LETTER

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Global convergence in the vulnerability of forests to drought

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Shifts in rainfall patterns and increasing temperatures associated with climate change are likely to cause widespread forest decline in regions where droughts are predicted to increase in duration and severity[1]. One primary cause of productivity loss and plant mortality during drought is hydraulic failure[2–4]. Drought stress creates trapped gas emboli in the water transport system, which reduces the ability of plants to supply water to leaves for photosynthetic gas exchange and can ultimately result in desiccation and mortality. At present we lack a clear picture of how thresholds to hydraulic failure vary across a broad range of species and environments, despite many individual experiments. Here we draw together published and unpublished data on the vulnerability of the transport system to drought-induced embolism for a large number of woody species, with a view to examining the likely consequences of climate change for forest biomes. We show that 70% of 226 forest species from 81 sites worldwide operate with narrow ($<$1 megapascal) hydraulic safety margins against injurious levels of drought stress and therefore potentially face long-term reductions in productivity and survival if temperature and aridity increase as predicted for many regions across the globe[5,6]. Safety margins are largely independent of mean annual precipitation, showing that there is global convergence in the vulnerability of forests to drought, with all forest biomes equally vulnerable to hydraulic failure regardless of their current rainfall environment. These findings provide insight into why drought-induced forest decline is occurring not only in arid regions but also in wet forests not normally considered at drought risk[7,8].

Sensitivity to drought is fundamentally important in shaping the geographic distribution of individual species as well as communities[9,10]. Drought has underpinned many large-scale forest mortality events over the past century, often in combination with other abiotic and biotic factors[1,11]. Recent evidence suggests rising global temperatures are already amplifying drought-induced forest change and affecting terrestrial net primary productivity[12–14]. The consequences of longer droughts and higher temperatures are potentially dramatic. For example, rapid forest collapse as a result of drought could convert the world's tropical forests from a net carbon sink into a large carbon source during this century[8,15]. Predicting how forests will respond to future climate changes hinges on a quantitative understanding of the physiological mechanisms governing drought stress at the species level. One of the most promising avenues for characterizing the sensitivity of plants to drought stress is by quantifying the strength of the liquid (hydraulic) connection between soil and leaves through the water-transporting xylem tissue.

Cavitation, a phase change from liquid water to vapour, occurs in plants because water transported through the xylem is under negative pressure[16]. The resultant air emboli block xylem conduits and reduce the plant's ability to move water from soil to sites of photosynthesis[17]. Recent evidence indicates that the ability of woody plants to survive and recover from periods of sustained drought is strongly related to their embolism resistance[2,3]. This property varies widely among species and is largely determined by differences in the structure of the xylem[18–20]. Although xylem structure can acclimate to environmental variation during growth and development, subsequent acclimation of embolism resistance to environmental stress is not possible because xylem conduits are dead at maturity. Embolism resistance therefore represents a critically important trait for defining the limits of drought tolerance across woody species and predicting drought-induced forest decline at regional and global scales.

In drying soil, stomata initially regulate water loss from the leaves to maintain xylem pressure (Ψ_x; measured as water potential below 0) within a range that will protect the xylem from extensive embolism[17,21]. As drought continues, stomatal closure slows but does not halt the decline of xylem pressure and hydraulic capacity. If soil water is not replenished before complete hydraulic failure occurs then the plant will desiccate and potentially die. The resistance of a plant to embolism is described by the relationship between xylem pressure and loss of hydraulic conductivity due to conduit occlusion by gas emboli (Supplementary Fig. 1). The Ψ_x at which 50% loss of conductivity occurs (Ψ_{50}) is the most commonly used index of embolism resistance. When Ψ_x falls below Ψ_{50} the water transport function of the xylem is markedly impaired and the plant is exposed to considerable risk of accelerated embolism leading to long-term reductions in productivity, tissue damage, and ultimately death[2]. To examine vulnerability of forest biomes to drought-induced hydraulic failure we assembled a database of Ψ_{50} (Supplementary Table 1, including 480 woody species). Site

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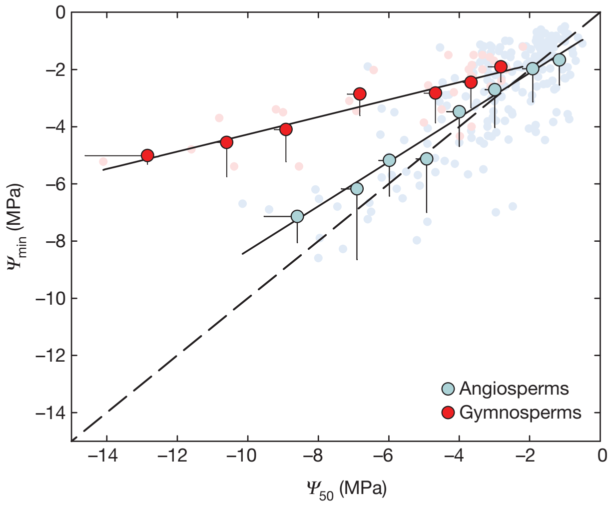

Figure 1 | Minimum xylem pressure as a function of embolism resistance for 191 angiosperm and 32 gymnosperm species. The safety margin is the distance between each point and the 1:1 (dashed) line. Data were binned in 1.0-MPa increments for embolism resistance (Ψ_{50}). Bins were pooled with the next lowest bin if they contained only one sample. Raw data are shown as smaller points behind binned data. Error bars, s.d. Regression lines shown were fitted to raw data (angiosperms, $r^2 = 0.57$, $P < 0.0001$; gymnosperms, $r^2 = 0.59$, $P < 0.0001$; data set available in Supplementary Table 1). Ψ_{min}, minimum xylem pressure.

climate varied widely, for example, mean annual precipitation (MAP) ranged from 300 to 4,500 mm, and mean annual temperature from −4 to 27 °C. Data for angiosperms (flowering plants) and gymnosperms (mainly conifers) were analysed separately because of fundamental differences in xylem structure between these two groups.

We observed a significant ($P < 0.0001$) linear relationship between the minimum Ψ_x measured in plants under natural conditions (Ψ_{min}) and Ψ_{50} for both angiosperms and gymnosperms, showing that embolism resistance is tightly linked with the level of drought stress experienced by plants across a broad range of environments (Fig. 1). The difference between Ψ_{min} and Ψ_{50} represents a highly informative 'safety margin' within which the plant operates in a given environment[22,23]. This safety margin quantifies the degree of conservatism in a plant's hydraulic strategy, indicating that plants with low (or even negative) safety margins experience large amounts of embolism and therefore potential risk of hydraulic failure (Supplementary Fig. 1). Measurements of Ψ_{min} were available for 226 of the 480 species included in our database.

Across all forest biomes, 70% of all species operated at narrow (<1 megapascal (MPa)) safety margins (Fig. 2a), indicating that both arid and mesic biomes are vulnerable to drought-induced decline if extreme drought events become more frequent as predicted under global climate change[5,6]. Applying more conservative safety margins, for example, the difference between Ψ_{min} and almost complete xylem failure (Ψ_{88}), showed a similar convergence of vulnerability across forest biomes (Fig. 2b).

Overall, gymnosperms showed greater hydraulic safety margins than angiosperms, with 42% of all angiosperms versus only 6% of all gymnosperms operating at negative safety margins, that is, Ψ_{min} below Ψ_{50} (Figs 1, 2). The seemingly risky embolism-tolerance strategies seen in angiosperms suggest that flowering plants may have a greater capacity to reverse embolism, a process by which gas is dissolved and the conduits are restored to a water-filled and functional status. Although this process is still poorly understood, it is clear that recovery can only occur if periods of drought are followed by sufficient precipitation and a return to favourable water status[24,25]. Therefore, refilling does not represent an effective escape strategy for mitigating the effects of severe and persistent drought.

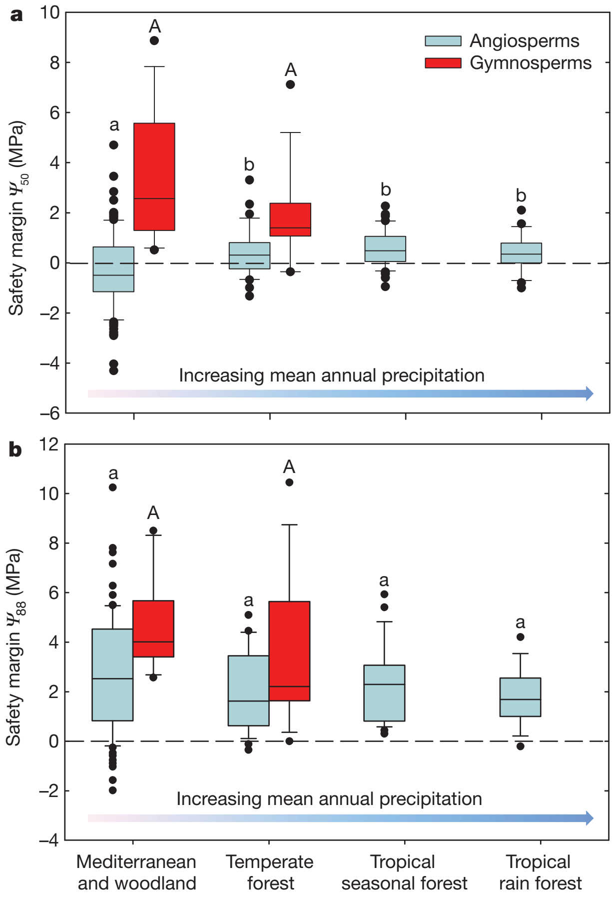

Figure 2 | Box plot of hydraulic safety margins for angiosperm and gymnosperm species across forest biomes. **a**, **b**, The Ψ_{50} ($\Psi_{\mathrm{min}} - \Psi_{50}$) safety margin is shown in **a** ($n = 223$), and the Ψ_{88} ($\Psi_{\mathrm{min}} - \Psi_{88}$) safety margin is shown in **b** ($n = 222$). Boxes show the median, 25th and 75th percentiles, error bars show 10th and 90th percentiles, and filled symbols show outliers. Gymnosperm species were not represented in tropical forests. Significant differences ($P < 0.05$) between biome means are indicated by letters above boxes with angiosperms (lowercase a, b) and gymnosperms (uppercase A) considered separately. Data set available in Supplementary Table 1.

Wider safety margins in gymnosperms than angiosperms do not mean that gymnosperms are immune to the threat of hydraulic failure. In fact, Pinaceae species have significantly lower embolism resistance and safety margins than Cupressaceae[19,20,26], which is reflected in the greater frequency of dieback events involving Pinaceae[1,13,26]. In the severe 2002–2003 drought, for example, *Pinus* (Pinaceae) species suffered widespread mortality in the south western United States, whereas co-existing *Juniperus* (Cupressaceae) survived[13].

In our data set, Ψ_{50} was strongly associated with MAP (Fig. 3) such that both the mean and upper tenth quantile trends showed decreasing resistance to embolism (less negative Ψ_{50}) with increasing rainfall ($P < 0.05$). Similar relationships were found between Ψ_{50} and climate variables that account for both the variation in potential evapotranspiration (PET) and seasonality of precipitation: aridity index (MAP divided by PET) and mean precipitation of the driest quarter (Supplementary Fig. 2). However, a wide range of hydraulic strategies occur within any given climate region, with the greatest variation in Ψ_{50} occurring at sites with a MAP of between 300 and 1,000 mm. In high MAP sites, represented by tropical rainforests in our data set, variation is compressed to less negative Ψ_{50}, suggesting that low embolism resistance is associated with high transport efficiency and low structural 'costs', making this an advantageous strategy in highly productive, wet tropical environments[18].

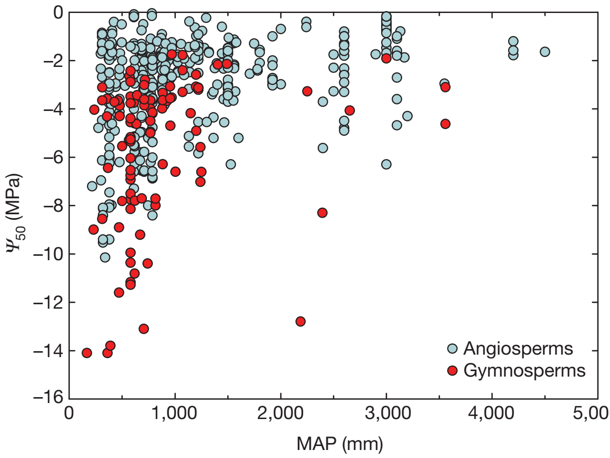

Figure 3 | Embolism resistance as a function of mean annual precipitation for 384 angiosperm and 96 gymnosperm species. Each point represents one species. A generalized model indicated that embolism resistance (Ψ_{50}) was significantly related ($P < 0.00001$) to mean annual precipitation (MAP) for angiosperms and gymnosperms (see Methods for details), with decreasing resistance to embolism corresponding to increasing rainfall. The full data set is available in Supplementary Table 1.

It is clear from Fig. 3 that Ψ_{50} and MAP are decoupled in certain cases, implying that some species growing in drier environments escape from water stress, therefore alleviating the need for high embolism resistance. There are many examples in the literature of species with low embolism resistance growing in areas of low rainfall or seasonal drought. This includes riparian and ground-water-dependent vegetation[10], and drought-deciduous trees in tropical dry forests[27]. These species avoid very negative Ψ_x by some combination of predictable access to ground water (deep roots), internal water storage and reduced leaf area or other shifts in biomass allocation[10,23,28]. Although these adjustments decouple Ψ_{50} and $\Psi_{\min}$ from MAP, it seems that the majority of species operate close to their functional limits. They are therefore exposed to xylem failure during anomalously low rainfall in a manner that is largely independent of rainfall region and biome (Fig. 2).

The convergence on a 'risky' hydraulic strategy exhibited by many species can be understood as the result of a trade-off that balances growth with protection against risk of mortality in a given environment[17,21,25]. Thus, a low safety margin to Ψ_{50} also indicates that stomatal regulation takes full advantage of the range of xylem pressures that are within the tolerance of the hydraulic system of that species. This stomatal behaviour carries with it the benefit of increased carbon gain but may come at the cost of extensive loss of photosynthetic area or death.

A fundamental question concerns the plasticity and genetic diversity of embolism resistance within species[22,29,30]. If the tight link between embolism resistance and water availability is the product of natural selection over many generations and adaptation is limited by a long generation cycle of perennial plants, then the rapid pace of climate change may outstrip the capacity of populations to adapt. This could lead to long-term reductions in net primary productivity of forest systems, loss of biodiversity and changes to the composition of forest and woodland communities. Although it is evident that multiple mechanisms (hydraulic failure, carbohydrate depletion and insect attack) are involved in drought-induced mortality, these mechanisms are highly interdependent[11,12]. Embolism formation is a key mechanism of vegetation shifts and forest decline because it sets the thresholds for stomatal closure, leading to limitations on photosynthesis, increased heat and light damage, and a run-down of carbohydrate reserves over time. Our findings demonstrate the necessity of integrating long-term monitoring of $\Psi_{\min}$ with measurements of embolism resistance and safety margins. The inclusion of these data in process-based vegetation models will improve the accuracy with which the responses of forest ecosystems to climate change can be predicted.

METHODS SUMMARY

Xylem traits were compiled from published and unpublished sources (Supplementary Table 1). When values of Ψ_{50} and Ψ_{88} were not reported in numerical form, they were extracted from published graphs of vulnerability curves. $\Psi_{\min}$ data are the minimum midday water potential recorded for each species in the field, indicating a seasonal, rather than daily minimum value. Two types of safety margins were calculated: the Ψ_{50} margin ($\Psi_{\min} - \Psi_{50}$) and the Ψ_{88} margin ($\Psi_{\min} - \Psi_{88}$) (Supplementary Fig. 1).

Data in Fig. 1 were binned in 1.0-MPa increments of Ψ_{50}. Bins were pooled with the next lowest bin if they contained only one sample. Regression lines in Fig. 1 presented are for raw data to avoid bias associated with uneven bin size. Differences in biome means for safety margin were analysed using a general linear model, with differences between angiosperms and gymnosperms considered separately. Climate data were taken from the paper in which Ψ_{50} data were published, or from the WorldClim database or CRU climate database, whichever gave an elevation closest to that given in the paper. Relationships between Ψ_{50} and climate variables (MAP, aridity index, mean precipitation of the driest quarter) were analysed using a generalized model assessed by restricted maximum likelihood in which variance was simultaneously modelled as a power function of the same climate variables. Quantile regression was also used to assess the boundary relationship between Ψ_{50} and climate variables. As Ψ_{50} is a negative variable, the 10% quantile was used, which is equivalent to the 90% quantile for a positive response variable.

Forest biomes were assigned based on site descriptions contained in the primary sources. We defined 'forest' broadly to include Mediterranean, savanna and woodland environments that are not commonly classified as forests. The data set therefore encompasses tree, shrub and liana species from vegetation communities with a significant component of woody plants.

Full Methods and any associated references are available in the online version of the paper.

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Supplementary Information is available in the online version of the paper.

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Author Contributions B.C. and S.J. led the initial working group and coordinated the analysis and write-up of the work. B.C., S.J., T.J.B., H.C., S.D., R.B., S.J.B., T.S.F., S.M.G., U.G.H., A.L.J., F.L., H.M., J.M.-V., S.M., M.M., P.J.M., A.N., J.P., R.B.P., J.S.S., M.W., I.J.W. and A.E.Z. contributed to compilation and organization of the data set and writing of the manuscript. S.M.G. and I.J.W. extracted climate data from the WorldClim and CRU climate databases. H.M., M.M. and J.M.-V. assisted in statistical analyses of the data set.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to S.J. (steven.jansen@uni-ulm.de).

METHODS

The resistance of a species to embolism is described by a vulnerability curve, which shows the percentage loss of hydraulic conductivity (PLC, %) as a function of decreasing xylem pressure (Ψ_x, MPa); that is, as plant drought stress increases (Supplementary Fig. 1). We define three parameters on this curve: first, the xylem pressure at which 50% of conductivity is lost (Ψ_{50}, MPa); second, the xylem pressure at which 88% of conductivity is lost (Ψ_{88}, MPa), which represents the upper inflection of the curve; and third, the slope of the curve between Ψ_{50} and Ψ_{88}.

The most negative Ψ_x observed for a species is defined as Ψ_{min} (MPa). 'Lethal' Ψ_{min} values reported in manipulative trials were not included in the database. If Ψ_{min} is equal to Ψ_{50}, this means that the plant has lost 50% of its hydraulic capacity. Ψ_{50} is the most commonly used index of xylem embolism resistance in literature and represents the steepest part of the vulnerability curve, meaning that even a slight drop in Ψ_x will result in a substantial reduction in hydraulic function. However, Ψ_{50} does not represent the mortality point per se because the Ψ_x value corresponding to lethal levels of embolism may vary among species, depending on the water-use strategy of the whole plant. In our data set, 42% of the angiosperm species (versus 6% of the gymnosperm species) show Ψ_{min} values below Ψ_{50}.

A hydraulic safety margin was defined as the difference between Ψ_{min} and Ψ_{50} (Supplementary Fig. 1 and Fig. 2a). An alternative, more conservative safety margin was defined as the difference between Ψ_{min} and Ψ_{88} (Fig. 2b). Both the Ψ_{50} and the Ψ_{88} safety margins should be interpreted as relative vulnerability indices with a low (or even negative) value indicating a higher-risk strategy for hydraulic failure compared to a high safety margin.

The data set was compiled from published papers and unpublished results of the authors (see Supplementary Table 1), including 480 species from 172 sites, with 384 angiosperm and 96 gymnosperm species. Genera and species names were checked for orthography and synonymy using TaxonScrubber (version 2.1; www.salvias.net/pages/taxonscrubber.html), the International Plant Names Index (www.ipni.org), Tropicos (www.tropicos.org), Phylomatic (www.phylodiversity.net/phylomatic/) and the Angiosperm Phylogeny Website (http://www.mobot.org/MOBOT/research/APweb/). Samples based on measurements of roots, petioles or trunks were removed for the analyses. Data presented for Ψ_{50} and Ψ_{88} were from distal branches (approximately 0.5–1.2 cm in diameter) of 1- to 3-year-old stems and therefore represent a conservative estimate of embolism resistance, as roots and leaves are normally less embolism resistant than stems within a species. All but 2% of the samples are from mature trees with 2% of samples coming from saplings or seedlings. PET data were extracted from the Global Aridity Index (Global-Aridity) and the Global Potential Evapo-Transpiration (Global-PET) Geospatial Database (http://www.cgiar-csi.org/2010/04/134/).

The data set was then filtered for the target parameters. The data set was first filtered for samples in which both Ψ_{50} and Ψ_{min} were available, and filtered separately for Ψ_{50} and MAP, which accounted for the majority of samples initially included. Only Ψ_{88} data for Ψ_{min} filtered species were included. Relationships between Ψ_{50} and climate variables (MAP, aridity index, mean precipitation of the driest quarter) were analysed using a generalized model assessed by restricted maximum likelihood in which variance was simultaneously modelled as a power function of the same climate variables. Quantile regression was also used to assess the boundary relationship between Ψ_{50} and climate variables. As Ψ_{50} is a negative variable, the 10% quantile was used, which is equivalent to the 90% quantile for a positive response variable.

Ψ_{50} and Ψ_{min} were collected from the same population of plants with the exception of a few cases in which Ψ_{min} data were extracted from another study or from unpublished sources. In 67% of our samples Ψ_{min} was measured as xylem or stem water potential, that is, the leaves were covered with plastic and aluminium foil such that leaf and stem water potentials were equilibrated. In the remaining 33% of cases Ψ_{min} was measured as leaf water potential. In this case, Ψ_x may be less negative than leaf water potential because of the pressure drop across the leaf hydraulic pathway caused by transpiration. Because of the difference in leaf and xylem water potential it is possible the amount of embolism in the stem could be overestimated, that is, the safety margin would appear narrower than it actually was.

However, there are two main reasons why this issue would not alter the results. First, Ψ_{min} has most probably been underestimated in most cases because we lack continuous long-term data sets of water potential. Second, 48% of the species for which leaf water potential was recorded were below −2.0 MPa. At this point the stomata are assumed to be closed in isohydric species (that is, species that close their stomata to prevent Ψ_x from dropping) and thus leaf water potential would be close to equilibrium with stem water potential. To estimate the magnitude of any potential error, we correlated Ψ_{min} pre-dawn and Ψ_{min} midday for studies in which both were available. Although there is equilibrium for Ψ_{min} pre-dawn between leaves and stems, in theory there should be a more significant drop in Ψ_{min} midday for leaves than for stems. However, the slope of the relationship between Ψ_{min} midday and Ψ_{min} pre-dawn was statistically indistinguishable for leaves and stems, indicating that no bias was introduced by combining leaf and stem Ψ_{min} data (analysis of covariance (ANCOVA) interaction term, $F_{1,112} = 0.944$, $P = 0.333$).

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I. Supplementary Figures

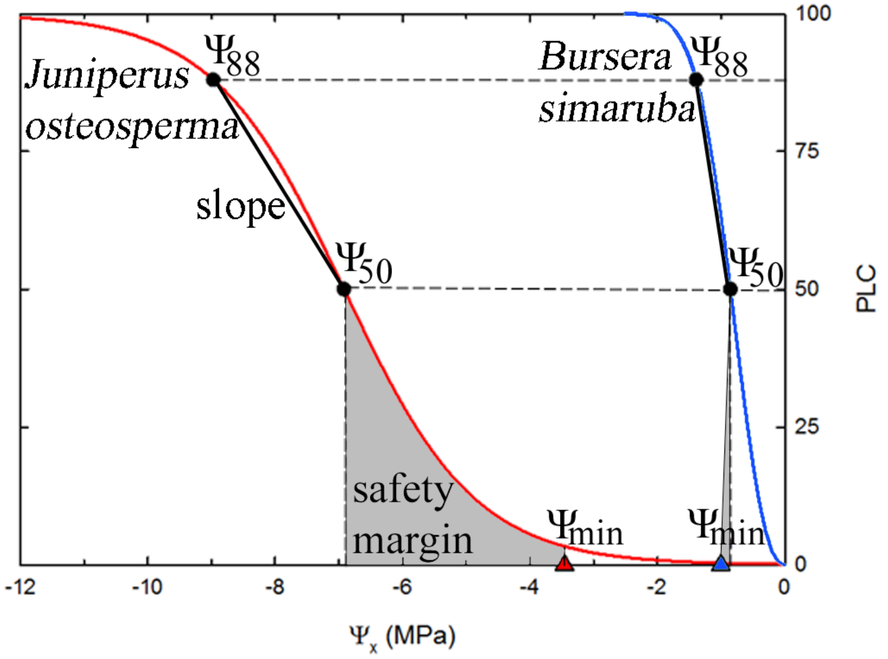

Figure S1: Embolism vulnerability curves showing percentage loss of hydraulic conductivity (PLC) as a function of xylem pressure (Ψ_x). Curves are shown for the angiosperm species *Bursera simaruba*, a tropical rainforest species (blue curve), and the gymnosperm *Juniperus osteosperma*, a dry forest species (red curve). Points show the xylem pressures at which PLC = 50% (Ψ_{50}) and PLC = 88% (Ψ_{88}) for each species (Ψ_{50} = – 6.9 MPa and – 1 MPa for *J. osteosperma* and *B. simaruba*, respectively). A smaller decrease in xylem pressure is required to move from Ψ_{50} to Ψ_{88} in *B. simaruba* because of the steeper slope of the curve between Ψ_{50} and Ψ_{88}. Ψ_{min} values are indicated by triangles and represent the minimum Ψ_x measured in the field. The difference between Ψ_{min} and Ψ_{50} (grey area) corresponds to a "safety margin", which is 3.4 MPa for *J. osteosperma*, while Ψ_{min} passes the Ψ_{50} point marginally for *B. simaruba*, resulting in a slightly negative safety margin and thus a more risky hydraulic strategy than *J. osteosperma*. Curves were redrawn from literature[1,2].

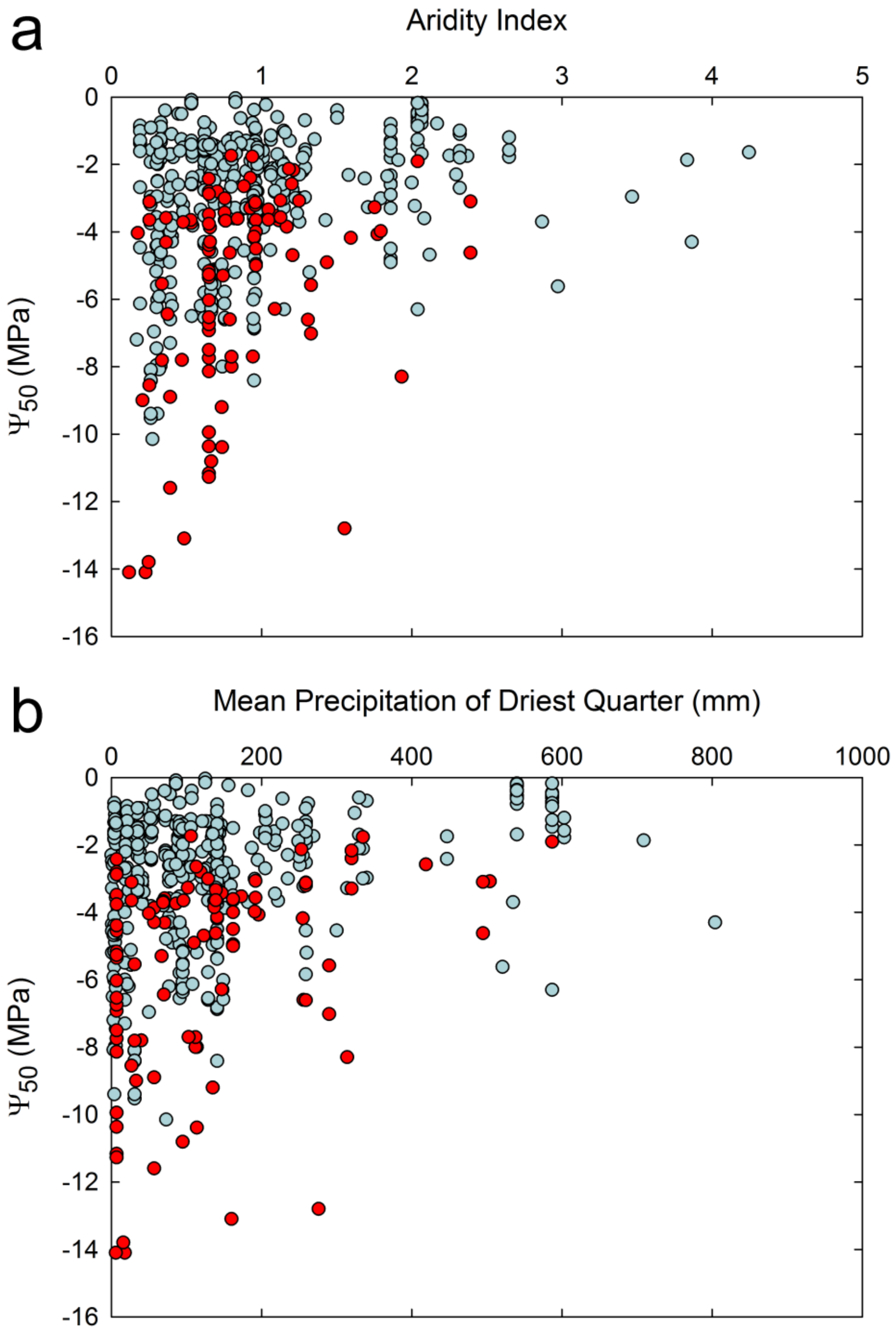

Figure S2: Embolism resistance (Ψ_{50}) as a function of (a) Aridity Index (AI, calculated as the ratio of MAP to PET as defined by the United Nations Environment Programme) and (b) Mean Precipitation of the Driest Quarter (mm) for 384 angiosperm (blue dots) and 96 gymnosperm (red dots) species with each point representing one species. The mean precipitation of the driest quarter is the sum of the average precipitation in the three driest successive months, a measure that takes into account the seasonality of rainfall. A generalised model indicated Ψ_{50} was significantly related to AI ($P < 0.00001$) and Mean Precipitation of the Driest Quarter ($P < 0.0001$) for both angiosperms and gymnosperms, illustrating a similar relationship as observed for Ψ_{50} and MAP (Figure 3).

II. Supplementary Table

The dataset compiled from published work and unpublished data of the authors is provided in **Supplementary Table 1**, including species names, Ψ_{50}, Ψ_{88}, Ψ_{min}, safety margins, climate data, life form, biome, site data, and the sources of published data

III. References

1 Lopez, O. R., Kursar, T. A., Cochard, H. & Tyree, M. T. Interspecific variation in xylem vulnerability to cavitation among tropical tree and shrub species. *Tree Physiol.* **25**, 1553-1562 (2005).

2 Linton, M. J., Sperry, J. S. & Williams, D. G. Limits to water transport in *Juniperus osteosperma* and *Pinus edulis*: implications for drought tolerance and regulation of transpiration. *Funct. Ecol.* **12**, 906-911 (1998).