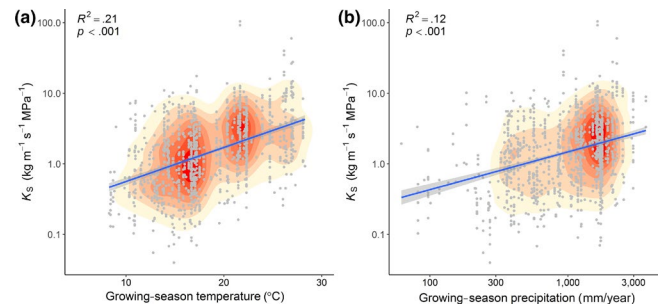


FIGURE 2 Global variation in K_S in relation to climate: global variation in K_S in relation to growing-season temperature (a) and growing-season precipitation (b). Colors indicate the density of points from highest density (red) to lowest (yellow). Solid lines represent fitted ordinary least squares regression models with 95th confidence intervals. K_S , stem xylem-specific hydraulic conductivity ($\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$). OLS, ordinary least squares

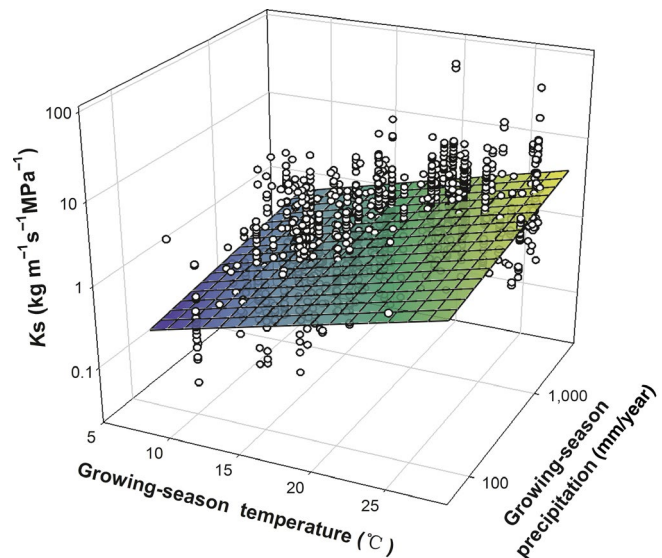


FIGURE 3 Global variation in K_S in relation to T_{gs} and P_{gs} . The best-fit function estimated by multiple linear regression was $\log K_S = 0.14 \log P_{gs} + 0.04 T_{gs} - 1.04$ (all parameters $p < .01$; $R^2 = .22$). K_S , stem xylem-specific hydraulic conductivity ($\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$); P_{gs} , growing-season precipitation (mm); T_{gs} , growing-season temperature ($^{\circ}\text{C}$)

all climatic variables, PFTs, and biomes explained up to 41% variation in K_S (Table S2). K_S differed significantly between PFTs ($F = 26.0$, $p < .0001$) and biomes ($F = 6.0$, $p < .0001$), and was mostly influenced by T_{gs} ($F = 397.4$, $p < .0001$; Table S3).

On average, lianas had higher K_S ($14.43 \text{ kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) than other PFTs (Figure 4A; Table S4). Deciduous trees and evergreen trees had similar mean values of K_S ($3.06 \text{ kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ and $2.71 \text{ kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$, respectively; Table S4). Evergreen shrubs had lower K_S than those of deciduous shrubs. Conifers had the lowest mean value of K_S ($0.95 \text{ kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$). Additionally, the variance in K_S was lowest among conifers and evergreen shrubs, but highest among lianas (Figure 4B; Figure S4).

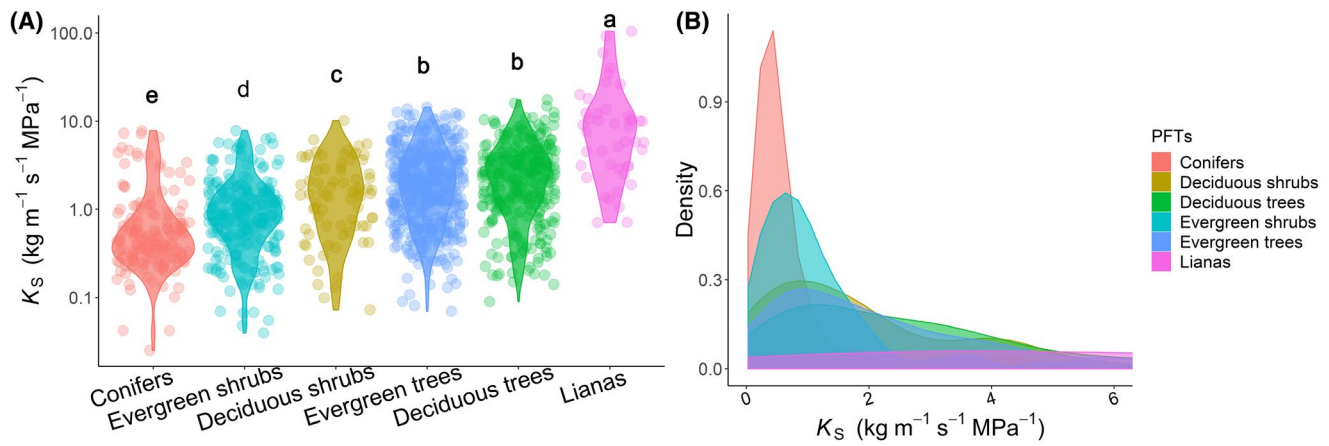


FIGURE 4 Patterns of K_S across PFTs: (A) Differences in K_S among PFTs. Significant differences ($p < .05$) among PFTs are indicated by different lowercase letters (a–e). (B) Density distribution of K_S among PFTs. K_S , stem xylem-specific hydraulic conductivity ($\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$). PFTs, plant functional types

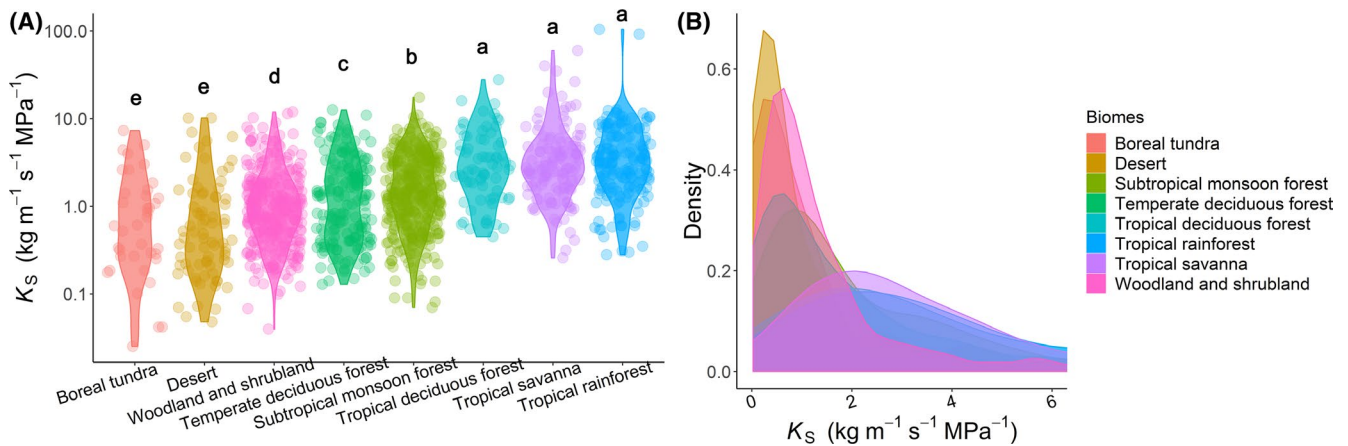


FIGURE 5 Patterns of K_S across biomes: (A) Differences in K_S among plant biomes. Significant differences ($p < .05$) among biomes are indicated by different lowercase letters (a–e). (B) Density distribution of K_S among plant biomes. K_S , stem xylem-specific hydraulic conductivity ($\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$)

Considering plant biomes, tropical rainforest species had the highest K_S ($5.29 \text{ kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$; Figure 5A; Table S5), and boreal tundra and desert species had the lowest ($1.25 \text{ kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ and $1.28 \text{ kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$, respectively). Interestingly, the variance in K_S increased from biomes with low temperature (e.g., boreal tundra) or low precipitation (e.g., desert) to biomes with high temperature and high precipitation (e.g., tropical rainforests; Figure 5B; Figure S5).

4 | DISCUSSION

In this study, we analyzed the global patterns of plant K_S , including how this trait differs among PFTs and biomes, and its coordination with climatic variables, thus providing new insights into how climate affects plant water use and the evolution of plant water use strategies.

Our results showed that air temperature was a more significant explanatory variable than precipitation, but both temperature and

precipitation were influential. Moreover, species from warm regions (e.g., tropical rainforests and tropical savannas) had relatively high K_S , whereas species in cold regions (e.g., boreal tundra and woodland plus shrubland) had relatively low K_S . There are three possible interpretations for these results: first, plants in warm habitats tend to have high transpiration rates (Yuan et al., 2010), supported by high K_S , to avoid overheating during warm periods (Wright et al., 2017). In contrast, in cold sites such as tundra and woodland/shrubland, PET is never high, so there is less selective advantage in having higher K_S . Second, species at warm sites need to compete for light and grow fast, and thus, require high photosynthetic rates and high water transport capacity (Apgaua et al., 2017; Chen et al., 2015; Fan et al., 2012). Third, there is a benefit of small conduits for resistance to embolism arising from the freezing and thawing of sap (Feild & Brodribb, 2001; Pittermann & Sperry, 2003), and small conduits are usually associated with low K_S (Morris et al., 2018). In contrast, high K_S achieved via wide conduits has a greater risk of embolism arising from freeze–thaw cycles (Mayr, Rothart, & Dämon, 2003; Niu et al., 2017).

We found K_S was high at high rainfall sites, which is consistent with Gleason et al. (2013), suggesting that differences in K_S between wet and dry climates reflect the competing requirements among water transport, embolism, and maintenance cost per unit water transported through the vasculature. As such, we might expect high K_S to confer a fitness advantage in habitats with low risk of embolism and high potential for CO_2 assimilation, whereas low K_S to confer a fitness advantage in shaded and/or arid environments where there is a meaningful risk of hydraulic failure and/or high requirement for low xylem construction and maintenance costs. Although this idea may account for the evolution of highly conductive xylem in high-rainfall habitats, it does not provide a satisfying explanation for why low K_S should arise in arid or shaded habitats. This is because, even in these habitats, higher K_S should confer either greater water transport per unit cross-sectional investment or confer less cross-sectional investment per unit water transport (i.e., thinner stems or less living sapwood). Only in the case where higher K_S results in compromised mechanical stability (but see Zanne et al., 2010), increased susceptibility to drought or cold weather injury, or a significant carbon expenditure (amortized over the lifetime of the plant), should natural selection favor the evolution of low K_S .

Compared to MAT and precipitation, we found that mean temperature and precipitation over the growing season alone explained more variance in K_S (Figure 2; Figure S3a,b), indicating the important role of growing season in mediating the variation in K_S . One possible interpretation of this result is that xylogenesis takes place mainly during the growing season. Therefore, excessive cold or dry conditions during growing season may adversely affect xylem growth and limit the number and size of xylem elements (Petit et al., 2011; Zhang et al., 2018).

We noted that the minimum temperature of coldest month explained 11.7% of the variation in K_S , suggesting that markedly cold temperatures may affect the water transport capacity of plant xylem, despite relatively less significant as compared to the effect of growing-season temperature (explained 21.3%). These findings are consistent with the freezing tolerance hypothesis, that is, the frequency of freezing temperatures is an important climatic factor in determining large-scale patterns of species richness and distribution (Sakai & Weiser, 1973; Wang, Fang, Tang, & Lin, 2010; Woodward, 1990). According to the freeze-thaw-induced embolism theory, gas bubbles are formed in conduits upon freezing and expand when the sap thaws, but importantly, bubble size is limited by the width of the conduits in which the bubbles form. Thus, the formation, ultimate size of bubbles, and the subsequent spread of gas from conduit to conduit may result in damage to the water transport vasculature (Charrier et al., 2014; Mayr, Cochard, Améglio, & Kikuta, 2007; Mayr & Sperry, 2010). Considering that larger bubbles are more likely to form in wider conduits, species exhibiting wider conduits (and higher K_S) may be more susceptible to freeze-thaw embolism (Davis, Sperry, & Hacke, 1999; Pittermann & Sperry, 2003, 2006).

Although our models provide a measure of the alignment between K_S and temperature/precipitation, most of the variation in these models remains unexplained. We acknowledge some uncertainties and limitations in our data. First, construction and

maintenance costs of xylem are largely unknown. Plant vasculature appears to conform with Murray's law and similar hydraulic models (Gleason et al., 2018; McCulloh, Sperry, & Adler, 2003; McCulloh, Sperry, Meinzer, Lachenbruch, & Atala, 2009), that is, xylem has been designed to achieve maximum conductance for a given investment in carbon and energy. It is unlikely that vasculature would align with Murray's law if xylem costs were negligible. As such, it is possible that the construction and maintenance costs associated with efficient xylem have been underestimated. Second, it should be noted that our results are based on observations of plants at the biome and PFT levels under present climate conditions. Whether the observed sensitivities to temperature and precipitation are influenced mainly by phenotypical variation within the same species or by genotypic variation across species would likely influence the distribution of species in the future under climate change (Anderegg, 2015; Anderegg et al., 2018; Osnas et al., 2018; Pfautsch et al., 2016). If phenotypical variation dominates, climate change would likely be less impactful on species distributions than if genotypic variation was dominant. This warrants further investigation in the future. Third, much of the variation in K_S exists within sites, rather than across climate gradients. It is clear that species occurring in cold or dry habitats always have low K_S , whereas species occurring in warm and wet habitats exhibit the entire range of K_S . As such, it appears that high K_S can only occur in warm and wet habitats, and this is clearly a temperature/precipitation effect, but the reason for why most species in warm and wet habitats do not achieve high K_S remains an important and interesting research question.

This work represents an important step toward a better understanding of geographic variation in plant hydraulic strategies, and builds toward a more reliable conceptual model of global vegetation functioning and the risks of climate change. In particular, K_S is an important parameter in plant hydraulic models and is used to simulate root water uptake, leaf water stress, plant carbon-water trade-offs, and mortality (Kennedy et al., 2019; Xu, Medvigy, Powers, Becknell, & Guan, 2016). A better understanding at the biome level could inform these models and improve the representation of physiological processes, and thus, improve future simulations of vegetation structure and carbon dynamics. Our data support the continued development and improvement of process-based global vegetation models that explicitly link K_S to performance, such as plant growth, death, and dispersal (Prentice et al., 2007; Zhou, Duursma, Medlyn, Kelly, & Prentice, 2013). We suggest that the continued measurement and inclusion of important plant hydraulic traits in these modeling efforts will improve our understanding of species-climate linkages as well as our ability to predict demographic shifts in the face of climate change.

ACKNOWLEDGEMENTS

We are grateful to the editor and reviewers for their constructive suggestions and comments on an earlier version of this manuscript. We thank Brendan Choat for his suggestions on data collection, Megan K. Bartlett and Yusuke Onoda for their comments on the manuscript, and Zeqing Ma for his suggestions on figure presentation. We also

thank Xiaojuan Liu and Shaowei Jiang for their data contribution. This work was funded by the National Natural Science Foundation of China (31825005 and 31570405), and the Institution of South China Sea Ecology and Environmental Engineering, Chinese Academy of Sciences (ISEE2018YB01). The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

P.H. and Q.Y. designed the study and wrote the initial manuscript. P.H. collected and analyzed the data, with help from I.J.W. P.H., S.Z., and R.L. performed trait measurements across 188 species at five study sites in China. S.M.G., Q.L., G.W., E.Y., Y.S., X.M., and G.H. contributed to the data collection. I.J.W., S.M.G., E.W., H.L., S.Z., M.L., G.H., P.B.R., Y.P.W., and D.S.E. contributed to improving the manuscript.

DATA AVAILABILITY STATEMENT

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

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: He P, Gleason SM, Wright IJ, et al. Growing-season temperature and precipitation are independent drivers of global variation in xylem hydraulic conductivity. *Glob Change Biol*. 2019;00:1–9. <https://doi.org/10.1111/gcb.14929>