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Leaf economics and plant hydraulics drive leaf : wood area ratios

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Abstract

Biomass and area ratios between leaves, stems and roots regulate many physiological and ecological processes. The Huber value H_v (sapwood area/leaf area ratio) is central to plant water balance and drought responses. However, its coordination with key plant functional traits is poorly understood, which prevents developing trait-based prediction models.

Based on theoretical arguments, we hypothesise that global patterns in H_v of terminal woody branches can be predicted from variables related to plant trait spectra, i.e., plant hydraulics and size and leaf economics.

Using a global compilation of 1135 species-averaged H_v , we show that H_v varies over 3 orders of magnitude. Higher H_v are seen in short small-leaved low-SLA shrubs with low K_s in arid relative to tall large-leaved high-SLA trees with high K_s in moist environments. All traits depend on climate but climatic correlations are stronger for explanatory traits than H_v . Negative isometry is found between H_v and K_s , suggesting a compensation to maintain hydraulic supply to leaves across species.

This work identifies the major global drivers of branch sapwood/leaf area ratios. Our approach based on widely available traits facilitates the development of accurate models of aboveground biomass allocation and helps predict vegetation responses to drought.

Introduction

Plant growth and survival depend in large part on the traits of individual plant organs and on the partitioning of resources to these organs (Thornley 1972; Grime 1979; Tilman 1988; Westoby 1998). Hence, biomass partitioning integrates key physiological and ecological processes (Hunt & Cornelissen 1997; Shipley 2006; Poorter *et al.* 2015). At the global scale, the biomass ratios between leaves, stems and roots are known to be affected by abiotic factors such as temperature (Gill & Jackson, 2000; Lapenis *et al.*, 2005; Reich *et al.*, 2014a; Reich *et al.*, 2014b; Freschet *et al.*, 2017), light (Poorter *et al.* 2012, 2019), potential evapotranspiration (Ledo *et al.* 2017), soil water stress (Lapenis *et al.*, 2005; Poorter *et al.*, 2012) and nutrients (Poorter *et al.* 2012; Freschet *et al.* 2017), and biotic factors such as plant size (Poorter *et al.* 2015; Ledo *et al.* 2017). Biomass ratios globally have also been reported to vary among plant functional types, e.g., eudicots invest more in leaf tissues than monocots and gymnosperms more than angiosperms (Poorter *et al.* 2012; Duursma & Falster 2016). While global patterns in biomass ratios are beginning to be elucidated, how specific traits affect the partitioning among plant tissues is not well understood.

Functional balance and adaptive dynamics theories (Thornley 1972; Bloom *et al.* 1985; Franklin *et al.* 2012; Fariior *et al.* 2013) suggest that, over evolutionary time scales, partitioning should be regulated to guarantee access to the most limiting resource in competitive and variable

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environments. However, complications arise because plant size declines with reduced resource availability (Coleman *et al.* 1994; McCarthy & Enquist 2007), biomass partitioning varies with plant size (Enquist & Niklas 2002; Poorter *et al.* 2015), and because biomass ratios reflect both partitioning and turnover times (Thornley 1972; Gill & Jackson 2000; Reich 2002; Niinemets 2010). Additionally, hydraulic (Tyree & Ewers 1991) and biomechanical (Niklas & Spatz 2010) properties of stems depend on stem cross-sectional areas and their geometry, rather than their mass. Similarly, leaf gas exchange occurs *via* the leaf surface. Thus, in order to predict tissue partitioning, relationships between leaf and xylem cross-section areas should be considered in addition to mass ratios; indeed, links to water relations and plant hydraulics can only be understood this way.

To develop predictions of the area ratios between stem and leaves, we employ here the Huber value (xylem sapwood area / leaf area, H_v) of crown-top branches (Tyree & Ewers 1991). The H_v can be viewed as the ratio of investment in xylem area (i.e., excluding pith, heartwood, stem bark and phloem) over the expected gains obtained by leaf display and thus, it is an essential parameter in models of water use by vegetation (Mencuccini *et al.* 2019). It is employed to convert xylem-area specific conductivity K_s into a more physiologically meaningful variable, i.e., leaf-area specific conductivity K_L ($K_L = K_s H_v$), thereby linking the unit-area water flux through plants with the water potential gradient necessary to drive that flux. To facilitate understanding and prediction of H_v , we explore here the idea that H_v may be constrained by the functional properties of leaves and xylem, which in turn are dependent on climate and resource availability.

The need to build sufficient xylem hydraulic capacity to supply the canopy, given a certain distance between roots and leaves (Zimmermann 1983; Tyree & Ewers 1991), provides a first constraint; i.e., higher K_s may be required for thin and long stems to compensate pressure losses along a longer hydraulic pathway. A second trade-off comes from Corner's rules (Corner 1949). Corner's rules state that larger individual leaves are generally subtended by thicker stems and are more widely spaced in branches. While the second rule describes an axis of plant architectural variation, Corner's first rule relates to leaf packing, implying that for a given leaf area, the trade-offs between building many small leaves or few large ones have consequences for stem size (Westoby & Wright 2003; Kleiman & Aarssen 2007; Olson *et al.* 2009; Smith *et al.* 2017). A third trade-off relates to the partitioning towards leaf area construction in relation to the carbon returned by photosynthesis (Kikuzawa 1991; Reich *et al.* 1997; Wright *et al.* 2004; Shipley *et al.* 2006). The central trait mediating this trade-off is *SLA*, which is the ratio between radiation-intercepting leaf area and required mass investment (Niinemets 1999, 2001). Finally, wood density (*WD*) might control the amount of biomass investment in xylem cross-sectional areas. High *WD* increases

mechanical stiffness, resistance to breakage (Niklas & Spatz 2006; Chave *et al.* 2009) and cavitation (Hacke *et al.* 2001), but results in high carbon costs, especially for tall trees (Mencuccini 2003). Hence, the trade-offs between building thin terminal branches with dense wood or building thick branches with low density (Niklas & Spatz 2010) may have consequences for the ratios between xylem and leaf areas. Although some of the relationships highlighted above are employed in other plant leaf-seed-size spectra (e.g., Westoby 1998; Díaz *et al.* 2016; Hodgson *et al.* 2017; Pierce *et al.* 2017), the focus on hydraulic traits makes this global analysis distinctive. While Corner's rules do not distinguish between the components of branch cross-sectional area, H_v only considers tissues potentially involved in water transport. Additionally, because H_v is defined based on actively-conducting sapwood, turnover times of sapwood into heartwood are implicitly considered. Finally, although the H_v dataset reported here refers to samples of crown-top terminal branches only, variations in H_v within a plant canopy are relatively constrained (cf., review in Mencuccini *et al.* 2019).

Based on the considerations above, we develop a trait-based predictive model for H_v . As a starting point, we employ the definition of H_v ($\text{cm}^2 \text{m}^{-2}$) to partition the identity into component variables:

$$H_v = \frac{A_x}{A_{L,tot}} = \frac{A_x}{\sum A_L} = \frac{A_x}{SLA n M_L}, \quad (\text{Eqn. 1})$$

where A_x and $A_{L,tot}$ are xylem sapwood area (cm^2) and subtended leaf area (m^2), respectively. The capital sigma in the denominator indicates a summation over all leaves of a crown-top twig; A_L , M_L and SLA are mean area of a leaf (m^2), mean mass of a leaf (kg) and mean specific leaf area ($\text{m}^2 \text{kg}^{-1}$), respectively; n is the number of leaves in a branch of a given length. SLA is known to depend on light availability within tree crowns (e.g., Niinemets *et al.* 2015), while H_v reflects only conditions of canopy-top branches. Eqn. 1 predicts a negative scaling for H_v against both M_L and SLA , equivalent to slopes of -1 once variables are log-transformed. In practice, negative isometric scaling ($b=-1.00$) is not expected between these variables, because of, among other factors, non-zero covariances between M_L and SLA and between M_L and n . SLA and M_L act very distinctively with regard to how they might affect H_v . Doubling SLA halves H_v without changes in leaf biomass. Conversely, doubling M_L halves H_v by doubling leaf biomass. The presence of A_x in the numerator of Eqn. 1 suggest a size-dependency. To incorporate it, the potential hydraulic conductance of a plant can be expressed as $K_p = K_s A_x / H_{max}$, where K_p ($\text{kg MPa}^{-1} \text{s}^{-1}$), K_s ($\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$) and H_{max} (m) are potential plant hydraulic conductance, branch specific conductivity and plant maximum height (strongly related to maximum hydraulic path length), respectively. Conductance K_p is referred to as 'potential' because it does not

account for actual path length, only maximum height, and neglects reductions of water flow due to cavitation. We employ H_{\max} instead of actual plant height, because sampling heights are not available for the majority of our samples. Hence our results must be understood with regard to the effects of plant potential stature (i.e., maximum height), not actual height *per se*, on these relationships. We recognise that metabolic scaling theory (MST, West *et al.* 1999; Savage *et al.* 2010) provides suitable expressions for scaling against plant height. We do not employ quarter-power relationships, as our intention is not to test our global dataset against predictions from MST, but to explore the joint covariation of leaf economics, xylem and plant traits in relation to H_v . Substituting $K_p H_{\max} / K_s$ for A_x into Eqn.1 gives:

$$H_v = \frac{K_p}{n} \frac{H_{\max}}{SLA K_s M_L} \quad (\text{Eqn.2})$$

The first term on the right hand side of the equation contains the ratio K_p/n , the total stem hydraulic supply capacity to each leaf. Both K_p and n are dependent on stem diameter (Mencuccini 2002; Savage *et al.* 2010; Smith *et al.* 2017), while K_p/n is much less so (West *et al.* 1999). The second term on the right hand side of Eqn. 2 predicts a direct scaling of H_v with H_{\max} and an inverse scaling with K_s , SLA and M_L . The direct scaling of H_v with H_{\max} ensures that taller plants have greater relative allocation to xylem area to compensate for their stature (McDowell *et al.* 2002). This compensation is moderated by other processes; i.e., vertical conduit tapering (West *et al.* 1999; Anfodillo *et al.* 2006) and larger conduits at the apex of tall plants (Olson *et al.* 2014, 2018), both of which affect K_s . An inverse scaling of H_v with H_{\max} may thus also be obtained, if K_s scaled with H_{\max} more than proportionally. A negative scaling of H_v with H_{\max} may also be obtained if tall trees grow relatively less sapwood than shorter plants (for a given leaf area) to minimise sapwood construction and/or maintenance costs, instead of hydraulic resistance (Anfodillo *et al.* 2016; Fajardo *et al.* 2019). An inverse relationship between H_v and K_s is expected because of functional balance between water supply and demand (Whitehead & Jarvis, 1981; see derivation in the Supplementary Information, Methods S1) and it has been found empirically before for smaller datasets (Choat *et al.* 2011; Gleason *et al.* 2012).

Equations 1-2 express H_v in term of the constituent traits, thus providing a predictive reference framework for tissue partitioning based on organ-specific traits. Following Eqn.2, we test the hypotheses that the relative partitioning between sapwood area and leaf area (H_v) is affected jointly by leaf, xylem and plant traits. Specifically, we test the hypotheses that H_v declines with a) SLA and leaf size, b) xylem hydraulic efficiency K_s , but c) increases with maximum tree height H_{\max} . Additionally, we also test a hypothesis related to wood economics, i.e., that d) H_v declines with WD

(strictly, stem specific density). A negative relationship between H_v and WD may arise because of xylem carbon construction costs (cf., Supplementary Materials Methods S1 for in-depth discussion). Although WD is not employed in Eqns. 1 and 2, it allows pointing more precisely at additional physiological variables not explored in the analysis and it is a widely available trait. Because biomass ratios are known to vary with abiotic factors, we explore also e) whether this is the result of direct climatic effects on H_v as previously proposed (e.g., Mencuccini & Grace 1995) or whether they only act indirectly on the component traits. Finally, we tested a model excluding K_s from the set of traits employed to predict H_v . The advantage of excluding K_s is that it allows obtaining a model for H_v based only on widely available easy-to-measure traits, making it possible to employ global databases to predict sapwood-leaf area ratios. Overall, our analyses provide the first approximation to a framework explaining the variability in a difficult-to-predict allocation trait, based on standard leaf and xylem traits and plant stature. Understanding how partitioning between leaves and wood in terminal branches is jointly determined by leaf and wood properties is a significant step towards predicting how organ-level traits can affect global patterns of biomass partitioning and vegetation responses to drought.

Materials and Methods

Datasets

Measured values of crown-top branch H_v were obtained from a) an updated version of the hydraulic dataset by Choat *et al.* (2012) (i.e., XFT, xylem functional traits), including several new datasets from China, b) an Amazonian dataset from RAINFOR (Patiño *et al.* 2012), c) an Australian dataset (from Togashi *et al.* 2015) and d) an African/S. American dataset from TROBIT (Schrodt *et al.* 2015). Smaller datasets from China were obtained from (Niu *et al.*, 2017; Song *et al.*, 2018). The geographical distribution of sampling sites/species location is given in Fig.S1 and the biome distribution plot in Fig. S2. The RAINFOR and the TROBIT projects (accounting for ~50% of all H_v here) followed a single protocol for the measurement of leaf area, mass, xylem area, SLA and wood density (Patiño 2005). Specifically, 1-m-long top-canopy branches were sampled typically at the end of the rainy season (leaf phenology can be variable and is poorly predictable in the tropics, e.g., Wu *et al.*, 2016) from sun-exposed crowns of trees of diameter at breast height >10cm. Bark, heartwood if present, and xylem pith were visually excluded from xylem measurements. However, since dyes were not routinely used, hydraulically active xylem was not identified. For the hydraulic dataset (~50% of the entries), crown top samples were also typically collected. Units and protocols were

checked by experts, although study-to-study variability in sampling/measurement methods may be present in our sample (especially, regarding use of dyes and sample length). Measurements conducted on seedlings, inside greenhouses and those subjected to experimental treatments were excluded from this study. Values of wood specific conductivity K_s were obtained from the updated XFT, leaf economics traits (SLA , leaf lifespan LL), H_{max} and WD from XFT and Glopnet (Wright *et al.* 2004), (Patiño *et al.* 2012), (Schrodt *et al.* 2015) and/or TRY (Kattge *et al.*, 2011). Xylem vulnerability to embolism from XFT was employed for one analysis, for which r-shaped curves were excluded. Individual, one-sided projected leaf areas A_L were obtained from (Wright *et al.* 2017) and leaf masses M_L calculated by dividing A_L by SLA .

Information on genus-level woodiness, leaf habit, leaf type, leaf shape and plant growth form were obtained from the sources above or from (Zanne *et al.* 2014). When required, missing pieces of information were extracted by web scraping of wiki pages from Wikipedia (https://en.wikipedia.org/wiki/Main_Page), Encyclopaedia of Life (<http://eol.org/>), Flora of China (<http://www.efloras.org>) and Useful Tropical Plants (<http://tropical.theferns.info/>) using *xml2*, *rvest* and *httr* in R (R Core Team 2017). When a certain species was given different categories of growth form, we followed (Castorena *et al.* 2015) and classified the plant in the largest category (e.g., if the species was listed as shrub and tree, we classed the species as tree). The dataset was finally trimmed to the following levels for each categorical variable: woodiness (woody only), leaf habit (winter and drought-deciduous, evergreen), leaf shape (compound, simple), leaf type (needle leaf, broadleaf), plant habit (shrub, tree) and taxon group (Angiosperm, Gymnosperm). The final dataset contained 1135 species-averaged H_v values from 736 sites (1618 unique values when including lianas, vines, succulents and cacti). The other quantitative variables had somewhat lower coverage (i.e., >90% for SLA and WD , >70% for H_{max} and leaf size, 40% for K_s).

For each species record, species climatic envelopes were calculated with *speciesmap* (https://remkoduursma.github.io/speciesmap/articles/Using_speciesmap.html), an R package that combines species occurrences from GBIF (Global Biodiversity Information Facility, <http://www.gbif.org>), with climate layers from WorldClim (<http://www.worldclim.org>) and CGIAR-CSI, cf. Trabucco *et al.*, 2008). *speciesmap* rasterizes species occurrences and extracts 0.025, 0.5 and 0.975 quantiles for mean annual temperature (MAT), precipitation (MAP) and potential evapotranspiration (PET) across all grid cells of the species occurrence region. Converting the occurrence data into presence/absence grid cells equally weighs over- and under-sampled areas in the climate envelope estimates. Species classification into biomes was obtained from a Whittaker diagram of MAT and MAP (Wright *et al.* 2004). For those H_v measurements where

Latitude/Longitude were available from the original publications, we compared MAT/MAP at the sampling site against values obtained for the GBIF climate envelope (slope=0.96, $R^2=0.94$, $n=686$, and slope=0.90, $R^2=0.91$, $n=686$, for MAT and MAP, respectively; the slopes <1.0 suggest, as expected, a 4-10% underestimation of MAT/MAP from GBIF relative to local values). Because annual MAP/MAT values may be poorly related to relative water supply particularly during the growing season, a Moisture index (MI) was calculated as MAP/PET . To bring species binomials to a common taxonomy, names were matched against accepted names in The Plant List using *taxonstand* (Cayuela *et al.* 2012). Any binomials not found in this list were matched against the International Plant Names Index (IPNI; <http://www.ipni.org/>), eFloras and Tropicos (<http://www.tropicos.org>). The final list with unresolved species nomenclature was carefully checked manually.

Statistical analyses

To assess functional scaling between variables, bivariate relationships between H_v and other traits (SLA , M_L , K_s , H_{max} and WD) were summarised using standardised major axis (SMA) slopes using *smatr* (Warton *et al.* 2006). All traits were log-10 transformed to improve residual distribution and examine relationships across order of magnitude differences. Global scaling patterns (i.e., overall line slopes and intercepts $\pm 95\%$ confidence intervals) were obtained from the fitted regressions. Slopes were compared between categorical groupings by leaf type (broad/needle leaves), leaf shape (simple/compound) leaf habit (winter deciduous/drought deciduous/evergreen), plant growth form (shrub/tree) and taxon group (Angiosperm/Gymnosperm) using a likelihood ratio test (Warton *et al.* 2006). Where slopes were deemed not to significantly differ, we tested for intercept differences between the common-slope lines and/or shifts of the data clouds along the common-slope line using a Wald test with one degree of freedom (Warton *et al.* 2006).

Path models (SEM) were used to examine whether the hypothesised correlation structures were consistent with the observed multivariate relationships among traits determining H_v . We used the *sem* function in *lavaan* (Rosseel 2012) and followed Brown (2006) for model selection and diagnostics. SLA , M_L , H_{max} (in some models also WD and/or K_s) were allowed to co-vary with each other as they jointly affected H_v . To explore the possibility that these relationships were modulated by additional factors, we allowed for trait covariance to depend on additional categorical variables (i.e., leaf shape, leaf type, plant growth form and taxon group), included as fixed effects in some models. Directed climate effects (MAT, MAP, MI) on leaf, xylem traits and H_{max} were included in some models, together with directed climate effects on H_v . The saturated path models were simplified by removing non-significant paths (using z tests and ΔAIC values) until a minimal adequate

model was found. Goodness of fit was assessed using absolute fit, parsimony and comparative fit (Brown 2015). Full-information Maximum Likelihood allowed including species with partially missing traits. Finally, the path model coefficients were used to predict H_v based on organ-specific traits.

To test whether the relationships of organ traits with H_v were affected by leaf turnover times, the models above were modified to include leaf lifespan LL . Also, as an alternative, we employed leaf habit (deciduous/evergreen) in some models, because the sample size for LL ($n=105$ coupled values of LL and H_v) was much lower than for leaf habit. Leaf habit strongly relates to LL (t-test, $P=1.14 \cdot 10^{-10}$). Variation in LL is high among evergreen species, but the consequences for our interpretation are minimal because models with LL , leaf habit, or without are almost identical.

To check for the possibility that systematic biases were present across the original datasets (XFT; RAINFOR; TROBIT; Togashi *et al.*, 2015; Niu *et al.*, 2017; Song *et al.*, 2018), we treated these datasets as a random factor in a linear mixed model (*nlme*, Pinheiro & Bates, 2000). We modelled H_v as a function of leaf and xylem traits, by varying intercept and slope as a function of dataset. We tested the significance of the factor “dataset” by running an ANOVA comparison of the model accounting for dataset as a random factor against a simpler linear model without the random factor. The test showed that the simpler linear model was equally effective ($P=0.9998$). We therefore discard the possibility that systematic biases across pooled datasets can affect our conclusions, although we acknowledge that study-to-study variability within each dataset is likely. All analyses were carried out in R version 3.4.3 (R Core Team 2017).

Data accessibility

All data are archived and are available from the TRY plant trait data base: www.try-db.org (<https://doi.org/10.1111/j.1365-2486.2011.02451.x>).

Results

In bivariate analyses, H_v scales inversely and with similar correlation strength (r from -0.54 to -0.60) with each of the three leaf traits, i.e., SLA , individual leaf area A_L and individual leaf mass M_L (all $P < 2.2 \cdot 10^{-16}$, Figure 1A, B and C, Table 1). H_v also scales inversely with xylem specific conductivity K_s and plant stature H_{max} (Figure 1D and E, $r = -0.53$ and $r = -0.45$; both $P < 2.2 \cdot 10^{-16}$). Finally, H_v and WD are positively but poorly related (Figure 1F, $P=0.09$, $r=0.06$). In log10 scale, H_v varies over 3 orders of magnitude, much more than SLA (>1 order), slightly more than K_s and H_{max} (<3 orders), but less than leaf size (6 orders). Apart from a few gymnosperms, species with very high H_v are often

short shrubs with needle-like leaves in the Proteaceae, Ericaceae, and Asteraceae of the steppes/semi-deserts of South America or Australia. Those with very low H_v tend to be large-leaved tall tropical trees in a large number of families (esp., Fabaceae and Malvaceae) in either wet or dry forests. The scaling slope of H_v against SLA (- 1.93) is far steeper than -1.0 ($P < 2.2 \cdot 10^{-16}$). By contrast, the scaling slopes against M_L and A_L are significantly flatter than -1.0 ($b = -0.50$ and -0.44 , respectively; $P < 2.2 \cdot 10^{-16}$). The slopes against K_s and H_{max} are not significantly different from negative isometry (Table 1, $b = -1.04$ and $b = -0.96$, respectively).

Plant growth form (shrub/tree) and taxon group (Angiosperm/Gymnosperm) affect the magnitude but not the direction of these relationships (cf., Figure 1, Table S1). Relative to trees, shrubs are characterised by leaves with lower SLA , smaller A_L and M_L and by a xylem with lower K_s , while having a higher H_v (Figure 1). In contrast, Gymnosperms are shifted vertically downwards and tend to have lower H_v for a given SLA , leaf size but not K_s relative to Angiosperms (Table S1). For a given stature, shrubs are shifted downward and Gymnosperms upward, relative to Angiosperms. When LL is tested in bivariate relationships, it co-varies positively and significantly with H_v , but the relationship is weak ($P < 0.05$, $r = 0.28$). Similar results are obtained for leaf habit and H_v ($P < 0.01$, $r = 0.10$).

Many of the bivariate relationships between H_v , M_L , A_L , K_s , WD , H_{max} and SLA are affected by various categorical variables (Table S1). Regardless of the specific comparison, the inverse relationships between H_v and other traits are conserved, although low sample size makes the relationships non-significant for some groups (needle-like leaves, winter-deciduous plants). Generally, categorical variables related to leaf shape (simple/compound), leaf type (broad/needle leaves) and leaf habit (deciduous/evergreen) are associated with changes in the bivariate slopes between H_v and traits. Out of the possible 18 relationships, nine have heterogeneous slopes (cf., Table S1 for the P slope test values). In contrast, growth form (shrub/tree) and taxon group (Angiosperm/Gymnosperm) are only associated with elevation changes and shifts in data clouds along the common-slope lines (Tables 1 and S1).

SEM analyses (Table S2) confirmed that each of SLA , M_L , H_{max} and K_s contribute substantially ($SLA > M_L > K_s > H_{max}$) and independently to variation in H_v (Figure 2A). H_v remains negatively related to H_{max} , leaf (SLA , M_L) and xylem (K_s) properties, with this model being strongly supported ($P = 0.697$, Table S2; Figure 2A). All four traits strongly co-vary. In this and subsequent models, substituting A_L for M_L leads to almost identical results (data not shown).

We verified the robustness of the dependency of H_v against H_{max} , leaf and xylem traits, by incorporating one additional categorical variable (i.e., taxon group, plant growth form, leaf habit, leaf form, leaf shape) with effects on these traits. In no case do we find that the scaling of H_v against leaf/xylem traits disappears or is strongly altered (with the partial exception of the scaling of H_{max} , Figure S3). In all cases, the categorical variables affect the traits directly, while their effects on H_v are either very small (Fig. S3E) or non-significant (other panels in Fig. S3). Conversely, highly significant differences in H_v are always found across the levels of all these categorical variables using a general linear model (i.e., when trait effects on H_v are not accounted for; always $P < 0.0001$; data not shown). When LL is tested with the co-varying leaf/xylem traits, it is not found to be a contributor to H_v and it is excluded ($P \gg 0.05$). Similarly, despite its much larger sample size, leaf habit is not a significant contributor to H_v (Fig.S3C).

We also explored the robustness of these relationships to differences in climatic conditions, by incorporating MAT, MAP or MI across the species climatic envelopes (MAP and MAT are highly and positively correlated in our dataset, $P < 2.2 \cdot 10^{-16}$, $R^2 = 0.48$). Highly significant negative effects of MAT, MAP and MI are found when tested directly in correlations against H_v ($P < 2.2 \cdot 10^{-16}$, $r = -0.49$; $P < 2.2 \cdot 10^{-16}$, $r = -0.43$, and $P < 2.2 \cdot 10^{-16}$, $r = -0.28$, respectively). When examined within the network of trait relationships explaining H_v , all four plant traits (SLA , M_L , H_{max} and K_s) increase at higher MAT, MAP and MI. Interestingly, direct climatic effects on H_v are comparatively small or non-existent (Figure 3). In addition, the proportions of explained variance of H_v in models with the direct effects of climate on H_v are lower than the proportions for the model without climate (i.e., $r^2 = 0.48-0.50$ versus 0.54, when climate is versus when it is not included, respectively; cf., Fig.2A with Fig. 3). Importantly, the path coefficients from traits to H_v change minimally up or down compared to previous models.

Having examined the relationships between H_v and H_{max} , leaf and xylem traits, WD was included in the path models. WD co-varies with all four other traits and negatively affects H_v , contributing to increase the model r^2 for H_v from 0.54 to 0.57 (Table S2, Figure 2B). The direction of the effect of WD on H_v remains identical (and its magnitude similar) also with the inclusion of additional categorical variables (data not shown). Overall among all models, the best one explains 57% of the variance in H_v (Figure S4 and Table S2).

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Finally, we examined the performance of a model based only on widely available traits, i.e., excluding the trait with the lowest coverage (K_s) (Figure 4). A model based on SLA , M_L , H_{max} and WD explains almost the same amount of variance (i.e., 53%) as the one including xylem conductivity (54%) and somewhat less compared to the model with all five traits (57%, cf., Figures 2 and 4), but with comparable standardised root mean square residuals (SRMSR) (Tables S2 and S3).

Discussion

We provide evidence of consistent global scaling of H_v with plant stature, leaf and wood traits. We report relationships robust to the incorporation of climatic variables and major plant groupings, with the best model explaining close to 60% of the global-scale variability in H_v in a sample of >1,100 species. By comparison, a regression against MAT and MAP explains only 26% of the variance of H_v (data not shown). This result generalises findings previously reported based on smaller datasets, of relationships between H_v and/or K_s with SLA and/or WD (Stratton *et al.* 2000; Meinzer *et al.* 2004; Pickup *et al.* 2005; Gleason *et al.* 2012; Patiño *et al.* 2012), of H_v with H_{max} (Liu *et al.* 2019) and of a negative H_v - K_s relationship (Martínez-Vilalta *et al.* 2004; Choat *et al.* 2011; Togashi *et al.* 2015). Our findings can be employed to improve models' skills for the prediction of vegetation functions in biomes where a lack of empirical data currently limits the parameterization of plant hydraulic processes.

About 40% of the variance in H_v remains unaccounted for in our models. Part of this variance could be explained by variations in the factor K_p/n , which is incorporated in Eqn. 2 but is not quantified due to lack of data. Similarly, lack of size (A_x , distance from apex, sampling height) measurements prevent us from investigating additional constraints, such as axial variability in K_s . Methodological uncertainties for K_s (e.g., Espino & Schenk 2011) and study-to-study variability in the sampling strategy for H_v (leaf and xylem phenology; infrequent use of dyes) add to the same problem. A better understanding of H_v scaling within plants is essential to estimate how leaf/wood allocation can be scaled from branches to whole plants (Mencuccini *et al.* 2019).

Covariation between K_s and H_v in relation to leaf size and SLA

As hypothesised (Eqns. 1-2), H_v scales negatively against individual leaf mass M_L (Table 1, slope of ~ -0.5). Strictly speaking, Equation 2 predicts a scaling of -1.00 , although, as explained above, additional variables may affect this slope. Given the lack of information regarding these variables at the global scale, we refrain from interpreting the discrepancy between predicted and observed exponent of this relationship. It is tempting to explain the scaling between K_s and M_L (or A_L ; in both cases slope of ~ 0.5) as a consequence of the longer path length inside longer leaves, leading to greater conduit tapering and larger K_s down the branch. Such analysis should consider the potential covariations with all the other hydraulic variables (cf., Supplementary Information Methods S1 and Whitehead & Jarvis (1981)). The positive K_s - M_L slope almost exactly matches the negative H_v - M_L slope, effectively leading to an invariance of the product of these two variables (i.e., leaf specific hydraulic conductivity K_L , $K_L = K_s H_v$) across leaf sizes (data not shown). Changes in M_L impact on many other functional aspects, including proportion of supporting versus physiologically active tissues (Niinemets *et al.* 2007), radiation load and boundary layer conductances (Wright *et al.* 2017). Hence, it is remarkable that no trends are found in the relationship between M_L and K_L .

With regard to the H_v -SLA relationship, we find a negative slope, consistent with the negative scaling predicted by Eqns. 1-2. The steep slope (~ -1.9 , Table 1) implies a more-than-proportional decline in H_v with SLA. Similar to the case above, K_s scales positively against SLA with a slope that is so steep (slope of ~ 1.6 , Table 1) to effectively negate the negative scaling of H_v . Hence the increase of K_s with SLA balances the decline of H_v with SLA, again leading to no relationship between SLA and leaf-specific conductivity K_L (data not shown). Although the processes leading to these specific scaling exponents are not known, their consequences are apparent. Stomatal conductance and unit-area photosynthetic rates are positively associated with hydraulic capacity in leaves and stems (Mencuccini 2003; Brodribb *et al.* 2004; Santiago *et al.* 2004; Scoffoni *et al.* 2016). All else being equal, high SLA leads to lower H_v (Figs. 1 to 4). Hence, without the compensation between K_s and H_v (keeping K_L constant), high-SLA leaves would paradoxically be associated with lower hydraulic capacity and lower unit-area gas exchange, whereas observations show that SLA is unrelated to unit-area photosynthetic rates (Wright *et al.* 2004, 2005). The general result is that high-SLA (or “acquisitive”) leaves are necessarily associated with larger canopy areas (for a given investment in sapwood area), while an absolute increase in xylem K_s helps maintain hydraulic supply to the larger canopy (cf., SI Methods S1). While SLA values obtained from TRY may reflect conditions of partial canopy shading (Keenan & Niinemets 2016), this is unlikely to lead to different conclusions.

Overall, cross-species changes in H_v against either M_L or SLA are compensated for by changes in K_s . This is confirmed both by the scaling of H_v directly against K_s (negative isometry, i.e., $b=-1.00$, Table 1, consistent with predictions from Eqns.1-2) and by the fact that the negative relationship between these two variables remains even after accounting for the covariance among traits (Figure 2). Therefore, covariation between H_v and K_s changes the cross-species balance between conductive areas and specific conductivity per unit area, maintaining similar levels of leaf hydraulic supply (proportional to K_L) with varying SLA and M_L . The existence of a compensation between these two hydraulic properties has been reported already (Ewers & Fisher 1991; Martínez-Vilalta *et al.* 2004; Choat *et al.* 2011; Togashi *et al.* 2015), but its significance at the global scale had not been realised. While a trade-off between hydraulic efficiency and safety prevents the occurrence of plants with high efficiency and high safety (Gleason *et al.* 2016), the negative isometric scaling between xylem efficiency and H_v separates high relative allocation to a hydraulically inefficient xylem from low allocation to xylem with high hydraulic efficiency. This is similar to the trade-off generally observed across wood types, i.e., from tracheid-based conifer wood to diffuse-porous and ring-porous angiosperm wood. Interestingly, the same scaling is seen also separately for angiosperms and gymnosperms. This compensation justifies a broadly constant leaf-specific hydraulic conductivity K_L with varying SLA , M_L , WD (cf., Table 1) and, as discussed later, plant stature. Other things being equal, a broadly constant K_L allows sustaining similar transpiration rates across species adopting contrasting hydraulic strategies in the same environment (Manzoni *et al.* 2013).

The regulation of H_v by leaf and xylem traits takes place via different processes. In the case of SLA , the regulation is assured partly by the mathematical link between these two variables at constant leaf biomass investment (Lloyd *et al.* 2013; Osnas *et al.* 2013). The association between SLA and H_v therefore links water transport traits to the ecological trade-offs behind LES traits. In the case of M_L , the regulation occurs because changes in M_L inevitably lead to changes in total mass investment in leaves, although reductions in leaf numbers n partly compensate increases in M_L . Therefore, the M_L - H_v effect is mediated via the effect of Corner's rules on leaf packing (Smith *et al.* 2017). Finally, in the case of the regulation of H_v by K_s , a compensation takes place between investment in thick but inefficient versus thin but efficient xylem. From this perspective, Corner's rules, LES and hydraulic supply to leaves are only partially connected with each other, at least at the global scale chosen for this analysis of species-specific traits.

The role of plant stature

Plant stature (i.e., H_{\max}) is negatively correlated with H_v . If the relationship between stature and Huber values was determined by gravity or the need to counter frictional losses during water transport, one would predict a positive effect (cf., Eqn.2). Indeed, this is typically observed within species (i.e., when H_v changes during development at constant H_{\max} ; McDowell *et al.* 2002). The occurrence of a negative isometric relationship suggests instead that stature brings about the need to reduce relative biomass allocation to sapwood, possibly as a consequence of sapwood carbon costs versus leaf gains (Mencuccini 2003; Niinemets 2010; Anfodillo *et al.* 2016; Fajardo *et al.* 2019). This may especially be the case under high competitive (i.e., closed canopy) conditions, where carbon balance may be less favourable (Togashi *et al.* 2015). Nonetheless, the correlation coefficient of H_{\max} with H_v is lower than for almost all other traits (Table 1). Equivalently, the standardised coefficient for H_{\max} is the lowest among the variables controlling changes in H_v in our path models (Figs. 2-4), suggesting that changes in stature are not strongly correlated with sapwood-leaf area ratios, when all the other variables are partialled out. This low correlation is likely caused by the covariation between H_{\max} and other leaf/xylem traits (Liu *et al.* 2019) and the compensation between H_v and K_s . In our path models, K_s is negatively related to H_v while it co-varies positively with H_{\max} , hence net size effects of H_{\max} on H_v are strongly reduced. The overall negative isometric scaling (slope of -1.00, cf., Table 1) between H_v and H_{\max} suggests that sapwood volume per unit of leaf area may be conserved across species. However, shrubs had a lower branch-top H_v than trees for a given H_{\max} and relationships for each growth form were steeper than negative isometry (Fig.1E, Table S1). The difference between these two growth forms may not have been found, had we examined the relationship of H_v with actual H as opposed to H_{\max} . Similarly, we did not attempt to employ scaling relationships explicitly accounting for vertical variability in hydraulics with height (e.g., Couvreur *et al.* 2018).

Isometric scalings were also found for K_s against H_{\max} (slope of +1.00) and H_v against K_s (slope of -1.00). Hence, a broadly constant branch-top leaf-specific hydraulic conductivity K_L is maintained (cf., West *et al.* 1999), despite the increasing stature of tall trees. This occurs *via* increases in specific conductivity (likely caused by increased canopy-top conduit diameters, Olson *et al.* 2014, 2018) and reductions in H_v , probably to avoid stature-related carbon costs (Mencuccini 2003). Plant stature also co-varies with M_L and with SLA , albeit less strongly. Compared to shrubs (most of them, from desert or woodland, not boreal, biomes), tall (mainly tropical) trees are characterised by larger leaves and, less consistently, leaves with high specific leaf area. This also contrasts with trends

occurring within individual trees, where leaf size and SLA strongly decline with height (Koch *et al.* 2004; Burgess & Dawson 2007).

The role of wood density

The negative association between WD and H_v was not predicted in our theoretical framework (Eqns.1-2) but is robust to the covariation with other organ-level traits, categorical and climatic variables. A mechanistic interpretation of the role of WD is complicated by its involvement in several processes (cf., discussion in Supplementary Materials Methods S1). The direct negative effect of WD on H_v most likely reflects a bio-mechanical / carbon cost trade-off between smaller but denser sapwood areas versus larger areas made up of cheaper wood. This trade-off is probably mediated by the relationships between WD and wood mechanical properties (Chave *et al.* 2009; Niklas & Spatz 2010). WD also acts indirectly via conduit size and packing (which leads to negative covariance of WD with K_s , cf., derivation in SI, Methods S1) and via its covariances with SLA and M_L . WD may also be linked to abundance of fibres, fibre wall thickness and parenchyma wood fractions (Ziemińska *et al.* 2015). We considered that WD may act on H_v via hydraulic safety. This analysis however shows no significant effect of P50 on H_v in a path model with the other traits (data not shown).

Climate and other moderating variables

Within species, H_v can respond to climatic conditions, e.g., radiation, site water balance, vapour pressure deficit and/or temperature (Mencuccini & Grace 1995; Delucia *et al.* 2000). We confirm these findings globally, with significant cross-species effects of MAT, MAP and MI on H_v . One of the most interesting results of our analysis is that, contrary to our initial hypothesis, direct climatic effects on H_v become non-significant or very small when the effects of MAT, MAP and MI are tested in a path model, accounting for indirect climatic effects via H_{max} and leaf/xylem traits. This finding suggests that evolutionary pressure by climate on H_v may largely occur via the component traits, e.g., reducing H_{max} , K_s , M_L and SLA under dry conditions.

Prediction of hydraulic traits for global models

Global models increasingly need to be parameterised with wood-to-leaf ratios and hydraulic traits (Fatichi *et al.* 2016; Matheny *et al.* 2017; Mencuccini *et al.* 2019), including H_v and K_s specific to different plant functional types. However, adequate parameterisation of hydraulic and biomass scaling in terrestrial biosphere models requires understanding how the relevant traits are integrated and co-vary with one another. A model for sapwood/leaf allocation based entirely on organ-specific traits has the advantage of increasing model consistency and avoid over-parameterization. The fact that the model including only four easily measured and widely available traits (SLA , M_L , H_{max} and WD) performs similarly to the models including the less available xylem efficiency K_s raises the possibility that H_v may be estimated globally from parameters already employed in models. Additionally, the negative isometric scaling between H_v and K_s is robust to several comparisons across potential grouping variables and to the covariation with other traits. Therefore, it may also be possible to predict K_s as a function of H_v , assuming a globally constant K_L .

Our conclusion that relative allocation to sapwood/leaf area can be explained via component traits is limited to the canopy-top branches where H_v was measured. Using the limited available data, Mencuccini *et al.* (2019) showed that, while varying from species to species, H_v tend to remain relatively constant from twig to trunk base. A constant sapwood-leaf ratio along the plant axis is consistent with metabolic scaling theory (West *et al.* 1999; Savage *et al.* 2010). However, neither the dataset we previous employed (Mencuccini *et al.* 2019), nor metabolic scaling theory account for light-dependent variation in traits within tree canopies. In addition, we employed species-level averages to estimate relationships between traits and H_v . A complementary approach would be to examine this scaling at ecosystem and biome scales, using available plot-level information on species distributions across biomes. Further investigations are required to determine the robustness of this approach for modelling H_v and other hydraulic traits in different plant functional types.

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Supporting Information.

Supporting Information may be found online in the Supporting Information section at the end of the article.

Table S1. Standardised Major Axis analyses of plant traits in relation to Huber Value.

Table S2. First path Model analysis of leaf and xylem traits in relation to Huber Value.

Table S3. Second path Model analysis of leaf and xylem traits in relation to Huber Value

Figure S1. Plot of the approximate sampling locations for Huber values.

Figure S2. Box-and-whisker plot of Huber values distribution by biome.

Figure S3. Results of the path model explaining Huber values based on traits and additional categorical variables.

Figure S4. Relationship between observed and predicted Huber values for the best-performing model.

Methods S1. Derivation of the inverse relationship between H_v and xylem specific conductivity K_s and effects of wood density on K_s

Table 1. Results of Standardised Major Axis analyses of the bivariate relationships among the plant traits affecting H_v .

X_2	X_1	Y-Intercept	95% CI of the elevation	Slope (95% CI)	95% CI of the slope	n	r	(P value)
H_v	<i>SLA</i>	2.126	2.021 / 2.231	-1.934	-2.041 / -1.833	1039	0.60	$<2.2 \cdot 10^{-16}$
H_v	A_L	0.874	0.824 / 0.923	-0.442	-0.470 / -0.416	822	0.60	$<2.2 \cdot 10^{-16}$
H_v	M_L	0.459	0.422 / 0.497	-0.497	-0.532 / -0.464	780	0.54	$<2.2 \cdot 10^{-16}$
H_v	K_s	0.481	0.432 / 0.531	-1.039	-1.126 / -0.960	448	0.53	$<2.2 \cdot 10^{-16}$
H_v	H_{max}	1.413	1.339 / 1.486	-0.963	-1.021 / -0.908	798	0.45	$<2.2 \cdot 10^{-16}$
H_v	<i>WD</i>	1.118	1.045 / 1.192	1.721	1.608 / 1.842	1018	0.06	0.09
K_s	<i>SLA</i>	-1.300	-1.450 / -1.151	1.601	1.458 / 1.758	397	0.35	$4.9 \cdot 10^{-12}$
K_s	A_L	-0.326	-0.415 / -0.236	0.494	0.438 / 0.557	218	0.48	$2.5 \cdot 10^{-13}$
K_s	M_L	0.145	0.075 / 0.215	0.557	0.492 / 0.632	208	0.45	$2.0 \cdot 10^{-11}$
K_s	<i>WD</i>	-0.667	-0.774 / -0.560	-1.673	-1.845 / -1.514	386	0.18	0.0006
K_s	H_{max}	-0.879	-0.994 / -0.764	1.004	0.913 / 1.104	316	0.30	$7.1 \cdot 10^{-8}$
M_L	<i>SLA</i>	-3.622	-3.943 / -3.300	4.101	3.802 / 4.424	780	0.30	$8.8 \cdot 10^{-14}$
M_L	A_L	-0.869	-0.896 / -0.842	0.911	0.896 / 0.927	780	0.98	$<2.2 \cdot 10^{-16}$
M_L	<i>WD</i>	-1.019	-1.170 / -0.867	-3.022	-3.277 / -2.787	746	0.18	$2.5 \cdot 10^{-5}$
M_L	H_{max}	-2.276	-2.481 / -2.071	2.173	2.026 / 2.330	598	0.48	$<2.2 \cdot 10^{-16}$
<i>SLA</i>	A_L	0.676	0.674 / 0.705	0.222	0.207 / 0.238	802	0.44	$<2.2 \cdot 10^{-16}$
<i>SLA</i>	<i>WD</i>	0.477	0.438 / 0.516	-0.956	-1.021 / -0.894	976	0.29	$6.4 \cdot 10^{-16}$
<i>SLA</i>	H_{max}	0.323	0.277 / 0.369	0.539	0.505 / 0.575	754	0.38	$<2.2 \cdot 10^{-16}$
<i>WD</i>	A_L	-0.060	-0.105 / -0.015	-0.296	-0.320 / -0.273	759	0.20	$9.3 \cdot 10^{-7}$
<i>WD</i>	H_{max}	0.236	0.179 / 0.293	-0.609	-0.652 / -0.569	722	0.23	$2.4 \cdot 10^{-10}$
A_L	H_{max}	-1.369	-1.568 / -1.169	2.260	2.116 / 2.414	638	0.53	$<2.2 \cdot 10^{-16}$

All variables are base-10 log-transformed. Formulas are given as: $X_2=f(X_1)$. Legend: CI, confidence intervals; H_v , Huber value; *SLA*, Specific Leaf Area; A_L , leaf area; M_L , leaf mass; K_s , xylem specific conductivity; H_{max} , maximum plant height; *WD*, wood density. Sample size (n), correlation coefficient (r) and probability level (P value) for each regression are also given.

Figure legends.

Figure 1. Bivariate plots of Huber Value H_v against other plant traits, i.e., A) specific leaf area (SLA), B) leaf area (A_L), C) leaf mass (M_L) and D) xylem specific conductivity (K_s), E) plant stature (H_{max}) and F) wood density (WD). All variables are base-10 log-transformed. Points are coloured to distinguish Gymnosperms (black triangles) from Angiosperms (circles), and among these, trees (red circles) from shrubs (blue circles). The thin black dashed line gives the overall model II regression scaling across all data points (cf., Table 1). Thick black, blue and red lines give separate scaling for the three respective groups. Statistics of the regressions and the comparisons among groups (shrub vs. trees; Angiosperms vs. Gymnosperms) are given in Supporting Information Table S1.

Figure 2. Results of the Path models explaining Huber Value (H_v) based on A) specific leaf area (SLA), leaf mass (M_L), plant stature (H_{max}) and xylem specific conductivity (K_s) or B) the same variables plus wood density (WD). Data from both angiosperms and gymnosperms are included. All variables are base-10 log-transformed. All coefficients are standardised. Green single-headed lines (and respective numbers) indicate positive relationships, red single-headed lines (and numbers), negative relationships (from cause to effect). Double-headed arrows (and numbers) indicate covariances among variables. The thicknesses of the lines are proportional to the intensity of the effect. Green numbers close to the rounded arrows around each rectangle give the proportion of unexplained variance for each model (values of 1 are given for the predictor variables). The difference between observed and modelled covariance structure is not significant in either of the two models based on a chi-square test ($P=0.697$ and $P=0.727$, respectively).

Figure 3. Results of the Path model explaining Huber values (H_v) based on specific leaf area (SLA), leaf mass (M_L), xylem specific conductivity (K_s), plant stature (H_{max}) and climatic variables. Plots give the relative fits for A) mean annual temperature MAT, B) mean annual precipitation MAP and C) moisture index MI (ratio of precipitation to potential evapotranspiration). All variables are log10-transformed. All coefficients are standardised to vary between 0 and 1. Green lines and numbers indicate positive relationships, red lines and numbers, negative relationships. Double-headed arrows indicate covariance among variables. The thicknesses of the lines are proportional to the intensity of the effect. Green numbers close to the rounded arrows around each rectangle give the proportion of unexplained variance for each model. Observed and modelled covariance structure were not significantly different in any of the models, based on a chi-square test ($P=0.461$, $P=0.227$ and $P=0.294$, respectively, from A–C).

Figure 4. Results of the Path model explaining Huber Value (H_v) based on specific leaf area (SLA), individual leaf mass (M_L), plant stature (H_{max}) and wood density (WD). All variables are base-10 log-transformed. All coefficients are standardised. Green single-headed lines (and respective numbers) indicate positive relationships, red single-headed lines (and numbers), negative relationships (from cause to effect). Double-headed arrows (and numbers) indicate covariances among variables. The thicknesses of the lines are proportional to the intensity of the effect. Green numbers close to the rounded arrows around each rectangle give the proportion of unexplained variance for each model (values of 1 are given for the predictor variables). The difference between observed and modelled covariance structure is not significant based on a chi-square test ($P=0.469$).













