

Comparison of wood physical and mechanical traits between major gymnosperm and angiosperm tree species in China

Meixia Zhang¹ · Chengjun Ji² · Jiangling Zhu² ·
Xiangping Wang³ · Donghui Wang⁴ · Wenxuan Han¹

Received: 11 April 2016 / Published online: 13 September 2017
© Springer-Verlag GmbH Germany 2017

Abstract Many wood physical and mechanical traits are important functional attributes for tree species, but variation in these traits among taxonomic categories such as between gymnosperms and angiosperms is still poorly documented. Here, the systematic differences in 12 traits and their allometric relationships between the two tree categories and the potential effects of phylogeny are explored based on a database for major gymnosperm and angiosperm tree species across China. The results are summarized below: (1) means of wood traits were all significantly lower in gymnosperms than in angiosperms. (2) Air-dried density (ADD) and tangential shrinkage coefficient (TSC) are key traits that summarize the correlations among wood traits for gymnosperms, while ADD and radial shrinkage coefficient (RSC) represent those for angiosperms. The allometric slopes of other traits, except for hardness of transverse section (HES), against ADD for gymnosperms were significantly steeper than or similar to the corresponding slopes for angiosperms. On the

Electronic supplementary material The online version of this article (doi:[10.1007/s00226-017-0954-1](https://doi.org/10.1007/s00226-017-0954-1)) contains supplementary material, which is available to authorized users.

✉ Chengjun Ji
Jiej@pku.edu.cn

✉ Wenxuan Han
hanwenxuan@cau.edu.cn

¹ Beijing Key Laboratory of Biodiversity and Organic Farming, College of Resources and Environmental Sciences, China Agricultural University, No. 2 West Yuanmingyuan Road, Haidian District, Beijing 100193, China

² Department of Ecology, College of Urban and Environmental Sciences, Peking University, Beijing 100871, China

³ The Key Laboratory of Silviculture and Conservation of the Ministry of Education, and the National Engineering Laboratory for Forest Genetics and Tree Breeding, Beijing Forestry University, Beijing 10083, China

⁴ College of Life Sciences, Peking University, Beijing 100871, China

contrary, the slopes of other traits (except TSC) against RSC for gymnosperms were shallower than or similar to their counterparts for angiosperms. Generally, wood traits were positively related with each other, except that TSC was negatively related to density-related (ADD, BD) and hardness-related traits (HES, HRS and HTS) in gymnosperms. (3) Phylogeny had significant effects on some wood traits of gymnosperms, but had no effects on traits of angiosperms. The present analyses demonstrated a systematic difference in wood traits between two major plant categories, which suggests the evolutionary divergence (TSC, RSC) and convergence (ADD) in key functional traits among woody plants.

Introduction

Wood physical and mechanical properties are not only related to the mechanical support of stems and limbs (Niklas 1992), and the hydraulic function (low density with high hydraulic conductivity) (Hacke et al. 2001; Preston et al. 2006), but also affect the morphological structure of individual plants (Sterck et al. 2001; Poorter et al. 2006). Some wood traits (e.g., density) are closely linked with the survival and mortality rate, reproductive time (Swenson and Enquist 2007; Wright et al. 2003) and life span (Sterck et al. 2001) of trees, as well as the growth rate (Sotelo et al. 2007b) of stem diameter and canopy (King et al. 2005). Wood traits are also connected with resource competition among species (Baker et al. 2004), community dynamics and ecosystem functions (Chave et al. 2006; Zhang et al. 2011). Therefore, studying of wood physical and mechanical properties can benefit our understanding of ecological processes from individual plants to ecosystem scales.

Current studies mainly focused on wood density (Swenson and Enquist 2007; Chave et al. 2009; Zanne et al. 2010; Zheng and Martínez-Cabrera 2013). A number of studies reported other traits, such as correlations between wood shrinkage and tree growth (Sotelo et al. 2007b); bending strength (MOR) and bending modulus of elasticity (MOE) of wood in a tropical rain forest (Van et al. 2006); crushing strength, stem-growth traits and branch-wood traits of *Calycophyllum spruceanum* (Sotelo et al. 2007a, 2003), wood color variables among trees and shrub species (Sotelo et al. 2013). Nevertheless, few studies have ever addressed the variations in wood traits and their interrelations between gymnosperms and angiosperms (Zhu et al. 2015). Therefore, a comprehensive comparison of wood traits between gymnosperms and angiosperms is of great importance.

Gymnosperm and angiosperm trees differ markedly not only in evolutionary history and distribution, but also in wood structure. Gymnosperms are the original seed plants, mainly distributed in areas with nutrient-poor soils (Aerts 1995). The structure of gymnosperms wood is relatively simple, consisting of tracheid and rays, with tracheids mainly responsible for the function of transport and mechanical support. On the other hand, angiosperm wood is mostly composed of vessels, rays, fibers and parenchyma cells. These differences are expected to cause quite different wood physical and mechanical attributes between gymnosperms and angiosperms. However, the differences, if any, in wood traits and their interrelations were seldom

documented between these two plant categories, and it is also unclear whether these traits are affected by phylogeny.

Based on a database of wood traits across major tree species in China, the difference in 12 wood physical and mechanical properties between gymnosperms and angiosperms, and the phylogenetic effects on these traits were examined. In addition, the allometric relationships (Niklas 1994) between wood traits of gymnosperms versus angiosperms were explored. Specifically, the following hypotheses were tested: (1) gymnosperms have lower values of wood physical and mechanical traits than angiosperms. (2) Allometric relationships between wood traits of gymnosperms are different from those of angiosperms. (3) Phylogeny may have effects on wood traits of both gymnosperms and angiosperms. Thus, based on the above hypotheses, the similarity and differences of the 12 wood traits between gymnosperms and angiosperms across China were explored and it was attempted to afford more information about the criteria to determine wood usage.

Materials and methods

Wood physical and mechanical properties

A comprehensive database of wood traits for major gymnosperm and angiosperm tree species across China, collected from the studies, was established (Anatomy and Properties of Chinese Woods, Wood Physical and Mechanical Properties of Main Tree Species in China, Atlas of Gymnosperms Woods of China, Wood Properties of Main Tree Species from Plantation in China; see Reference S1 for more details). Description and definition of the 12 wood traits are as below.

BD, basic density: the oven-dry mass of a wood sample divided by its green volume. ADD, air-dried density: the air-dry mass of a wood sample divided by its air-dried volume. RSC/TSC/VSC, radial/tangential/volumetric shrinkage coefficient: the relative change of dimension with change of wood moisture content across the radial/tangential/volumetric plane. MOR, bending strength: the stress in a material just before it yields in a flexure test. MOE, bending modulus of elasticity: an intensive property that is computed as the ratio of stress to strain in flexural deformation, or the tendency for a material to bend. CSG, compression strength parallel to grain: maximum stress sustained by a compression parallel-to-grain specimen. RES, resilience: the capacity of wood to absorb energy when it is deformed elastically and then upon unloading to have this energy recovered. HES/HRS/HTS, hardness of transverse/radial/tangential section: resistance to indentation using a modified Janka hardness test, measured by the load required to embed an 11.28-mm ball to one-half its diameter in transverse/radial/tangential plane (Green et al. 1999). More detailed description of the mathematical formulas for the 12 wood physical and mechanical traits is shown as supporting information (Appendix S1).

These traits can well characterize the main wood properties in density (ADD, BD), dry shrinkage coefficient (RSC, TSC and VCS), resilience (MOE, RES), strength and hardness (MOR, CSG, HES, HRS and HTS).

The gymnosperms in this study involve 98 species belonging to 27 genera and six families: *Cupressaceae*, *Taxaceae*, *Podocarpaceae*, *Cephalotaxaceae*, *Pinaceae* and *Taxodiaceae*. The woody angiosperms consist of 372 species belonging to 66 genera and 76 families (Fig. 1).

Data analysis

Shapiro–Wilk test was used for data normality (Shapiro and Wilk 1965). For both gymnosperms and angiosperms, the 12 wood physical and mechanical traits did not follow a normal distribution (Fig. 2). Consequently, MOE, RES, HRS and HTS were log-transformed, and other traits were square-root transformed, to improve normality before data analyses. Then, *t* test was used to compare the mean values of the 12 individual wood traits between gymnosperms and angiosperms. Principal component analysis (PCA) was conducted for the 12 wood traits, for gymnosperms and angiosperms separately. Traits with the greatest contribution to the first two PCA axes were identified as the key traits that summarized the correlations among wood traits in this study. Then, it was examined how the allometric relationships between other traits and these key traits differ among gymnosperms and angiosperms (Warton et al. 2012). Allometric analyses were conducted with type-II regressions (standard major axis regression). The type-II regression slopes were compared with the standard *F* tests (Warton et al. 2006) between gymnosperms and angiosperms.

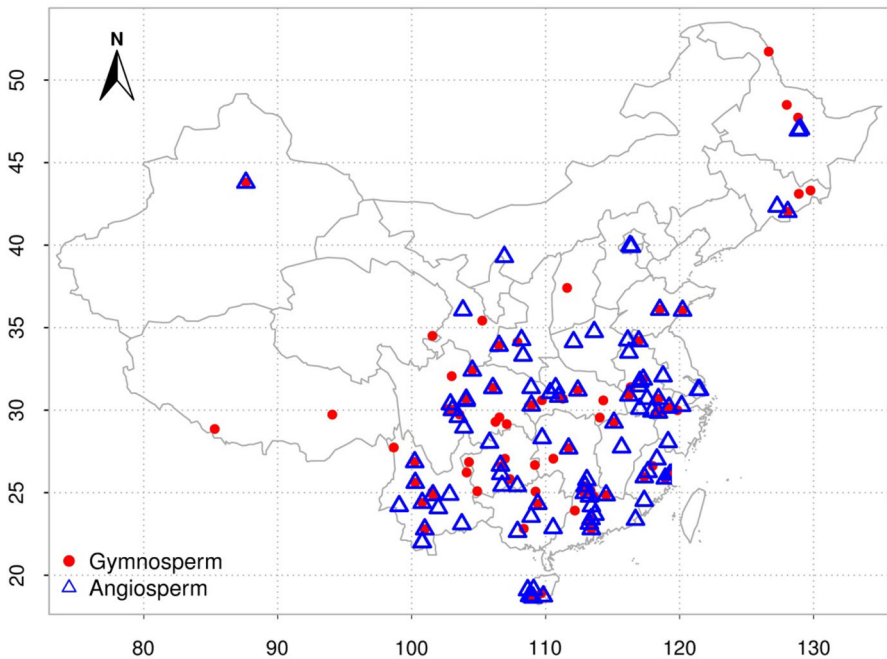


Fig. 1 Wood sampling sites for all the gymnosperm and angiosperm tree species in this study

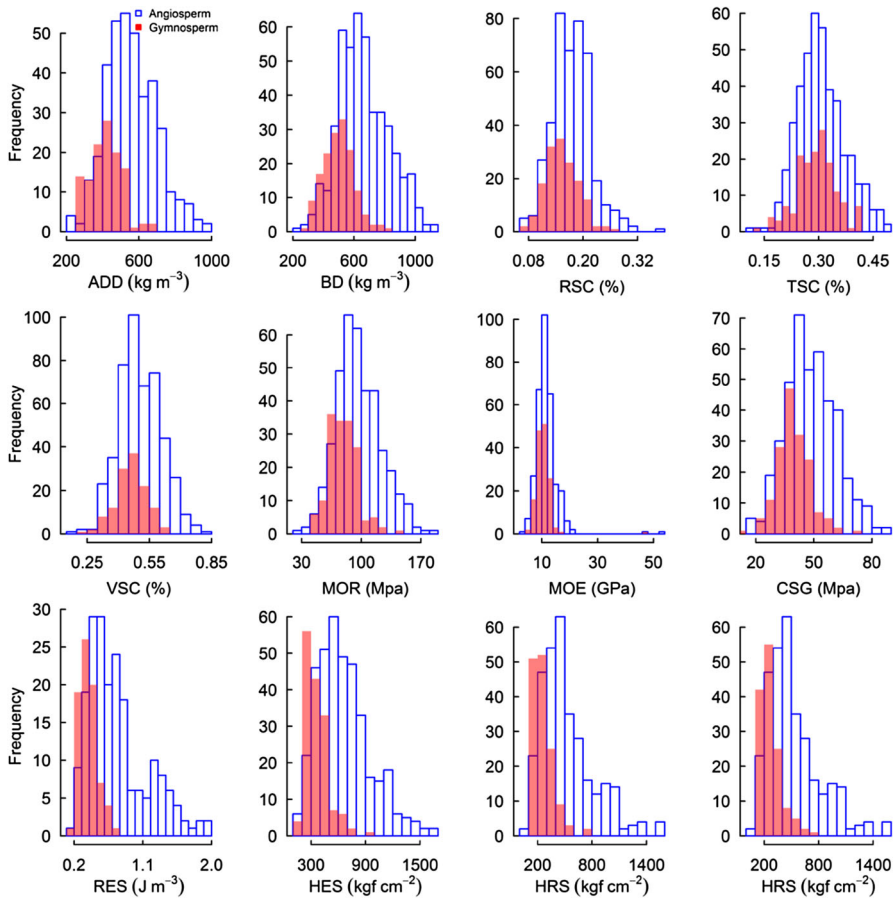


Fig. 2 Histograms showing the distribution of 12 wood physical and mechanical traits of gymnosperms and angiosperms. *BD* basic density; *ADD* air-dried density; *RSC* radial shrinkage coefficient; *TSC* tangential shrinkage coefficient; *VSC* volumetric shrinkage coefficient; *MOR* bending strength; *MOE* bending modulus of elasticity; *CSG* compression strength parallel to grain; *RES* resilience; *HES* hardness of transverse section; *HRS* hardness of radial section; *HTS* hardness of tangential section

Based on the APG III system (Bremer et al. 2009), a phylogenetic tree for the species was generated in this study. The tree topology was obtained with the online Phylomatic [storedtree = Phylomatic tree R20120829 (plants)] (Webb and Donoghue 2005). The branch lengths were estimated with the *bladj* function of Phylcom (Wikstrom et al. 2001; Webb et al. 2008), based on the node ages (Wikstrom et al. 2001). Then, the phylogenetic Euclidean distances (Greenacre and Primicerio 2008) among gymnosperms (or angiosperms) species were calculated at the family level. Euclidean distance is the physical distance in two- or three-dimensional space to multidimensional space, often referred to as the “Pythagorean distance” as well (Greenacre and Primicerio 2008). The equation:

$$d_{x,y} = \sqrt{\sum_{n=1}^n (x_n - y_n)^2}. \text{ Euclidean distance among species is based on the}$$

distance in phylogeny, which relies on a measure of “genetic distance” between the sequences being classified. Then, a set of coordinates marking the positions of the species will be generated based on node age within the phylogenetic trees. The Euclidean distance, i.e., the evolutionary distances among species, can be obtained with the above equation. For each wood trait, the Euclidean distances among gymnosperms (or angiosperms) were also calculated. Mantel test (Mantel 1967) was used to relate Euclidean distance matrix of species to Euclidean distance matrix of wood traits. This analysis was conducted separately for gymnosperms and angiosperms to examine whether they differed in the phylogenetic control of wood traits.

All statistical analyses were performed using R package 3.0.2 software. PCA was performed with FactoMineR package (Josse et al. 2008), while allometric analysis was conducted with the smart package (Warton et al. 2012). The phylogenetic and trait Euclidean distances between species pairs were calculated with ape package (Paradis et al. 2004) and simba package, respectively.

Results

Statistics of wood traits for gymnosperms and angiosperms

Wood traits varied greatly but with different coefficients of variance (CV): HRS and HTS had larger CV than the other traits (Table 1). Consistent with the current hypothesis, means of all wood traits were lower ($P < 0.05$) in gymnosperms than angiosperms (e.g., 411 vs. 552 kg m⁻³ for ADD, 0.15 vs. 0.18% for RSC, 0.29 vs. 0.30% for TSC; all $P < 0.05$) (Table 1; Fig. 2). Gymnosperms had smaller CV of wood traits than angiosperms, except for RSC.

Key wood traits for gymnosperms and angiosperms

For gymnosperms, the PCA analysis on 12 wood traits showed that the first two axes of PCA explained most (85.9%) of the variation (Table 2, Table S2, S3), which is enough to reflect the majority of information on wood physical and mechanical traits of gymnosperms. For the first axis of PCA, the traits of density (ADD, BD), resilience (MOE, RES), strength and hardness (MOR, CSG, HES, HRS and HTS) had high contributions, with ADD the most important (12%). For the second axis, only RSC, TSC and VSC had high explanatory powers, and TSC was the most important (33.5%). Thus, ADD and TSC, with the highest relative contribution to the first and second axis, respectively, can serve as “key traits” to characterize the two major axes of wood trait variations for gymnosperms.

PCA analysis on wood traits of angiosperms also showed that the first two PCA axes together explained 88.4% of the variation. ADD was the most important contributor (9.7%) to the first PCA axis. However, RSC was the most important (30%) for the second axis, which is different from gymnosperms. Thus, ADD and RSC can be regarded as the key wood traits for angiosperms tree species.

Table 1 Statistics of wood physical and mechanical traits for gymnosperms and angiosperms

Wood traits	Units	Taxonomic category	Sample size	Average*	Range	CV (%)
ADD	kg m ⁻³	Gymnosperm	118	411 ^a (417)	260–694	21.4
		Angiosperm	366	552 ^b (560)	200–966	24.9
BD	kg m ⁻³	Gymnosperm	158	496 ^a (501)	291–835	19.7
		Angiosperm	467	653 ^b (664)	240–1130	24.7
RSC	%**	Gymnosperm	156	0.15 ^a (0.16)	0.07–0.45	27.3
		Angiosperm	420	0.18 ^b (0.17)	0.06–0.36	24.4
TSC	%**	Gymnosperm	157	0.29 ^a (0.30)	0.13–0.52	19.1
		Angiosperm	421	0.30 ^b (0.31)	0.11–0.49	20.9
VSC	%**	Gymnosperm	127	0.46 ^a (0.46)	0.25–0.62	16.2
		Angiosperm	468	0.50 ^b (0.51)	0.19–0.81	20.0
MOR	Mpa	Gymnosperm	158	78.2 ^a (79.0)	42.7–145	21.6
		Angiosperm	382	95.3 ^b (97.0)	29.40–183	26.8
MOE	GPa	Gymnosperm	148	10.0 ^a (10.5)	4.79–47.5	34.9
		Angiosperm	322	11.2 ^b (11.7)	3.1–53.4	36.5
CSG	Mpa	Gymnosperm	163	39.2 ^a (39.7)	13.1–71.5	21.5
		Angiosperm	415	47.7 ^b (48.6)	16.0–87.3	26.7
RES	J m ⁻³	Gymnosperm	78	0.37 ^a (0.39)	0.18–0.79	29.9
		Angiosperm	201	0.67 ^b (0.76)	0.16–1.94	50.7
HES	Kgf cm ⁻²	Gymnosperm	152	350 ^a (359)	107–937	35.0
		Angiosperm	382	625 ^b (658)	131–1650	44.5
HRS	Kgf cm ⁻²	Gymnosperm	142	240 ^a (260)	113–748	44.3
		Angiosperm	322	457 ^b (525)	88.0–1598	55.8
HTS	Kgf cm ⁻²	Gymnosperm	138	251 ^a (274)	106–788	43.0
		Angiosperm	326	468 ^b (539)	96.0–1554	52.2

*The average values were calculated using the transformed data (retransformed average values in original units), with the arithmetic averages based on the original data in parentheses aside. Different letters denote significant difference in the average values of the same trait between taxonomic categories ($P < 0.05$). CV (%), the coefficient of variation, calculated from the original data. **or, $\times 10^{-2}\%$ (%-moisture)⁻¹; see formula (S3) in Formulae S1 for more details

BD basic density; *ADD* air-dried density; *RSC* radial shrinkage coefficient; *TSC* tangential shrinkage coefficient; *VSC* volumetric shrinkage coefficient; *MOR* bending strength; *MOE* bending modulus of elasticity; *CSG* compression strength parallel to grain; *RES* resilience; *HES* hardness of transverse section; *HRS* hardness of radial section; *HTS* hardness of tangential section

Allometric relationships of wood traits against ADD, TSC and RSC

Most wood physical and mechanical traits had positive effect on the key traits (ADD, RSC and TSC) based on the allometric analysis, except for the traits reflecting density (ADD and BD) and hardness (HES, HRS and HTS) against TSC for gymnosperms (Fig. 3).

The allometry slopes of RSC, TSC, MOE against ADD for gymnosperms were 1.2–1.3 times greater than the corresponding slopes for angiosperms ($P < 0.05$). The slope of HES against ADD for gymnosperms was 1.2 times smaller than that of

Table 2 PCA analysis on the twelve wood traits for gymnosperm and angiosperm tree species

Wood trait	Relative contribution (%)			
	Gymnosperm		Angiosperm	
	First axis	Second axis	First axis	Second axis
BD	11.88	0.39	9.47	1.36
ADD	11.91	0.15	9.68	0.44
RSC	7.28	12.76	6.24	30.03
TSC	0.49	33.51	7.35	13.04
VSC	3.04	26.96	8.05	25.40
MOR	10.86	0.02	9.17	1.66
MOE	8.02	6.71	8.33	2.22
CSG	8.95	0.54	8.46	3.68
RES	8.17	0.37	5.89	2.17
HES	8.77	8.11	8.90	6.96
HRS	10.53	4.48	9.22	6.67
HTS	10.10	5.99	9.25	6.38
Sum of the contribution (%)	63.84	22.11	82.54	5.90

Values in bold indicate that the corresponding traits have the highest contributor to the PCA axis

BD basic density; *ADD* air-dried density; *RSC* radial shrinkage coefficient; *TSC* tangential shrinkage coefficient; *VSC* volumetric shrinkage coefficient; *MOR* bending strength; *MOE* bending modulus of elasticity; *CSG* compression strength parallel to grain; *RES* resilience; *HES* hardness of transverse section; *HRS* hardness of radial section; *HTS* hardness of tangential section

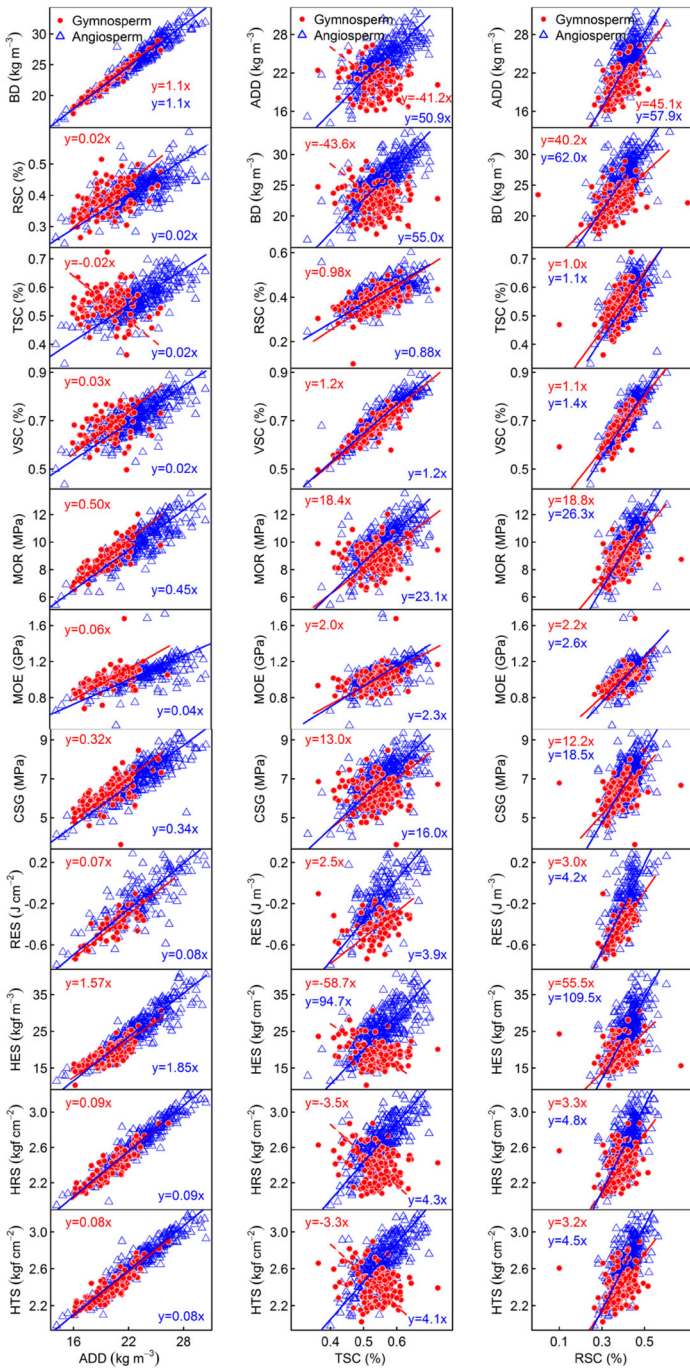
angiosperms ($P < 0.05$). There was no significant difference in the allometric slopes of the other six traits against ADD between gymnosperms and angiosperms ($P > 0.05$; Fig. 3, Table S1).

The allometric analysis on TSC versus other traits showed that the slopes of most traits against TSC for angiosperms were 1.2–1.6 times greater than those for gymnosperms ($P < 0.05$; Fig. 3), except that the slopes for RSC, VSC and MOE were not significantly different between gymnosperms and angiosperms.

The slopes of most traits (except TSC) against RSC for angiosperms were 1.2–2.0 times greater than the corresponding slopes for gymnosperms ($P < 0.05$; Fig. 3, Table S1). All slopes were greater than 1.0, except that the slope of TSC against RSC was not significantly different from 1.0 ($P > 0.05$), for both gymnosperms and angiosperms.

Influence of phylogeny on wood mechanical and mechanical traits

There were significant positive correlations between the Euclidean distance matrix of the traits (BD, TSC, VSC and CSG) and the phylogenetic Euclidean distance matrix for gymnosperms ($r > 0.1$, $P < 0.05$; Table 3, Fig S1), suggesting that between-species differences in these traits were significantly associated with phylogenetic distance between species. However, no significant correlation between trait distance and phylogenetic distance was found in angiosperms (Table 3).



◀ **Fig. 3** Allometric relationships between the three key traits (ADD, TSC and RSC) and the other wood traits. The fitted lines show the standardized major axis regression results ($P < 0.05$). Equation above is for gymnosperms. Below is for angiosperms. *BD* basic density; *ADD* air-dried density; *RSC* radial shrinkage coefficient; *TSC* tangential shrinkage coefficient; *VSC* volumetric shrinkage coefficient; *MOR* bending strength; *MOE* bending modulus of elasticity; *CSG* compression strength parallel to grain; *RES* resilience; *HES* hardness of transverse section; *HRS* hardness of radial section; *HTS* hardness of tangential section

Discussion

Difference in wood traits between gymnosperm and angiosperm tree species

Comparison of 12 wood physical and mechanical traits between major gymnosperm and angiosperm tree species showed that the values of all wood traits of angiosperms were higher than those of gymnosperms. The high trait values might suggest a generally better wood functioning or some competitive advantages for angiosperms, which may contribute to the currently wider spread of angiosperm versus gymnosperm trees over the Earth.

Functions (which can be indicated by traits) are consistent with structures. Wood physical and mechanical traits are important functional attributes for tree species. So, the difference in these wood traits may be explained by the different wood anatomical features of gymnosperms versus angiosperms. Gymnosperm wood consists of tracheids, rays and parenchyma. The relative proportions of the three tissues are generally similar among gymnosperms (Cheng 1985). On the other hand, angiosperm wood is structurally more complex, composed of vessels, fibers, rays and parenchyma. The relative proportions of these wood tissues, however, are markedly variable across angiosperm tree species. Consistently, the current results showed that gymnosperm wood traits demonstrated smaller CVs than angiosperms (Table 1). Previous studies also found that wood traits of angiosperms varied more dramatically with climate than those of gymnosperms (Cheng 1985; Carlquist 2001). Tracheid and wood fiber cells are mainly responsible for mechanical support in gymnosperms and angiosperms, respectively. However, the tracheid walls are thinner than the fibers walls, which explained why gymnosperms had lower values of strength-related (CSG and MOR) and hardness-related (HES, HRS and HTS) traits than angiosperms (Table 1).

The difference in wood traits between gymnosperms and angiosperms is further reflected in their “key traits.” Previous studies have determined the central role of wood density in woody plant functioning (Swenson and Enquist 2007), as shown by the current PCA analysis that ADD was the common “key traits” of the two taxonomic categories. Furthermore, TSC was another key trait for gymnosperms, while RSC was another major trait for angiosperms. For gymnosperms, cross-field pitting (i.e., the pores between the ray parenchyma cells and the adjacent vertical tracheids) usually occurs on radial walls, leading to much more pits on the tracheid radial walls than on tangential walls (Cheng 1985). Therefore, radial shrinkage is more limited than tangential shrinkage in wood of gymnosperms, which may be the possible reason that TSC was the key trait of gymnosperms. No difference was found in the number and size of pits between the radial and tangential vessel walls

Table 3 Significance level (*P* value) for the correlations between Euclidean distance matrix of species and Euclidean distance matrix of wood traits for gymnosperms and angiosperms, respectively

Taxonomic category	ADD	BD	RSC	TSC	VSC	MOR	MOE	CSG	RES	HES	HRS	HTS
Angiosperm	0.62	0.95	0.07	0.63	0.97	0.72	0.50	0.54	0.27	0.69	0.56	0.93
Gymnosperm	0.20	0.0004****	0.18	0.03*	0.01***	0.17	0.75	0.02***	0.38	0.46	0.28	0.65

The null hypothesis is no significant correlation between the two kinds of matrices. Mantel test was used to relate Euclidean distance matrix of species to Euclidean distance matrix of wood traits

BD basic density; *ADD* air-dried density; *RSC* radial shrinkage coefficient; *TSC* tangential shrinkage coefficient; *VSC* volumetric shrinkage coefficient; *MOR* bending strength; *MOE* bending modulus of elasticity; *CSG* compression strength parallel to grain; *RES* resilience; *HES* hardness of transverse section; *HRS* hardness of radial section; *HTS* hardness of tangential section

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$

of angiosperm woods (Bao et al. 1984). However, the number, size and cell wall thickness of vessels and fibers are much more variable radially than tangentially. This structural feature of wood might partly explain why RSC was a key wood trait besides ADD for angiosperms.

Wood traits are the main criteria to determine wood usage (Bowyer et al. 2007). Density is currently considered as an important criterion in determining wood strength, elasticity and hardness. The current results supplied useful references for wood applications. In addition to density, the key traits (TSC for gymnosperms and RSC for angiosperms) can also be used as the primary indicators to judge the qualities and usages of the two categories of wood, respectively.

Allometries of wood traits against ADD, TSC and RSC

Although the “key traits” of gymnosperms (ADD and TSC) and angiosperms (ADD and RSC) were generally positively correlated with most other wood traits, TSC of gymnosperms was negatively but nonsignificantly correlated with density traits (ADD and BD) and hardness traits (HES, HRS and HTS) based on the allometric analysis, contrary to the corresponding relations in angiosperms (Fig. 3). The different allometries of TSC versus density and hardness traits between gymnosperms and angiosperms may also reflect the difference in wood structures of the two taxonomic groups. Vessels usually have higher shrinkage than tracheids; the shrinkage of angiosperm wood is mainly controlled by its vessels in both radial and tangential directions. Similarly, the radial shrinkage of gymnosperm wood is controlled by its tracheids. However, tangential tracheid walls are thicker in the ray-contact areas, which is a general characteristic of coniferous wood, called “raythickness” (Ladell 1967; Keith 2007). The thicker tangential tracheid walls (raythickness), together with the concomitant smaller lumina, in the tangential versus radial direction may possibly result in relatively low shrinkage of tracheids tangentially versus radially, thus leading to nonsignificant allometric relationships ($P > 0.05$; Fig. 3) of TSC against density traits (ADD and BD) and hardness traits (HES, HRS and HTS) of gymnosperm wood. However, the underlying mechanisms need to be further explored.

Influence of phylogeny on wood physical and mechanical traits

Correlation analysis between the Euclidean distance matrixes (Table 3) suggested that wood traits of gymnosperms were significantly affected by phylogeny, but traits of angiosperms did not show phylogenetic effects. Phylogeny may interact with the environment in shaping the spatial patterns of wood traits (Zhang et al. 2011). Gymnosperms are ancient seed plants with many epibiotic species (Mutke and Barthlott 2005), which suggests that their phylogenetic tree covers long time span (e.g., the longest Euclidean distance between gymnosperm species is 603, much longer than that (390) between angiosperms in this study). These plants mostly grow in relative similar habitats, for example, with poor soils, dry and cool climate (Aerts 1995). Thus, phylogeny might impose relatively stronger influences on the wood traits of gymnosperms than the habitat environments did. In contrast, angiosperms

appeared later on the Earth but have successfully spread to diverse habitats. Consequently, phylogeny may play a less important role than the habitats in shaping the wood traits of angiosperms. Unfortunately, there are no habitat data for these plants to test this hypothesis at the present time. The fact that phylogeny affects only wood traits of gymnosperms may suggest the differential evolutionary controls on plant functional traits of the two categories (gymnosperms vs. angiosperms).

Conclusion

Comparison of wood traits between gymnosperms and angiosperms revealed markedly patterns of evolutionary divergence and convergence in key functional traits of woody plants. Means of wood traits were all significantly lower in gymnosperms than in angiosperms. Air-dried density (ADD) and tangential shrinkage coefficient (TSC) are key traits that summarize the correlations among wood traits (or represent the major axis of wood traits syndrome) for gymnosperms, while ADD and radial shrinkage coefficient (RSC) are key traits for angiosperm. Generally, wood traits for both plant categories were positively related to each other, except that TSC was negatively but nonsignificantly related to density- and hardness-related traits in gymnosperms. The allometry slopes of most traits against ADD for gymnosperms were steeper than those for angiosperms, while the slopes of most traits against RSC were shallower for gymnosperms than those for angiosperms. Phylogeny may have significant effects on some wood traits of gymnosperms, but did not show influences on any wood trait of angiosperms.

Acknowledgements The authors thank the anonymous referees and the editor for their valuable suggestions, which have improved the manuscript. They also thank Dr. Jinlong Zhang from Kadoorie Farm and Botanic Garden, Hong Kong for his great help with phylogenetic analysis. The project was funded by the National Natural Science Foundation of China (#41473068, 31370419, 31370620) and Ministry of Science and Technology of China Special Funding for Basic Works project (#2011FY110300).

References

- Aerts R (1995) The advantages of being evergreen. *Trends Ecol Evol* 10:402–407
- Baker TR, Phillips OL, Malhi Y, Almeida S, Arroyo L, Di Fiore A, Ewin T, Killeen TJ, Laurance SG, Laurance WF, Lewis SL, Lloyd J, Monteagudo A, Neill DA, Patino S, Patino S, Pitman NCA, Silva JNM, Martinez RV (2004) Variation in wood density determines spatial patterns in Amazonian forest biomass. *Glob Chang Biol* 10:545–562
- Bao FC, Hu R, Tan O, Zhang XP (1984) Fluid permeability in wood and factors affecting on it. *Scientia silvae sinicae* 20:277–290
- Bowyer JL, Shmulsky R, Haygreen JG (2007) *Forest products and wood science: an introduction*. Blackwell Publishing, Ames
- Bremer B, Bremer K, Chase M, Fay MF, Reveal JL, Soltis DE, Soltis PS, Stevens PF, Anderberg AA, Moore MJ, Olmstead RG, Rudall PJ, Sytsma KJ, Tank DC, Wurdack K, Xiang JQY, Zmarzty S (2009) An update of the angiosperm phylogeny group classification for the orders and families of flowering plants: APG III. *Bot J Linn Soc* 161:105–121
- Carlquist S (2001) *Comparative wood anatomy: systematic, ecological, and evolutionary aspects of dicotyledon wood*. Springer, Berlin

- Chave J, Muller-Landau HC, Baker TR, Easdale TA, Steege HT, Webb CO (2006) Regional and phylogenetic variation of wood density across 2456 neotropical tree species. *Ecol Appl* 16:2356–2367
- Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE (2009) Towards a worldwide wood economics spectrum. *Ecol Lett* 12:351–366
- Cheng JQ (1985) Wood science. Forestry Publishing House, Beijing
- Green DW, Winandy JE, Kretschmann DE (1999) Mechanical properties of wood. Wood handbook: wood as an engineering material. Madison, USDA Forest Service, Forest Products Laboratory. General technical report FPL GTR-113: 4.1–4.45
- Greenacre M, Primicerio R (2008) Measures of distance between samples: Euclidean. In: Fundacion BBVA Publication (December 2013), pp 978–84
- Hacke UG, Sperry JS, Pockman WT, Davis SD, McCulloh KA (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* 126:457–461
- Josse J, Lê S, Husson F (2008) FactoMineR: an R package for multivariate analysis. *J Stat Softw* 25:1–18
- Keith CT (2007) Tangential wall thickenings in conifer tracheids at ray-contact areas. *Wood Fiber Sci* 7:129–135
- King DA, Davies SJ, Supardi MN, Tan S (2005) Tree growth is related to light interception and wood density in two mixed dipterocarp forests of Malaysia. *Funct Ecol* 19:445–453
- Ladell JL (1967) Ray thickenings in the walls of conifer tracheids. *Nature* 213:470–473
- Mantel N (1967) The detection of disease clustering and a generalized regression approach. *Can Res* 27:209–220
- Mutke J, Barthlott W (2005) Patterns of vascular plant diversity at continental to global scales. *Biologische Skrifter* 55:521–531
- Niklas KJ (1992) Plant biomechanics: an engineering approach to plant form and function. The University of Chicago Press, Chicago
- Niklas KJ (1994) Plant allometry: the scaling of form and process. The University of Chicago Press, Chicago
- Paradis E, Claude J, Strimmer K (2004) APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20:289–290
- Poorter L, Bongers L, Bongers F (2006) Architecture of 54 moist-forest tree species: traits, trade-offs, and functional groups. *Ecology* 87:1289–1301
- Preston KA, Cornwell WK, DeNoyer JL (2006) Wood density and vessel traits as distinct correlates of ecological strategy in 51 California coast range angiosperms. *New Phytol* 170:807–818
- Shapiro SS, Wilk MB (1965) An analysis of variance test for normality (complete samples). *Biometrika* 52:591–611
- Sotelo MC, Vidaurre H, Weber J (2003) Variation in stem-growth and branch-wood traits among provenances of *Calycophyllum spruceanum* Benth. from the Peruvian Amazon. *New For* 26:1–16
- Sotelo MC, Beaulieu J, Hernández RE (2007a) Genetic variation in wood mechanical properties of *Calycophyllum spruceanum* at an early age in the Peruvian Amazon. *Wood Fiber Sci* 39:578–590
- Sotelo MC, Hernandez J, Beaulieu RE (2007b) Genetic variation in wood shrinkage and its correlations with tree growth and wood density of *Calycophyllum spruceanum* at an early age in the Peruvian Amazon. *Can J For Res* 37:966–976
- Sotelo MC, Weber JC, García RA, Silva DA, Muñoz GI (2013) Variation in wood color among natural populations of five tree and shrub species in the Sahelian and Sudanian ecozones of Mali. *Can J For Res* 43:552–562
- Sterck FJ, Bongers F, Newbery DM (2001) Tree architecture in a Bornean lowland rain forest: intraspecific and interspecific patterns. *Plant Ecol* 153:279–292
- Swenson NG, Enquist BJ (2007) Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. *Am J Bot* 94:451–459
- Van GH, Poorter L, Sterck F (2006) Wood mechanics, allometry, and life-history variation in a tropical rain forest tree community. *New Phytol* 171:367–378
- Warton DI, Wright IJ, Falster DS, Westoby M (2006) Bivariate line-fitting methods for allometry. *Biol Rev* 81:259–291
- Warton DI, Duursma RA, Falster DS, Taskinen S (2012) Smatr 3—an R package for estimation and inference about allometric lines. *Method Ecol Evol* 3:257–259
- Webb CO, Donoghue MJ (2005) Phylomatic: tree assembly for applied phylogenetics. *Mol Ecol Notes* 5:181–183

- Webb CO, Ackerly DD, Kembel SW (2008) Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics* 24:2098–2100
- Wikstrom N, Savolainen V, Chase MW (2001) Evolution of the angiosperms: calibrating the family tree. *Proc R Soc B Biol Sci* 268:2211–2220
- Wright SJ, Muller-Landau HC, Condit R, Hubbell SP (2003) Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. *Ecology* 84:3174–3185
- Zanne AE, Westoby M, Falster DS, Ackerly DD, Loarie SR, Arnold SE, Coomes DA (2010) Angiosperm wood structure: global patterns in vessel anatomy and their relation to wood density and potential conductivity. *Am J Bot* 97:207–215
- Zhang SB, Slik JW, Zhang JL, Cao KF (2011) Spatial patterns of wood traits in China are controlled by phylogeny and the environment. *Glob Ecol Biogeogr* 20:241–250
- Zheng JM, Martínez-Cabrera HI (2013) Wood anatomical correlates with theoretical conductivity and wood density across China: evolutionary evidence of the functional differentiation of axial and radial parenchyma. *Ann Bot* 112:927–935
- Zhu JL, Shi Y, Fang LQ, Liu XE, Ji CJ (2015) Patterns and determinants of wood physical properties across major tree species in China. *Sci China Life Sci* 58:602–612