

Variation of xylem traits reveals evidence of adaptation to climatic conditions in conifers along a latitudinal gradient across China

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March 30, 2022

Abstract

Extant conifer species are adapted to a range of climate conditions, which would be reflected in their xylem structure, especially in tracheid characteristics of early-and-latewood. With an anatomical dataset of 79 conifer species native to China, an interspecific study was conducted within a phylogenetic context to find latitudinal patterns in tracheid cell dimensions in response to climate. The analyses showed that there is a significant difference in tracheid length and diameter between early-and-latewood, but no significant difference in cell wall thickness. An opposite divergence pattern was found based on the PC1 axis of tracheid traits, with species of Pinaceae showing strong divergence in their xylem structure in contrast to a conservative xylem structure for species of the other families studied. Except for tracheid diameter in earlywood, tracheid characteristics decreased as latitude increased. Mean annual temperature, precipitation, and their interaction could explain 24.7% to 49.2% of the variance of the tracheid features measured, while phylogeny accounted for 12.5 to 50.5%, suggesting that both temperature and precipitation play a major role in shaping conifer xylem structure. These results provide valuable insight into the effect of climate on the xylem structure of conifers, helping to further our understanding of trees' adaptation to climate.

Introduction

Understanding how tree growth responds to changes in temperature and precipitation along latitude is crucial for an accurate prediction of future changes in forest dynamics caused by global climate change, especially in Northern boreal ecosystems (Huang et al. 2020; Zhang, Belien, Ren, Rossi, and Huang 2020). A latitudinal gradient is associated with consistent temperature changes, which acts as a potential natural laboratory to help infer forest responses to global warming (De Frenne et al. 2013). Although there are many studies on tree growth response to latitude, most of them have focused on ring width and latewood density in the context of specific regions and/or species. For instance, using a tree ring database from a dozen species and 762 sites in the International Tree-Ring Data Bank (ITRDB), Wettstein et al. (2011) showed that high-latitude ring-width series were more likely to positively correlate with summer temperature while low-latitude sites commonly showed negative correlations; different species respond differently to temperature and precipitation anomalies (Wettstein, Littell, Wallace, and Gedalof 2011). Björklund et al. (2017) analyzed the latewood density parameters from 27 species and 349 sites in ITRDB and found that correlations between density and width shifted from negative to positive when moving from earlywood to latewood, and temperature response of density varied intra-seasonally in strength and sign (positive or negative correlation coefficients) (Björklund et al. 2017).

Although wood density and ring width are sensitive indicators of a tree's response to climate, the changes might be driven by traits at the cell level or lower (i.e. micro-structure of cell wall). Conduit dimensions of xylem are accepted as important traits in respect to plant hydraulics and adaptation for both angiosperms and gymnosperms (Baas, Ewers, Davies, and Wheeler 2004). Similar to angiosperm vessels, tracheid characteristics can provide us with valuable information about how conifer species adapt to diverse habitats and their possible responses to global climate change. For instance, stem heating and water manipulation experiments were carried out to study tree growth based on timing and kinetics of the tracheid development process, which showed that xylem traits responded to a significant change in temperature and water availability (Begum, Nakaba, Yamagishi, Oribe, and Funada 2013; Vieira, arvalho, and Campelo 2020). However, latitudinal patterns of tracheids have been surprisingly understudied when compared to vessel traits (Brodribb, Pittermann, and Coomes 2012).

Conifer xylem consists of two types of cells: tracheid (approx. 90-93% xylem surface area) and parenchyma (approx. 7-10% surface area), which is more uniform in pattern and has less cellular diversity than angiosperm xylem (Panshin and Zeeuw 1980; Hacke 2015). Temperate conifer tree rings are mainly composed of two types of tracheid: large and thin-walled earlywood cells that are produced early in the growing season (i.e. springwood) and primarily responsible for water transport, and small but thick-walled latewood tracheids (i.e. summerwood) that are produced after the earlywood cells and serving primarily in mechanical support (Fonti et al. 2013). Therefore, tracheid diameter, length and wall thickness represent useful proxies to examine tracheid cell profiles within a growth rings and across xylem. Understanding the temporal pattern of these traits and how the environment shapes them is of high importance for forest management.

Recent studies on wood formation dynamics have greatly increased our understanding of xylogenesis, i.e. xylem formation (Rossi et al. 2013; Cuny, Rathgeber, Frank, Fonti, and Fournier 2014; Cuny and Rathgeber 2016; Rathgeber, Cuny, and Fonti 2016; Rossi et al. 2016). In short, cell enlargement and secondary cell wall deposition and lignification (wall thickening) are the two fundamental sub-processes of xylogenesis that shape xylem cell dimensions and the resulting tree-ring structure (Cuny et al. 2014). The complex interplay between the duration and rate of xylogenesis determines the changes in cell features, e.g., cell and lumen diameter, lumen area and wall thickness, etc., which in turn creates the anatomical structure driving the wood density profile (Cuny et al. 2014; Cuny and Rathgeber 2016). A recent study on *Larix* sp. and *Picea* sp. showed that tracheid cell size and tracheid wall thickness drive variability of earlywood and latewood density in the Northern Hemisphere (Björklund et al. 2017). However, whether this conclusion can be applied to most conifer species remains unknown, especially pertaining to those distributed in humid tropical forests of the Southern Hemisphere (Leslie et al. 2012).

Although tracheid cell development across a tree ring follows a sequence in cell division from cell enlargement, secondary cell wall thickening to cell maturation, the duration and rate of the latter sub-processes are influenced by different climatic factors during their specific developmental periods (Castagneri Fonti, von Arx, and Carrer 2017; Ebisuya and Briscoe 2018). For instance, using a micro-core data set including members of Pinaceae belonging to four genera (i.e., *Abies*, *Larix*, *Picea*, and *Pinus*) from 39 sites in the Northern Hemisphere, Rossi et al. (2016) found that the timing of xylem phenology events and mean annual temperature of the sites were related linearly, with spring and autumn events being separated by constant intervals across the temperature range. The latter authors suggested that the uniformity of the process in wood formation was mainly determined by the environmental conditions occurring at the time of growth resumption (Rossi et al. 2016). In a three-year study on the kinetics of tracheid development of three conifer species (i.e., *Picea abies* , *Pinus sylvestris* , and *Abies alba*), Cuny et al. (2014) found that the amount of lumen wall material per cell was quite constant along growth rings, which challenges the widespread understanding that wall thickness is mainly driven by the wall-thickening duration (Cuny et al. 2014). Hence, there is no consensus on the role of the duration and rate of cell enlargement and wall thickening phases on final tracheid cell traits, such as cell size and cell wall area or thickness, while the effects of climatic factors on xylogenesis are often species-specific and site-dependent (Cuny et al. 2014; Rossi et al. 2016; Buttò, Rossi, Deslauriers, and Morin 2019).

Tree growth and xylem structure could be influenced by various climatic conditions along a latitudinal gradient. Towards the colder upper-end of the gradient, low temperatures limit tree growth and ultimately prevent the growth, reproduction, and survival of trees at the tree line (Körner 1998; Lyu et al. 2017). By contrast, at lower regions of latitude, the higher temperatures increase evapotranspiration, raising the level of drought stress on tree growth and changing tree phenology (Lian et al. 2020). Therefore, in such environments, tree growth is typically negatively correlated with temperature but positively with precipitation. Previous dendrochronology studies showed that tree growth of *Picea abies* responded to temperature and precipitation changes along latitudinal gradients; however, the effect of precipitation was dependent on temperature-induced water stress (Mäkinen et al. 2003). In addition to the gradually changing relationship between temperature and growth, the period of cambial activity and xylem cell growth gradually shortens towards colder areas owing to thermal limitations in wood formation (Rossi Deslauriers, Anfodillo, and Carraro 2007; Huang et al. 2020). The time window in which climatic conditions affect cell development and tree growth, tends to change most with increasing latitude (Körner 1998; Briffa et al. 2002; Henttonen et al. 2014). However, there are relatively few interspecific studies on the effect of climate on xylem anatomical traits compared to the tree ring width for conifer species.

Although previous research suggests that hydraulic traits are correlated with both precipitation and temperature (Martínez-Vilalta et al. 2004), temperature is increasingly recognized as the primary driver of growth reactivation in a cold climate. Both direct observations and controlled experiments have demonstrated that cambial activity is limited by low air temperatures in a cold climate (Rossi et al. 2012; Begum et al. 2013). However, most studies have only focused on temperate or boreal ecosystems where snowmelt provides abundant water especially at the beginning of spring and summer, and is therefore not a limiting factor for xylem formation (Cuny and Rathgeber 2016, Rathgeber et al. 2016, Rossi et al. 2016). Given that xylem cell expansion is a turgor-driven process depending on cellular water uptake and solute accumulation, water availability can affect xylogenesis (Kozłowski and Pallardy, 2002). Researchers have shown that both cell division and expansion are sensitive to water potential (Fonti et al. 2010), and that water deficit is the primary constraint for xylogenesis of *Pinus pinaster* in a Mediterranean climate (Vieira, Rossi, Campelo, Freitas, and Nabais 2014; Vieira Carvalho, and Campelo 2020). The large range in the thermal thresholds for the onset of xylogenesis in *Juniperus przewalskii* provides additional evidence that temperature was not the only factor initiating xylem growth under such cold and dry conditions (Ren Rossi, Gricar, Liang, and Cufar 2015; Ren et al. 2018). These results suggest that wood formation and xylem structure of various conifer species along a large latitudinal gradient are an interplay between genetics and multiple climatic factors. Therefore, an interspecific study within a phylogenetic context and along a wide latitudinal gradient could shed light on the role of temperature and precipitation on conifer xylem structure.

The global distribution of conifers is as wide as that of angiosperms. Boreal forests in high latitudes consist of a limited number of conifer species (low diversity), whereas at lower latitudes conifer species generally occur on mountains. The latter observations indicate that some conifer species are more adapted to stresses such as cold and drought than angiosperm trees, and therefore could occupy habitats that most angiosperm trees could not (Condamine Silvestro, Koppelhus, and Antonelli 2020), and their adaptation might be attributed to some characteristics of their xylem structure. Furthermore, adaptation to various climatic conditions along a wide latitudinal range should be reflected in the xylem structure, especially in tracheid cell and cell wall dimensions in early-and-latewood owing to construction costs and water transportation constraints of tracheids. To-date, the latitudinal patterns of conifer xylem anatomy has been understudied, and climatic factors driving the variance of xylem structure traits were shown to be ambiguous.

We hypothesize that the xylem structure of conifer species is mainly a consequence of adaptation to cold or drought, thus, differences in tracheid dimensions between early-and latewood would become stronger at higher latitudes, which could be viewed as an ecological strategy of adaptation to changing climate conditions. Among climatic factors, we predict that temperature and precipitation could both impact the xylem structure of conifers under cold or dry conditions, along with elevation. Specifically, we address the following questions: 1) Does a contrast of tracheid dimension between earlywood and latewood persist when accounting for phylogeny? 2) Are there clear trends in xylem structure along a latitudinal gradient? 3) Is

temperature the main driver of xylem structure under a monsoonal climate or does xylogenesis depend on the interaction between temperature and precipitation? 4) How much of the xylem structure variance can be explained by climate and phylogeny respectively? To the best of our knowledge, there are no existing cross-species studies that include up to 80 coniferous tree species making this study an important contribution to our knowledge of conifer adaptation.

Materials and Methods

Data collection

China is the country with the highest number of conifer species in the world among which more than 90 species are endemics (Li, Shen, Ying, and Fang 2009). Meanwhile, the land mass of China covers a large latitudinal gradient from 18° N to 54° N. Besides, although the precipitation is generally higher in lower latitude regions, seasonal drought is common in Southwest China, where a hotspot of conifer species is situated (Yang 2015; Sundaram et al. 2019). Such diverse species and environmental conditions provide an opportunity for a cross-species study on the correlation between xylem structure and climate. We compiled a tracheid trait dataset for Chinese conifer species (Cheng Yang, and Liu 1993, Yang Lu, Liu, and Wu 2001; Jiang Cheng, and Yin 2010). All taxonomic names were verified using the Plant List (<http://www.theplantlist.org/>) to correct for synonyms, and varieties and subspecies were removed since the study is at the interspecific level. Finally, we obtained wood anatomical data for 79 conifer species across China (Fig.1). Most tree samples were taken from the Eastern Monsoonal climate zone in China, where the temperate, subtropical, and marginal tropical natural forests are distributed (Wu 1995). The maximum plant height for each species was extracted from Fu (2012) to check their potential relationships with conduit size.

Five cell dimensional traits from both earlywood and latewood for the 79 conifer species were selected, including tangential and radial tracheid diameter, tangential and radial tracheid wall thickness, and tracheid length (Fig. 2, Appendix 1, and Appendix 2). The anatomical data was mainly collected from publications by The Chinese Academy of Forestry, which hosts the largest wood collection in China, and the wood anatomical traits were measured following their methods (Cheng et al. 1993; Zhou and Jiang 1994; Yang, Cheng, Yang, and Lu 2009). In brief, most conifer tree species were sampled from mature trees over 60 years old with a DBH of over 20 cm in natural forests, as previous studies suggest that tracheid size is consistent in the sapwood of old trees (Zhou and Jiang 1994). The sampled discs were collected at a height of 1.3m, avoiding compression wood. These discs were cut, from pith to bark, into six equal parts according to the equidistance method and anatomical samples were taken from the middle of the outermost part (closest to the bark). These outermost samples were sectioned with a microtome and the entire span of a randomly selected growth ring analysed. Wood anatomical traits were measured using a light microscope, including tracheid diameter, tracheid wall thickness, and tracheid length for earlywood and latewood respectively. The early-and-latewood subzones were chosen as close as possible to the ring boundaries, and tracheids at the very end of latewood with irregular shapes were avoided. For tracheid diameter and tracheid wall thickness, 100 tracheids were measured randomly in the earlywood and latewood subsection of each sample. For tracheid length, 50 tracheids in earlywood and latewood from a randomly selected growth ring were measured using the maceration method after wood samples were treated with glacial acetic acid and hydrogen peroxide for one to three days (Yang et al. 2001).

As the sampling locations were not recorded for most of the species in the database, geographical coordinates for the distribution of each species in China were retrieved from Atlas of the Gymnosperms of China (Ying, Chen, and Chang 2004) and combined with climatic data extracted from WorldClim (<https://www.worldclim.org/>) and the aridity index from the global aridity index database (<https://cgiaresci.community/data/global-aridity-and-pet-database/>) using the R package 'raster' (Hijmans, 2015). The environmental variables included: (1) Location indices: mid-point latitude (LAT, °), longitude (LON, °), and altitude (ALT, m). (2) Annual climatic indices: mean annual temperature (MAT, °C), mean annual precipitation (MAP, mm), and mean annual aridity index (MAI, mm) which is defined as the ratio of mean annual precipitation and mean annual potential evapotranspiration. Climatic variables retrieved from different locations were averaged for each conifer species for further analysis.

Previous studies demonstrated that xylogenesis and the resulting xylem structure were species-specific (Rathgeber et al. 2016; Chen et al. 2019). Therefore, the effect of phylogeny was taken into account using various phylogenetic models in this cross-species study. We firstly constructed a phylogenetic tree for the species using the largest dated vascular plant phylogeny presently available, the GBOTB mega-tree of Smith & Brown (2018), which includes 79,881 taxa and all families of extant vascular plants based on combined molecular data from GenBank and data from the Open Tree of Life project (Smith and Brown 2018). We then pruned the supertree using the R package ‘V.PhyloMaker’ (Jin and Qian 2019) to generate a phylogeny for 79 conifer species.

Data analysis

Anatomic traits and their contrast between earlywood and latewood were checked for normality using the ‘Shapiro.test’ function in R (R Core Team 2018). Phylogenetic independent contrast (Pics) of tracheid characters and maximum plant height were calculated using the R package ‘ape’ (Paradis and Schliep 2018), and their correlations were tested using the R package ‘psych’ (Revelle 2018). Phylogenetically paired T-test was performed to test for a significant difference between corresponding traits in earlywood and latewood using the R package ‘phytools’ (Revell 2012), which is similar to paired t-test but take phylogeny into account.

As all of the five tracheid traits were positively correlated (Appendix 3), we applied a Phylogenetic principal component analysis (pPCA) to aggregate traits into PCs and to detect non-independent values of variables (traits or PCs) with the phylogenetic relationship (phylogenetic autocorrelation) between species. Phylogenetic principal components were analyzed using the R package ‘ade4’ (Jombart, Balloux, and Dray 2010), in which phylogenetic proximities were calculated using Abouheif’s proximity, and the resulting matrix of phylogenetic proximities was used to calculate phylogenetic autocorrelation, i.e., Moran’s value (Jombart et al. 2010, Zheng and Martinez-Cabrera 2013). Phylogenetic generalized least square regression (PGLS) was used to build bi-variate and multi-variate models in a phylogenetic context using the R package ‘nlme’ (Pinheiro et al. 2015), in which cell traits were expressed as a function of environmental variables, i.e., mid-point latitude, MAT, MAP, and interactions between climatic variables. R^2 for phylogeny and environmental variables in each model were calculated using the R package ‘rr2’ (Ives 2019).

Results

Contrast of early-and-latewood traits

All five pairs of traits showed significant phylogenetic signals (Table 1). The average tangential and radial diameter of tracheid in earlywood was larger than these of latewood, and tracheid length was higher in latewood than in earlywood within a phylogenetic context. However, tangential and radial wall thickness of tracheids did not differ significantly between earlywood and latewood when taking phylogeny into account (Table 1). Pics of maximum plant height were not significantly ($p > 0.05$) related to any of the five pairs of traits, and therefore, plant height was excluded in subsequent analyses.

PC1 of tracheid characters differ between families

Different traits showed a different pattern for autocorrelation with phylogeny. All tracheid features except cell wall thickness of earlywood were closely correlated with PC1, which contained 80% of all the information, and the cell wall thickness of earlywood was mainly correlated with PC2, which contained 12% information (Fig. 3). Therefore, PC1 stands for the xylem structure including features of earlywood and latewood in terms of cell diameter, cell length and cell wall thickness. For the two species-rich families, Pinaceae and Cupressaceae, their respective species were at opposite ends along PC1 (Fig.3). Podocarpaceae and Taxaceae also appeared to be positioned at the opposite end of Pinaceae; however, this was hard to confirm due to the limited number of five species of Podocarpaceae and Taxaceae analysed (Fig.3).

According to PC1, the first node on the phylotree divided all species excluding *Ginkgo biloba* into two groups (Fig. 4). Species from Cupressaceae and other families at the lower part of the phylotree showed some high positive Moran’ values (i.e., global structure), while Pinaceae species were located at the upper part of the

phylogeny and showed mainly negative Moran' values (i.e., local structure). A positive autocorrelation is the result of similarity in related species at the tips of the phylogeny, especially in *Juniperus* and *Cephalotaxus*. Negative autocorrelation results from differences among closely related species in the tips of the phylogeny, and was most clear in *Larix* and *Keteleeria*. Traits closely related to PC1 diverged more strongly within Pinaceae than in other conifer species along the phylogeny (Fig. 4).

Variation in tracheid characteristics along a latitudinal gradient

Most of the traits, except for earlywood tracheid diameters (CTD, CRD), showed a latitudinal pattern (Fig. 5). However, no significant trends were found between traits and longitude (LON) and altitude (ALT) ($p > 0.05$). Generally, traits of latewood decreased faster than those of earlywood as latitude increased, suggesting a climatic shift along latitude is more related to the change of latewood than earlywood traits.

Explanatory power of phylogeny and climate to cell traits

Phylogeny alone could explain 12.5~50.5% variance of tracheid structure. The total variance explained by the best models with climatic variables as a function of traits ranged from 24.7% to 49.2%. The best models for different traits varied in their climatic variables. MAT, MAP, and their interaction were included; however, aridity index (MAI) was excluded from all multivariate models (Table 2). Taken together, phylogeny, MAT, and MAP all played a role in shaping the xylem structure.

Discussions

Tracheid morphology in earlywood and latewood

Tracheid diameters in early- and latewood differed significantly (Table 1), partly supporting the widely recognized premise that earlywood is composed of wide, thin-walled tracheids in contrast to the narrow thick-walled tracheids in latewood. An explanation for the latter could be that the duration of latewood tracheid development is shorter than earlywood tracheid development, while a large proportion of non-structural carbohydrate produced in the current growing season is consumed by earlywood cell wall thickening (Rathgeber et al. 2016). Since the principal function of tracheids in earlywood is water transport, while tracheids in latewood are primarily involved in mechanical support and possible water storage (Domec and Gartner 2002), the xylem structure presented by the cell diameter in early- and latewood of our study is in line with their functions. A large tracheid size in earlywood results in a large lumen diameter, enabling higher water conductivity (Pittermann and Sperry 2003). Moreover, a small tracheid diameter ($< 30 \mu\text{m}$) in latewood is assumed to protect against freezing-induced embolism in conifers at high latitudes and altitudes (Davis Sperry, and Hacke 1999; Pittermann and Sperry 2006).

The difference in tracheid wall thickness between early- and latewood was insignificant when taking phylogeny into account, which was unexpected. However, Cuny et al. (2014) found that the area of tracheid walls was quite constant along growth rings except for the last quarter of the ring, which may be explained by the strong negative correlation between the duration and rate of secondary wall deposition for the three studied members of Pinaceae, *Abies alba*, *Picea abies* and *Pinus sylvestris* (Cuny, Rathgeber, Frank, Fonti, and Fournier 2014). Wilkinson et al. (2015) also found that tracheid wall thickness in intra-ring cells was surprisingly constant for *Pinus pinaster* (Wilkinson, Ogée, Domec, Rayment, and Wingate 2015). A possible explanation for our result is that the difference in tracheid wall thickness between early- and latewood was species-specific and may not always manifest the same pattern for various conifers (Kim, Funada, and Singh 2016). Although some boreal conifer species have thicker cell walls in latewood compared to earlywood, the distinctiveness between the two regions may not apply to all conifer species, especially those conifer families of warm regions, e.g., Podocarpaceae and Araucariaceae. For instance, lumen diameter and cell size in the wood of *Podocarpus neriifolius* (an evergreen conifer species growing in tropical China), did not differ noticeably between earlywood and latewood (Jiang et al. 2010). The majority of conifer species in this study are distributed throughout subtropical climates (Fig.1), which could explain the insignificant difference in tracheid wall thickness between early- and latewood.

During the evolution of conifers, selection has acted on optimizing xylem structure to fulfill both safety

and transport requirements (Hacke 2015). Conifers have adapted to diverse and often difficult environments by adjustment of their xylem structure at different levels, such as the amount of ray parenchyma at the tissue level (Olano et al. 2013), tracheid size, wall composition and structure at the cell level (Lachenbruch and McCulloh 2014), and pit membrane structure at the pit level (Lachenbruch and McCulloh 2014; Hacke 2015). There is an assumption that coordinated traits combined, not just a single trait, determine the safety/efficiency trade-off and further determine species distribution (Martínez-Vilalta et al. 2004; Pittermann et al. 2010; Bouche et al. 2014; Pittermann, Stuart, Dawson, and Moreau 2015). Intraspecific studies over broad latitudinal and elevation gradients also suggest that anatomical traits might not be closely related to efficiency and safety in contrast to leaf to sapwood area ratio and plant height for *Pinus sylvestris* and *Juniperus communis* (Martínez-Vilalta et al. 2009; Unterholzner et al. 2020). Besides the importance of xylem adjustment at the pit level and other mechanisms, we here postulate that tracheid dimensional contrasts between early- and latewood may be an ecological strategy for various conifers when adapting to different environmental conditions along latitude, especially cold temperature at high latitude.

2. Evolutionary outcome of xylem structure

Previous studies of conifer species from Pinaceae, Cupressaceae, and Podocarpaceae suggest there are at least three evolutionary directions for conifers adapting to different stresses at a geological time scale: cold adaptation, drought adaptation, and shade adaptation (Appendix 5). Species of Pinaceae possessed the most evolutionary advanced structural type of pit membrane (Bauch, Liese, and Schultze 1972; Zhou, Jiang, and Zhang 1990), and were generally drought vulnerable but cold tolerant (Martínez-Vilalta, Sala, and Piñol 2004). Cupressaceae spp. possessed drought tolerant strategies (Pittermann et al. 2015), whereas Podocarpaceae species were thought to have evolved in response to light competition, not drought or cold (Brodibb 2011). Considering the distribution of conifers, boreal forests mainly consist of Pinaceae species that must cope with freeze-thaw cycles, while some species of Cupressaceae are found in very arid regions or tree lines with extreme drought. Podocarpaceae are generally growing in humid tropical/subtropical regions with many angiosperm counterparts. Taken together, the xylem structure of Pinaceae species could have evolved mainly in response to freezing temperature, while species of other families were more conserved in this respect but might be more diverged in other xylem properties, i.e., pit structure or parenchyma (Braun 1984).

Small alterations in xylem anatomy can lead to a different performance in terms of water transportation, embolism resistance and capacitance (Hacke 2015). Our phylogenetic analyses provide some evidence for such functional changes between species (Fig. 4). However, owing to a currently incomplete understanding of embolism formation in tracheids, it is unclear whether tracheid characteristics, pit dimension and pit membrane morphology, and other morphological traits such as leaf shape, evolved in parallel during conifer evolution, but it is certainly an interesting topic to study further.

The latitudinal pattern of xylem structure of conifer species

Although many anatomical traits of woody angiosperms demonstrate a latitudinal trend in xylogenesis (Lens, Luteyn, Smets, and Jansen 2004; Wheeler, Baas, and Rodgers 2007; Zheng, Zhao, Morris, and Jansen 2019), gymnosperm wood has been less studied until recently (St-Germain and Krause 2008; Rossi et al. 2016; Björklund et al. 2017; Huang et al. 2020). In our cross-species study, most tracheid traits showed a clear latitudinal pattern, especially in traits related to cell wall dimensions in latewood (Fig. 3). We also reveal a decrease in tracheid length and tracheid wall thickness for both early-and-latewood together with tracheid diameter in latewood along the latitudinal gradient. Regarding such a large latitudinal gradient under a monsoonal climate in China, the carbon investment for xylem formation would decrease in the northern regions due to a shortened photoperiod during the growing season, which may lead to a reduction in tracheid diameter and tracheid wall thickness in latewood. The latter finding is in good agreement with the fact that tree growth rate declines towards high latitudes. Besides, radial diameters of latewood tracheids were generally lower than 30 μm , which is consistent with the threshold diameter for frost-induced embolism (Pittermann and Sperry 2003). Therefore, the decreased stem hydraulic capacity in a cold climate might be a consequence of the evolution of reduced vulnerability of xylem to freezing-induced embolism (Creese,

Benscoter, and Maherali 2011), which represents an ecological strategy for conifers distributed in colder climates. For instance, the wide distribution of *Pinus* species in the Northern Hemisphere was thought to be due to adaptation to cold temperatures during the Eocene (Millar 1993).

Both temperature and precipitation play a role in shaping xylem structure

Climatic conditions (i.e., mean annual temperature; MAT and mean annual precipitation; MAP) and their interaction were correlated with different cell traits to various degrees (Table 2). Also, the shifting patterns of cell traits along MAT and MAP gradients had a similar increasing tendency as latitude (not shown). Responses of most latewood cell traits to MAT and MAP gradients were stronger than those of corresponding earlywood cell traits, except that no significant correlation was detected between tangential/radial cell diameter in earlywood and the two climatic variables. Although Rossi et al. (2016) found that the period of wood formation increased linearly with MAT in a range of 14 for 10 conifer species in cold biomes of the Northern Hemisphere (Rossi et al. 2013; Rossi et al. 2016), our results suggest that both temperature and precipitation contribute to tracheid size and tracheid wall dimensions for multiple conifer species across various climate conditions, i.e., temperate, subtropical, and tropical climate, while taking phylogeny into account. The similar impacts of MAT and MAP on xylem structure possibly lies in the fact that temperature and precipitation are largely synchronic under a monsoonal climate in the eastern part of China (Ding 2013), which is supported by a close correlation between MAT and MAP ($r=0.81$, $p<0.001$) (Appendix 4).

We did not find clear evidence for the association between drought and xylem structure using mean annual climatic variables, as MAI was not included in any top models with MAT and MAP as climatic variables. Although seasonal drought does exist in subtropical regions in Southwest China, the annual rainfall does not differ much among these regions (Ding 2013). Furthermore, it was the length of the drought season rather than other climatic variables that determined a plant’s response to climate in these regions (Lian et al. 2020), which could not be presented by the mean annual aridity index used in this study. Finer temporal resolution of climate data, such as weekly or daily data of air temperature and soil water deficit, together with long-term chronological anatomical data would help to address these questions. Given the fast development of image processing techniques and automatic climate and soil monitoring methods, we believe that a combination of information from radial growth, wood density and xylem anatomy will open up a new research area for tree-ring science and allow for the detection of large structural, biogeographical and environmental patterns and their interpretation.

Table Legend

Table 1. Description of tracheid characteristics measured and results of phylogenetic paired T-test between early- and latewood based on 79 conifer tree species from China. The mean and standard deviation of each trait were shown, and phylogenetic signals for traits represented by lambda values.

Tracheid character	Earlywood	Earlywood	Latewood	Latewood	Phylogenetic Paired
	Mean (SD)	lambda	Mean (SD)	lambda	T
Tracheid Length (CL, mm)	3.46 (1.39)	0.91	3.85 (1.33)	0.91	-6.07
Tracheid tangential diameter (CTD, μm)	37.04 (0.92)	0.88	34.78 (0.75)	0.87	2.32
Tracheid radial diameter (CRD, μm)	44.00 (1.05)	0.94	23.06 (0.95)	0.34	2.05
Tracheid tangential wall thickness (WRT, μm)	2.81 (0.89)	0.68	4.67 (1.37)	0.76	-0.91
Tracheid radial wall thickness (WTT, μm)	3.80 (0.82)	0.58	5.09 (1.24)	0.80	-1.07

Table 2. Summary of PGLS models of xylem tracheid characters as functions of MAT, MAP and their interaction, with models’ R^2 for phylogeny and climate partitioned by the method of Ives (2019). MAT, mean annual temperature; MAP, mean annual precipitation. Multivariate models included climatic variable interactions, i.e., MAT*MAP. For tracheid length (CL) in both earlywood and latewood, the interaction was not significant, as marked by a “*” next to the AIC-value. Models with the highest R^2 for each trait were bold and italicized. Acronyms of tracheid characters are according to Table 1.

		Earlywood model				
Trait	Climatic index	R^2_{tot}	R^2_{var}	R^2_{phy}	AIC	lambda
CL	MAT	0.426	0.033	0.407	187.7	0.91
	MAP	0.469	0.105	0.407	180.7	0.91
	MAT*MAP	0.469	0.104	0.407	182.7*	0.91
CTD	MAT	-	-	0.388	513.4	0.90
	MAP	-	-	0.388	513.4	0.90
	MAT*MAP	-	-	0.388	513.4	0.90
CRD	MAT	-	-	0.505	552.1	0.94
	MAP	-	-	0.505	552.1	0.94
	MAT*MAP	-	-	0.505	552.1	0.94
WTT	MAT	0.247	0.102	0.161	127.9	0.73
	MAP	0.205	0.053	0.161	132.0	0.74
	MAT*MAP	-	-	0.161	134.6	0.75
WRT	MAT	0.246	0.076	0.184	132.5	0.39
	MAP	0.126	0.126	0.000	141.7	0.00
	MAT*MAP	0.251	0.082	0.184	134.5	0.46

Figure Legend

Figure 1 . Spatial distribution of the data in this study. Each dot represents a species’ central distribution location in China, using the mid-latitude and mid-longitude values of the species’ range in the country as coordinates.

Figure 2 . Frequency distribution of five tracheid traits for 79 conifer species. Blue bars stand for earlywood and red bars for latewood.

Figure 3 . Phylogenetic PCA of earlywood and latewood characters for 79 conifer species from five families. Acronyms for tracheid traits are listed in Table 1. Trait names followed by ‘s’ stand for earlywood while ‘a’ is for latewood.

Figure 4 . Phylogenetic PCs of earlywood and latewood traits along the phylogenetic tree. Bubbles stand for Moran’ values for each species along the phylotree with a legend at the bottom-left. The node-1 label is added to emphasize two clades of the phylotree: Pinaceae species in the upper part of the phylotree generally showed negative values, suggesting there are more frequent divergences in traits related with PC1. On the contrary, Cupressaceae species and others in the lower branches showed positive values, suggesting xylem traits related with PC1 of the species were conserved.

Figure 5 . Interspecific variation in tracheid characters along a latitudinal gradient taking phylogeny into account. R^2 stands for the explanatory power of the climatic variable in PGLS models, subscript “s” in R^2 stands for earlywood, while “a” stands for latewood. Blue and red lines stand for fitted GPLS models for earlywood and latewood data, respectively.

Acknowledgements

We thank Dr. Fang Du for support with the preparation of Figure 1. This research was funded by the Beijing Municipal Bureau of Parks (2020-STBHXC-04-013) to J.Z.

Author Contributions

J.Z. planed the study, Y.L. and J.Z. collected data, performed the statistical analyses. J.Z, M.H. V.F. and J.S. wrote the manuscript.

Additional Information

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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