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short title: Embolism resistance in herbs

Herbaceous angiosperms are not more vulnerable to drought-induced embolism than angiosperm trees

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One sentence summary

Herbs display a wide range of embolism resistance, and do not show pronounced embolism formation throughout the growing season.

Summary

The water transport pipeline in herbs is assumed to be more vulnerable to drought than in trees due to the formation of frequent embolisms (gas bubbles), which could be removed by the occurrence of root pressure, especially in grasses. Here, we studied hydraulic failure in herbaceous angiosperms by measuring the pressure inducing 50% loss of hydraulic conductance (P_{50}) in stems of 26 species - mainly European grasses (Poaceae). Our measurements show a large range in P_{50} from -0.5 to -7.5MPa, which overlaps with 94% of the woody angiosperm species in a worldwide, published dataset, and which strongly correlates with an aridity index. Moreover, the P_{50} values obtained were substantially more negative than the midday water potentials for five grass species monitored throughout the entire growing season, suggesting that embolism formation and repair are not routine and mainly occur under water deficits. These results show that both herbs and trees share the ability to withstand very negative water potentials without embolism formation in their xylem conduits during drought stress. In addition, structure-function trade-offs in grass stems reveal that more resistant species are more lignified, which was confirmed for herbaceous and closely related woody species of the daisy group (Asteraceae). Our findings could imply that herbs with more lignified stems will become more abundant in future grasslands under more frequent and severe droughts, potentially resulting in lower forage digestibility.

Terrestrial biomes provide numerous ecosystem services to humans, such as biodiversity refuges, forage supply, carbon sequestration and associated atmospheric feedbacks (Bonan et al., 2008). Drought frequency and severity are predicted to increase across various ecosystems (Dai, 2013), and its impact on the fate of terrestrial biomes has aroused great concern for stakeholders over the past decade. For instance, world-wide forest declines have been associated with drought events (Allen et al., 2010), and the sustainability of grasslands - one of the most important agro-ecosystems representing 26% of the world land area - is threatened due to increasing aridity in the light of climate change (Tubiello et al., 2007; Brookshire and Weaver, 2015). Since the maintenance of grasslands is of prime importance for livestock, and several of the most valuable crops are grasses, herbaceous species deserve more attention from a hydraulic point of view to understand how they will cope with shifts in precipitation and temperature patterns.

During water deficit, hydraulic failure in trees has been put forward as one of the primary causes of forest decline (Anderegg et al., 2015, 2016). Drought exacerbates the negative pressure inside the water conducting cells, making the liquid xylem sap more metastable, and thus more vulnerable to air-entry (i.e., gas embolism; Lens et al., 2013). Extensive levels of embolisms may lead to desiccation, leaf mortality, branch sacrifice and ultimately plant death (Barigah et al., 2013; Urli et al., 2013). Plant resistance to embolism is therefore assumed to represent a key-parameter in determining the drought tolerance of trees and is estimated using so-called vulnerability curves (VCs), from which the P_{50} - i.e. the sap pressure inducing 50% loss of hydraulic conductivity - can be estimated (Cochard et al., 2013). P_{50} values are therefore good proxies for drought stress tolerance in woody plants and have been published for hundreds of angiosperm and gymnosperm tree species (Delzon et al., 2010; Choat et al., 2012), illustrating a wide range from -0.5 to -19MPa (Larter et al., 2015).

Studies focusing on P_{50} values of herbs are limited to stems of circa 14 angiosperm species (see Table S1 and references cited therein). Half of the herbaceous angiosperms studied so far (see Table S1) have a stem P_{50} between 0 and -2MPa, indicating that many herbs are highly vulnerable to embolism. Moreover, positive root pressure has been reported in various herbs – including many grasses (Poaceae) with hydathodes in their leaves (Evert, 2006) – and root pressure is hypothesised to refill embolized conduits overnight when transpiration is low (Miller et al., 1985; Neufeld et al., 1992; Cochard et al., 1994; Macduff and Bakken 2003; Saha et al., 2009; Cao et al., 2012). This could suggest that embolism formation and repair follow a daily cycle in herbs. In other words, the midday water potential that herbs experience in the field may often be more negative than P_{50}, which would result in an extremely vulnerable hydraulic pipeline characterised by a negative hydraulic safety margin (expressed as the minimum midday water potential - P_{50}). In contrast to herbs, most trees operate at a slightly positive hydraulic safety margin (Choat et al., 2013), and woody plants are often too tall to allow refilling by positive root and/or pressure in the upper stems (Ewers et al., 1997; Fisher et al., 1997). It could therefore be postulated that herbaceous species possess a hydraulic system that is more vulnerable to embolism than that of woody species. In this study, we want to underpin possible differences in embolism resistance between stems of herbaceous and woody angiosperms.

The scarcity of P_{50} measures in herbaceous angiosperms – including grasses and herbaceous eudicots – is mainly due to their fragile stems and low hydraulic conductivity, making VCs technically more challenging. Using minor adaptations to existing centrifuge techniques (see Supplemental Text S1), we obtained a P_{50} stem dataset of 26 herbaceous angiosperm species (mainly grasses) from various collection sites in France and Switzerland. In addition, we compared our dataset with published data from woody (gymnosperm and angiosperm) species, confronted some of our herbaceous eudicot measurements with original P_{50} data from derived, woody relatives, and we performed anatomical observations in grasses to investigate a possible link between stem anatomical characters and differences in P_{50} among the species studied. Three main research questions are central in our paper: (i) are stems of herbaceous angiosperms more vulnerable to embolism than those of woody angiosperms?; (ii) do grasses operate with highly vulnerable, negative hydraulic safety margins?; and (iii) do grasses show structure-function trade-offs in their stems with respect to embolism resistance?

RESULTS AND DISCUSSION

Comparable P_{50} Range in Herbs Compared to Woody Species

Our herbaceous dataset including 26 angiosperm species reveals a broad range in P_{50} from -0.5MPa to -7.5MPa (Fig. 1). If we compare the overlap between the range of this herbaceous dataset and the range observed in a large, published woody dataset (including P_{50} values of 404 woody angiosperm and gymnosperm species, see Material and Methods, Table S2), 89% of the woody species fall within this 0.5-7.5MPa range. This P_{50} overlap further increases to 94% when only the woody angiosperms are taken into account (301 species). Since herbaceous species (N = 28, Spearman's r = 0.6003, P = 0.0007) as well as woody species (N = 124, Spearman's r = 0.6006, $P < 0.0001$) with a more negative P_{50} grow in drier environments (lower aridity index; Fig. 2), we expect that further sampling of herbs from (semi-)desert-like environments will further increase the P_{50} range towards more negative extremes. This would generate an even stronger overlap in P_{50} between herbaceous and woody plants. Generally, we find that herbaceous angiosperms (mean P_{50} = -2.93MPa, CV = 57%) are significantly more vulnerable to embolism than woody species, including angiosperms and gymnosperms (mean P_{50} = -4.07MPa, CV = 62%; $F_{1,441}$ = 7.64, P = 0.0059; Fig. S1). However, when splitting up the dataset into grasses (Poaceae, mean P_{50} = -3.37MPa, CV = 57%), herbaceous eudicots (mean P_{50} = -2.3MPa, CV = 43%), woody angiosperms (mean P_{50} = -3.57MPa, CV = 59%), and woody gymnosperms (mean P_{50} = -5.55MPa, CV = 55%), only the woody gymnosperms are different from the rest (Fig. 3, Tables S1 and S2), while the differences between grasses, herbaceous eudicots and woody angiosperms are not significant (Table S3); especially the similarity in stem P_{50} between grasses and woody angiosperms is remarkable (LS-Means differences P=0.98; Table S3). These results emphasise that both herbaceous and woody angiosperms share the ability to withstand low water potentials without experiencing embolism formation in their xylem conduits during water deficit (Fig. 3).

Hydraulic Safety Margins in Stems of Grasses are Positive

We assessed the range of native embolism in five grass species with a P_{50} between -3 and -4.5MPa from the Swiss field sites (Table 1). Therefore, we measured the midday leaf water potential throughout the entire growing season from April to October, and related these values with their VCs in order to estimate native embolism over the operating range of water potential. Interestingly, midday leaf water potentials in spring were substantially less negative than P_{50}, suggesting very low levels of native embolism (< 16% loss of hydraulic conductance; Tables 1, S4). This contradicts the general assumption that grasses undergo daily or short-term embolism/repair cycles during mild conditions. Furthermore, the most negative leaf water potential (Psi min), experienced by the plants during the driest period of the year (July), corresponded to low levels of native embolism in the stems, ranging from 10 to 22% loss of hydraulic conductance, which is far below 50% as defined by P_{50} (Table 1). Consequently, midday leaf water potential data in the five grass species studied show evidence for positive hydraulic safety margins varying from 1.40 to 2.19MPa (Table 1).

In summary, our data suggest that daily embolism/repair cycles in grasses are not the rule throughout the growing season, at least not in stems, despite ample evidence for positive root pressure in grasses (Neufeld et al., 1992; Cochard et al., 1994; Miller et al., 1995; Saha et al., 2009; Cao et al., 2012). The broad range in embolism resistance of the grasses studied, in combination with these low levels of native embolism in the moderately resistant grasses studied suggest that embolism refilling may play a less significant role for grasses than previously thought (Cao et al., 2012). In other words, our findings suggest that frequent cycles of xylem embolism and repair are not pronounced in grasses, which is in agreement with observations in woody plants (Wheeler et al., 2013; Sperry, 2013; Delzon and Cochard, 2014). If the Psi min monitoring in our five grass species studied could be confirmed in a broader sampling of herbaceous species, this would raise questions about the generally accepted role of root pressure in repairing embolised conduits. Root pressure may simply be a byproduct of nutrient absorption by roots, allowing water transport via a leaky hydraulic pipeline with hydathodes. Evidently, root pressure needs to be quantified in relation to P_{50} and midday leaf/stem water potentials across a broad sampling of herbaceous species to better understand this enigmatic phenomenon. Moreover, we should know more about the specific climatic conditions under which root pressure development is physically possible, since drought will decrease the soil water content (Table S4), making root pressure more challenging.

Despite the observed conservative nature of embolism/refilling cycles in the grass stems studied, Holloway-Phillips and Brodribb (2011) showed that *Lolium perenne* – one of our Swiss species studied – operates very close to its hydraulic limits based on whole leaf hydraulic data, suggesting a hydraulic decoupling between stem and leaves. While the stem P_{50} reaches -3.21MPa in the individuals we studied (Table S1), the authors found a vulnerable whole leaf P_{50} (leaf P_{50}: -1MPa; leaf P_{95}: -2.2MPa), and complete stomatal closure happened very late at -2.35MPa. In other words, while our stem observations for *Lolium perenne* indicate no or low levels of native embolisms throughout the growing season in combination with a positive safety margin, leaf hydraulic measures suggest much narrower or even negative hydraulic safety margins. This contradicting result could be explained by recent papers on leaf hydraulics, showing that the observed decrease in hydraulic conductance in needles and leaves is not due to xylem embolism but rather to a conductivity drop in the extra-xylary pathway (Bouche et al., 2016; Scoffoni, personal communication). This suggests that there are no robust assessments of leaf vulnerability to embolism so far, but it is expected that the new optical technique developed by Brodribb et al. (2016) will shed new light into better understanding the hydraulic connection between stems and leaves.

Embolism Resistance in Herbs Comes at a Lignification Cost

Based on our 20 herbaceous species for which we have anatomical observations (mainly based on internode cross sections of grasses; Tables S1, S5, S6), Fig. 4 shows that the more resistant herbs have a higher proportion of lignified tissue in their stems (*P* =

0.0066, partial $R^2 = 0.40$; Figs. 4 a-d) and develop thicker cell walls in the fibres of this lignified zone ($P = 0.0005$, partial $R^2 = 0.57$; Figs. 4 a-c, e). When only the grass dataset is analysed, the relative proportion of lignified tissue becomes marginally significant ($P = 0.0457$, partial $R^2 = 0.32$), while the relative proportion of cell wall per lignified fibre remains highly significant ($P = 0.0014$, partial $R^2 = 0.62$; Table S6). Therefore, we argue that developing embolism resistant stems in herbs requires upregulation of the energy-consuming lignin pathway, which is a costly process. The relative size of the pith, and the hydraulically weighted (metaxylem) vessel diameter did not significantly contribute to variation in P_{50}. Likewise, there was no trade-off between P_{50} and the intervessel pit membrane thickness between adjacent metaxylem vessels in vascular bundles of six selected grass species, which ranged from on average 131nm in *Lolium perenne* to 313nm in *Elytrigia repens* ($F_{1,4} = 0.03$, $P = 0.87$). This is unexpected considering the strong evidence for functional relevance of intervessel pit membrane thickness amongst woody angiosperms (Jansen et al., 2009; Lens et al., 2011, 2013; Li et al., 2016).

The distribution pattern of lignified tissues between grasses and herbaceous eudicots is completely different. In grasses, lignification is mainly confined to the outer parts of the stems along the entire axis (Fig. 4A–C), and is related to provide mechanical strength and perhaps also to avoid water loss during periods of drought. Lignification in the herbaceous eudicots, however, is concentrated in the narrow wood cylinder at the base of the stem (Lens et al., 2012ab; Kidner et al., 2016; Fig. S2A, B). Our anatomical dataset, including mainly grass species, shows that lignification scales positively with embolism resistance. The link between increased embolism resistance and increased lignification has also been experimentally demonstrated in the herbaceous eudicot *Arabidopsis thaliana* (Lens et al., 2013; Tixier et al., 2013), in several transgenic poplars modified for lignin metabolism (Awad et al., 2012), and is further corroborated in this study by comparing the vulnerable, herbaceous daisies *Chamaemelum* (P_{50} -2.6MPa) and *Leucanthemum* (P_{50} -2.5MPa) with closely related members of the derived, more embolism resistant, woody genus *Argyranthemum* (P_{50} between -3 and -5.1MPa; Fig. S2A, C). Based on these observations, it seems that plants invest more energy resources to develop a mechanically stronger, embolism resistant stem (Lens et al., 2013), which is in agreement with previous studies linking embolism resistance with higher wood densities and thickness-to-span ratios of water conducting cells (Hacke et al., 2001), and thicker interconduit pit membranes (Jansen et al., 2009; Lens et al., 2011, 2013; Li et al., 2016). Likewise, intervessel pit membranes of the embolism resistant, woody *Argyranthemum* species are thicker than in the more vulnerable, herbaceous *Leucanthemum* and *Chamaemelum* (between on average 370-485nm vs 290-350nm, respectively).

However, more lignification/wood formation is not per definition needed to obtain a higher level of embolism resistance across flowering plants: the Gentianaceae sister pair *Blackstonia perfoliata* (herbaceous) and *Ixanthus viscosus* (woody) shows a similar P_{50} value (-4.5MPa), despite the marked difference in wood formation (Fig. S2B, D). Likewise, some other woody eudicot lineages that have evolved from herbaceous relatives grow in extremely wet environments, such as *Cyrtandra* (Cronk et al., 2005) or *Begonia* (Kidner et al., 2016). Also in ferns, where a thick ring of sclerenchyma fibres is located just below the epidermis of the leaf rachis – comparable to the situation in grass stems – no structural investment trade-offs in vulnerability to embolism were found (Watkins et al., 2010; Pittermann et al., 2011).

In conclusion, there is a remarkable range in P_{50} amongst 26 herbaceous species, overlapping with 94% of woody angiosperm species in a published dataset. The large variation in P_{50} in herbs and trees scales tightly with climatic conditions. Despite the potential refilling capacity by root pressure, embolism formation in grasses does not seem to be common throughout the growing season. This suggests that herbs and woody plants are more similar in their ability to avoid drought-induced embolism than previously expected, especially within the angiosperms. We also found that embolism resistance generally comes at a lignification cost in herbs. This could lead towards selection for species with more lignified stems in future grasslands that have to cope with more frequent and intensive droughts, potentially resulting in a lower forage digestibility.

MATERIAL AND METHODS

Sampling Strategy

In total, 26 herbaceous angiosperm species, including 18 grass species (family Poaceae) and eight eudicots, and four woody angiosperm species were investigated. Details about species and sampling sites are given in Supplemental Text S1 and Table S1. Canary Island species were collected in order to compare stem anatomy and P_{50} values of some of the herbaceous eudicots with closely related, woody descendants. Examples are *Argyranthemum* species that have evolved within the largely herbaceous daisy group including amongst others *Chamaemelum* and *Leucanthemum* (Fig. 1). Likewise, we studied *Ixanthus viscosus*, a woody Canary Island species that is derived from the herbaceous *Blackstonia* native to continental Europe (Lens et al., 2013; Fig. 1, Table S1). To expand the wood dataset, we used an updated version of the Xylem Functional Traits Database (Choat et al., 2012; Table S2 and references cited therein), in which we removed the angiosperms with long vessels and high P_{50} values (> -1MPa) to account for the vessel length artefact (Cochard et al., 2013), and adopted the P_{50} values with those published in Brendel and Cochard (2011) for 18 species that showed more than 40% intraspecific variation compared to other studies (mainly because of vessel length issues). In addition, we updated the wood dataset with more recent references and with four Canary Island species measured in this study (Table S2).

The variation in habitat among the herbaceous species and the adjusted dataset of Choat et al. (2012) was captured by the Julve index, an aridity index characterizing the edaphic humidity environment that was specifically designed for the French flora (Julve, 1998; http://perso.wanadoo.fr/philippe.julve/catminat.htm, download “French Flora Database (baseflor)”, column AD “Humidité_édaphique” corresponding to edaphic humidity). “Baseflor” is a floristic database indexing about 11,000 taxa from the French vascular flora. For each taxon, the database includes phytosociological characteristics and chorological, ecological and biological descriptions. In the “Baseflor” database, the Ellenberg’s “F”-values are modified to take into account the French ecological context of each taxon, describing xerophytic to aquatic species (from small to high values). The Julve index was documented for 28 herbaceous species and 124 woody species present in our datasets (Table S2).

Embolism Resistance Measurements

All the species were measured using the centrifuge technique. The static centrifuge technique (Alder et al., 1997) was applied when the conductance was too low (most of the grass species from France), while the cavitron (in-situ flow centrifuge) technique (Cochard et al., 2005) was used for the other species because the hydraulic conductivity was high enough (Table S1). Both centrifuge techniques are explained in

Supplemental Text S1, and S-shaped VCs were fitted according to a sigmoid function (Pammenter and Vander Willigen, 1998).

Leaf Water Potential Measures

For the species of the Swiss collection, midday leaf water potential was determined using a Scholander pressure chamber (SKPM, Skye instruments Ltd, Powys, UK) along the entire growing season 2015 (from April to October) between 11 a.m. and 1 p.m. on sunny days and every two weeks. Then, the minimum midday leaf water potential value experienced in the field for each species was used as minimum water potential (Psi min), which in all cases corresponded to the driest period of the year, i.e. in July.

Anatomical Observations

For all the French ($N = 20$) and Canary Island ($N = 4$) species, cross sections of three individuals per species were made at the level of the internodes according to resin embedding (Hamann et al., 2011) or standard wood sectioning (Lens et al., 2005), respectively, observed with the light microscope, photographed with a digital camera, and measured with ImageJ (Table S5). Details are given in the Supplemental Text S1. We also investigated intervessel pit membrane thickness based on transmission electron microscope (TEM) observations for six selected grass species from the French site with a P_{50} range between -0.5 and -6.2MPa (*Anthoxanthum odoratum*, *Brachypodium pinnatum*, *Elymus campestris, Elytrigia repens*, *Lolium perenne, Phalaris arundinacea*; stored in -20°C freezer before fixation, transverse sections through the nodes), and all the eight eudicot species belonging to the daisy and Gentianaceae lineage. After hydraulic measures, we immediately submerged the stems in Karnovsky fixative (Karnovsky, 1965), and followed the protocol explained in the Supplemental Text S1.

Statistics

The correlation between P_{50} and the aridity index (Fig. 2) was tested using Spearman correlation for herbaceous species ($N = 28$) and woody species ($N = 124$ species) separately (PROC CORR, in SAS Software, SAS University Edition). To assess differences between embolism resistance across plant groups (Fig. 3), we compared P_{50} variability (i) among angiosperms (including grasses, herbaceous eudicots, woody angiosperms) and gymnosperms, and (ii) between herbaceous species and woody species using General Linear Models (PROC GLM). For the first type of analysis (i), we used post-hoc least squares means using the 'Tukey-Kramer' approximation adapted for multiple comparisons with unbalanced sample sizes (Table S3).

We used multiple regression analyses (PROC REG) to test the contribution of anatomical features (independent variables) to P_{50} variability (dependent variable). Several of the anatomical features measured were correlated because many of them were merged to calculate additional traits. To select predictive factors, we screened for multi-collinearity by calculating variance inflation factors in multiple regression analyses (VIF option in PROC REG). This resulted in four predictive characters in our model: proportion of lignified tissues compared to entire stem diameter, proportion of pith compared to entire stem area, proportion of cell wall per fibre, hydraulically weighted (metaxylem) vessel diameter. The VIFs for the predictor variables in our regression model were <2, which indicates that multi-collinearity did not cause a loss of precision. This multiple regression model was applied independently to the 16 grasses and 20 herbaceous species for which we measured anatomical features (Tables S1, S5, S6). Finally, we tested the relationship between P_{50} and intervessel pit membrane thickness between metaxylem vessels in six grass species using a simple linear regression.

TABLES

Table 1. Embolism is not pronounced in grasses. Summary of hydraulic parameters for grasses from the Swiss collections, including mean leaf water potential during three time points in spring time (mean $\mathrm{Psi}_{\mathrm{midday}}$ during spring time), its corresponding native levels of embolism ($\mathrm{PLC}_{\mathrm{midday}}$, %), the minimum leaf water potential measured throughout the growing season (= $\mathrm{Psi}_{\mathrm{min}}$), and its corresponding PLC. Values are means ± 1 SE for n=6. More detailed information throughout the growing season is provided in Table S4.

Species	P_{50} (MPa)	Mean $\mathrm{Psi}_{\mathrm{midday}}$ in spring time (MPa)	Mean $\mathrm{PLC}_{\mathrm{midday}}$ in spring time (%)	$\mathrm{Psi}_{\mathrm{min}}$ (MPa)	PLC at $\mathrm{Psi}_{\mathrm{min}}$ (%)
Dactylis glomerata	-3.49	-1.47 ± 0.06	14.56 ± 0.67	-2.06 ± 0.14	22.30 ± 2.22
Lolium perenne	-3.21	-1.37 ± 0.03	15.80 ± 0.35	-1.81 ± 0.05	21.75 ± 0.73
Phleum pratense	-3.84	-1.24 ± 0.12	5.51 ± 0.86	-1.90 ± 0.10	10.49 ± 1.05
Poa pratensis	-3.65	species not yet growing	species not yet growing	-2.06 ± 0.15	11.06 ± 2.18
Agrostis capillaris	-4.50	-2.05 ± 0.15	8.98 ± 1.20	-2.31 ± 0.14	11.06 ± 1.20

FIGURE LEGENDS

Figure 1. P_{50} values of species measured. The range in P_{50} among the 26 herbaceous and 4 woody species studied varies from -0.5 up to -7.5MPa. Light green bars indicate grasses (Poaceae), dark green bars represent herbaceous eudicots and the orange ones are woody eudicot shrubs that have evolved from some of the herbaceous relatives studied (*daisy lineage, **gentian lineage). Each bar represents the average value for three specimens of the same species and error bars show SE.

Figure 2. P_{50} versus aridity index in herbs and woody species. Herbaceous as well as woody species that are more resistant to embolism formation (more negative P_{50}) grow in drier environments (lower aridity index; Julve, 1998). P_{50} values were averaged for each plant group every 2MPa (light green diamonds: grasses; dark green triangles: herbaceous eudicots; orange circles: woody angiosperms; brown triangles: woody gymnosperms). Error bars show SE.

Figure 3. Boxplots showing P_{50} range amongst different plant groups. There is a striking similarity in P_{50} between grasses, herbaceous eudicots, and woody angiosperms. On the other hand, woody gymnosperms have a statistically more negative P_{50} than each of the angiosperm groups. Mean values are shown with either a cross (grasses), triangle (herbaceous eudicots), circle (woody angiosperms) or plus sign (woody gymnosperms), 'a' and 'b' indicate statistical differences (Table S3).

Figure 4. Lignification and P_{50}. A-C, Cross sections of hollow stems through the internodes of the grasses *Phalaris arundinacea* (A, P_{50} = -0.5MPa)*, Lolium perenne* (B, P_{50} = -4.6MPa)*,* and *Brachypodium pinnatum* (C, P_{50} = -6.2MPa), showing more lignification in the outer zones of the stems (arrows), and thicker-walled fibres (inserts) with increasing P_{50}. D-E, Grasses and herbaceous eudicots that are more resistant to embolism have a higher proportion of lignified tissues in their stems (D) and thicker-walled fibres (E). Error bars show SE (only lower limits are presented for clarity purposes, each point represents the average value for three specimens of the same species). Marked zones apply to the 95% confidence limit of the regression. See Table S6 for multiple regression analysis of P_{50} and anatomical features as predictive variables.

Supplemental Data

The following supplemental data are available.

Supplemental Figure S1. Global P_{50} comparison between herbs and woody species.

Supplemental Figure S2. Differences in anatomy between herbs and related woody species.

Supplemental Table S1. P_{50} dataset of herbaceous species from our study and published papers.

Supplemental Table S2. Entire P_{50} and Julve dataset of woody and herbaceous species from our study and published papers.

Supplemental Table S3. Post-hoc comparisons of P_{50} LS-Means across species groups (see Fig. 3).

Supplemental Table S4. Hydraulic measures throughout the growing season for the five Swiss grass species.

Supplemental Table S5. List of the anatomical measurements carried out for the species in this study (3 replicates per species).

Supplemental Table S6. Multiple regression model of anatomical features as explaining factors of P_{50} variability in herbaceous species and grass species.

Supplemental Text S1. More detailed Material and Method descriptions about sampling strategy, embolism resistance measurements, and anatomical observations.

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LITERATURE CITED

Alder NN, Pockman WT, Sperry JS, Nuismer S (1997) Use of centrifugal force in the study of xylem cavitation. J Exp Bot 48: 665–674

Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg EH, Gonzalez P, Fensham R, Zhang Z, Castro J, Demidova N, Lim J-H, Allard G, Running SW, Semerci A, Cobb N (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecol Manag 259: 660–684

Anderegg WRL, Hicke JA, Fisher RA, Allen CD, Aukema J, Bentz B, Hood S, Lichstein JW, Macalady AK, McDowell N, Pan Y, Raffa K, Sala A, Shaw JD, Stephenson NL, Tague C, Zeppel M (2015) Tree mortality predicted from drought-induced vascular damage. Nature Geosci 8: 367–371

Anderegg WRL, Klein T, Bartlett M, Sack L, Pellegrini AFA, Choat B, Jansen S (2016) Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. Proc Natl Acad Sci USA 113: 5024–5029

Awad H, Herbette S, Brunel N, Tixier A, Pilate G, Cochard H, Badel E (2012) No trade-off between hydraulic and mechanical properties in several transgenic poplars modified for lignin metabolism. Environ Exp Bot 77: 185–195

Barigah TS, Charrier O, Douris M, Bonhomme M, Herbette S, Ameglio T, Fichot R, Brignolas F, Cochard H (2013) Water stress-induced xylem hydraulic failure is a causal factor of tree mortality in beech and poplar. Ann Bot 112: 1431–1437

Bonan GB (2008) Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science 320: 1444–1449

Bouche PS, Delzon S, Choat B, Badel E, Brodribb TJ, Burlett R, Cochard H, Charra-Vaskou K, Lavigne B, Li S, Mayr S, Morris H, Torres-Ruiz JM, Zufferey V, Jansen S (2016) Plant Cell Environ 39: 860–870

Brendel O, Cochard H (2011) In Y Birot, C Gracia, M Palahi, eds. Water for forest and people in the Mediterranean: a challenging balance, European Forest Institute, pp 76–80.

Brodribb T, Skelton RP, McAdam SAM, Bienaime D, Lucani CJ, Marmottant P (2016) Visual quantification of embolism reveals leaf vulnerability to hydraulic failure. New Phytol 209: 1403–1409

Brookshire ENJ, Weaver T (2015) Long-term decline in grassland productivity driven by increasing dryness. Nature Commun 6: 7148

Cao KF, Yang S-J, Zhang Y-J, Brodribb TJ (2012) The maximum height of grasses is determined by roots. Ecol Lett 15: 666–672

Choat B, Jansen S, Brodribb TJ, Cochard H, Delzon S, Bhaskar R, Bucci SJ, Feild TS, Gleason SM, Hacke UG, Jacobsen AL, Lens F, Maherali H, Martínez-Vilalta J, Mayr S, Mencuccini M, Mitchell PJ, Nardini A, Pittermann J, Pratt RB, Sperry JS, Westoby M, Wright IJ, Zanne AE (2012) Global convergence in the vulnerability of forests to drought. Nature 491: 752–755

Cochard H, Damour G, Bodet C, Tharwat I, Poirier M, Améglio T (2005) Evaluation of a new centrifuge technique for rapid generation of xylem vulnerability curves. Physiol Plant 124: 410–418

Cochard H, Badel E, Herbette S, Delzon S, Choat B, Jansen S (2013) Methods for measuring plant vulnerability to cavitation: a critical review. J Exp Bot 64: 4779–4791

Cochard H, Ewers FW, Tyree MT (1994) Water relations of a tropical vine-like bamboo (Rhipidocladum racemiflorum): root pressures, vulnerability to cavitation and seasonal changes in embolism. J Exp Bot 45: 1085–1089

Cronk QCB, Kiehn M, Wagner WL, Smith JF (2005) Evolution of Cyrtandra (Gesneriaceae) in the Pacific Ocean: the origin of a supertramp clade. Am J Bot 92: 1017–1024

Dai AG (2013) Increasing drought under global warming in observations and models. Nature Clim Change 3: 52–58

Delzon S, Cochard H (2014) Recent advances in tree hydraulics highlight the ecological significance of the hydraulic safety margin. New Phytol 203: 355–358

Delzon S, Douthe C, Sala A, Cochard H (2010) Mechanism of water-stress induced cavitation in conifers: bordered pit structure and function support the hypothesis of seal capillary-seeding. Plant Cell Environ 33: 2101–2111

Evert RF (2006) Esau's plant anatomy, meristems, cells, and tissues of the plant body: their structure, function, and development, 3rd edn, John Wiley & Sons, New Jersey.

Ewers FW, Cochard H, Tyree MT (1997) A survey of root pressures in vines of a tropical lowland forest. Oecologia 110: 191–196

Fisher JB, Angeles GA, Ewers FW, Lopez-Portillo J (1997) Survey of root pressure in tropical vines and woody species. Int J Plant Sci 158: 44–50

Hacke UG, Sperry JS, Pockman WT, Davis SD, McCulloh KA (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. Oecologia 126: 457-461

Hamann TD, Smets E, Lens F (2011) A comparison of paraffin and resin-based techniques used in bark anatomy. Taxon 60: 841–851

Holloway-Phillips M, Brodribb T (2011) Minimum hydraulic safety leads to maximum water-use efficiency in a forage grass. Plant Cell Environ 34: 302–313

Jansen S, Choat, B, Pletsers A (2009) Morphological variation of intervessel pit membranes and implications to xylem function in angiosperms. Am J Bot 96: 409–419

Julve P (1998) Baseflor. Index botanique, écologique et chorologique de la flore de France. Version Julve 2005-2014. http://perso.wanadoo.fr/philippe.julve/catminat.htm

Karnovsky MJ (1965) A formaldehyde-glutaraldehyde fixative of light osmolality for use in electron microscopy. J Cell Biol 27: 137A–138A

Kidner C. Groover A, Thomas D, Emelianova K, Soliz-Gamboa C, Lens F (2016) First steps in studying the origins of secondary woodiness in Begonia (Begoniaceae): combining anatomy, phylogenetics, and stem transcriptomics. Biol J Linnean Soc 117: 121–138

Larter M, Brodribb T, Pfautsch S, Burlett R, Cochard H, Delzon S (2015) Extreme aridity pushes trees to their physical limits. Plant Physiol 168: 804-807

Lens F, Tixier A, Cochard H, Sperry JS, Jansen S, Herbette S (2013) Embolism resistance as a key mechanism to understand plant adaptive strategies. Curr Opin Plant Biol 16: 287–292

Lens F, Sperry JS, Christman MA, Choat B, Rabaey D, Jansen S (2011) Testing hypotheses that link wood anatomy to cavitation resistance and hydraulic conductivity in the genus Acer. New Phytol 190: 709–723

Lens F, Davin N, Smets E, Del Arco M (2013) Insular woodiness on the Canary Islands: remarkable case of convergent evolution. Int J Plant Sci 174: 992–1013

Lens F, Dressler S, Jansen S, Van Evelghem L, Smets E (2005) Relationships within balsaminoid Ericales: a wood anatomical approach. Am J Bot 92: 941–953

Lens F, Eeckhout S, Zwartjes R, Smets E, Janssens S (2012a) The multiple fuzzy origins of woodiness within Balsaminaceae using an integrated approach. Where do we draw the line? Ann Bot 109: 783–799

Lens F, Smets E, Melzer S (2012b) Stem anatomy supports Arabidopsis thaliana as a model for insular woodiness. New Phytol 193: 12–17

Li S, Lens F, Espino S, Karimi Z, Klepsch M, Schenk HJ, Schmitt M, Schuldt B, Jansen S (2016) Intervessel pit membrane thickness as a key determinant of embolism resistance in angiosperm xylem. IAWA J 37: 152–171

Macduff JH, Bakken AK (2003) Diurnal variation in uptake and xylem contents of inorganic and assimilated N under continuous and interrupted N supply to Phleum pratense and Festuca pratensis. J Exp Bot 54: 431–444

Miller DM (1985) Studies of root function in Zea mays: III. Xylem sap composition at maximum root pressure provides evidence of active transport into the xylem and a measurement of the reflection coefficient of the root. Plant Physiol 77: 162–167

Neufeld HS, Grantz DA, Meinzer FC, Goldstein G, Crisosto GM, Crisosto C (1992) Genotypic variability in vulnerability of leaf xylem to cavitation in water-stressed and well-irrigated sugarcane. Plant Physiol 100: 1020–1028

Pammenter NW, Vander Willigen CA (1998) mathematical and statistical analysis of the curves illustrating vulnerability to cavitation. Tree Physiol 18: 589–593

Pittermann J, Limm E, Rico C, Christman MA (2011) Structure–function constraints of tracheid-based xylem: a comparison of conifers and ferns. New Phytol 192: 449–61

Saha S, Holbrook NM, Montti L, Goldstein G, Knust Cardinot G (2009) Water relations of Chusquea ramosissima and Merostachys claussenii in Iguazu national park, Argentina. Plant Physiol 149: 1992–1999

Sperry JS (2013) Cutting-edge research or cutting-edge artefact? An overdue control experiment complicates the xylem refilling story. Plant Cell Environ 36: 1916–1918

Tixier A, Cochard H, Badel E, Dusotoit-Coucaud A, Jansen S, Herbette S (2013) Arabidopsis thaliana as a model species for xylem hydraulics: does size matter? J Exp Bot 64: 2295–2305

Tubiello FN, Soussana JF, Howden SM (2007) Crop and pasture response to climate change. Proc Natl Acad Sci USA 104: 19686–19690

Urli M, Porté AJ, Cochard H, Guengant Y, Burlett R, Delzon S (2013) Xylem embolism threshold for catastrophic hydraulic failure in angiosperm trees. Tree Physiol 33: 672–683

Watkins JE, Holbrook NM, Zwieniecki MA (2010) Hydraulic properties of fern sporophytes: consequences for ecological and evolutionary diversification. Am J Bot 97: 2007–2019

Wheeler J, Huggett B, Tofte A, Rockwell FE, Holbrook NM (2013) Cutting xylem under tension or supersaturated with gas can generate PLC and the appearance of rapid recovery from embolism. Plant Cell Environ 36: 1938–1949

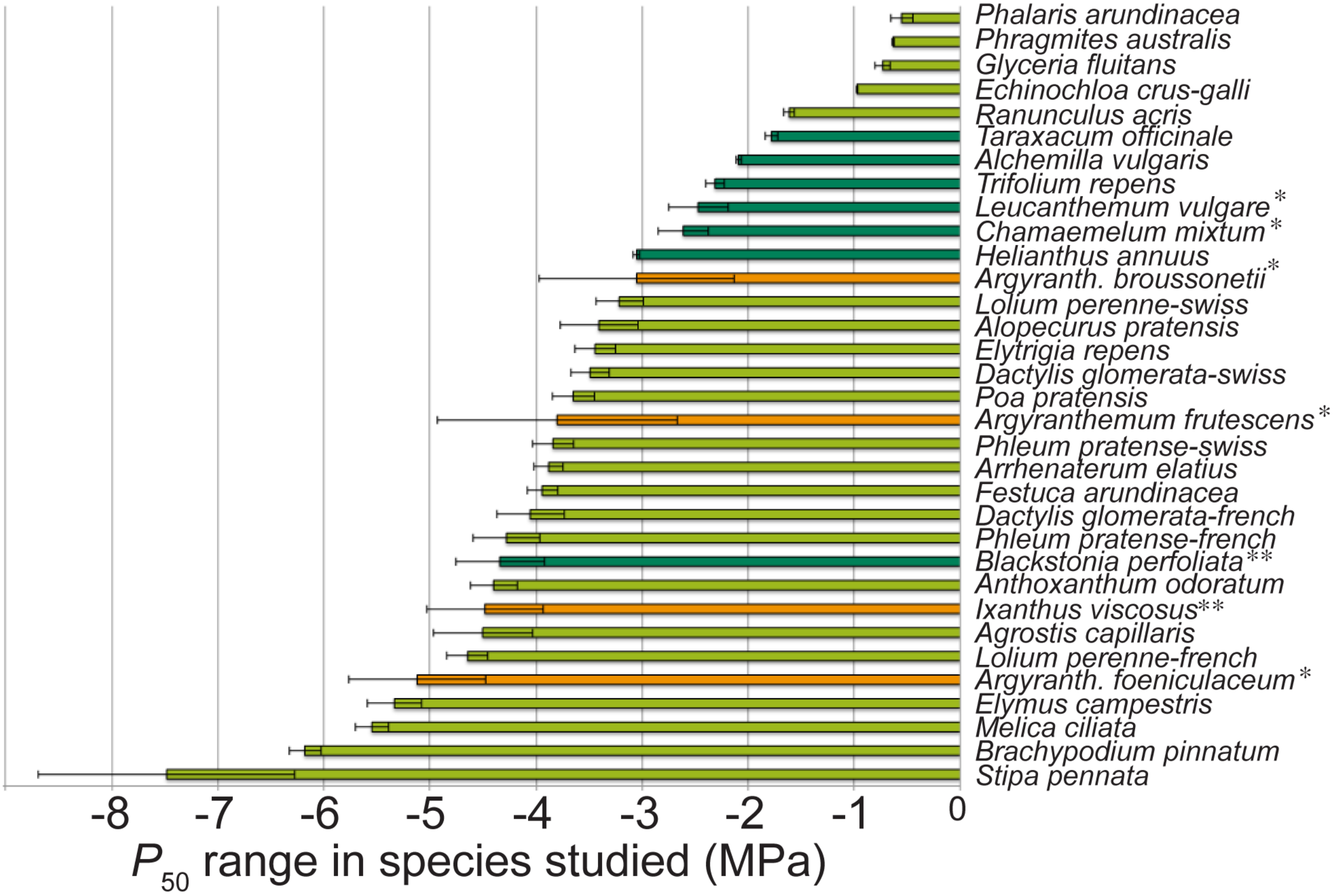

Figure 1. P50 values of species measured. The range in P50 among the 26 herbaceous and 4 woody species studied varies from -0.5 up to -7.5MPa. Light green bars indicate grasses (Poaceae), dark green bars represent herbaceous eudicots and the orange ones are woody eudicot shrubs that have evolved from some of the herbaceous relatives studied (*daisy lineage, **gentian lineage). Each bar represents the average value for three specimens of the same species and error bars show SE.

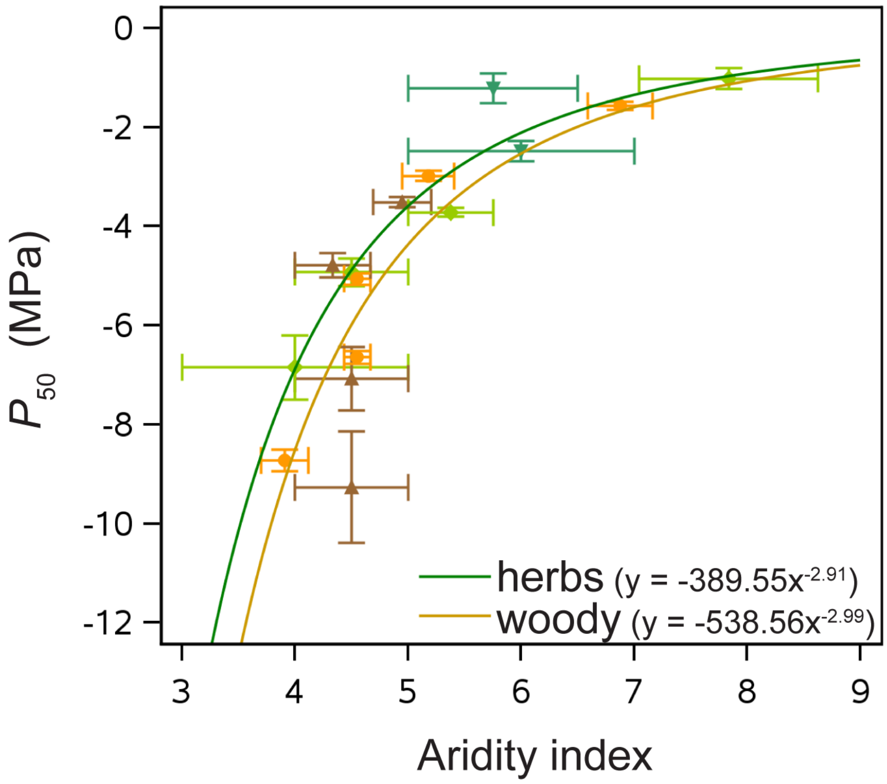

Figure 2. P50 versus aridity index in herbs and woody species. Herbaceous as well as woody species that are more resistant to embolism formation (more negative P50) grow in drier environments (lower aridity index; Julve, 1998). P50 values were averaged for each plant group every 2 MPa (light green diamonds: grasses; dark green triangles: herbaceous eudicots; orange circles: woody angiosperms; brown triangles: woody gymnosperms). Error bars show SE.

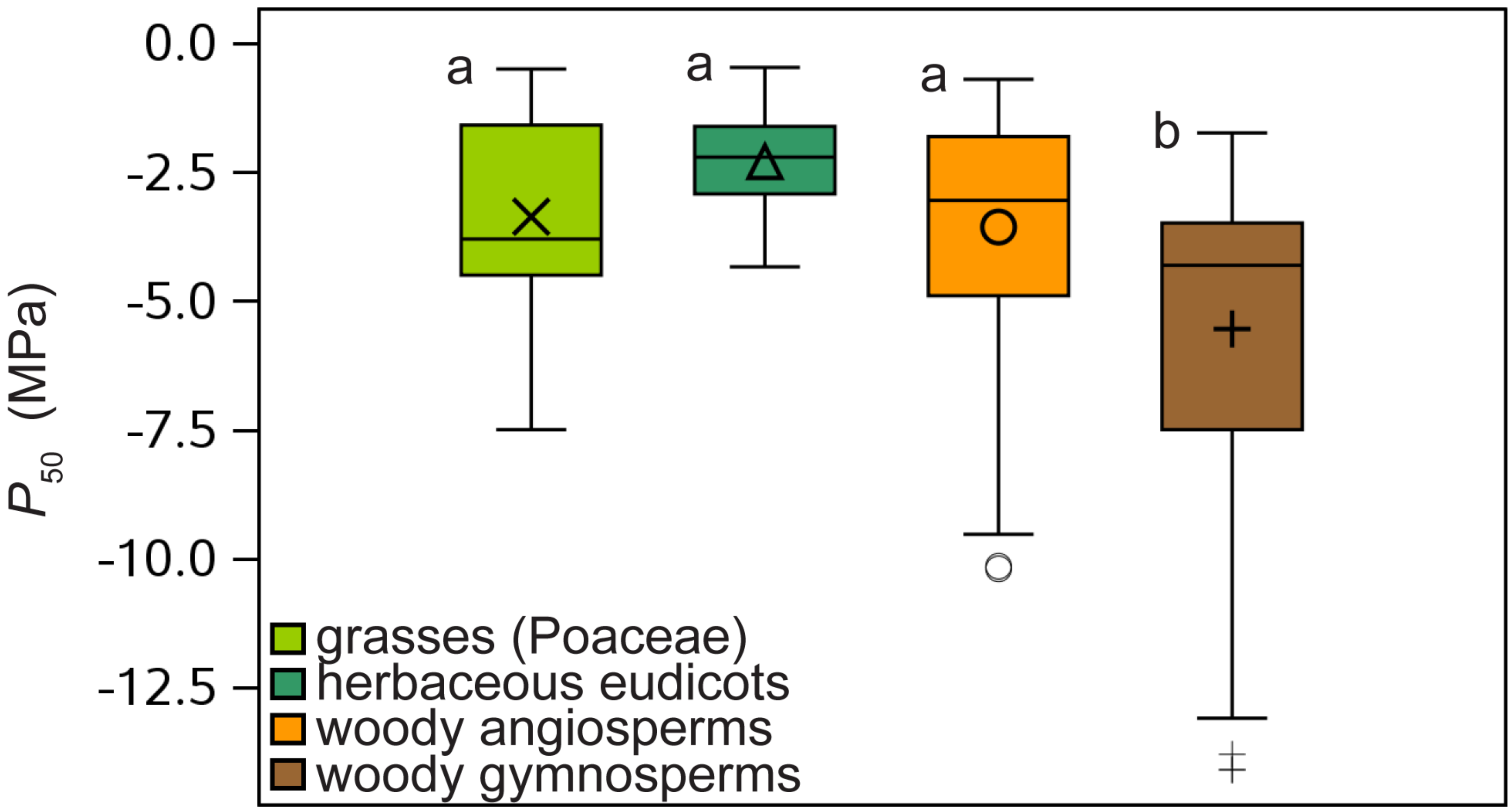

Figure 3. Boxplots showing P50 range amongst different plant groups. There is a striking similarity in P50 between grasses, herbaceous eudicots, and woody angiosperms. On the other hand, woody gymnosperms have a statistically more negative P50 than each of the angiosperm groups. Mean values are shown with either a cross (grasses), triangle (herbaceous eudicots), circle (woody angiosperms) or plus sign (woody gymnosperms), ‘a’ and ‘b’ indicate statistical differences (Table S3).

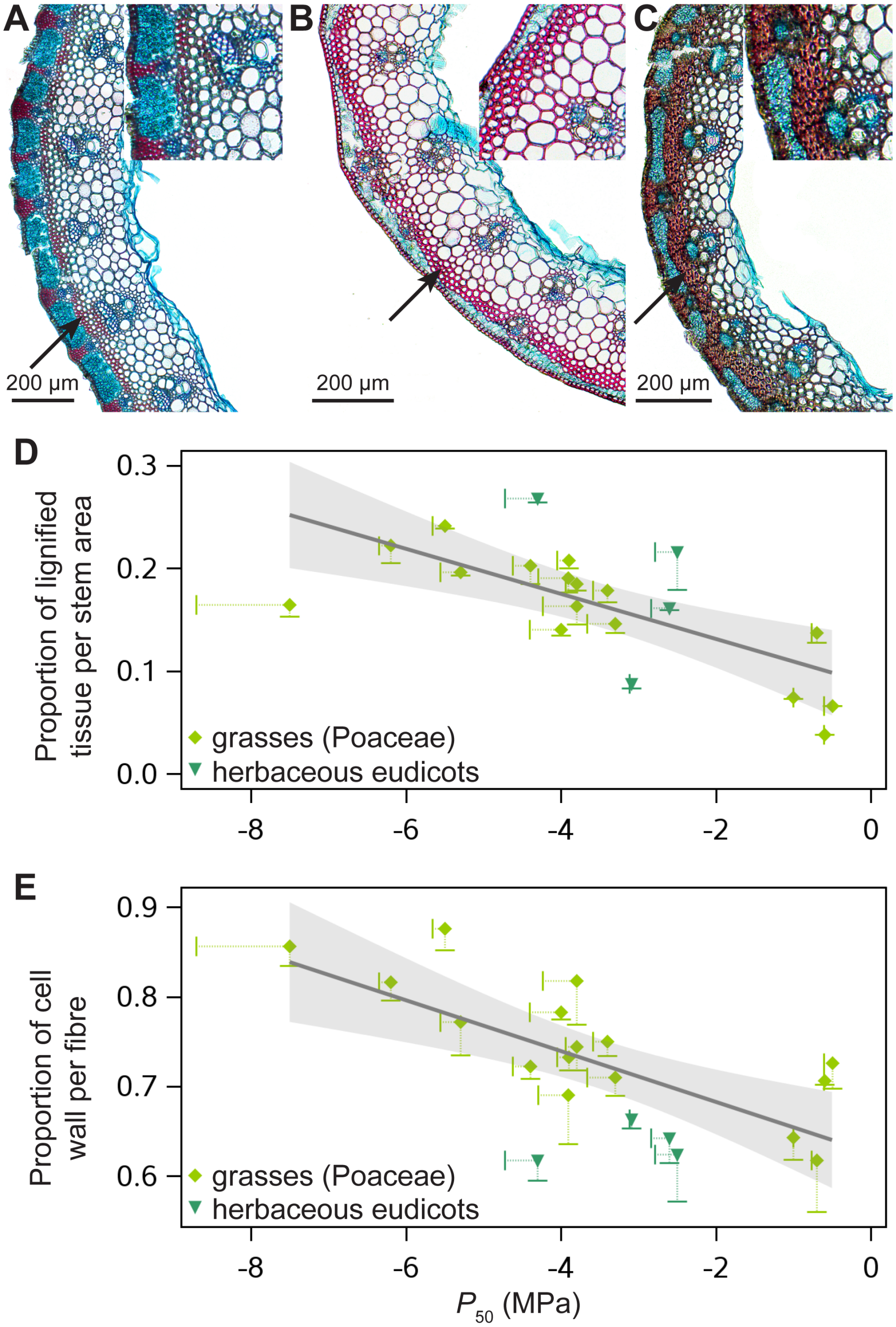

Figure 4. Lignification and P50. A-C, Cross sections of hollow stems through the internodes of the grasses Phalaris arundinacea (A, P50 = -0.5MPa), Lolium perenne (B, P50 = -4.6MPa), and Brachypodium pinnatum (C, P50 = -6.2MPa), showing more lignification in the outer zones of the stems (arrows), and thicker-walled fibres (inserts) with increasing P50. D-E, Grasses and herbaceous eudicots that are more resistant to embolism have a higher proportion of lignified tissues in their stems (D) and thicker-walled fibres (E). Error bars show SE (only lower limits are presented for clarity purposes, each point represents average value for three specimens of the same species). Marked zones apply to the 95% confidence limit of the regression. See Table S5 for multiple regression analysis of P50 and anatomical features as predictive variables.

Parsed Citations

Alder NN, Pockman WT, Sperry JS, Nuismer S (1997) Use of centrifugal force in the study of xylem cavitation. J Exp Bot 48: 665-674
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg EH, Gonzalez P, Fensham R, Zhang Z, Castro J, Demidova N, Lim J-H, Allard G, Running SW, Semerci A, Cobb N (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecol Manag 259: 660-684
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Anderegg WRL, Hicke JA, Fisher RA, Allen CD, Aukema J, Bentz B, Hood S, Lichstein JW, Macalady AK, McDowell N, Pan Y, Raffa K, Sala A, Shaw JD, Stephenson NL, Tague C, Zeppel M (2015) Tree mortality predicted from drought-induced vascular damage. Nature Geosci 8: 367-371
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Anderegg WRL, Klein T, Bartlett M, Sack L, Pellegrini AFA, Choat B, Jansen S (2016) Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. Proc Natl Acad Sci USA 113: 5024-5029
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Awad H, Herbette S, Brunel N, Tixier A, Pilate G, Cochard H, Badel E (2012) No trade-off between hydraulic and mechanical properties in several transgenic poplars modified for lignin metabolism. Environ Exp Bot 77: 185-195
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Barigah TS, Charrier O, Douris M, Bonhomme M, Herbette S, Ameglio T, Fichot R, Brignolas F, Cochard H (2013) Water stress-induced xylem hydraulic failure is a causal factor of tree mortality in beech and poplar. Ann Bot 112: 1431-1437
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Bonan GB (2008) Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science 320: 1444-1449
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Bouche PS, Delzon S, Choat B, Badel E, Brodribb TJ, Burlett R, Cochard H, Charra-Vaskou K, Lavigne B, Li S, Mayr S, Morris H, Torres-Ruiz JM, Zufferey V, Jansen S (2016) Plant Cell Environ 39: 860-870
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Brendel O, Cochard H (2011) In Y Birot, C Gracia, M Palahi, eds. Water for forest and people in the Mediterranean: a challenging balance, European Forest Institute, pp 76-80.
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Brodribb T, Skelton RP, McAdam SAM, Bienaime D, Lucani CJ, Marmottant P (2016) Visual quantification of embolism reveals leaf vulnerability to hydraulic failure. New Phytol 209: 1403-1409
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Brookshire ENJ, Weaver T (2015) Long-term decline in grassland productivity driven by increasing dryness. Nature Commun 6: 7148
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Cao KF, Yang S-J, Zhang Y-J, Brodribb TJ (2012) The maximum height of grasses is determined by roots. Ecol Lett 15: 666-672
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Choat B, Jansen S, Brodribb TJ, Cochard H, Delzon S, Bhaskar R, Bucci SJ, Feild TS, Gleason SM, Hacke UG, Jacobsen AL, Lens F, Maherali H, Martínez-Vilalta J, Mayr S, Mencuccini M, Mitchell PJ, Nardini A, Pittermann J, Pratt RB, Sperry JS, Westoby M, Wright IJ, Zanne AE (2012) Global convergence in the vulnerability of forests to drought. Nature 491: 752-755
Pubmed: Author and Title
CrossRef: Author and Title

Google Scholar: Author Only Title Only Author and Title

Cochard H, Damour G, Bodet C, Tharwat I, Poirier M, Améglio T (2005) Evaluation of a new centrifuge technique for rapid generation of xylem vulnerability curves. Physiol Plant 124: 410-418

Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Cochard H, Badel E, Herbette S, Delzon S, Choat B, Jansen S (2013) Methods for measuring plant vulnerability to cavitation: a critical review. J Exp Bot 64: 4779-4791

Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Cochard H, Ewers FW, Tyree MT (1994) Water relations of a tropical vine-like bamboo (Rhipidocladum racemiflorum): root pressures, vulnerability to cavitation and seasonal changes in embolism. J Exp Bot 45: 1085-1089

Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Cronk QCB, Kiehn M, Wagner WL, Smith JF (2005) Evolution of Cyrtandra (Gesneriaceae) in the Pacific Ocean: the origin of a supertramp clade. Am J Bot 92: 1017-1024

Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Dai AG (2013) Increasing drought under global warming in observations and models. Nature Clim Change 3: 52-58

Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Delzon S, Cochard H (2014) Recent advances in tree hydraulics highlight the ecological significance of the hydraulic safety margin. New Phytol 203: 355-358

Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Delzon S, Douthe C, Sala A, Cochard H (2010) Mechanism of water-stress induced cavitation in conifers: bordered pit structure and function support the hypothesis of seal capillary-seeding. Plant Cell Environ 33: 2101-2111

Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Evert RF (2006) Esau's plant anatomy, meristems, cells, and tissues of the plant body: their structure, function, and development, 3rd edn, John Wiley & Sons, New Jersey.

Ewers FW, Cochard H, Tyree MT (1997) A survey of root pressures in vines of a tropical lowland forest. Oecologia 110: 191-196

Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Fisher JB, Angeles GA, Ewers FW, Lopez-Portillo J (1997) Survey of root pressure in tropical vines and woody species. Int J Plant Sci 158: 44-50

Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Hacke UG, Sperry JS, Pockman WT, Davis SD, McCulloh KA (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. Oecologia 126: 457-461

Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Hamann TD, Smets E, Lens F (2011) A comparison of paraffin and resin-based techniques used in bark anatomy. Taxon 60: 841-851

Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Holloway-Phillips M, Brodribb T (2011) Minimum hydraulic safety leads to maximum water-use efficiency in a forage grass. Plant Cell Environ 34: 302-313

Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Jansen S, Choat, B, Pletsers A (2009) Morphological variation of intervessel pit membranes and implications to xylem function in angiosperms. Am J Bot 96: 409-419

Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Julve P (1998) Baseflor. Index botanique, écologique et chorologique de la flore de France. Version Julve 2005-2014.

http://perso.wanadoo.fr/philippe.julve/catminat.htm
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Karnovsky MJ (1965) A formaldehyde-glutaraldehyde fixative of light osmolality for use in electron microscopy. J Cell Biol 27: 137A-138A
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Kidner C. Groover A, Thomas D, Emelianova K, Soliz-Gamboa C, Lens F (2016) First steps in studying the origins of secondary woodiness in Begonia (Begoniaceae): combining anatomy, phylogenetics, and stem transcriptomics. Biol J Linnean Soc 117: 121-138
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Larter M, Brodribb T, Pfautsch S, Burlett R, Cochard H, Delzon S (2015) Extreme aridity pushes trees to their physical limits. Plant Physiol 168: 804-807
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Lens F, Tixier A, Cochard H, Sperry JS, Jansen S, Herbette S (2013) Embolism resistance as a key mechanism to understand plant adaptive strategies. Curr Opin Plant Biol 16: 287-292
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Lens F, Sperry JS, Christman MA, Choat B, Rabaey D, Jansen S (2011) Testing hypotheses that link wood anatomy to cavitation resistance and hydraulic conductivity in the genus Acer. New Phytol 190: 709-723
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Lens F, Davin N, Smets E, Del Arco M (2013) Insular woodiness on the Canary Islands: remarkable case of convergent evolution. Int J Plant Sci 174: 992-1013
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Lens F, Dressler S, Jansen S, Van Evelghem L, Smets E (2005) Relationships within balsaminoid Ericales: a wood anatomical approach. Am J Bot 92: 941-953
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Lens F, Eeckhout S, Zwartjes R, Smets E, Janssens S (2012a) The multiple fuzzy origins of woodiness within Balsaminaceae using an integrated approach. Where do we draw the line? Ann Bot 109: 783-799
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Lens F, Smets E, Melzer S (2012b) Stem anatomy supports Arabidopsis thaliana as a model for insular woodiness. New Phytol 193: 12-17
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Li S, Lens F, Espino S, Karimi Z, Klepsch M, Schenk HJ, Schmitt M, Schuldt B, Jansen S (2016) Intervessel pit membrane thickness as a key determinant of embolism resistance in angiosperm xylem. IAWA J 37: 152-171
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Macduff JH, Bakken AK (2003) Diurnal variation in uptake and xylem contents of inorganic and assimilated N under continuous and interrupted N supply to Phleum pratense and Festuca pratensis. J Exp Bot 54: 431-444
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Miller DM (1985) Studies of root function in Zea mays: III. Xylem sap composition at maximum root pressure provides evidence of active transport into the xylem and a measurement of the reflection coefficient of the root. Plant Physiol 77: 162-167
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Neufeld HS, Grantz DA, Meinzer FC, Goldstein G, Crisosto GM, Crisosto C (1992) Genotypic variability in vulnerability of leaf xylem to cavitation in water-stressed and well-irrigated sugarcane. Plant Physiol 100: 1020-1028

Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Pammenter NW, Vander Willigen CA (1998) mathematical and statistical analysis of the curves illustrating vulnerability to cavitation. Tree Physiol 18: 589-593
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Pittermann J, Limm E, Rico C, Christman MA (2011) Structure-function constraints of tracheid-based xylem: a comparison of conifers and ferns. New Phytol 192: 449-61
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Saha S, Holbrook NM, Montti L, Goldstein G, Knust Cardinot G (2009) Water relations of Chusquea ramosissima and Merostachys claussenii in Iguazu national park, Argentina. Plant Physiol 149: 1992-1999
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Sperry JS (2013) Cutting-edge research or cutting-edge artefact? An overdue control experiment complicates the xylem refilling story. Plant Cell Environ 36: 1916-1918
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Tixier A, Cochard H, Badel E, Dusotoit-Coucaud A, Jansen S, Herbette S (2013) Arabidopsis thaliana as a model species for xylem hydraulics: does size matter? J Exp Bot 64: 2295-2305
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Tubiello FN, Soussana JF, Howden SM (2007) Crop and pasture response to climate change. Proc Natl Acad Sci USA 104: 19686-19690
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Urli M, Porté AJ, Cochard H, Guengant Y, Burlett R, Delzon S (2013) Xylem embolism threshold for catastrophic hydraulic failure in angiosperm trees. Tree Physiol 33: 672-683
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Watkins JE, Holbrook NM, Zwieniecki MA (2010) Hydraulic properties of fern sporophytes: consequences for ecological and evolutionary diversification. Am J Bot 97: 2007-2019
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

Wheeler J, Huggett B, Tofte A, Rockwell FE, Holbrook NM (2013) Cutting xylem under tension or supersaturated with gas can generate PLC and the appearance of rapid recovery from embolism. Plant Cell Environ 36: 1938-1949
Pubmed: Author and Title
CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title