Allometric covariation of xylem and stomata across diverse woody seedlings

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May 19, 2020

Abstract

Leaf stomatal density is known to covary with leaf vein density. However, the functional underpinning of this relation, and how it scales to whole-plant water transport anatomy, is still unresolved. We hypothesized that the balance of water exchange between the vapour phase (in stomata) and liquid phase (in vessels) depends on the consistent scaling between the summed stomatal areas and xylem cross-sectional areas, both at the whole-plant and single-leaf level. This predicted size-covariation should be driven by the covariation of numbers of stomata and terminal vessels. We examined the relationships of stomatal traits and xylem anatomical traits from the entire plant to individual leaves across seedlings of 53 European woody angiosperm species. There was strong and convergent scaling between total stomatal area and stem xylem area per plant and between leaf total stomatal area and midvein xylem area per leaf across all the species, irrespective of variation in leaf habit, growth-form or relative growth rate (RGR). Moreover, strong scaling was found between stomatal number and terminal vessel number while not in their respective average areas. Our findings have broad implications for integrating xylem architecture and stomatal distribution, and deepen our understanding of the design rules of plants' water transport network.

Definitions of parameters: **Average stomatal area:** mean area of a guard cell pair, i.e. double ellipse 2*a*b*π, where a ar

Introduction

The xylem system of vascular plants generally features a "tip-to-base" widening with the maximal number of the narrowest conduits in the terminal parts; the size of these terminal conduits should not vary with plant size (or leaf size) (Lechthaler, Colangeli, Gazzabin & Anfodillo, 2019, Rosell & Olson, 2019, West, Brown & Enquist, 1999). With this hierarchical and basipetally widening xylem architecture, the energy cost of long-distance water transport is minimized (Anfodillo, Carraro, Carrer, Fior & Rossi, 2006, Shinozaki, Yoda, Hozumi & Kira, 1964, West *et al.* , 1999). Under the negative pressure created by stomatal transpiration, water ascends from the soil, progressively through stem and leaf xylem vessels, all the way up to the terminal stomata. Covariation of stomatal and xylem traits in leaves is required to maintain a balance in water exchange between the liquid (water delivery) and the vapor (water loss) phase (Brodribb, McAdam & Carins Murphy, 2017, Carins Murphy, Jordan & Brodribb, 2014, Zhang, Carins Murphy, Cardoso, Jordan & Brodribb, 2018).

There is mounting evidence that vein density is proportional to stomatal density in leaves, and this pattern

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is applicable to diverse plants within and across species (Brodribb *et al.* , 2017, Carins Murphy, Jordan & Brodribb, 2016, Fiorin, Brodribb & Anfodillo, 2016). However, the causality of this relationship is difficult to interpret for three reasons. Firstly, leaf vein traits have been proposed to be proxies for leaf xylem properties (Blonder, Violle, Bentley & Enquist, 2011, Sack, Scoffoni, McKown, Frole, Rawls, Havran, Tran & Tran, 2012). Veins consist of more than xylem (e.g. they also host phloem), so simply considering vein density will ignore xylem vessel number and vessel lumen diameter, which have been deemed the predictors of conductive path length and leaf area respectively (Echeverría, Anfodillo, Soriano, Rosell & Olson, 2019, Rosell & Olson, 2019). We are not aware of any studies linking stomatal traits to xylem traits *per se* (i.e. size covariation of stomata and xylem vessels) (but see Meinzer and Grantz (1990) about xylem-stomatal conductance relationships) within and across species. Secondly, stomatal and vein densities reflect leaf water relations in terms of a leaf plane, while it is a system of conduits within a three-dimensional system, obviously finely tuned by natural selection in a way that directs water nearly optimally given carbon costs, conductance, and embolism resistance (Enquist, 2002, West *et al.* , 1999). Thirdly, these vein-stomatal density studies (Brodribb *et al.* , 2017, Carins Murphy *et al.* , 2014, Sack, Dietrich, Streeter, Sanchez-Gomez & Holbrook, 2008) use the water balance of single leaves to implicate the whole-plant water balance. This approach might be an oversimplification for understanding the entire liquid phase and the vapour phase relation, even though leaf area has been proved to predict photosynthetic productivity precisely, from the single leaf, to the branch, to the whole-tree, to the forest level (Li, Reich, Schmid, Shrestha, Feng, Lyu, Maitner, Xu, Li & Zou, 2020).

We address this knowledge gap with a laboratory growth experiment that enabled us to obtain xylem and stomatal traits both at leaf and whole-plant level. We grew seedlings of 53 diverse woody species from cool-temperate and Mediterranean Europe in a standard growing environment (Cornelissen, Castro-Díez & Hunt, 1996, Zhong, Castro-Diez, Puyravaud, Sterck & Cornelissen, 2019).

We examined relations between xylem dimensions (Zhong *et al.* , 2019) and stomatal dimensions of these seedlings both at whole-plant level and at leaf level. Specifically, this study presents, for the first time, the allometric scaling relationships at two scales: (i) between stem xylem cross-sectional area (as well as stem xylem conductance area) and total stomatal area at the whole-plant level, and (ii) between leaf midvein xylem area and leaf total stomatal area at single leaf level. We hereby introduce uniformity in the analyzed pairwise traits as they are expressed in the same physical units, which helps to represent more directly the selection effect on the water flux and enlightens our understanding of the whole-plant water balance.

Furthermore, as was proposed by the West-Brown-Enquist (WBE) model, the terminal vessels should be 'invariant' with plant size (or leaf size) along with plant growth for a given individual (Roddy, Théroux-Rancourt, Abbo, Benedetti, Brodersen, Castro, Castro, Gilbride, Jensen & Jiang, 2020, Simonin & Roddy, 2018, West *et al.* , 1999). We tested the relations between terminal vessel traits (i.e. minor vessel number and individual minor vessel area) and plant size (represented by stem xylem area and/or total leaf area per plant) across these 53 species, which were grown in a similar environment, in order to understand whether the terminal vessels 'depended' on plant size across diverse species. Additionally, the relations between stomatal traits (i.e. stomatal number and individual stomatal area) and leaf size (represented by midvein xylem area and/or average leaf area) were tested empirically, in order to link with the large body of studies on the allocation mechanism of leaf surface to stomata (Boer, Price, Wagner-Cremer, Dekker, Franks & Veneklaas, 2016, Franks & Farquhar, 2007, Parlange & Waggoner, 1970). Additionally, as stomatal allocation at the leaf surface tends to simultaneously minimize water loss (e.g. water exchange from the minor vessels to stomata) while maximizing gas exchange to maintain a constant photosynthetic productivity per unit leaf area (Boer *et al.* , 2016), we expect that the number of stomata should scale linearly with the number of minor vessels (Fig. 1).

Fig.1 Conceptual framework of this research concerning allometric relations of plant hydraulics across woody species. Natural selection acts on heritable variation between individuals within the same species. Individuals with vessels that do not widen with height growth, or widen little, will experience continual declines in leaf-specific conductance with height growth and therefore declining growth and reproductive output per unit leaf area. Individuals with vessels that widen very markedly would have conduits of low resistance, in

contrast to the high-resistance variants with conduits that are 'too narrow', but they would have their own set of disadvantages. For example, for a given leaf area and transpirational demand, the wider conduits cost more for the same service provided. Each unit of carbon invested in excessively wide vessels is a unit that is not invested in further growth or reproduction, and so these variants should be at a selective disadvantage (Banavar, Cooke, Rinaldo & Maritan, 2014). Moreover, wider vessels are more vulnerable to gas embolisms that obstruct conductance, both from freezing ((Sevanto, Holbrook & Ball, 2012, Zanne, Tank, Cornwell, Eastman, Smith, FitzJohn, McGlinn, O'Meara, Moles, Reich, Royer, Soltis, Stevens, Westoby, Wright, Aarssen, Bertin, Calaminus, Govaerts, Hemmings, Leishman, Oleksyn, Soltis, Swenson, Warman & Beaulieu, 2014) and likely drought as well (Cai & Tyree, 2010, Jacobsen, Pratt, Venturas & Hacke, 2019, Liu, Gleason, Hao, Hua, He, Goldstein & Ye, 2019). As a result, plants with vessels that are 'too wide' would also be at a selective disadvantage (Zhong *et al.*(2019)). The variants that should have the largest amounts of surplus carbon to devote to growth and reproduction are those in the intermediate zone, in which conduits widen just enough that conductance remains constant per unit leaf area, but not so much as to incur excessive carbon costs and embolism vulnerability.

In our previous study, based on the same woody seedling populations, we found that, at the whole-plant level, the stem xylem cross-sectional area (X_{stem}) of stem medium (a) closely scales with stem height (H) and total leaf area per plant (LA) as X_{stem} [?] $H^{1.52}$ and X_{stem} [?] $LA^{0.75}$ across all the studied species. For individual leaves, vessel diameter (D_{leaf}) in the medium of leaf midvein (b) closely scales with average leaf area (MLA) as D_{leaf} [?] $MLA^{0.21}$ (Zhong *et al.* (2019). In this study, we test the poorly understood xylem-stomata covariation from the size perspective We ask: are there scaling relationships between total stomatal area and xylem cross-sectional area across species, at the entire plant and at individual leaf level? Specifically, we zoom in on the terminal part of water exchange (from minor vessels to stomata), and ask: does the minor vessel number (which scales with leaf area; see (Lechthaler *et al.*, 2019, Rosell & Olson, 2019)) scale with stomatal number per leaf and per plant across these woody seedlings? The conceptual picture should deepen our understanding of plants' water transport system and have broad implications for integrating xylem architecture and stomatal distribution.

Based on the expectations above, we test the hypothesis that, despite large interspecific differences in leaf-habit, growth-form and relative growth rate (RGR), similar scaling should exist between total stomatal area and xylem area across woody seedlings, both at the entire plant and at individual leaf level, to ensure the balance between liquid- and vapour-phase water conductance. We also expect that the hypothesized scaling of total stomatal area to xylem area should be driven by the number covariation of stomatal and minor vessel elements; we also expect a scaling relation between mean stomatal area and mean minor vessel area as we presumed the distal element size for a given plant to be limited under long-term nature selection.

Materials and Methods

Seedling growth protocol

Seeds of 53 diverse woody species, belonging to different growth-forms (19 trees, 22 shrubs, 6 subshrubs and 6 climbers or scramblers) and leaf habits (34 deciduous and 19 evergreens), were collected from cool-temperate and Mediterranean Europe (Table S1). These species are a subset of those used by Cornelissen *et al.* (1996), and the seedlings sampled for this anatomical study were subpopulations of those grown in that growth rate focused study, which was conducted in standard environmental conditions at the Unit of Comparative Plant Ecology, Sheffield University. In brief, throughout 1994 and 1995, all seeds were first germinated and then transplanted into experimental pots that were filled with quarried, prewashed silica sand. An environmental condition of 14 h 20-22 : 10 h 15-17 light : dark was provided, with 135 +- 10 µmol m^{-2}s^{-1} of photosynthetically active radiation (classified as partial shade, see Hendry and Grime (1993)).

The population of each species was evenly divided into two halves for initial and final harvest. After the seedlings opened the first true leaf or leaf pair (i.e. at standardized ontogenetic stage), we harvested the first half population and determined the total plant dry weight. The second half of the population was cultivated for another 21 days within the same standard environment with 0.25 ml per sand volume full-strength Rorison

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nutrient solution (N, P and K at 56, 31 and 78 mg l^{-1}, respectively, plus Ca, Mg, Fe and trace elements) and sufficient deionized water on alternate days. The seedlings were then harvested, dry-weighed and further treated for anatomy analysis (details see Cornelissen *et al.* (1996)).

Relative growth rate (RGR) and leaf area

Mean relative growth rate (RGR) was derived as: RGR = $(\log_e W_2 - \log_e W_1)/(t_2 - t_1)$, where W_1 and W_2 was the plant dry weight at the first (t_1) and second (t_2) harvest, respectively. At the final harvest, plant total leaf area was measured after saturation in wet tissue paper at 5 overnight, with a Delta-T Area Meter (Burwell, Cambridge, UK) for most species, while a 1 mm paper grid was used to calculate leaf area visually for some species with tiny leaves. Average leaf area was calculated as the ratio of total leaf area to leaf number per individual. For each species, 8-30 individuals were used for quantifying the above parameters (details see Cornelissen *et al.* (1996), Cornelissen, Cerabolini, Castro-Diez, Villar-Salvador, Montserrat-Marti, Puyravaud, Maestro, Werger and Aerts (2003a)).

Xylem traits

At the final harvest, three to four seedlings per species were chosen randomly for xylem traits measurements. For each individual, one fully expanded leaf as well as the stem was pickled, and the middle part of each leaf (including the middle of the midvein) as well as the middle of each stem were cut transversely. The materials were embedded in 5% agar and progressively dehydrated in 50, 70 and 95% ethanol (2h per solution), after which the small blocks of agar were infiltrated for 15 days with resin JB 4 Polysciences (Polysciences Inc., Warington, Pa., USA). After polymerisation of the resin, 2 μm thick cross-sections were obtained with a glass ultra-microtome, then sections were stained with 5% toluidine blue and permanently mounted onto slides with DPX (dibutyl phthalate in xylene). The cross-sections of leaves and stems were studied with a light microscope (Zeiss Axioskop; Carl Zeiss, Jena, Germany) on a computer screen with image analysis software (Aequitas IA v. 1.25) (Castro-Díez, Puyravaud & Cornelissen, 2000, Castro-Díez, Puyravaud, Cornelissen & Villar-Salvador, 1998).

For stems, stem xylem area and stem xylem conductance area (stem xylem area minus cell wall area) were circled and measured. The proportion of cell wall area relative to xylem area in transverse section was measured in three to four microscopic fields per slide using Aequita tools (Castro-Díez *et al.* , 1998). For leaves, leaf midvein xylem area and minor vessel area were circled in light microscope images and measured, and the minor vessel area was calculated as the average area of the ten smallest vessels of the cross-section of leaves, which were defined as the distal conduits. The plant minor vessel number (N_{vessel}) was theoretically approximated as: $N_{vessel} = A/(\pi * R_s * R_m)$, where A is stem xylem conductance area, R_s is the radius of the biggest vessel in stem medium, and R_m is the radius of the minor vessel in leaves. This calculation was based on the pipe model, which states that the sum of all vessel inner diameters at each vein order is equal (Shinozaki *et al.* , 1964). We used the stem (rather than leaf) xylem conductance area to calculate N_{vessel} because it is difficult to gain the leaf xylem conductance area in a representative way from entire leaf cross-sections, especially for species that have big leaves.

Stomatal traits

At the final harvest, one leaf from each of three different seedlings was randomly selected for epidermal prints; the representative leaf section at about one third from the apex and one third from the midvein was examined. We first brushed acetone onto surfaces of these leaves, and then pressed an acetate layer onto them firmly for 30 s and waited for them to dry. Subsequently, we peeled off the acetate layer and mounted it onto a slide for stomatal analysis. Stomatal number of each of ten randomly selected views (0.12 mm^2 at 100 × magnification) was counted and averaged. When prints did not have sufficient large undamaged and clear areas, smaller areas (0.01- 0.05 mm^2 at 400 × magnification) were examined. Stomatal density was determined as the summed number of stomata on both upper and lower surface per one-sided leaf area. The stomatal area was defined as the area of a guard cell pair, *i.e.* double ellipse 2*a*b*π, where a and b are the maximum length and maximum width of the guard cells of ten randomly selected closed stomata, respectively (Cornelissen *et al.* , 2003a). Leaf total stomatal area was defined as stomatal density multiplied

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by average leaf area and average stomatal area. Correspondingly, plant total stomatal area was defined as stomatal density multiplied by plant total leaf area times average stomatal area. Leaf total stomatal number was defined as stomatal density multiplied by average leaf area. Similarly, plant total stomatal number was defined as stomatal density multiplied by plant total leaf area.

Statistics

Bivariate line-fitting of pair-wise traits across species with contrasting life strategy (*i.e.* different leaf habits, growth-forms and RGRs) was conducted with the standardized major axis (SMA) model using the 'smatr' package in R (R Development Core Team, 2014). All data were first ln-transformed before line fitting. Homogeneity among slopes and Y elevations of fitted lines were determined referring to different groups (leaf habits and growth-forms). Elevation homogeneity, as well as the overall slope homogeneity with 1, were analyzed when these individual slopes of ecological groups were homogeneous. As the absolute values of stomatal area or xylem area should vary due to different measuring methods, we did not compare the elevations of these regression against the one-to-one line. The impact of RGR on these scaling relationships was defined by fitting lines of Y/X to RGR.

Results

All relations reported below are based on linear SMA regressions on ln-transformed values. We found strong similarity in scaling relationships across seedlings of woody species between total stomatal area and xylem tissue area from the whole-plant level to single-leaf level. Across the 53 species, plant total stomatal area scaled to stem xylem area (slope = 1.29, $r^2 = 0.81$, $P < 0.001$; Fig. 2a), and to stem xylem conductance area (slope = 1.22, $r^2 = 0.77$, $P < 0.001$; Fig. 2b); leaf total stomatal area scaled to midvein xylem area (slope = 1.30, $r^2 = 0.79$, $P < 0.001$) (Fig. 3). The slopes of the regression lines were substantially and significantly larger than 1 (the 95% confidence intervals did not bracket zero, Table 1).

Fig. 2 Size-covariation of stomata and xylem at the whole plant level, across seedlings of 53 European woody species varying in leaf-habit, growth-form and relative growth rate (RGR). (a) Convergent scaling of plant total stomatal area and stem xylem transect area. (b) Convergent scaling of plant total stomatal area and stem xylem conductance area. Growth forms: *T* tree, *S* shrub, *SS* subshrub,*C+Sc* scrambler or climber. Regression coefficients of standardized major axis (SMA) are documented in Table 1.

Fig. 3 Convergent scaling of leaf total stomatal area and midvein xylem transect area, across seedlings of 53 European woody species varying in leaf-habit, growth-form and relative growth rate (RGR). Lines indicate significant scaling relationships. Growth forms: *T* tree, *S*shrub, *SS* subshrub, *C+Sc* scrambler or climber. Regression coefficients of standardized major axis (SMA) are documented in Table 1.

Table 1. Ln – Ln scaling relationships were analyzed with standardized major axis regression (SMA) analyses, with additional reference to the contributions of different growth forms, leaf habits and relative growth rates (RGRs) to these relationships. Y-intercept and slopes as well as slope homogeneity with 1 are reported for pairwise relationships with significant results. 95% confidence intervals (CI) are in parentheses. Growth-form: *T* tree, *S* shrub, *SS* subshrub,*C+Sc* scrambler or climber; Leaf-habit: *D* deciduous,*E* evergreen. Y/X – *RGR* SMA regression of Y/X (ratio of Y values to X values) and RGR. ***, $P < 0.001$; **$P < 0.05$; ns, not significant.

Moreover, leaf total stomatal number had a strong scaling relation with leaf midvein xylem area (slope = 1.32, $r^2 = 0.79$, $P < 0.001$) as well as average leaf area (slope = 0.97, $r^2 = 0.97$, $P < 0.001$) (Fig. 4a). For the former, the slope of the regression line was significantly larger than 1 (the 95% confidence intervals did not bracket zero), while slope of the latter was convergent to 1 (Table 1). In contrast, average stomatal area was independent of leaf midvein xylem area ($r^2 = 0.01$, $P > 0.05$) or average leaf area ($r^2 < 0.01$, $P > 0.05$) (Fig. 4b; Table 1). Similarly, plant minor vessel number scaled with stem xylem area (slope = 0.88,$r^2 = 0.88$, $P < 0.001$) and total leaf area (slope = 0.69, $r^2 = 0.62$,$P < 0.001$; Fig. 4c) (Table 1). Average minor vessel area was independent of stem xylem area ($r^2 < 0.01$, $P > 0.05$) or total leaf area ($r^2 < 0.01$, $P > 0.05$) (Fig. 4d; Table 1).

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Fig. 4 (a) Covariation of leaf total stomatal number and midvein xylem area (or average leaf area, insert). (b) Relationship between average stomatal area and midvein xylem area (or average leaf area, insert). (c) Covariation of plant total stomatal number and stem xylem area (or total leaf area, insert). (d) Relationship between minor vessel area and stem xylem area (or total leaf area, insert). Lines indicate significant scaling relationships. Growth forms: T tree, S shrub, SS subshrub, $C+Sc$ scrambler or climber. Regression coefficients of standardized major axis (SMA) are documented in Table 1.

Furthermore, plant total stomatal number strongly scaled with plant minor vessel number (slope = 1.51, $r^2 = 0.62, P < 0.001$; Fig. 5a); while the average area of stomata and minor vessels did not show any relation with each other ($r^2 = 0.05$, $P > 0.05$; Fig. 5b) (Table 1).

Fig. 5 (a) Covariation of plant total stomatal number and plant minor vessel number. (b) Relation between average stomatal area and average minor vessel area. Lines indicate significant scaling relationships. Growth forms: T tree, S shrub, SS subshrub, $C+Sc$ scrambler or climber. Regression coefficients of standardized major axis (SMA) are documented in Table 1.

Discussion

Woody seedlings are a convenient life stage to acquire water conductance parameters at the whole-plant level because of their size advantage, even though patterns of seedlings may could not completely reflect the water relation in adult woody plants. Nevertheless, how woody seedlings regulate water relations, in terms of the xylem-stomatal covariation, is important for their survival and growth into adulthood. Based on an anatomical analysis across ontogenetically comparable seedlings of 53 diverse woody species (Table S1), we have presented here key new findings on xylem-stomata coordination from a previously neglected aspect: we started from the water balance between the liquid (water delivery) and vapor (water loss) phase at the whole-plant level by scaling plant total stomatal area to stem xylem (conductance) cross-sectional area (Fig. 2; Table 1). This area-scaling pattern was driven by the covariation of stomata numbers and minor vessel numbers per plant (Fig. 5a; Table 1). We then zoomed in on the water exchange in individual leaves by showing the coordination of leaf total stomatal area and midvein xylem area (Fig. 3; Table 1). We also found that plant size (or leaf size) scales with stomatal (or minor vessel) number, while it does not scale with individual stomatal (or minor vessel) area (Fig. 4; Table 1), which has an important implication for our understanding of the design of xylem structure and stomatal distribution.

Convergent size coordination of stomata and xylem from whole-plant level to single-leaf level

The convergent size coordination of stomata and xylem in the case of entire plants and individual leaves implies that individual leaves have a tight control over the whole-plant water conductance (Fig. 2; Fig. 3; Table 1). Previously we showed, based on the same seedling populations, that the xylem vessels widen basipetally from the tip to the base for both single leaf (midvein) and the whole plant (stem) and that the remarkably tight covariation in vessel diameter between different organs (especially between leaf and stem) (Zhong *et al.* , 2019). When we now combine all three findings, we can conclude that natural selection has led to rather tight regulation of water-related architecture featuring similar size-driven variation across seedlings of diverse woody species, both for single leaves and entire plant individuals. Their xylem vessels widen basipetally from the tip to the base, from leaves to the entire individuals, in a way that maintains a constant leaf-specific conductance (Sterck & Zweifel, 2016, Zhong *et al.* , 2019) and a constant xylem-stomatal size scaling. Using hydraulic properties of single leaves to predict the entire plant water transport is an alternative choice, as numerous studies have done (Brodribb *et al.* , 2017, Carins Murphy *et al.* , 2014, Meinzer, 2002), especially when the conductance-related parameters of entire plants are difficult to acquire, for example in adult trees. Specifically, knowing leaf size (i.e. leaf area) is of the utmost importance, not only to predict photosynthetic productivity precisely (Li *et al.* , 2020), but also to understand plant water transport (Echeverría *et al.* , 2019), from the single leaf, to the branch, to the whole-tree, and even to the forest level.

The slopes of the ln-scaling regression lines between stomatal and xylem traits are notably larger than the slope of 1 (Fig. 2; Fig. 3; Table 1), which means that stomata do not scale linearly to xylem but exponentially.

In actual fact, it should be the stem xylem conductance area, rather than stem xylem area, that scales with the total stomatal area, while we gave the pattern for both in order to enable comparison with a previous study which used the same seedling population (Zhong et $al.$, 2019). In that study, the total leaf area (LA) scaled with stem xylem area (X_{stem}) at mid stem height as LA [?] $X_{stem}^{1.25}$ (Zhong et $al.$, 2019). Together with isometric scaling of leaf area and total stomatal area, we could elicit that total stomatal area should scale with X_{stem} with an exponent approximating 1.25. Our finding in the current paper (exponents 1.29 and 1.30 for entire plants and individual leaves respectively) is in line with this theoretical prediction. When considering the total water path length (e.g. by sampling the anatomical cross-section at the stem base), our results are in line with our prediction that there should be isometric scaling both between total leaf area and xylem conductance area and between total stomatal conductance area and xylem conductance area (see also Echeverriaet $al.$, 2019, Fiorin et $al.$, 2016, Lechthaler et $al.$, 2019, Meinzer & Grantz, 1990). Further studies are needed to integrate the relations between leaf area, stomatal area and xylem conductance area from the perspective of the (3-dimensional) water transport system from single-leaf level to whole-plant level. Ideally, such studies should be carried out also on adult woody plants and across different biomes.

Number coordination of stomata and minor vessels and its implication

We also found strong covariation between terminal xylem vessel number and stomatal number per plant (Fig. 5a; Table 1). That is: in order to ensure the balance between liquid- and vapour-phase water conductance, convergent scaling exists between total stomatal area and xylem area, both at the entire plant and at individual leaf level; and this area-scaling pattern was driven by the covariation of stomata numbers and minor vessel numbers per plant.

These findings provide empirical support for, as well as a better functional understanding of the xylem structure models and have broad implications for integrating xylem widening (Anfodillo et $al.$, 2006, Olson, Anfodillo, Rosell, Petit, Crivellaro, Isnard, Leon-Gomez, Alvarado-Cardenas & Castorena, 2014, Zhong et $al.$, 2019) and stomatal distribution; these linkages are illustrated in Fig. 1. Further studies on plant water relations should incorporate the transport mechanism of water from the minor vein xylem vessels to stomata with xylem architecture.

Conclusion

Woody seedlings across ecologically and morphologically wide-ranging species modulate the balance between the vapor (water loss) and liquid (water delivery) phase, via a convergent allometric covariation of xylem area and total stomatal area from entire individuals to individual leaves. Having a sufficient number of stomata relative to the minor vein xylem number is imperative for ensuring the force (generated by evaporation through stomata) of water delivery (through xylem vessels). The whole-leaf and whole-plant allometric relationships related to water transport and export in this study deepen our understanding of the vascular structure models and has broad implications for integrating xylem architecture and stomatal distribution across species.

Acknowledgements

Author contributions

JHCC, BELC, PC-D and J-PP carried out the experimental work. JHCC, BELC, PC-D, J-PP and MYZ gathered the data. MYZ and JHCC conceived the present study and designed the analyses. MYZ analyzed the data and wrote the first draft of the manuscript, and all authors made important suggestions on at least two drafts of the manuscript.

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Fig.1 Conceptual framework of this research concerning allometric relations of plant hydraulics across woody species. Natural selection acts on heritable variation between individuals within the same species. Individuals with vessels that do not widen with height growth, or widen little, will experience continual declines in leaf-specific conductance with height growth and therefore declining growth and reproductive output per unit leaf area. Individuals with vessels that widen very markedly would have conduits of low resistance, in contrast to the high-resistance variants with conduits that are 'too narrow', but they would have their own set of disadvantages. For example, for a given leaf area and transpirational demand, the wider conduits cost more for the same service provided. Each unit of carbon invested in excessively wide vessels is a unit that is not invested in further growth or reproduction, and so these variants should be at a selective disadvantage (Banavar, Cooke, Rinaldo & Maritan, 2014). Moreover, wider vessels are more vulnerable to gas embolisms that obstruct conductance, both from freezing ((Sevanto, Holbrook & Ball, 2012, Zanne, Tank, Cornwell, Eastman, Smith, FitzJohn, McGlinn, O'Meara, Moles, Reich, Royer, Soltis, Stevens, Westoby, Wright, Aarssen, Bertin, Calaminus, Govaerts, Hemmings, Leishman, Oleksyn, Soltis, Swenson, Warman & Beaulieu, 2014) and likely drought as well (Cai & Tyree, 2010, Jacobsen, Pratt, Venturas & Hacke, 2019, Liu, Gleason, Hao, Hua, He, Goldstein & Ye, 2019). As a result, plants with vessels that are 'too wide' would also be at a selective disadvantage (Zhong *et al.* (2019)). The variants that should have the largest amounts of surplus carbon to devote to growth and reproduction are those in the intermediate zone, in which conduits widen just enough that conductance remains constant per unit leaf area, but not so much as to incur excessive carbon costs and embolism vulnerability.

In our previous study, based on the same woody seedling populations, we found that, at the whole-plant level, the stem xylem cross-sectional area (X_{stem}) of stem medium (a) closely scales with stem height (H) and total leaf area per plant (LA) asX_{stem} [?] H $^{1.52}$ andX_{stem} [?] LA $^{0.75}$ across all the studied species. For individual leaves, vessel diameter (D $_{leaf}$) in the medium of leaf midvein (b) closely scales with average leaf area (MLA) as$D$ $_{leaf}$ [?] MLA $^{0.21}$ (Zhong*et al.* (2019). In this study, we test the poorly understood xylem-stomata covariation from the size perspective We ask: are there scaling relationships between total stomatal area and xylem cross-sectional area across species, at the entire plant and at individual leaf level? Specifically, we zoom in on the terminal part of water exchange (from minor vessels to stomata), and ask: does the minor vessel number (which scales with leaf area; see (Lechthaler *et al.* , 2019, Rosell & Olson, 2019)) scale with stomatal number per leaf and per plant across these woody seedlings? The conceptual picture should deepen our understanding of plants' water transport system and have broad implications for integrating xylem architecture and stomatal distribution.Fig. 2 Size-covariation of stomata and xylem at the whole plant level, across seedlings of 53 European woody species varying in leaf-habit, growth-form and relative growth rate (RGR). (a) Convergent scaling of plant total stomatal area and stem xylem transect area. (b) Convergent scaling of plant total stomatal area and stem xylem conductance area. Lines indicate significant scaling relationships. Growth forms: *T* tree, *S* shrub, *SS* subshrub,*C+Sc* scrambler or climber.

Regression coefficients of standardized major axis (SMA) are documented in Table 1.

Fig. 2 Size-covariation of stomata and xylem at the whole plant level, across seedlings of 53 European woody species varying in leaf-habit, growth-form and relative growth rate (RGR). (a) Convergent scaling of plant total stomatal area and stem xylem transect area. (b) Convergent scaling of plant total stomatal area and stem xylem conductance area. Growth forms: *T* tree, *S* shrub, *SS* subshrub, *C+Sc* scrambler or climber. Regression coefficients of standardized major axis (SMA) are documented in Table 1.

Fig. 3 Convergent scaling of leaf total stomatal area and midvein xylem transect area, across seedlings of 53 European woody species varying in leaf-habit, growth-form and relative growth rate (RGR). Lines indicate significant scaling relationships. Growth forms: *T* tree, *S* shrub, *SS* subshrub, *C+Sc* scrambler or climber. Regression coefficients of standardized major axis (SMA) are documented in Table 1.

Fig. 4 (a) Covariation of leaf total stomatal number and midvein xylem area (or average leaf area, insert). (b) Relationship between average stomatal area and midvein xylem area (or average leaf area, insert). (c) Covariation of plant total stomatal number and stem xylem area (or total leaf area, insert). (d) Relationship between minor vessel area and stem xylem area (or total leaf area, insert). Lines indicate significant scaling relationships. Growth forms: *T* tree, *S* shrub, *SS* subshrub, *C+Sc* scrambler or climber. Regression coefficients of standardized major axis (SMA) are documented in Table 1.

Fig. 5 (a) Covariation of plant total stomatal number and plant minor vessel number. (b) Relation between average stomatal area and average minor vessel area. Lines indicate significant scaling relationships. Growth forms: *T* tree, *S* shrub, *SS* subshrub, *C+Sc* scrambler or climber. Regression coefficients of standardized major axis (SMA) are documented in Table 1.

Table 1. Ln – Ln scaling relationships were analyzed with standardized major axis regression (SMA) analyses, with additional reference to the contributions of different growth forms, leaf habits and relative growth rates (RGRs) to these relationships. Y-intercept and slopes as well as slope homogeneity with 1 are reported for pairwise relationships with significant results. 95% confidence intervals (CI) are in parentheses. Growth-form: *T* tree, *S* shrub, *SS* subshrub, *C+Sc* scrambler or climber; Leaf-habit: *D* deciduous, *E* evergreen. Y/X – RGR SMA regression of Y/X (ratio of Y values to X values) and RGR. ***, $P < 0.001$; **$P < 0.05$; ns, not significant.

Model	Intercept (95% CI)	Slope (95% CI)	r^2 (P)	Slope.test= 1 r (P)	Y~X+ Leaf habit (P)	Y~X+ Leaf habit (P)	Y~X + Growth form (P)	Y~X + Growth form (P)	Y/X – RGR (P)
					Slope homogeneity	Elevation homogeneity	Slope homogeneity	Elevation homogeneity	
Plant total stomatal area ~ Stem xylem area	2.52 (0.50, 4.55)	1.29 (1.14, 1.47)	0.81***	0.51***	ns	ns	ns	ns	ns

Model	Intercept (95% CI)	Slope (95% CI)	r^2 (P)	Slope.test= 1 r (P)	Y~X+ Leaf habit (P)	Y~X+ Leaf habit (P)	Y~X + Growth form (P)	Y~X + Growth form (P)	Y/X – RGR (P)
Plant total stomatal area ~ Stem xylem conductance area	3.76 (1.70,5.82)	1.22 (1.06, 1.41)	0.77***	0.39**	ns	ns	ns	ns	ns
Leaf total stomatal area ~ Midvein xylem area	4.78 (3.16, 6.39)	1.30 (1.13, 1.49)	0.79***	0.50***	ns	ns	ns	ns	ns
Leaf total stomatal number ~ Midvein xylem area	-1.48 (-3.09, 0.13)	1.32 (1.16, 1.51)	0.79***	0.53***	ns	ns	ns	ns	ns
Leaf total stomatal number ~ Average leaf area	5.38 (5.02, 5.74)	0.97 (0.91, 1.04)	0.94***	-0.12ns	ns	ns	**	–	ns
Stomatal cell area ~ Midvein xylem area	8.08 (7.47, 8.68)	-0.22 (-0.30, 0.17)	0.01 ns	–	–	–	–	–	–
Stomatal cell area ~ Average leaf area	6.93 (6.66, 7.20)	-0.16 (-0.22,-0.13)	0.006ns	–	–	–	–	–	–
Plant minor vessel number ~ Stem xylem area	-2.73 (-3.86, -1.61)	0.88 (0.79, 0.98)	0.87***	–	ns	**	ns	**	**

Model	Intercept (95% CI)	Slope (95% CI)	r^2 (P)	Slope.test= 1 r (P)	Y~X+ Leaf habit (P)	Y~X+ Leaf habit (P)	Y~X + Growth form (P)	Y~X + Growth form (P)	Y/X – RGR (P)
Plant minor vessel number ~ Total leaf area	3.17 (2.24, 4.10)	0.69 (0.57, 0.83)	0.62***	–	ns	**	ns	ns	**
Minor vessel area ~ Stem xylem area	4.91 (4.08, 5.74)	-0.23 (-0.31, -0.17)	0.003ns	–	–	–	–	–	–
Minor vessel area ~ Total leaf area	3.46 (3.04, 3.88)	-0.19 (-0.25, -0.14)	0.01ns	–	–	–	–	–	–
Plant total stomatal number ~ Plant minor vessel number	0.19 (-2.10, 2.47)	1.51 (1.25, 1.82)	0.62***	–	ns	ns	ns	–	ns
Stomatal cell area ~ Minor vessel area	3.48 (2.71, 4.24)	1.22 (0.91, 1.62)	0.05ns	–	–	–	–	–	–

Table S1 Growth-form, Leaf-habit and seedling traits of the 53 studied woody species. Growth-form: *T* tree, *S* shrub, *SS* subshrub, *C+Sc* scrambler or climber; Leaf-habit: *D* deciduous, *E* evergreen. *RGR* relative growth rate (dataset could be found in Cornelissen *et al.* (1996)). Majority part of these datasets -*Stem xylem area* , *Leaf (midvein) xylem area* , *Total leaf area* and *Average leaf area* - could be found in (Zhong *et al.* , 2019). The dataset of *average stomatal area* could be found in (Cornelissen, Cerabolini, Castro-Díez, Villar-Salvador, Montserrat-Martí, Puyravaud, Maestro, Werger & Aerts, 2003b). The entire dataset of this research was provided here for easy access.

Species	Growth form	Leaf habit	RGR	Plant total stomatal area (μm^2)	Leaf total stomatal
Acer platanoides	T	D	0.0755	223804929	106603260
Acer pseudoplatanus	T	D	0.0808	186377155	89310035
Aesculus hippocastanum	T	D	0.0935	2537142026	253714203
Alnus glutinosa	T	D	0.1106	23416451	8519951
Arbutus unedo	T	E	0.0919	14208189	3830456
Berberis vulgaris	S	D	0.0844	21345164	5157241

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Species	Growth form	Leaf habit	RGR	Plant total stomatal area (μm^2)	Leaf total stomatal
Betula pendula	T	D	0.1280	8928559	3989847
Buddleja davidii	S	D	0.2000	66779051	11589874
Buxus sempervirens	S	E	0.0579	14440719	3759371
Calluna vulgaris	SS	E	0.0541		82431
Castanea sativa	T	D	0.0746	659912449	173246507
Cornus sanguinea	S	D	0.1028	56448859	14903255
Corylus avellana	S	D	0.1309	597659121	99609853
Crataegus monogyna	S	D	0.1059	59703754	11651733
Cytisus scoparius	S	E	0.0918	41138286	5072802
Empetrum nigrum	SS	E	0.0587	2220093	261786
Fagus sylvatica	T	D	0.0412	304853187	152426594
Frangula alnus	S	D	0.1164	38324802	9223801
Fraxinus excelsior	S	E	0.1017	147861778	36789017
Hebe x franciscana	C+Sc	E	0.1025	12333030	3866248
Hedera helix	C+Sc	E	0.0257	68535534	29306295
Helianthemum nummularium	SS	E	0.1129		2941751
Hippophae rhamnoides	S	D	0.0744	37317548	5519993
Ilex aquifolium	T	E	0.0137	17026164	7218047
Juglans regia	T	D	0.0643	2186734626	838486789
Laburnum anagyroides	T	D	0.0824	62620395	18136573
Ligustrum vulgare	S	E	0.072	92734988	16910829
Lonicera periclymenum	C+Sc	D	0.0773	27182339	6170674
Malus sylvestris	T	D	0.1087	181004476	35085012
Prunus laurocerasus	S	E	0.0794	156932580	74277221
Prunus lusitanica	S	E	0.1001	113721032	36432187
Prunus spinosa	S	D	0.1416	345051252	40525534
Quercus cerris	T	D	0.0645	794869756	215056379
Quercus ilex ilex	T	E	0.0630	419506213	83111179
Quercus petraea	T	D	0.0615	320599019	67059123
Quercus robur	T	D	0.0472	446422644	87661045
Rhamnus alaternus	S	E	0.054	23379549	4553052
Rhamnus cathartica	S	D	0.0720	56354993	15417573
Rhododendron ponticum	S	E	0.0570		1111068
Ribes nigrum	S	D	0.1761	223802657	24133735
Ribes uva-crispa	S	D	0.1207	48489246	10525089
Rosa arvensis	C+Sc	D	0.1439	65827185	13143722
Rubus fruticosus	C+Sc	D	0.1778	127053969	18354321
Salix caprea	T	D	0.1913	24352804	4847936
Sambucus nigra	S	D	0.1393	181928719	43208882
Solanum dulcamara	C+Sc	D	0.2271		47749004
Sorbus aucuparia	T	D	0.1167	36145255	10221650
Thymus polytrichus	SS	E	0.1308		369414
Ulex europaeus	S	E	0.0781	32604769	3818019
Ulmus glabra	T	D	0.1200	240512411	60001258
Vaccinium myrtillus	SS	D	0.0524	1102862	277584
Vaccinium vitis-idaea	SS	E	0.0492	801863	201557
Viburnum opulus	S	D	0.0767	66860566	38275083