



Correlation between leaf size and hydraulic architecture in five compound-leaved tree species of a temperate forest in NE China[☆]



Jia Song^{a,b}, Da Yang^{a,b}, Cun-Yang Niu^{a,b}, Wei-Wei Zhang^a, Miao Wang^a, Guang-You Hao^{a,*}

^a CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, 72 Wenhua Road, Shenhua, Shenyang, Liaoning, China

^b University of Chinese Academy of Sciences, Beijing 100049, China

ARTICLE INFO

Keywords:

Compound-leaved tree species
Fast growth hypothesis
Hydraulic segmentation hypothesis
Hydraulic-photosynthetic coordination
Temperate forest

ABSTRACT

The divergence between simple and compound leaf form is a fundamental division in leaf architecture that has great impact on environmental adaptations of plants. Two hypotheses regarding the adaptive significance of compound leaf form have long been hypothesized: (1) it enables trees to have higher growth rates under favorable environmental conditions; (2) it contributes to better adaptation to seasonal and unpredictable drought stresses since dropping the whole leaf units could function as a protective mechanism of hydraulic segmentation and hence avoiding diebacks of the more carbon costly stems. These hypotheses, however, have not been firmly supported by mechanistic studies on the underlying physiology and more importantly the inter-specific variations within this functional group in relation to these two proposed hypotheses have largely been overlooked. In the present study, using a common garden setup we investigated the impact of leaf size, an important characteristic of leaf architecture, on xylem hydraulics and carbon economy of five commonly found sympatric compound-leaved tree species from a typical temperate forest of NE China. We specifically tested the hypotheses that larger compound leaf size would be associated with higher hydraulic conductance, increased efficiency of carbon assimilation and greater degree of hydraulic segmentation. Our results showed that the majority of the hydraulic resistance in shoots was allocated to leaf lamina (53–77% among the five species) and the compound leaf petiole only accounts for a small portion of the shoot hydraulic resistance (9–24%). Both stem hydraulic conductivity and whole-shoot hydraulic conductance showed strong positive correlations with compound leaf size contributing to significantly higher carbon assimilation efficiency in species with larger leaf sizes. The magnitude of water potential drop across transpiring leaves showed a strong positive correlation with leaf size resulting in less negative stem xylem water potential in species with larger leaf sizes, which supports our hypothesis that larger compound leaf enhances hydraulic segmentation. Our results also showed that the advantages associated with larger leaf size can be traded off by a greater susceptibility to freeze-thaw induced hydraulic dysfunction. Besides a deeper understanding of the environmental adaptation of compound-leaved tree species, these findings may contribute to a better utilization of this important type of trees in forestry.

1. Introduction

Keystone and dominant tree species play vital roles in maintaining stable structure and function of forest ecosystems and perform essential ecosystem services (Ehrlich and Wilson, 1991; Grime 1998; Ellison et al., 2005). They also contribute most to the forest productivity and often act as ecosystem engineers by changing the environments via their physical structures and controlling the availability of resources to other species (Naiman et al., 1988; Jones et al., 1994; Lawton and Jones, 1995; Grime 1998; Geider et al. 2001; Mallik, 2003). In forest

ecosystems, the decline of some keystone or dominant tree species can show a disproportionately large influence on the reduction of total above-ground net primary productivity (Smith and Knapp, 2003). One of the major problems in forest management is the missing or decline of some keystone and dominant tree species, especially in forest ecosystems that have undergone strong human disturbances including the typical temperate forests of Northeast China (Runkle, 1981; Dai et al., 2004; Ellison et al., 2005). *Fraxinus mandshurica* Rupr. *Juglans mandshurica* Maxim. and *Phellodendron amurense* Rupr., well-known as “the three most valuable hardwood trees”, are important dominant species

[☆] This article is part of a special issue entitled “Current advances in plant water-relations research, implications for forest management and restoration stemming from the Ecosummit 2016 conference”, published in the Journal of Forest Ecology and Management 418, 2018.

* Corresponding author.

E-mail address: haogy@iae.ac.cn (G.-Y. Hao).

<http://dx.doi.org/10.1016/j.foreco.2017.08.005>

Received 27 May 2017; Received in revised form 27 July 2017; Accepted 4 August 2017

Available online 30 August 2017

0378-1127/ © 2017 Elsevier B.V. All rights reserved.

in the conifer and hardwood mixed forest of NE China at the climax state of succession (Sun et al., 2008; Yu et al., 2015). The decline of these tree species in the vast areas of secondary forests of this region, however, is very common due to changed environmental conditions than those of the primary forests (Dai et al., 2004; Sun et al., 2008; Yu et al., 2015). Knowledge in the ecophysiology of these tree species is relatively rare and would contribute to better forest management that is aimed at promoting the success of these species (Zhu, 2002; Qin, 2016). Coincidentally, these three species exclusively have compound leaves of relatively large leaf sizes. In the current study, we focus on investigating the adaptive significance of tree species with compound leaf form in the typical temperate forest of NE China, including the three above-mentioned tree species, through an interspecific comparison in some key physiological characteristics.

Leaf form reflects an optimal solution to the complex multi-dimensional environmental problems including capturing enough light for carbon fixation while maintaining water balance (Westoby et al., 2002; Chitwood and Sinha, 2016). Whether a leaf has simple or compound (multiple leaflets attached to the same rachis) form is a fundamental division in leaf architecture that has great adaptive significance for a plant species (Malhado et al., 2010; Efroni et al., 2010). Compound leaf form is a derived characteristic in angiosperms that independently evolved in multiple lineages (Cronquist, 1988; Bharathan et al., 2002; Klingenberg et al., 2012). Numerous studies have been aimed at teasing apart the evolutionary histories of compound leaves as well as the genetic basis controlling the divergence of simple vs. compound leaf forms (Franks and Britton, 2000; Friedman et al., 2004; Champagne et al., 2007). Many efforts have also been made to identify major biotic and abiotic environmental conditions favoring higher occurrence of compound-leaved tree species and in describing the patterns of geographic distribution of compound-leaved species relative to simple-leaved tree species (Stowe and Brown, 1981; Bongers and Popma, 1990; Martgers-Garza and Howe, 2005; Warman et al., 2011). However, the adaptive significance of compound leaf form is still under debate and the underlying physiological mechanisms remain poorly understood (Malhado et al., 2010).

Compound leaf form in trees has been found to occur more frequently in certain communities (e.g. warmer and water limited habitats), indicating its greater adaptive values for such environments (Turner, 2001). Compound-leaved tree species are mostly light demanding and are found to be more common in warmer and arid or semi-arid environments with high irradiance levels (Givnish, 1978; Stowe and Brown, 1981). It has also been suggested that trees with compound leaves are more likely to be pioneer and early successional species (Cochard et al., 2002; Mokany et al., 2003; Rosati et al., 2006; Tulik et al., 2010). Moreover, many compound-leaved tree species are very important timber species for plantations (Chen et al., 1994; Wang, 2006). The physiological characteristics that underlie the success of some compound-leaved tree species in certain environments and in becoming importing timber species are still waiting for further investigations.

Two major hypotheses about the adaptive significance of compound leaf form have long been proposed: (1) it is an adaptation allowing for rapid growth during favorable environmental conditions (Givnish, 1978, 1984; Niinemets, 1998). By producing relatively large and inexpensive petioles, which are functionally equivalent to stems in terms of supporting leaflets and performing hydraulic conduction, the compound-leaved species can allocate greater resources to vertical growth for light capture than simple-leaved species under conditions of strong interspecific competition. (2) It can be an adaptation to seasonal and unpredictable drought stresses since by dropping their leaf units during drought conditions compound-leaved species could minimize water loss while protecting the more carbon costly stems from catastrophic hydraulic failure and diebacks, which is known as a typical type of hydraulic segmentation (Gates, 1980; Yazaki et al., 2010; Liu et al., 2015; Merine et al., 2015). These hypotheses, however, have not been firmly supported due to a lack of data and to solve the mystery of compound leaf adaptation more theoretical and empirical evidences regarding

environmental adaptation of this type of species are needed (Aarssen, 2012).

Compound-leaved tree species have been shown to have some important ecophysiological differences from simple-leaved species. For example, trees with compound leaves usually have higher transpiration rates and higher stem hydraulic conductivities than simple-leaved trees (Tulik et al., 2010; Renninger and Phillips, 2011). Moreover, compound leaf form often permits tree species bearing larger leaves than their simple-leaved counterparts under similar water regimes (Malhado et al., 2010). However, not all compound leaves are homologous since compound leaf form has arisen independently many times in diverse lineages and probably in response to different selective pressures (Bharathan and Sinha, 2001; Friedman et al., 2004). One of the traits that is strikingly different among compound-leaved species is the size of the whole leaf unit, which spans a couple of orders of magnitudes from drought adapted species to species from humid conditions (Niinemets, 1998). Even within the same forest community, different compound-leaved tree species can vary substantially in leaf size and exhibit contrastingly different dominances. For example, in the typical temperate forest of NE China, the three important dominant tree species with compound leaves (*Fraxinus mandshurica*, *Juglans mandshurica* and *Phellodendron amurense*) have substantially larger leaves than the non-dominant tree species with compound leaves (e.g. *Sorbus pohuashanensis*). It is thus important for further ecophysiological investigations to take into account the functional variations in different compound-leaved tree species with different leaf sizes.

Leaf size is a fundamental physiognomic characteristic in foliage and in general it can strongly influence plant adaptation from local to global scales (Grubb, 1977; Tanner, 1980; Givnish, 1984; Royer et al., 2005). Across species and environments, larger leaf size is usually associated with increased total plant leaf area for higher whole-plant level photosynthetic carbon assimilation and higher growth rates (Bucci et al., 2006; Hacke et al., 2010; Goldstein et al., 2013). For a compound leaf, the costs and effectiveness associated with mechanical support to the leaf lamina in the leaf unit are strongly tied to the size of the whole leaf (Niinemets, 1998; Niinemets and Kull, 1999; Niinemets et al., 2006). Large differences in hydraulic architecture between compound-leaved species of different leaf sizes may thus likely exist but the leaf size mediated functional covariation regarding xylem hydraulics is largely overlooked by ecophysiological investigations. Moreover, most of the studies on hydraulic architecture focused on either stems or leaves but much less studies involve hydraulic architecture at the whole shoot level although it may be more tightly associated with plant performances (Wang et al., 2016).

In the present study, we investigated the interspecific variations in functional traits related to xylem hydraulics and carbon economy in five sympatric compound-leaved tree species in Changbai Mountain of NE China that span a relatively large range of leaf size. We aimed to look at the potential impacts of a relatively large leaf size variation on the whole-shoot level changes in hydraulic architecture and its consequences on associated physiological performances. More specifically we hypothesized that: (1) Larger leaf size in compound-leaved species is associated with greater hydraulic conductance at the whole shoot level that allows for higher photosynthetic rate, which would support rapid growth under favorable conditions; (2) Larger compound leaf size is associated with larger water potential gradient from stem to leaf that would favor a higher degree of hydraulic segmentation between leaves and stems, which are expected to be beneficial in case of unexpected severe drought; (3) Trade-offs between hydraulic efficiency and safety due to biophysical constraints are likely exist across compound-leaved species with different leaf sizes, which permits different species to succeed in their respective environmental conditions along the environmental gradient. To test these hypotheses, we studied the whole-shoot level hydraulics, water relations and photosynthetic characteristics in five sympatric compound-leaved tree species commonly found in the typical temperate forests of NE China using a common garden

setup.

2. Materials and methods

2.1. Study site and plant species

The study was conducted at the Research Station of Changbai Mountain Forest Ecosystems of the Chinese Academy of Sciences (128°28'E, 42°24'N; 736 m altitude), located on the north slope of Changbai Mountain, Jilin province, NE China. Strongly influenced by the monsoon, this region has a temperate continental mountain climate. The winter is long and cold and summer is short and cool. At the elevation equal to that of the research station, there is snow cover for about five months each year (October to March) and for about two months the daily minimum temperatures commonly fall below -20 °C (December to January; Niu et al., 2017). The mean annual precipitation at an elevation of the present study site is 695 mm and more than 70% occurs during the growing season from June to September. Altitude increases from the mountain foot (500 m) to the peak (2744 m) with concurrent decreases in the mean annual temperature, from 3.5 to -7.4 °C. Consequently, four distinct vertical vegetation zones have been developed with the change of the elevation, i.e. *Pinus koraiensis* and broadleaf deciduous tree species mixed forest (500–1100 m), *Picea* and *Abies* forest (1100–1800 m), *Betula ermanii* forest (1800–2000 m), and alpine tundra (2000–2744 m). The *Pinus koraiensis* and broadleaf deciduous tree species mixed forest, where our study site is located, is the most typical forest type of the climax succession in NE China and are well-known for relatively high species richness among temperate forests.

For the present study, we selected five most commonly found compound-leaved tree species native to the *Pinus koraiensis* and broadleaf deciduous tree species mixed forests that span a relatively large range of leaf size (Table 1), namely *Juglans mandshurica* (JM), *Fraxinus mandshurica* (FM), *Maackia amurensis* (MA), *Phellodendron amurense* (PA) and *Sorbus pohuashanensis* (SP). The trees used in this study were growing in the arboretum of the research station (740 m altitude) under similar environmental conditions, which minimizes the effect of plastic adjustment to variation in growing conditions. For each species, we randomly sampled six individuals of adult trees in the arboretum. Only sun-exposed branches were measured or sampled. All the measurements in xylem hydraulics and leaf gas exchange were conducted in the middle part of the growing season from June to August.

Table 1

Hydraulic related traits of the five studied compound-leaved tree species. LS, compound-leaf size; K_{shoot} , shoot hydraulic conductance; K_{stem} , hydraulic conductivity of a bare stem; $K_{petiole}$, hydraulic conductivity of petioles; $K_{leaflet}$, hydraulic conductivity of leaflets; K_s , the sapwood specific hydraulic conductivity; K_l , the leaf-specific hydraulic conductivity; LA/SA, the ratio of distal leaf area (LA) to sapwood conducting area (SA). D_v , mean vessel diameter; D_h , mean hydraulic weighted vessel diameter; VD, vessel density; PLC_{winter} , percent loss of hydraulic conductivity in winter. JM, *Juglans mandshurica*; FM, *Fraxinus mandshurica*; MA, *Maackia amurensis*; PA, *Phellodendron amurense*; SP, *Sorbus pohuashanensis*. Values are means ± 1SE (n = 6).

	JM	FM	MA	PA	SP
LS (m ²)	0.120 ± 0.004	0.043 ± 0.004	0.025 ± 0.003	0.021 ± 0.003	0.017 ± 0.002
K_{shoot} (× 10 ⁻⁴ kg m ⁻² s ⁻¹ MPa ⁻¹)	0.91 ± 0.07	0.62 ± 0.07	0.55 ± 0.02	0.43 ± 0.05	0.09 ± 0.01
K_{stem} (× 10 ⁻⁴ kg m ⁻² s ⁻¹ MPa ⁻¹)	4.33 ± 1.06	8.69 ± 3.55	6.30 ± 1.06	6.43 ± 0.88	6.39 ± 0.36
$K_{petiole}$ (× 10 ⁻⁴ kg m ⁻² s ⁻¹ MPa ⁻¹)	8.55 ± 0.20	14.52 ± 6.89	9.12 ± 1.08	11.97 ± 1.33	4.61 ± 0.51
$K_{leaflet}$ (× 10 ⁻⁴ kg m ⁻² s ⁻¹ MPa ⁻¹)	1.07 ± 0.53	2.63 ± 1.00	1.10 ± 0.19	3.37 ± 0.38	1.95 ± 0.28
K_s (kg m ⁻¹ s ⁻¹ MPa ⁻¹)	10.97 ± 1.02	6.93 ± 1.91	2.16 ± 0.68	2.16 ± 0.02	1.06 ± 0.23
K_l (× 10 ⁻⁴ kg m ⁻¹ s ⁻¹ MPa ⁻¹)	4.52 ± 0.71	3.54 ± 0.38	2.50 ± 0.64	2.66 ± 0.18	1.74 ± 0.68
LA/SA (m ² cm ⁻²)	2.39 ± 0.07	1.65 ± 0.04	1.61 ± 0.06	1.45 ± 0.04	0.33 ± 0.01
D_v (µm)	60.99 ± 3.48	60.79 ± 3.22	51.15 ± 2.80	46.97 ± 2.70	19.76 ± 1.48
D_h (µm)	86.99 ± 5.86	82.15 ± 3.84	74.86 ± 1.67	57.75 ± 4.41	24.60 ± 1.35
VD (no.mm ⁻²)	38.64 ± 3.80	43.45 ± 3.88	46.13 ± 4.77	81.42 ± 6.07	577.72 ± 49.78
PLC_{winter} (%)	28.69 ± 4.85	98.19 ± 6.65	82.98 ± 1.85	66.84 ± 1.94	30.44 ± 4.04

2.2. Stem hydraulic conductivity

Stem hydraulic conductivity (K_h) measurements were made on sun-exposed terminal branches from six different individuals per species. Large branches about 1.5 m in length, each from a different individual for all species, were collected at predawn (05:00–07:00 h). Branches were then re-cut under water (about 5 cm removed) and transported to the laboratory immediately with the cut end submerged in the water and the crown covered with black plastic bags. Six branches each from a different individual for each species were sampled. An unbranched stem segment of ~20 cm in length and 0.6–1.2 cm in diameter was sampled from each of these sampled branches for stem hydraulic conductivity (K_h) measurements. Leaflets terminal to each of the stem segments used for hydraulic conductivity measurements were kept in plastic bags for later measurements of leaf areas. Degassed and distilled 20 mmol L⁻¹ KCl solution was used as the perfusion fluid. The hydrostatic pressure that drove water flow through the stem segments was generated by a constant hydraulic head of 50 cm. Before each measurement of flow rate, both ends of a segment were shaved with a sharp razor blade immediately to avoid vessel clogging by wound reactions. Then 0.1% methyl aniline blue dye was perfused into one end of the branch segment under the same pressure head of 50 cm. Sapwood area (SA) was determined as the geometric mean of the area of dye stained wood on the cross section from both ends of each segment. Thus, we photographed the stained cross section from both end of each segment using an optical scanner (HP Scanjet G3110, Hewlett-Packard Development Co., Beijing, China), and the dye stained cross sectional area were calculated using Image-J image analysis software (US National Institutes of Health, Bethesda, MD, USA). Hydraulic conductivity (kg m s⁻¹ MPa⁻¹) was calculated as:

$$K_h = J_v / (\Delta P / \Delta L)$$

where J_v is the flow rate through the stem or petiole segment (kg s⁻¹), and the $\Delta P / \Delta L$ is the pressure gradient across the segment (MPa m⁻¹). The sapwood-specific hydraulic conductivity (K_s ; kg m⁻¹ s⁻¹ MPa⁻¹) was calculated as the ratio of K_h to SA and the leaf-specific hydraulic conductivity (K_l ; kg m⁻¹ s⁻¹ MPa⁻¹) was calculated as the ratio of K_h to LA. Leaf to sapwood area ratio (LA/SA) was determined for each segment used for hydraulic conductivity measurement.

2.3. Measurement of winter native embolism

After the determination of hydraulic conductivity, stem segments were reserved for measuring the percent loss of stem hydraulic conductivity (PLC), and the segments were flushed for 20 min using degassed 20 mmol L⁻¹ KCL solution under a 0.1 MPa pressure to remove air bubbles in the xylem. Then shaving both ends of the segments with a

sharp razor blade, the flushed segments were connected to an apparatus with degassed and filtered 20 mmol L⁻¹ KCl solution for maximum hydraulic conductivity (K_{h-max}) determination, and the percent loss of stem hydraulic conductivity (PLC) was calculated as:

$$PLC = 100(K_{h-max} - K_h) / K_{h-max}$$

where K_{max} represents the stem maximum hydraulic conductivity determined on flushed segments. In this research, we measured the PLC of the five compound-leaved species in winter, six hydraulic conductivity measurements were made for each of the five compound-leaved tree species.

2.4. Shoot hydraulic resistance distribution

In August of 2015, hydraulic conductances of shoots (K_{shoot}) and their components (stems, petioles, leaflets) were measured by the water perfusion method using a high-pressure flow meter (HPFM Gen3; Dynamax Corp., Elkhart, Indiana, USA) under quasi-steady state mode (Tyree et al., 1993; Sack et al., 2002). We collected shoots c. 1.5 m in length from six different individuals for each species in the early morning, which were then re-cut under water (~5 cm removed) and transported to the laboratory with the cut end immersed in water and the other part covered with a opaque plastic bag. The perfusion solution in the HPFM tubing system used for hydraulic measurements was degassed, deionization water that was filtered to 0.2 μ m pore diameter. The surface of the stem segment was washed carefully with degassed, deionized water before connecting to the tubing system of the HPFM. To avoid xylem embolism formation, the cut end of the stem was kept under water during the sample preparation and connection procedures. The shoots used to connect to the HPFM were c. twice the length of its compound leaf petioles. The shoot was then perfused with the water in the HPFM tubing system at a pressure of c. 0.5 MPa until a stable flow rate was reached (mostly within 10 min) for determining the K_{shoot} . To measure the resistance allocation between different parts of the shoot (i.e., stem, petiole and leaflet), all leaflets were then cut off to measure the hydraulic conductance of the shoot with stem and compound leaf petiole ($K_{stem+petiole}$). Finally, all compound leaf petioles were cut off and the hydraulic conductance of the stem (K_{stem}) was measured. It took 2–3 min to reach stable water flow rates following the removal of leaflets and the petioles. Hydraulic conductance measurements for shoots and all the components were made on six different individuals per species. Hydraulic resistance is the reciprocal of conductance, and the hydraulic resistance of the shoot (R_{shoot}), stem (R_{stem}), petioles ($R_{petiole}$) and leaflets ($R_{leaflet}$) can thus be calculated (Wang et al. 2016). The data on hydraulic conductance were standardized to 25 °C to correct for changes induced by the temperature dependence of water viscosity and normalized by the total area of leaflets of the whole shoot.

2.5. Wood anatomical traits

Xylem anatomical traits were measured on six stem segments per species previously used for hydraulic conductivity measurements. Stem cross-sections c. 15–30 μ m in thickness were made using a sliding microtome (Model 2010-17, Shanghai Medical Instrument Corp., China) and then stained with 0.1% toluidine blue to increase visual contrast. Wood sections were fixed on slides and examined using a light microscope (Leica ICC50, Wetzlar, Germany) and images were taken under magnifications of 100 \times with an inbuilt digital camera. Tension wood was avoided due to its minimal contribution to water transport. The photographs were prepared and analyzed using the software Image J (US National Institutes of Health, Bethesda, MD) for calculating anatomical variables. The diameter of each vessel was the diameter of the circle having the same area as the measured vessel lumen. For each species, mean vessel diameter (D_v , μ m) was determined as the mean value of each segment ($n = 6$ segments), a minimum of 100 vessels was measured per segment. Vessel density (VD, no. mm⁻²) was calculated

as the number of vessels per unit cross-sectional area. Mean hydraulic diameter (D_h , μ m) was calculated as:

$$D_h = \sum D_v^5 / \sum D_v^4$$

2.6. Leaf gas exchange

Leaf net CO₂ assimilation rate (A_{net}) and stomatal conductance (g_s) were measured using a LI-6400 photosynthetic system (LI-COR Inc., Lincoln, NE, USA) during sunny days. The mature sunlit leaves from six trees for each species were measured under ambient temperature (20–25 °C) and CO₂ concentration (350–400 μ mol mol⁻¹), photosynthetic photon flux density in the cuvette was held at about 1000 μ mol m⁻² s⁻¹. Intrinsic photosynthetic water use efficiency (WUE_i) was calculated as the ratio of A_{net} to g_s .

2.7. Water potential measurements

Water potentials were measured in consecutive sunny days of mid-June 2016 with a pressure chamber (ZLZ-4, Lanzhou University, Lanzhou, China). Leaflet samples from six individuals of each species for predawn and midday potentials were taken before sunrise and at midday, all the samples were cut from trees and sealed immediately in plastic bags with a moist paper towels in them and kept it in a cooler during the transportation to the laboratory. To evaluate the midday water potentials of the stem xylem (Ψ_{xylem}) of the terminal branches, the whole compound leaves on each of six individuals per species were covered with aluminum foil and plastic bags containing moist paper towels in the evening before measurement days. The compound leaf samples remain covered with aluminum foil and plastic bags when they were cut off from trees. The bagged leaves were kept in a cooler until water potentials were measured in the laboratory within an hour from excision.

2.8. Data analysis

Linear and nonlinear regression analyses were used to determine the relationships between functional trait pairs of interests using Sigmaplot 10.0 (Software, Inc., San Jose, CA, USA). Pearson correlation analyses across all the five compound-leaved tree species was used to test the possible significance among all the hydraulic, photosynthetic and phenotypic traits (SPSS 17.0 software package, SPSS Inc. Chicago, IL, USA).

3. Results

The $R_{leaflet}$ accounted for the largest resistance for water flow among the three components of the whole-shoot hydraulic system in all the five compound-leaved tree species, i.e. ranged from 52.5 to 76.7% (Fig. 1). For each of the five species, the hydraulic resistance in petioles only accounts for a small portion of the whole-shoot hydraulic resistance (8.9–24.2%) despite the fact that it accounts for a relatively large portion of the water transport pathway (c. 50%) in the shoots used for hydraulic conductance measurements (Fig. 1). There is no clear pattern in the allocation of hydraulic resistance in comparing the five species that span a relatively large range of leaf size.

Relatively large variations in traits related to xylem hydraulic conductances were observed among the five studied tree species. The K_{shoot} ranged from 0.09 ($\times 10^{-4}$ kg m⁻² s⁻¹ MPa⁻¹) in *SP* with the smallest leaf size to 0.91 ($\times 10^{-4}$ kg m⁻² s⁻¹ MPa⁻¹) in *JM* with the largest leaf size (Table 1). Similarly, K_s and K_l found of *JM* were 10.3 and 2.6 times of those observed in *SP*. Across these studied species, whole-shoot hydraulic conductance showed a strong positive correlation with the compound leaf size (Fig. 2a; $P < 0.05$). Consistently, stem hydraulic conductivity expressed on both sapwood area and leaf area basis were

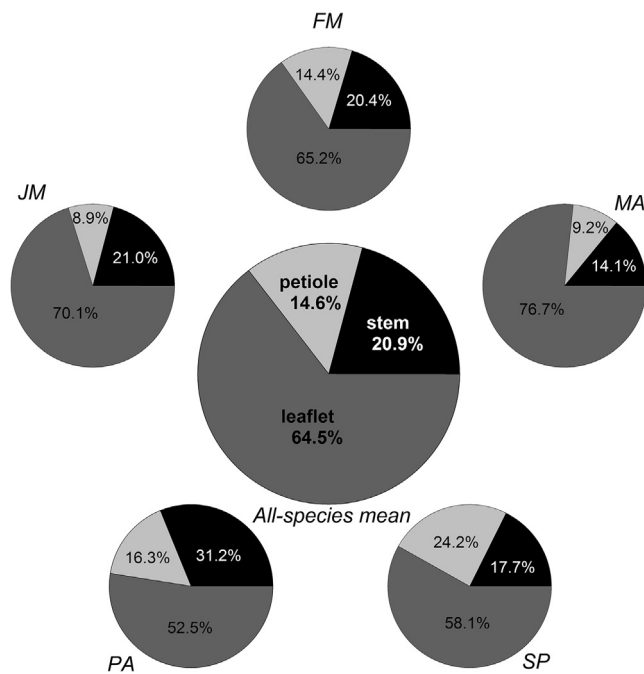


Fig. 1. Partitioning of the whole-shoot hydraulic resistance between stem (R_{stem}), compound leaf petiole ($R_{petiole}$) and leaflet ($R_{leaflet}$) for the five studied tree species. Species name abbreviations are as defined in Table 1. The pie chart in the center shows mean values of the five species. The color code for each of the small pie chart is consistent with the big chart in the center.

also positively correlated with compound leaf size (Fig. 2b and c; both $P < 0.01$).

Consistent with the trend found for hydraulic conductance, stomatal conductance and leaf net assimilation rate also varied substantially among the five species with clear trends of increase with the increase of leaf size (Table 2, Fig. 3a). Moreover, species with larger compound leaf size also showed higher LA/SA, i.e. larger leaf surface area that can be supported per xylem investment in the stem (Fig.3b). Overall, leaf gas exchange characteristics showed strong linear relations with both shoot hydraulic conductance and leaf-specific hydraulic conductivity (Table S1; Fig.4a–f). Specifically, both A_{net} and g_s showed significant positive correlations with hydraulic traits, whereas WUE_i showed significant negative correlations with K_{shoot} and K_l (Fig.4e and f).

There was no clear trend when predawn and midday water potentials were compared in freely transpiring leaves between the five studied species (Fig. 5); however, when stem xylem water potential (estimated in covered leaves) were compared, a strong trend emerged, i.e. species with larger leaf size consistently showed less negative midday stem xylem water potentials (Fig.5b). This is resulted from the fact that larger water potential drops occurred across the whole compound leaf in species with larger leaf sizes (Fig. 6).

Consistent with the increase of hydraulic conductance with leaf size, tree species with larger leaf sizes had larger vessel diameters (Fig. 7a). The hydraulic weighed vessel diameter showed a significant logarithm relationship with leaf size across the studied species. Across the five compound-leaved tree species, stem PLC values measured in winter ranged from 28.69% to 98.19% (Table 1). Notably, JM with the largest stem vessel diameter showed the smallest winter PLC degree (28.69%), which might be due to the fact that this is the only species that can generate positive xylem pressure during the winter and early spring for embolism refilling. When JM was excluded from the regression analysis, there is a significant positive relationship between D_h and winter PLC values across species (Fig. 7b).

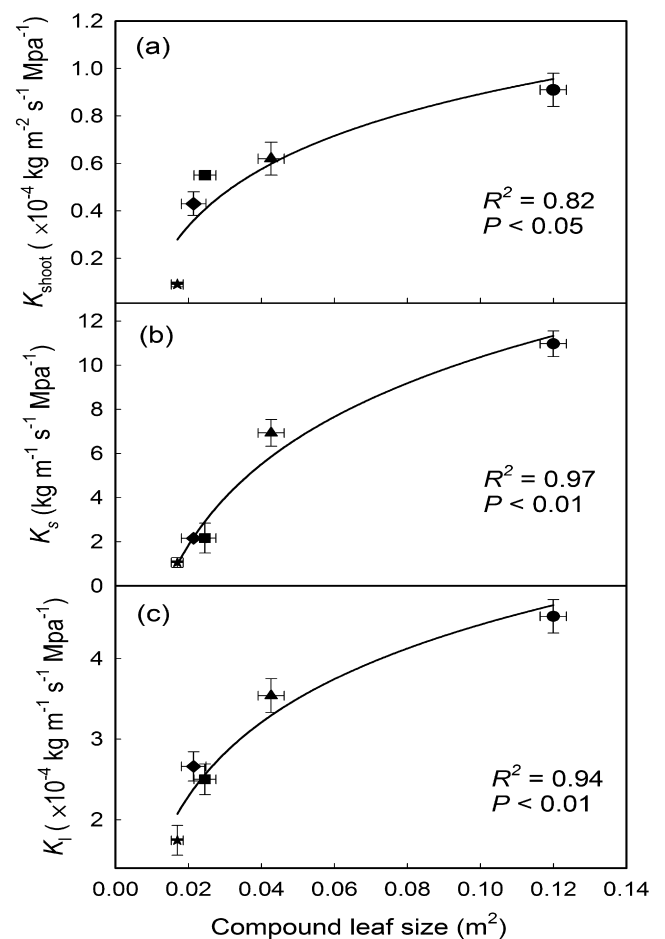


Fig. 2. (a) Whole-shoot hydraulic conductance (K_{shoot}); (b) sapwood-specific hydraulic conductivity (K_s) and (c) leaf-specific hydraulic conductivity (K_l) as a function of compound-leaf size. Error bars show \pm 1 SE ($n = 6$). *Juglans mandshurica* (●); *Fraxinus mandshurica* (▲); *Maackia amurensis* (■); *Phellodendron amurense* (◆); *Sorbus pohuashanensis* (★).

4. Discussion

4.1. The fast growth hypothesis

The variation of physiological traits across these compound-leaved tree species differing in leaf sizes seems to follow a slow-fast axis of resource acquisition and utilization (Coley et al., 1985; Lambers and Poorter, 1992; Reich et al., 1992; Méndez-Alonzo et al., 2012), which is partially in line with the fast growth hypothesis of compound-leaved tree species. The strong positive correlation between leaf size and shoot hydraulic conductance across these studied species indicates that compound leaf form needs to be in combination with larger leaf size in order to allow trees to build more efficient hydraulic systems. The higher shoot hydraulic conductive efficiency in species with larger compound leaf sizes would be able to meet higher water demand that is necessary for greater instantaneous rates of carbon fixation than in species with lower shoot hydraulic conductance and smaller compound leaf sizes. Under favorable water conditions, higher xylem hydraulic conductance enables more efficient water transport to transpiring leaves and contributes to a reduced stomatal limitation to leaf gas exchange and enhanced carbon assimilation capacity (Meinzer, 2003; Ackerly, 2004; Santiago et al., 2004; Hao et al., 2011, 2013). Consistently, under a relatively humid environmental conditions at the present study site, the photosynthetic rate showed a strong positive correlation with leaf size across the five sympatric compound-leaved tree species, which is underlain by a commonly observed strong

Table 2

Photosynthetic and hydraulic related traits of the five studied tree species. A_{net} , net photosynthetic rate; g_s , maximum stomatal conductance; WUE_i , intrinsic photosynthetic water use efficiency; Ψ_{pd} , predawn leaf water potential; Ψ_{md} , midday leaf water potential; Ψ_{xylem} , midday stem xylem water potential. $\Delta\Psi$, water potential difference between stem xylem and compound leaf measured at midday ($\Psi_{xylem} - \Psi_{md}$). Species name abbreviations are as defined in Table 1. Values are means \pm 1SE ($n = 6$).

	JM	FM	MA	PA	SP
A_{net} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	21.15 \pm 0.75	18.41 \pm 0.85	13.87 \pm 0.82	12.88 \pm 0.81	7.01 \pm 0.80
g_s ($\text{mmol m}^{-2} \text{s}^{-1}$)	0.60 \pm 0.03	0.38 \pm 0.03	0.33 \pm 0.02	0.30 \pm 0.02	0.09 \pm 0.01
WUE_i ($\mu\text{mol mmol}^{-1}$)	35.31 \pm 1.07	48.72 \pm 2.77	42.15 \pm 0.59	42.83 \pm 0.47	80.09 \pm 2.53
Ψ_{pd} (MPa)	-0.28 \pm 0.02	-0.34 \pm 0.02	-0.29 \pm 0.02	-0.36 \pm 0.03	-0.38 \pm 0.03
Ψ_{md} (MPa)	-1.51 \pm 0.09	-1.56 \pm 0.07	-1.73 \pm 0.04	-1.66 \pm 0.06	-1.75 \pm 0.04
Ψ_{xylem} (MPa)	-0.54 \pm 0.02	-0.70 \pm 0.03	-1.07 \pm 0.03	-1.24 \pm 0.04	-1.50 \pm 0.04
$\Delta\Psi$ (MPa)	0.97 \pm 0.04	0.86 \pm 0.04	0.66 \pm 0.03	0.42 \pm 0.02	0.25 \pm 0.02

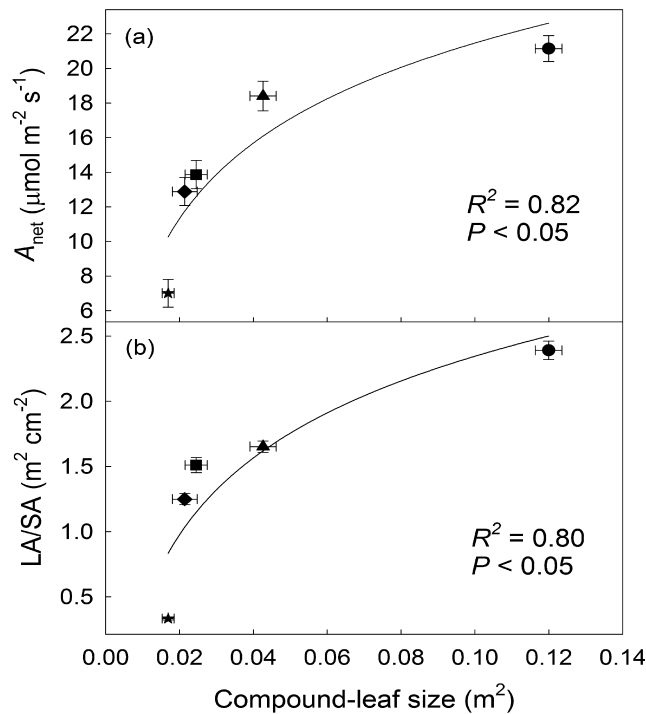


Fig. 3. (a) Leaf net photosynthetic rate (A_{net}) and (b) ratio of distal leaf area to sapwood conducting area (LA/SA) as a function of compound-leaf size. Error bars show \pm 1SE ($n = 6$). Symbols are as defined in Fig. 2.

hydraulic-photosynthetic coordination across a variety of species (Hao et al., 2011; Zhu et al., 2013; Scoffoni et al., 2016).

Besides increased hydraulic efficiency and carbon assimilation capacity, compound leaf form may allow trees to deploy their shoots in a more carbon efficient manner, which becomes especially true with the increase of leaf size. One of the important reasons is the relatively high hydraulic efficiency in rachis of compound leaves that are equivalent to terminal stems (Liu et al. 2015; Wang et al. 2016). Although compound leaf petioles accounts for a relatively large proportion (20–70%) of the total length of the water transport pathway in shoots (Niklas, 1991a, 1991b, 1991c), they only make up for 8.9–24.2% of the whole-shoot hydraulic resistance (Fig. 1). Compound leaf petioles are functionally equivalent to terminal stems of simple-leaved species in terms of efficiencies of water transport and in spreading leaf lamina for light interception (Niklas, 1992; Liu et al., 2015), while petioles are much cheaper to build in terms of carbon investment allowing these species to deploy shoots in a more carbon economically manner (Bonser and Aarssen, 1994; Sims and Percy, 1994; Niinemets, 1998). Moreover, increasingly higher stem hydraulic conductivity with the increase of leaf size allows species of larger compound leaves to be able to support larger areas of leaf lamina per sapwood area (Fig. 3b), which means larger surface area for carbon assimilation and more carbon return per investment in stem hydraulic system. In this way, especially under

conditions of sufficient water supply, longer petioles with cheaper investment and high hydraulic conductance, would allow compound-leaved tree species having better physiological performances and higher rate of vertical growth (Givnish 1978, 1979).

4.2. The hydraulic segmentation hypothesis

High hydraulic resistance in compound leaves relative to that of the stems found in the present study is consistent with the hydraulic segmentation hypothesis (Zimmermann, 1978, 1983). According to the Ohm’s Law analogy of plant hydraulic system (van den Honert, 1948; Tyree and Ewers, 1991; Tyree and Zimmermann, 2002), the near 80% hydraulic resistance allocated in the compound leaves would confine the steepest water potential gradient between the leaf transpiring sites of the substomatal cavities and the petiole insertion points. Consistently, stem xylem water potentials estimated by measuring covered leaves were considerably higher than transpiring leaves. It has been shown that leaves are much more vulnerable to drought induced loss of hydraulic conductance than that of the stems (Hao et al., 2008; Zufferey et al., 2011; Liu et al., 2015). Under unfavorable water conditions, such as during midday, leaf vascular systems may routinely lose a considerably large portion of hydraulic conductance and it can function as a signal to induced stomatal closure for prevention of further water loss (Sperry et al., 1998; Brodrribb et al., 2003; Brodrribb and Holbrook, 2003a; Brodrribb and Holbrook, 2004a, 2004b). Moreover, the compound leaf petioles are found to be considerably more sensitive to drought-induced embolism than the stems they are attached to (Liu et al. 2015). Higher vulnerability to embolism in combination with lower water potentials makes the leaflets and the rachis efficient hydraulic ‘safety fuses’ (Brodrribb and Holbrook, 2003b; Bucci et al., 2013; Liu et al. 2015), which provides a physiological basis for hydraulic segmentation facilitated by compound leaf form and explains the commonly observed diebacks of whole compound leaves under severe drought while the terminal stems remain intact (Tyree et al. 1993, Malhado et al. 2010).

Moreover, the strong positive correlation between leaf size and the magnitude of water potential drop across the whole compound leaf strongly support our hypothesis that hydraulic segmentation in compound-leaved tree species is enhanced by the increase of leaf size. Greater water potential drop across compound leaves of larger size results in significantly higher water potential in the stem xylem during periods of active transpiration, which reduces the risk of catastrophic embolism in the stem xylem and may avoid the unnecessary restrictions on photosynthetic gas exchange (Zimmermann, 1983; Tyree and Ewers, 1991; Liu et al. 2015). Under conditions of prolonged and severe drought stresses, larger water potential gradients across the leaf units of species with larger leaf sizes would results in greater susceptibility of the compound leaf to hydraulic failure and diebacks than the terminal branches, i.e. enhancing hydraulic safety of the stems at the expense of leaves due to stronger hydraulic segmentation (Zimmermann, 1983; Tyree and Ewers, 1991; Tyree et al., 1993; Liu et al., 2015).

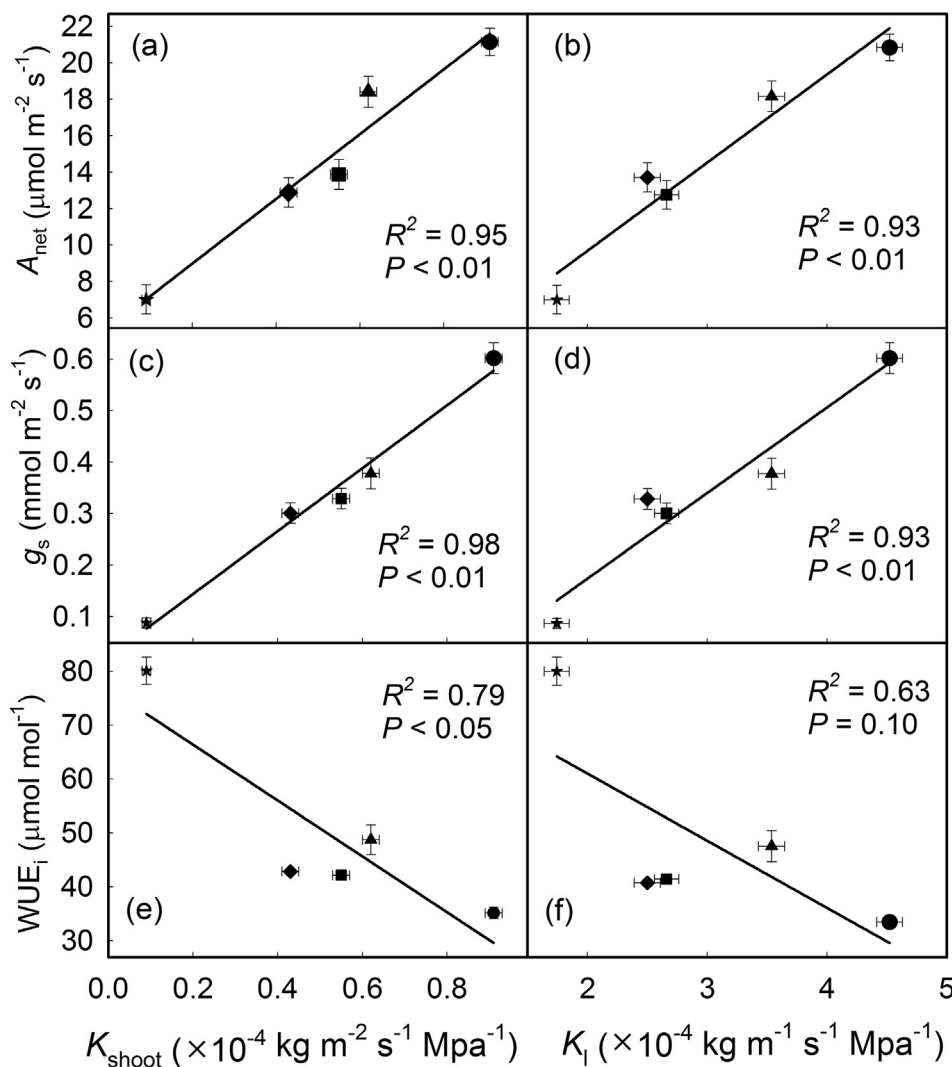


Fig. 4. Relationships between hydraulic conductance of the whole shoot (K_{shoot}) and (a) net photosynthetic rate (A_{net}), (c) stomatal conductance (g_s), (e) intrinsic photosynthetic water use efficiency (WUE_i) across the five compound-leaved tree species. Relationship between leaf-specific hydraulic conductivity (K_l) and (b) leaf net photosynthetic rate (A_{net}), (d) stomatal conductance (g_s), (f) intrinsic photosynthetic water use efficiency (WUE_i) across the five compound-leaved tree species. Error bars show \pm 1SE ($n = 6$). Symbols are as defined in Fig. 2.

4.3. Functional trade-offs mediated by variation in leaf size

Greater stem and shoot level hydraulic conductance and a higher degree of hydraulic segmentation related to larger compound leaf size, however, do not necessarily mean superiority under all circumstances but rather there is a functional trade-off mediated by variation in leaf size, which is reflected by their differences in distribution along the altitudinal gradients in the current study site of Changbai Mountain. The two compound-leaved tree species with the largest leaf sizes, i.e. *JM* and *FM*, are widely distributed dominant tree species in riparian, foothill and low-elevation mountain habitats (700–1000 m altitude) and the species with the third and fourth largest leaf size, i.e. *PA* and *MA*, are dominant species in many secondary forests at relatively low elevations (300–1100 m altitude) (Hu et al., 2010; Park et al., 2012). *SP* with the smallest leaf sizes is never dominant species under any circumstances in the region but it can naturally occur in substantially higher elevations even to the alpine timber line, i.e. 900–2500 m (Yang and Shen, 2011; Yang et al., 2012). The nonrandom association between leaf size and altitude of distribution among these studied species may at least partially underlain by a trade-off between hydraulic efficiency and safety against freeze-thaw induced xylem embolism under the temperate climate conditions of the present study area.

The strong positive correlation between compound leaf size and stem vessel diameter emerged as a central factor resulting in the trade-off between hydraulic efficiency and safety against freeze-thaw induced stem xylem embolism. Wider conduit is usually positively related to

photosynthetic capacity and plant growth rates given water is readily available; however, it is also strongly associated with greater vulnerability to freeze-thaw-induced embolism (Sperry et al., 1994; Davis et al., 1999; Feild and Brodrigg, 2001; Hacke and Sperry, 2001; Pittermann and Sperry, 2003; Cobb et al., 2007; Stuart et al., 2007). Notably, *JM* with the largest vessel diameter showed the lowest level of winter embolism that seemingly contradict with this pattern. However, this is due to the fact that *JM* is a stem pressure generating species that can effectively keep the embolism at low levels in spite of its large vessel diameters (Améglio et al., 2001; Ewers et al., 2001; Niu et al., 2017).

Aside from the case of embolism refilling in root or stem pressure generating species, greater resistance to freeze-thaw-induced embolism allows the species with smaller leaf size and conduit diameter to survive habitats of higher elevations, whereas their lower hydraulic conductance would impose greater limit on the carbon assimilation and hence results in reduced competitiveness under more favorable growth conditions (Wang et al., 1992; Sperry et al., 1994; Feild and Brodrigg, 2001). Across species, variation in hydraulic conductance and resistance to freeze-thaw-induced embolism among these studied compound-leaved species of varying leaf sizes thus reflects a trade-off between xylem water transport efficiency and safety against hydraulic failure under a temperate climate condition (Martínez-Vilalta et al. 2002).

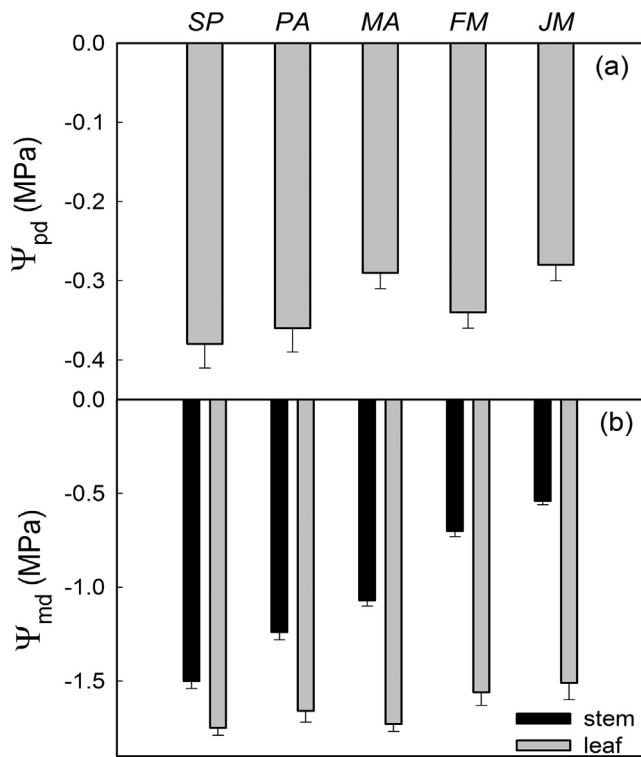


Fig. 5. (a) Predawn leaf water potential (Ψ_{pd}), (b) midday water potential (Ψ_{md}) of stem xylem (estimated by measuring water potentials of covered leaves) and freely transpiring leaves for the five compound-leaved tree species. Symbols are as defined in Fig. 2.

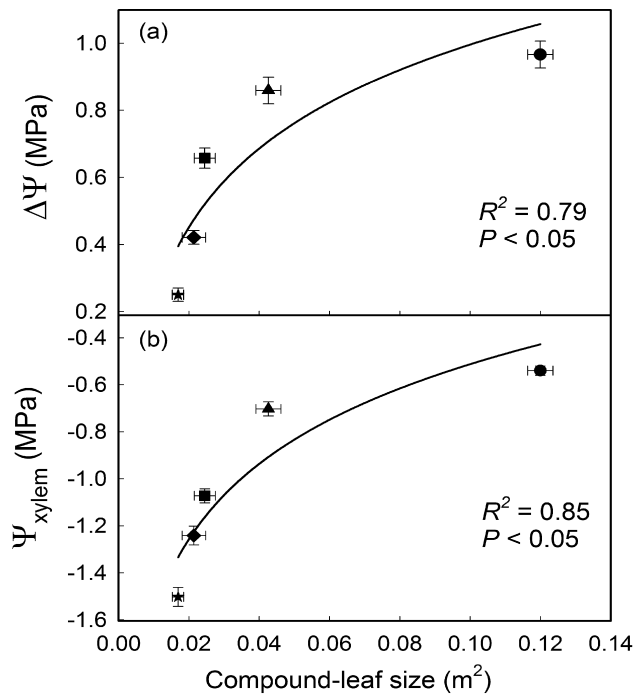


Fig. 6. (a) Water potential difference between stem xylem and compound leaf measured at midday ($\Delta\Psi$) and (b) midday stem xylem water potential (Ψ_{xylem}) as a function of compound leaf size across the five tree species. Error bars show $\pm 1SE$ ($n = 6$). Symbols are as defined in Fig. 2.

5. Conclusions

Our results suggest that, across the sympatric compound-leaved tree species of a typical temperate forest of NE China, larger leaf size results in higher carbon assimilation capacity and likely stronger

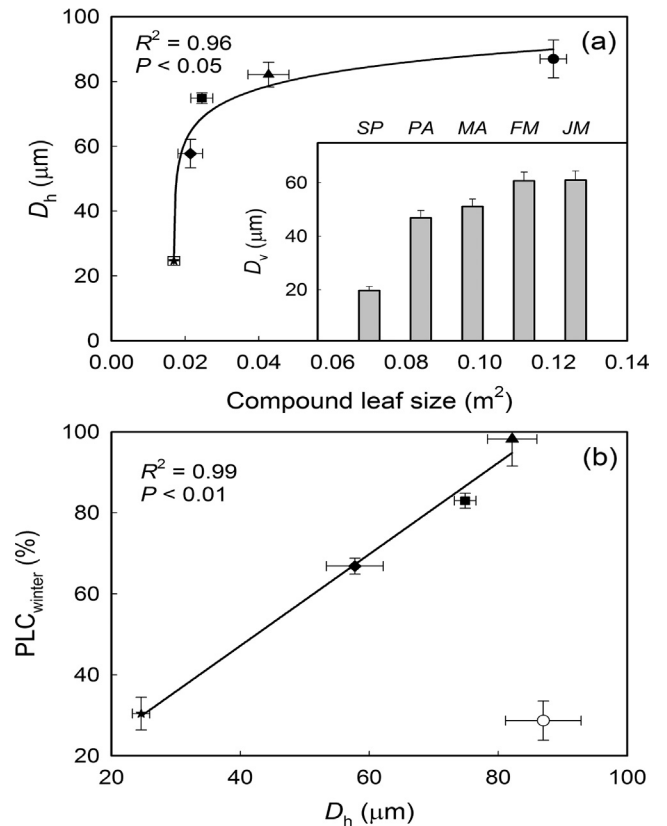


Fig. 7. (a) The relationship between mean hydraulic weighted vessel diameter (D_h) and compound-leaf size. Data were fitted using logarithm function ($y = y_0 + a \ln(x - x_0)$). (b) Winter-time percent loss of hydraulic conductivity (PLC_{winter}) as a function of mean hydraulic weighted vessel diameter (D_h) for the five compound-leaved tree species. Error bars show $\pm 1SE$ ($n = 6$). The insert in panel (a) shows mean vessel diameters (D_v) for the five species. Symbols are as defined in Fig. 2.

competitiveness under favorable environmental conditions, which is underlain by greater whole-shoot level hydraulic conductance and more efficient branch architecture (higher LA/SA) with the increase of leaf size. Larger leaf size also enhanced significantly the hydraulic segmentation between terminal branches and compound leaves resulting in greater hydraulic safety against drought-induced embolism in species with larger compound leaves. Higher susceptibility to freeze-thaw induced xylem embolism in overwintering stems of species with larger vessel diameters, however, results in reduced ability to succeed in habitats of higher elevations. Results of our study are overall in line with the long proposed fast growth and hydraulic segmentation hypotheses of compound leaf adaptation but deepened our understanding to these two hypotheses by showing the importance of compound leaf size in affecting both hydraulic efficiency and hydraulic segmentation.

Acknowledgements

We thank the staff at the Research Station of Changbai Mountain Forest Ecosystems for supporting this study. Luxin Zhao and Luxiang Zhao are greatly acknowledged for field assistances. The authors declare no conflict of interests. The authors declare no conflicts of interest.

Funding

This work was supported by the National Key Research and Development Program of China (2016YFA0600803), the National Natural Science Foundation of China (31722013, 31500222), the Hundred-Talents Program and the project QYZDJ-SSW-DQC027 from the Chinese Academy of Sciences.

Appendix A. Supplementary materials

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.08.005>.

References

- Aarssen, L., 2012. Reducing size to increase number: a hypothesis for compound leaves. *Ideas Ecol. Evol.* 5, 1–5.
- Ackerly, D., 2004. Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. *Ecol. Monogr.* 74, 25–44.
- Améglio, T., Ewers, F.W., Cochard, H., Martignac, M., Vandame, M., Bodet, C., Cruziat, P., 2001. Winter stem xylem pressure in walnut trees: effects of carbohydrates, cooling and freezing. *Tree Physiol.* 21, 387–394.
- Bharathan, G., Sinha, N.R., 2001. The regulation of compound leaf development. *Plant Physiol.* 127, 1533–1538.
- Bharathan, G., Goliber, T.E., Moore, C., Kessler, S., Pham, T., Sinha, N.R., 2002. Homologies in leaf form inferred from KNOXI gene expression during development. *Science* 296, 1858–1860.
- Bongers, F., Popma, J., 1990. Leaf characteristics of the tropical rain forest flora of Los Tuxtlas, Mexico. *Bot. Gaz.* 151, 354–365.
- Bonser, S.P., Aarssen, L.W., 1994. Plastic allometry in young sugar maple (*Acer saccharum*): adaptive responses to light availability. *Am. J. Bot.* 81, 400–406.
- Brodribb, T.J., Holbrook, N.M., 2003a. Stomatal closure during leaf dehydration, correlation with other leaf physiological traits. *Plant Physiol.* 132, 2166–2173.
- Brodribb, T.J., Holbrook, N.M., 2003b. Changes in leaf hydraulic conductance during leaf shedding in seasonally dry tropical forest. *New Phytol.* 158, 295–303.
- Brodribb, T.J., Holbrook, N.M., Edwards, E.J., Gutierrez, M.V., 2003. Relations between stomatal closure, leaf turgor and xylem vulnerability in eight tropical dry forest trees. *Plant, Cell Environ.* 26, 443–450.
- Brodribb, T.J., Holbrook, N.M., 2004a. Diurnal depression of leaf hydraulic conductance in a tropical tree species. *Plant, Cell Environ.* 27, 820–827.
- Brodribb, T.J., Holbrook, N.M., 2004b. Stomatal protection against hydraulic failure: a comparison of coexisting ferns and angiosperms. *New Phytol.* 162, 663–670.
- Bucci, S.J., Scholz, F.G., Goldstein, G., Meinzer, F.C., Franco, A.C., Campanello, P.I., Villalobos-Vega, R., Bustamante, M., Miralles-Wilhelm, F., 2006. Nutrient availability constrains the hydraulic architecture and water relations of savannah trees. *Plant, Cell Environ.* 29, 2153–2167.
- Bucci, S.J., Scholz, F.G., Peschiutta, M.L., Arias, N.S., Meinzer, F.C., Goldstein, G., 2013. The stem xylem of Patagonian shrubs operates far from the point of catastrophic dysfunction and is additionally protected from drought-induced embolism by leaves and roots. *Plant, Cell Environ.* 36, 2163–2174.
- Champagne, C.E., Goliber, T.E., Wojciechowski, M.F., Mei, R.W., Townsley, B.T., Wang, K., Paz, M.M., Geeta, R., Sinha, N.R., 2007. Compound leaf development and evolution in the legumes. *Plant Cell* 19, 3369–3378.
- Chen, D.K., Zhou, X.F., Zhu, N., 1994. Natural Secondary Forest-Structure, Function, Dynamics and Management. Northeast Forestry University Press, Haerbin, China.
- Chitwood, D.H., Sinha, N.R., 2016. Evolutionary and environmental forces sculpting leaf development. *Curr. Biol.* 26, R297–R306.
- Cobb, A.R., Choat, B., Holbrook, N.M., 2007. Dynamics of freeze–thaw embolism in *Smilax rotundifolia* (Smilacaceae). *Am. J. Bot.* 94, 640–649.
- Cochard, H., Coll, L., Le Roux, X., Améglio, T., 2002. Unraveling the effects of plant hydraulics on stomatal closure during water stress in walnut. *Plant Physiol.* 128, 282–290.
- Coley, P.D., Bryant, J.P., Chapin, F.S.I.I.I., 1985. Resource availability and plant anti-herbivore defense. *Science* 230, 895–899.
- Cronquist, A., 1988. *The Evolution and Classification of Flowering Plants*. New York Botanical Garden, New York.
- Dai, L.M., Chen, G., Deng, H.B., Ji, L.Z., Hao, Z.Q., Wang, Q.L., 2004. Structure characteristics and health distance assessment of various disturbed communities of Korean pine and broadleaved mixed forest in Changbai Mountains. *Chin. J. Appl. Ecol.* 15, 1750–1754 (in Chinese with English abstrat).
- Davis, S.D., Sperry, J.S., Hacke, U.G., 1999. The relationship between xylem conduit diameter and cavitation caused by freezing. *Am. J. Bot.* 86, 1367–1372.
- Efroni, I., Eshed, Y., Lifschitz, E., 2010. Morphogenesis of simple and compound leaves: a critical review. *Plant Cell* 22, 1019–1032.
- Ehrlich, P.R., Wilson, E.O., 1991. Biodiversity studies: science and policy. *Science* 253, 758–762.
- Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N.L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Holle, B.V., Webster, J.R., 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Front. Ecol. Environ.* 3, 479–486.
- Ewers, F.W., Améglio, T., Cochard, H., Beaujard, F., Martignac, M., Vandame, M., Bodet, C., Cruziat, P., 2001. Seasonal variation in xylem pressure of walnut trees: root and stem pressures. *Tree Physiol.* 21, 1123–1132.
- Feild, T.S., Brodribb, T.J., 2001. Stem water transport and freeze–thaw xylem embolism in conifers and angiosperms in a Tasmanian treeline heath. *Oecologia* 127, 314–320.
- Franks, N.R., Britton, N.F., 2000. The possible role of reaction–diffusion in leaf shape. *P. Roy. Soc. B: Biol. Sci.* 267, 1295–1300.
- Friedman, W.E., Moore, R.C., Purugganan, M.D., 2004. The evolution of plant development. *Am. J. Bot.* 91, 1726–1741.
- Gates, D.M., 1980. *Biophysical Ecology*. Springer-Verlag, New York.
- Geider, R.J., Delucia, E.H., Falkowski, P.G., Finzi, A.C., Grime, J.P., Grace, J., Kana, T.M., Roche, J.L., Long, S.P., Osborne, B.A., Platt, T., Prentice, I.C., Raven, J.A., Schlesinger, W.H., Smetacek, V.S., Stuart, V., Sathyendranath, S., Thomas, R.B., Vogelmann, T.C., Williams, P., Woodward, F.I., 2001. Primary productivity of planet earth: biological determinants and physical constraints in terrestrial and aquatic habitats. *Global Change Biol.* 7, 849–882.
- Givnish, T.J., 1978. On the adaptive significance of compound leaves, with particular reference to tropical trees. In: Tomlinson, P.B., Zimmerman, M.H. (Eds.), *Tropical Trees as Living Systems*. Cambridge University Press, Cambridge, pp. 351–380.
- Givnish, T.J., 1979. On the adaptive significance of leaf form. In: Solbrig, O.T., Jain, S., Johnson, G.B., Raven, P.H. (Eds.), *Topics in Plant Population Biology*. Columbia University Press, New York, pp. 375–407.
- Givnish, T.J., 1984. Leaf and canopy adaptations in tropical forests. In: Medina, E., Mooney, H.A., Vázquez-Yanes, C. (Eds.), *Physiological Ecology of Plants of the Wet Tropics*. Junk, W., The Hague, pp. 51–84.
- Goldstein, G., Bucci, S.J., Scholz, F.G., 2013. Why do trees adjust water relations and hydraulic architecture in response to nutrient availability? *Tree Physiol.* 33, 238–240.
- Grime, J.P., 1998. Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. *J. Ecol.* 86, 902–910.
- Grubb, P., 1977. Control of forest growth and distribution on wet tropical mountains: with special reference to mineral nutrition. *Annu. Rev. Ecol. Syst.* 8, 83–107.
- Hacke, U.G., Plavcová, L., Almeida-Rodriguez, A., King-Jones, S., Zhou, W., Cooke, J.E., 2010. Influence of nitrogen fertilization on xylem traits and aquaporin expression in stems of hybrid poplar. *Tree Physiol.* 30, 1016–1025.
- Hacke, U.G., Sperry, J.S., 2001. Functional and ecological xylem anatomy. *Perspect. Plant Ecol.* 4, 97–115.
- Hao, G.Y., Goldstein, G., Sack, L., Holbrook, N.M., Liu, Z.H., Wang, A.Y., Cao, K.F., 2011. Ecology of hemiepiphytism in fig species is based on evolutionary correlation of hydraulics and carbon economy. *Ecology* 92, 2117–2130.
- Hao, G.Y., Hoffmann, W.A., Scholz, F.G., Bucci, S.J., Meinzer, F.C., Franco, A.C., Cao, K.F., Goldstein, G., 2008. Stem and leaf hydraulics of congeneric tree species from adjacent tropical savanna and forest ecosystems. *Oecologia* 155, 405–415.
- Hao, G.Y., Wheeler, J.K., Holbrook, N.M., Goldstein, G., 2013. Investigating xylem embolism formation, refilling and water storage in tree trunks using frequency domain reflectometry. *J. Exp. Botany* 64, 2321–2332.
- Hu, L.J., Uchiyama, K., Shen, H.L., Ide, Y., 2010. Multiple-scaled spatial genetic structures of *Fraxinus mandshurica* over a riparian–mountain landscape in Northeast China. *Conserv. Genet.* 11, 77–87.
- Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *Oikos* 69, 373–389.
- Klingenberg, C., Duttke, S., Whelan, S., Kim, M., 2012. Developmental plasticity, morphological variation and evolvability: a multilevel analysis of morphometric integration in the shape of compound leaves. *J. Evol. Biol.* 25, 115–129.
- Lambers, H., Poorter, H., 1992. Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Adv. Ecol. Res.* 23, 187–261.
- Lawton, J.H., Jones, C.G., 1995. Linking species and ecosystems: organisms as ecosystem engineers. In: Jones, C.G., Lawton, J.H. (Eds.), *Linking Species and Ecosystems*, pp. 141–150 New York.
- Liu, Y.Y., Song, J., Wang, M., Li, N., Niu, C.Y., Hao, G.Y., 2015. Coordination of xylem hydraulics and stomatal regulation in keeping the integrity of xylem water transport in shoots of two compound-leaved tree species. *Tree Physiol.* 35, 1333–1342.
- Mallik, A.U., 2003. Conifer regeneration problems in boreal and temperate forests with ericaceous understory: role of disturbance, seedbed limitation, and keystone species change. *Crit. Rev. Plant Sci.* 22, 341–366.
- Malhado, A.C.M., Whittaker, R.J., Malhi, Y., Ladle, R.J., Ter Steege, H., Phillips, O., Aragão, L.E.O.C., Baker, T.R., Arroyo, L., Almeida, S., Higuchi, N., Killeen, T.J., Monteagudo, A., Pitman, N.C.A., Prieto, A., Salomão, R.P., Vásquez-Martínez, R., Laurance, W.F., Ramírez-Angulo, H., 2010. Are compound leaves an adaptation to seasonal drought or to rapid growth? Evidence from the Amazon rain forest. *Glob. Ecol. Biogeogr.* 19, 852–862.
- Martínez-Garza, C., Howe, H., 2005. Developmental strategy or immediate responses in leaf traits of tropical tree species? *Int. J. Plant Sci.* 166, 41–48.
- Martínez-Vilalta, J., Prat, E., Oliveras, I., Piñol, J., 2002. Xylem hydraulic properties of roots and stems of nine Mediterranean woody species. *Oecologia* 133, 19–29.
- Meinzer, F.C., 2003. Functional convergence in plant responses to the environment. *Oecologia* 134, 1–11.
- Méndez-Alonzo, R., Paz, H., Cruz-Zuluaga, R., Rosell, J.A., Olson, M.E., 2012. Coordinated evolution of leaf and stem economics in tropical dry forest trees. *Ecology* 93, 2397–2406.
- Merine, A.K., Rodríguez-García, E., Alfa, R., Pando, V., Bravo, F., 2015. Effects of water stress and substrate fertility on the early growth of *Acacia senegal* and *Acacia seyal* from Ethiopian Savanna woodlands. *Trees* 29, 593–604.
- Mokany, K., McMurtrie, R.E., Atwell, B.J., Keith, H., 2003. Interaction between sapwood and foliage area in alpine ash (*Eucalyptus delegatensis*) trees of different heights. *Tree Physiol.* 23, 949–958.
- Naiman, R.J., Johnston, C.A., Kelley, J.C., 1988. Alteration of North American streams by beaver. *Bioscience* 38, 753–762.
- Niinemets, Ü., 1998. Are compound-leaved woody species inherently shade-intolerant? An analysis of species ecological requirements and foliar support costs. *Plant Ecol.* 134, 1–11.
- Niinemets, Ü., Kull, O., 1999. Biomass investment in leaf lamina versus lamina support in relation to growth irradiance and leaf size in temperate deciduous trees. *Tree Physiol.* 19, 349–358.
- Niinemets, Ü., Portsmuth, A., Tobias, M., 2006. Leaf size modifies support biomass distribution among stems, petioles and mid-ribs in temperate plants. *New Phytol.* 171,

- 91–104.
- Niklas, K.J., 1991a. Biomechanical responses of *Chamaedorea* and *Spathiphyllum* petioles to tissue dehydration. *Ann. Bot.* 67, 67–76.
- Niklas, K.J., 1991b. Effects of tissue volume and location on the mechanical consequences of dehydration of petioles. *Am. J. Bot.* 78, 361–369.
- Niklas, K.J., 1991c. Flexural stiffness allometries of angiosperm and fern petioles and rachises: evidence for biomechanical convergence. *Evolution* 45, 734–750.
- Niklas, K.J., 1992. *Plant Biomechanics*. University of Chicago Press, Chicago.
- Niu, C.Y., Meinzer, F.C., Hao, G.Y., 2017. Divergence in strategies for coping with winter embolism among co-occurring temperate tree species: the role of positive xylem pressure, wood type and tree stature. *Funct. Ecol.* <http://dx.doi.org/10.1111/1365-2435.12868>.
- Park, G., Jang, D.S., Oh, M.S., 2012. *Juglans mandshurica* leaf extract protects skin fibroblasts from damage by regulating the oxidative defense system. *Biochem. Biophys. Res. Commun.* 421, 343–348.
- Pittermann, J., Sperry, J.S., 2003. Tracheid diameter is the key trait determining the extent of freezing-induced embolism in conifers. *Tree Physiol.* 23, 907–914.
- Qin, J., 2016. Research progress of secondary forest management in Northeast China. *J. Liaoning For. Sci. Technol.* 2, 61–63 (in Chinese).
- Reich, P.B., Walters, M.B., Ellsworth, D.S., 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecol. Monogr.* 62, 365–392.
- Renninger, H.J., Phillips, N., 2011. Hydraulic properties of fronds from palms of varying height and habitat. *Oecologia* 167, 925–935.
- Rosati, A., Metcalf, S., Buchner, R., Fulton, A., Lampinen, B., 2006. Tree water status and gas exchange in walnut under drought, high temperature and vapour pressure deficit. *J. Hort. Sci. Biotechnol.* 81, 415–420.
- Royer, D.L., Wilf, P., Janesko, D.A., Kowalski, E.A., Dilcher, D.L., 2005. Correlations of climate and plant ecology to leaf size and shape: potential proxies for the fossil record. *Am. J. Bot.* 92, 1141–1151.
- Runkle, J.R., 1981. Gap Regeneration in Some Old-growth Forests of the Eastern United States. *Ecology* 62, 1041–1051.
- Sack, L., Melcher, P.J., Zwieniecki, M.A., Holbrook, N.M., 2002. The hydraulic conductance of the angiosperm leaf lamina: a comparison of three measurement methods. *J. Exp. Bot.* 53, 2177–2184.
- Santiago, L., Goldstein, G., Meinzer, F., Fisher, J., Machado, K., Woodruff, D., Jones, T., 2004. Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. *Oecologia* 140, 543–550.
- Scoffoni, C., Chatelet, D.S., Pasquet-kok, J., Rawls, M., Donoghue, M.J., Edwards, E.J., Sack, L., 2016. Hydraulic basis for the evolution of photosynthetic productivity. *Nat. Plants* 2, 16072.
- Sims, D., Pearcy, R., 1994. Scaling sun and shade photosynthetic acclimation of *Alocasia macrorrhiza* to whole-plant performance—I. Carbon balance and allocation at different daily photon flux densities. *Plant, Cell Environ.* 17, 881–887.
- Smith, M.D., Knapp, A.K., 2003. Dominant species maintain ecosystem function with non-random species loss. *Ecol. Lett.* 6, 509–517.
- Sperry, J.S., Adler, F.R., Campbell, G.S., Comstock, J.P., 1998. Limitation of plant water use by rhizosphere and xylem conductance: results from a model. *Plant, Cell Environ.* 21, 347–359.
- Sperry, J.S., Nichols, K.L., Sullivan, J.E., Eastlack, S.E., 1994. Xylem embolism in ring-porous, diffuse-porous, and coniferous trees of northern Utah and interior Alaska. *Ecology* 75, 1736–1752.
- Stowe, L.G., Brown, J.L., 1981. A geographic perspective on the ecology of compound leaves. *Evolution* 35, 818–821.
- Stuart, S.A., Choat, B., Martin, K.C., Holbrook, N.M., Ball, M.C., 2007. The role of freezing in setting the latitudinal limits of mangrove forests. *New Phytol.* 173, 576–583.
- Sun, X.C., Zhang, Y.Z., Fan, X.N., 2008. The status and operating management of broad leaved *Pinus koriensis* forests in Changbai Mountain. *J. Jilin Normal Univ. (Natural Science Edition)* 29, 105–107 (in Chinese with English abstrat).
- Tanner, E., 1980. Studies on the biomass and productivity in a series of montane rain forests in Jamaica. *J. Ecol.* 68, 573–588.
- Tulik, M., Marciszewska, K., Adamczyk, J., 2010. Diminished vessel diameter as a possible factor in the decline of European ash (*Fraxinus excelsior* L.). *Ann. For. Sci.* 67, 103.
- Turner, I.M., 2001. *The Ecology of Trees in the Tropical Rain Forest*. Cambridge University Press, Cambridge.
- Tyree, M., Cochard, H., Cruziat, P., Sinclair, B., Ameglio, T., 1993. Drought-induced leaf shedding in walnut: evidence for vulnerability segmentation. *Plant, Cell Environ.* 16, 879–882.
- Tyree, M.T., Ewers, F.W., 1991. The hydraulic architecture of trees and other woody plants. *New Phytol.* 119, 345–360.
- Tyree, M.T., Zimmermann, M.H., 2002. *Xylem Structure and the Ascent of Sap*. Springer, New York.
- van den Honert, T.H., 1948. Water transport in plants as a catenary process. *Discuss. Farad. Soc.* 3, 146–153.
- Wang, C., 2006. Biomass allometric equations for 10 co-occurring tree species in Chinese temperate forests. *For. Ecol. Manage.* 222, 9–16.
- Wang, A.Y., Wang, M., Yang, D., Song, J., Zhang, W.W., Han, S.J., Hao, G.Y., 2016. Responses of hydraulics at the whole-plant level to simulated nitrogen deposition of different levels in *Fraxinus mandshurica*. *Tree Physiol.* 36, 1045–1055.
- Wang, J., Ives, N., Lechowicz, M., 1992. The relation of foliar phenology to xylem embolism in trees. *Funct. Ecol.* 6, 469–475.
- Warman, L., Moles, A.T., Edwards, W., 2011. Not so simple after all: searching for ecological advantages of compound leaves. *Oikos* 120, 813–821.
- Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A., Wright, I.J., 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annu. Rev. Ecol. Syst.* 33, 125–159.
- Yang, L., Li, Y., Shen, H., 2012. Somatic embryogenesis and plant regeneration from immature zygotic embryo cultures of mountain ash (*Sorbus pohnuashanensis*). *Plant Cell Tiss. Org. Cult.* 109, 547–556.
- Yang, L., Shen, H.I., 2011. Effect of electrostatic field on seed germination and seedling growth of *Sorbus pohnuashanensis*. *J. Forestry Res.* 22, 27–34.
- Yazaki, K., Sano, Y., Fujikawa, S., Nakano, T., Ishida, A., 2010. Response to dehydration and irrigation in invasive and native saplings: osmotic adjustment versus leaf shedding. *Tree Physiol.* 30, 597–607.
- Yu, D.P., Zhou, W.M., Bao, Y., Qi, L., Zhou, L., Dai, L.M., 2015. Forest management of Korean pine and broadleaf mixed forest in Northeast China since the implementation of Natural Forest Protection Project. *Acta Ecol. Sin.* 35, 0010–0017 (in Chinese with English abstrat).
- Zhu, J.J., 2002. A review on fundamental studies of secondary forest management. *Chin. J. Appl. Ecol.* 13, 1689–1694 (in Chinese with English abstrat).
- Zhu, S.D., Song, J.J., Li, R.H., Ye, Q., 2013. Plant hydraulics and photosynthesis of 34 woody species from different successional stages of subtropical forests. *Plant, Cell Environ.* 36, 879–891.
- Zimmermann, M.H., 1978. Hydraulic architecture of some diffuse-porous Trees. *Can. J. Bot.* 56, 2286–2295.
- Zimmermann, M.H., 1983. *Xylem Structure and the Ascent of Sap*. Springer-Verlag, Berlin, Germany.
- Zufferey, V., Cochard, H., Ameglio, T., Spring, J.L., Viret, O., 2011. Diurnal cycles of embolism formation and repair in petioles of grapevine (*Vitis vinifera* cv. Chasselas). *J. Exp. Bot.* 62, 3885–3894.