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

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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 disproportionally 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 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

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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