UNIVERSITY OF LEEDS

This is a repository copy of *Taller trees exhibit greater hydraulic vulnerability in southern Amazonian forests*.

White Rose Research Online URL for this paper:
https://eprints.whiterose.ac.uk/215008/

Version: Accepted Version

Article:

Araújo, I., Marimon, B.S., Marimon, B.H. et al. (9 more authors) (2024) Taller trees exhibit greater hydraulic vulnerability in southern Amazonian forests. Environmental and Experimental Botany, 226. 105905. ISSN 0098-8472

https://doi.org/10.1016/j.envexpbot.2024.105905

© 2024, Elsevier. This manuscript version is made available under the CC-BY-NC-ND 4.0 license http://creativecommons.org/licenses/by-nc-nd/4.0/. This is an author produced version of an article published in Environmental and Experimental Botany. Uploaded in accordance with the publisher's self-archiving policy.

Reuse

This article is distributed under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs (CC BY-NC-ND) licence. This licence only allows you to download this work and share it with others as long as you credit the authors, but you can’t change the article in any way or use it commercially. More information and the full terms of the licence here: https://creativecommons.org/licenses/

Takedown

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.

White Rose
university consortium
Universities of Leeds, Sheffield & York

eprints@whiterose.ac.uk
https://eprints.whiterose.ac.uk/

Taller trees exhibit greater hydraulic vulnerability in southern Amazonian forests

Igor Araújo, Beatriz S. Marimon, Ben Hur Marimon Junior, Carla H.L. Oliveira, Jose W.S. Silva, Raiane G. Beú, Ivone Vieira da Silva, Priscila F. Simioni, Julia V. Tavares, Oliver L. Phillips, Manuel U Gloor, David R. Galbraith

PII: S0098-8472(24)00263-6

DOI: https://doi.org/10.1016/j.envexpbot.2024.105905

Reference: EEB105905

To appear in: *Environmental and Experimental Botany*

Received date: 14 February 2024
Revised date: 12 July 2024
Accepted date: 13 July 2024

Please cite this article as: Igor Araújo, Beatriz S. Marimon, Ben Hur Marimon Junior, Carla H.L. Oliveira, Jose W.S. Silva, Raiane G. Beú, Ivone Vieira da Silva, Priscila F. Simioni, Julia V. Tavares, Oliver L. Phillips, Manuel U Gloor and David R. Galbraith, Taller trees exhibit greater hydraulic vulnerability in southern Amazonian forests, *Environmental and Experimental Botany,* (2024) doi:https://doi.org/10.1016/j.envexpbot.2024.105905

Taller trees exhibit greater hydraulic vulnerability in southern Amazonian forests

Igor Araújo [1*] (ORCiD 0000-0002-9226-7321), Beatriz S. Marimon [1,2] (ORCiD 0000-0003-3105-2914), Ben Hur Marimon Junior [1,2] (ORCiD 0000-0002-6359-6281), Carla H. L. Oliveira [1] (ORCiD 0000-0003-0374-1640), Jose W. S. Silva [1] (ORCiD 0000-0003-1076-8374), Raiane G. Beú [1,3] (ORCiD 0000-0003-0237-2409), Ivone Vieira da Silva [4], Priscila F. Simioni [5] (ORCiD 0000-0002-1395-2866), Julia V. Tavares [6] (ORCiD 0000-0003-3784-5720), Oliver L. Phillips [7] (ORCiD 0000-0002-8993-6168), Manuel U Gloor [7], David R. Galbraith [7]

[1] Universidade do Estado de Mato Grosso, Programa de Pós-Graduação em Ecologia e Conservação, Nova Xavantina, MT, Brazil.

[2] Universidade do Estado de Mato Grosso, Departamento de Ciências Biológicas, Nova Xavantina, MT, Brazil.

[3] Universidade de Brasília, Instituto de Ciências Biológicas, Programa de Pós-Graduação em Ecologia, Brasília, DF, Brazil.

[4] Universidade do Estado de Mato Grosso, Curso de Ciências Biológicas, Alta Floresta, MT, Brazil.

[5] Universidade do Estado do Rio de Janeiro, Laboratório de Anatomia Vegetal, Rio de Janeiro, RJ, Brazil.

[6] University of Uppsala, Department of Ecology and Genetic, Evolutionary Biology Centre, Uppsala, Sweden

[7] School of Geography, University of Leeds, Leeds, LS2 9JT, UK.

* Corresponding author. Tel.: +55 (66) 9 9251-3188
E-mail address: igor.araujo@outlook.com.br

Abstract

1. Potential increases in drought frequency and vapour pressure deficit pose a risk to the future function of tropical trees. Previous studies have found that taller tropical trees show a stronger increase in mortality than shorter trees in response to dry anomalies, but the mechanisms behind this are unclear. Here we investigate whether

canopy branches of taller tropical trees have different hydraulic traits compared to shorter conspecifics.

2. We determined xylem resistance to embolism (P_{50}), hydraulic safety margin (HSM), xylem functional traits and xylem theoretical hydraulic conductivity for canopy branches of four tree species across a range of tree heights (sapling to maximum tree height) in an ecotonal forest near the Amazonia-Cerrado transition.
3. We found that canopy branches of taller trees within each species have lower HSM, suggesting that they are more susceptible to hydraulic failure under drought than smaller conspecifics. Height-related trends in HSM were driven by variation in P_{50} with height and not by variation in leaf water potential which did not vary with height. We find that canopy branches with greater xylem vessel diameters are generally more vulnerable to embolism, suggesting a potential role for a diameter-safety linkage in explaining observed patterns of decreasing HSM with height. However, we find no evidence of a branch-level trade-off between theoretical hydraulic conductivity and hydraulic vulnerability.
4. The greater hydraulic vulnerability of larger trees provides a potential explanation for the higher drought-induced mortality observed in taller tropical trees. The consistency of the height-P_{50} relationship across species opens the door to a more accurate prediction of southern Amazon forest responses to future droughts. Whether the findings for forests in southern Amazonia can be generalized to other Amazonian regions remains an open question.

Keywords

Height-hydraulic operation, hydraulic sensitivity, resistance to embolism, tropical trees, xylem anatomical traits

1. Introduction

Several climate models project an increase of dry season water stress over the eastern Amazon (Duffy *et al.,* 2015), with potentially significant consequences for forest function, biomass storage and composition. Furthemore, marked increases in tree mortality have been observed following natural and experimental droughts in Amazonia (Phillips *et al.,* 2010; da Costa *et al.,* 2010; Meir *et al.,* 2015). The most significant changes in recent climate have been observed in the southeastern Amazon, where deforestation has been most extensive (Marques *et al.,* 2020; Gatti *et al.,* 2021). In this region, temperature increases have been particularly marked (Jiménez-Muñoz *et al.,*

2013) and a lengthening of the dry season has been documented (Haghtalab *et al.,* 2020; Marimon *et al.,* 2020). Field observations suggest that forests in southeastern Amazonia have the lowest hydraulic safety margins of all Amazon forests (Tavares *et al.,* 2023), may already be approaching temperatures that may limit photosynthetic function (Tiwari *et al.,* 2020; Araújo *et al.,* 2021) and exhibit the highest mortality rate of all Amazonian regions (Esquivel-Muelbert *et al.,* 2020, Reis *et al.,* 2022). Therefore, forests in this region are at the frontline of climate change in Amazonia and a mechanistic understanding of their climatic sensitivity is critical for predicting forest responses to future climate change.

Water is transported in trees in narrow xylem conduits under high tensions (negative water potentials), which intensify during periods of soil water deficit and high atmospheric evaporative demand. Under very negative water potentials, air embolism may form in the xylem (Tyree & Sperry, 1988), disrupting the continuity of the plant water column and interrupting the transport of water to the leaves. Severe embolism of the xylem vessels may lead to failure of the water transport system (i.e., hydraulic failure) and ultimately cause tissue and tree mortality (Tyree & Sperry, 1988; Adams *et al.,* 2017). Embolism-induced hydraulic failure (Brodribb & Cochard, 2009; Rowland *et al.,* 2015; Bittencourt *et al.,* 2020) has been found to be the dominant mechanism of tree death under drought conditions (Adams *et al.,* 2017), although other mechanisms including carbon deprivation (Adams *et al.,* 2009) and insect outbreaks (Ferrell *et al.,* 1994), can also contribute to tree mortality. Given the observed recent changes in climate in the region, remaining forests in the southern Amazon may face a significant risk of drought-induced mortality (Tiwari *et al.,* 2020; Esquivel-Muelbert *et al.,* 2020; Araújo *et al.,* 2021; Reis *et al.,* 2022), but their hydraulic properties have been little evaluated (Jancoski *et al.,* 2022; Tavares *et al.,* 2023).

The hydraulic limitation hypothesis predicts that hydraulic resistance increases with increasing xylem path length, making the transport of water to the leaves more difficult in tall trees (Ryan & Yoder, 1997; Koch *et al.,* 2004), although tapering of xylem vessels with height partially compensates for these increases in resistance (e.g., Becker *et al.,* 2000 a, b; Becker & Gribben, 2001; Zaehle, 2005). Taller trees generally have wider xylem vessels, which could make them more vulnerable to embolism than shorter trees with narrower vessels (Olson *et al.,* 2018; Liu *et al.,* 2019), mostly during drought events. Indeed, predictions based on Darcy's law suggest that tall trees are most at risk of drought-induced mortality (McDowell & Allen, 2015).

The greater vulnerability of large trees is supported by several lines of empirical evidence. In tropical forests in Amazonia and worldwide, natural drought events tend to impact taller trees more than shorter trees (Phillips *et al.,* 2010; Bennett *et al.,* 2015). In a long-running experimental drought study in the Brazilian Amazon, high mortality of tall trees drove a 40% reduction of standing biomass over a 15-year period (Rowland *et al.,* 2015), attributed to a greater risk of hydraulic failure in taller trees than in smaller trees as xylem resistance to embolism was found to decline with increasing tree height (Rowland *et al.,* 2015). In a global scale study, Liu *et al.,* (2019) showed that tree species attaining higher height are generally less resistant to embolism (less negative P_{50}); on the other hand, they have greater xylem efficiency than species with lower maximum height. These findings have been attributed to a vessel diameter-vulnerability link (Olson *et al.,* 2023), whereby large-vesseled tall trees are also more prone to cavitation. The potential mechanisms underlying this relationship include the heightened likelihood of spontaneous embolism formation in larger vessels and the increased capacity for embolism transmission to adjacent vessels. Wider vessels may possess larger pores in their pit membranes and a greater number of intervascular depressions, thereby augmenting their susceptibility to water stress-induced embolism (Hargrave *et al.,* 1994; Isasa *et al.,* 2021).

Studies investigating ontogenetic variation in hydraulic traits within taxa are rare, with substantial divergences between them. For example, Olson *et al.,* (2018), demonstrated that taller individuals of some subtropical plantation species are less resistant to embolism than shorter individuals (e.g., *Moringa oleifera*; <150 cm, P_{50} = -1.3 MPa; >250 cm, -0.7 MPa). In the only study to date in Amazon forests, Bittencourt *et al.,* (2020), showed that the relationship between tree diameter and P_{50} is widely variable in eastern Amazonian tree genera (e.g., P_{50} becomes more negative with diameter for *Virola* and *Inga* but less negative for *Vouacapoua* and *Eschweilera*). Understanding these relationships (e.g., between tree height and P_{50} and hydraulic safety margin) is particularly important for the southern Amazon, where there are no relevant empirical data but where there are urgent implications for forest structure and carbon storage due to the rapid deforestation and climate change observed in the region.

In this study, we evaluated the relationship between tree height and key branch-level hydraulic traits related to the conductivity and safety of xylem water transport (e.g., P_{50}, vessel lumen diameter and frequency) as well as plant hydraulic status (minimum leaf water potentials, hydraulic safety margins) in one of the Amazon's southernmost closed canopy forest fragments, located at the transition of the Amazon and Cerrado (savannah) biomes. This combination of hydraulic architecture traits and hydraulic status variables allows us to integratively examine the implications of plant height for hydraulic conductivity and safety. With this dataset, we address the following research questions: **(1)** Do tall trees exhibit less embolism resistance and lower hydraulic safety margins than shorter conspecifics? **(2)** Are theoretical hydraulic conductivity and xylem functional traits coordinated with tree height? **(3)** Is there evidence of a trade-off between theoretical hydraulic conductivity (K_h estimated from xylem anatomical traits) and resistance to embolism (branch P_{50}) in tree species in the southern Amazon?

2. Materials and Methods

2.1 Study area and species

We carried out the study in a 1 ha plot in a large forest fragment located in the legal reserve area of Fazenda Vera Cruz (14º49'32''S and 52º06'20''W), Nova Xavantina, Mato Grosso, Brazil, at the transition of the Amazon and Cerrado biomes (Marimon *et al.,* 2014; Marques *et al.,* 2020). The plot is a closed canopy mixed forest with emergent trees that can reach 25 m in height but with an average tree height of 13.6 m, classified as a pre-Amazonian transitional forest (Marimon *et al.,* 2014; Araújo *et al.,* 2022) where > 80% are commonly-occurring Amazon species, but also containing some typical *Cerrado* species, as is the case in other savanna-forest contact areas (Ratter *et al.,* 1973; Mews *et al.,* 2012; Morandi *et al.,* 2016; Araújo *et al.,* 2023).

The altitude is approximately 200 m above sea level, with plinthosol, dystrophic, alic and medium-textured soil (Marimon *et al.,* 2014; Marimon-Junior *et al.,* 2020). Mean annual precipitation (based on CHIRPS) for our study site is 1544 +/- 192 mm (mean +/- SD). Total annual precipitation in 2021, the year of our P_{MIN} measurements was 1715 mm and thus within one standard deviation of the mean. The region's climate is strongly seasonal with well-defined rainy (March to October) and dry (April to September) periods. The climate is classified as Aw type, according to the Köppen classification (Alvares *et al.,* 2013).

We selected four dominant evergreen species: *Brosimum rubescens* Taub. (Moraceae), *Amaioua guianensis* Aubl. (Rubiaceae), *Cheiloclinium cognatum* (Miers) A. C. Sm. (Celastraceae) and *Protium altissimum* (Aubl.) Marchand (Burseraceae) that jointly contribute 34% of the total plot basal area for individuals with diameter > 10 cm

(Mews *et al.,* 2011, 2012). For *A. guianensis* and *C. cognatum*, we selected 15 individuals distributed among three height classes (five trees per class; intermediate 10-15m, low 5-10m and saplings < 1m) for each species, while for the species *B. rubescens* and *P. altissimum* we selected 20 individuals in order to include a fourth class (tall >15m) due to their greater height variation. A laser hypsometer was used to measure tree heights.

2.2 Leaf water potential measurements

We determined the minimum water potential in canopy leaves (P_{MIN}) in August 2021 (peak of the dry period) between 12:00 and 14:00 on leaves from branches collected by a trained tree climber. Total dry season rainfall (April – September) in 2021 was 126 mm and within one standard deviation of the long-term (1982-2023) mean values (161 +/- 56 mm). For each sampled individual, P_{MIN} was measured on three healthy (i.e., free from pathogens) and fully-expanded top-of-canopy leaves, using a Scholander pressure chamber (PMS Instruments Co., Albany, USA; model: 1505D-EXP; Scholander *et al.,* 1965) and took the mean of the three leaves to represent the P_{MIN} for that individual. All leaf water potential measurements were made *in situ*, with a maximum time interval between branch collection and water potential measurement of 1-2 minutes.

2.3 Xylem hydraulic vulnerability

Field procedure

Xylem vulnerability curves were constructed between February and May 2022, during or immediately after the rainy season at which point plants were fully hydrated. Wet season rainfall (October – March) corresponding to the year of sampling was 1697 mm and within two standard deviations of the long-term (1982-2023) mean wet season rainfall (1372 +/- 173 mm). We harvested two sunlit branches between 50 cm and 1 m in length from the upper part of the crown between 5:00 and 6:00 a.m. for each individual and species. Branches were then identified with a collection code (i.e., species name, branch and individual numbers) and kept in black plastic bags, wrapped with a damp cloth at their base and with 20 ml of water added to keep the branch hydrated during transport to the laboratory (one hour away by vehicle).

Preparation and handling of samples in the laboratory

We assessed the vulnerability of the xylem to embolism using sigmoidal curves of the relationship between the percentage loss of conductivity (PLC) and the water potential in the xylem. We used the percentage of air discharge (PAD) from the xylem as a proxy for PLC using a pneumatic method (Pereira *et al.,* 2016). In the laboratory, we prepared the connections for each branch and covered them with a black plastic bag for one hour to allow the leaf water potential to equilibrate with the branch xylem water potential. We induced cavitation using the bench-top dehydration method (Sperry *et al.,* 1988) and simultaneously measured the leaf water potential (P_X) with a pressure chamber (Scholander *et al.,* 1965) and the PAD at frequent intervals during the branch dehydration cycle (we used at least five points to fit each curve). We calculated P_{50} (i.e., water potentials at which the tissue loses 50% of its conductivity) for each individual (see Figures **S4** to **S17**) using the equation of Pammenter & Willigen, (1998):

$$PAD = \frac{100}{1 + \mathrm{e}^{[\frac{S}{25}(\mathrm{P}_x - P_{50})]}}$$

where PAD (percentage of air discharge) and P_X (xylem water potential, MPa) are measured values and P_{50} (xylem water potential when PAD equals 50%) and S (slope of the curve, % PAD MPa^{-1}) are parameters extracted from the best model fits.

2.4 Hydraulic safety margin

We considered the hydraulic safety margin (HSM) with respect to P_{50} as an estimate of vulnerability to drought, which we calculated as: $HSM_{50} = P_{MIN} - P_{50}$ (Brodribb *et al.,* 2017) where P_{50} is derived from the vulnerability curve for each individual and P_{MIN} is the minimum leaf water potential measured in the field for the same individual.

2.5 Xylem anatomy

For each individual, we selected a 10 cm-long sample from the same branches for which we determined P_{50}. Initially, to soften the material, we put the stem samples in an oven with water and liquid glycerin (3:1 ratio) at 75 °C for 72 h. We obtained cross-sections (16-20 µm thick) with a rotary microtome (RM2235, Leica, Germany). We clarified the cuts in sodium hypochlorite (50%) and acidulous water (0.1%), dehydrated them in an ascending series (50% to 100%) of ethanol (Johansen 1940) stained the sections with Safranin (Berlyn & Miksche, 1976) and mounted the slides in glycerin gelatin. From the histological slides, we obtained photomicrographs using the Leica LAS E.Z 1.7.0 software coupled to a Leica ICC50 photomicroscope with 10x magnification.

We made 25 measurements per individual branch samples of the tangential diameter of the vessel (µm) and vessel frequency (number of vessels per mm²) using the Image Pro-Plus 4.0 digital image processing system (Media Cybernetics, EUA), following the standards of the IAWA Committee (1989). We note that all diameter measurements presented in this study refer to the tangential diameter. Due to the high correlation between tangential and longitudinal diameters, it is common practice in anatomical studies to report only the tangential diameter (e.g., Castelar *et al.,* 2023; Freitas *et al.,* 2024).

2.6 Theoretical hydraulic conductivity K_h

In line with previous studies (e.g., Castelar *et al.,* 2023), theoretical hydraulic conductivity (K_h) was calculated using the Hagen-Poiseuille equation as follows:

$$K_h = (\pi/128\eta) \bullet F_v \bullet D_h^4$$

where K_h = Theoretical hydraulic conductivity in m^4 MPa^{-1} s^{-1}, η = water viscosity at 20 °C (1.002×10^{-9} MPa. s), F_v is the vessel density (*n* vessels mm^2) and D_h is the hydraulically weighted diameter (m). For ease of reporting, the theoretical hydraulic conductivity was multiplied by 10^{12} to express in mm^4 MPa^{-1} s^{-1}.

The hydraulically weighted diameter per segment was calculated following Scholz *et al.,* (2013):

$$D_h = \left(\frac{\sum d^4}{n}\right)^{\frac{1}{4}}$$

where *d* is the measured vessel diameter (m) and n is the number of vessels measured (25 per segment).

2.7 Vulnerability index

As an alternative measure of xylem vulnerability, the vulnerability index (VI) was calculated using the equation proposed by Carlquist (1977):

$$VI = D_v/F_v$$

where D_v = mean vessel lumen diameter per segment in mm, and F_v = vessel frequency in mm^2.

3. Data analysis

We constructed linear regression models to assess relationships between tree height and hydraulic and anatomical characteristics of xylem vessels with *ggbiplot* package (Wickham, 2011). In addition, we also built linear regression models to understand how resistance to embolism was related to xylem anatomical traits and theoretical hydraulic conductivity. Before performing the analysis, we tested the normality and homoscedasticity of the data using the Shapiro-Wilk and Levene tests (Levene, 1961; Shapiro-Wilk, 1965), and performed all analysis in R software version 4.2.1 (R Core Team, 2022).

4. **Results**

4.1 Tree height influences hydraulic behavior

In general, we found for all tree species that as the height increases, canopy branch xylem resistance to embolism decreases (less negative P_{50}, $P < 0.0001$, $R^2 = 0.45$, Fig. **1a**). Interestingly, minimum leaf water potential generally does not change with height, except for *B. rubescens* (Fig. **1b**). A negative relationship between tree height and hydraulic safety margin was found for three of the evaluated species, where taller trees tend to have lower HSM_{50} (Fig. **1c**). Slopes did not vary between species but had different intercepts. For a given height, *B. rubescens* and *P. altissimum* had higher HSM_{50} than *C. cognatum* and *A. guianensis* (Fig. 1c), reflecting the less negative minimum water potentials observed in those species.

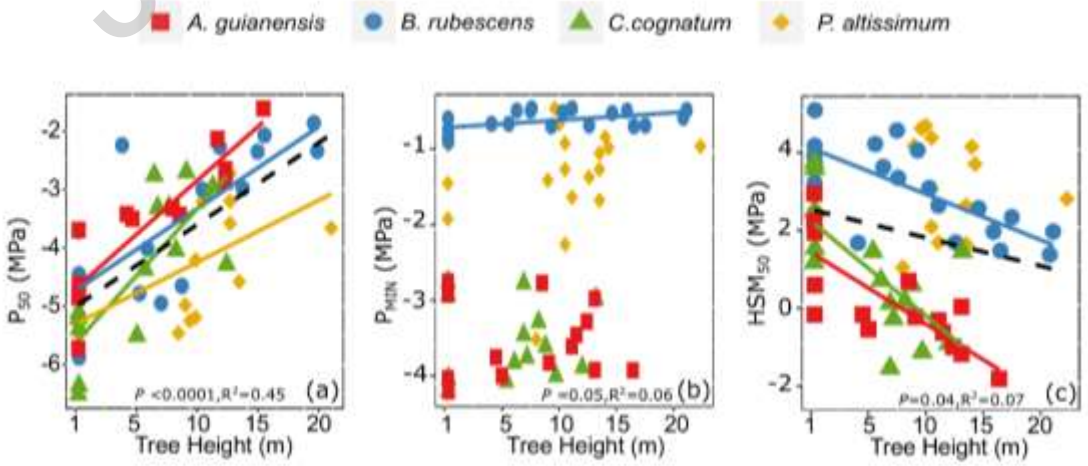

Fig. 1 Relationship between tree height and hydraulic traits: (a) resistance to xylem embolism - P_{50}, (b) minimum leaf water potential - P_{MIN} and (c) hydraulic safety margins - HSM_{50}. The solid lines provide the predicted linear regression for each species. The bold dashed black line provides the general linear regression best-fit line for all species together (The R^2 in the figure and P value refers to the general linear regression best-fit line for all species together, extended data Tables **S1** to **S3**).

4.2 Theoretical hydraulic conductivity and xylem functional traits coordination with tree height

In general, canopy branches of taller trees within each species have wider mean vessel lumen diameter and a smaller number of vessels than those of shorter conspecifics (Fig. **2a, b**). With increasing height, mean vessel lumen diameter increases for all species evaluated ($P < 0.0001$, $R^2 = 0.48$, Fig. **2a**). A weaker trend was found for hydraulically weighted vessel diameter, which increased significantly with height for two of the evaluated species (Fig. **S1**). On the other hand, as trees increase in height, vessel frequency decreases in all species ($P < 0.0001$, $R^2 = 0.35$, Fig. **2b**). Theoretical hydraulic conductivity K_h, which combines vessel frequency and diameter, does not change with height (Fig. **2c**).

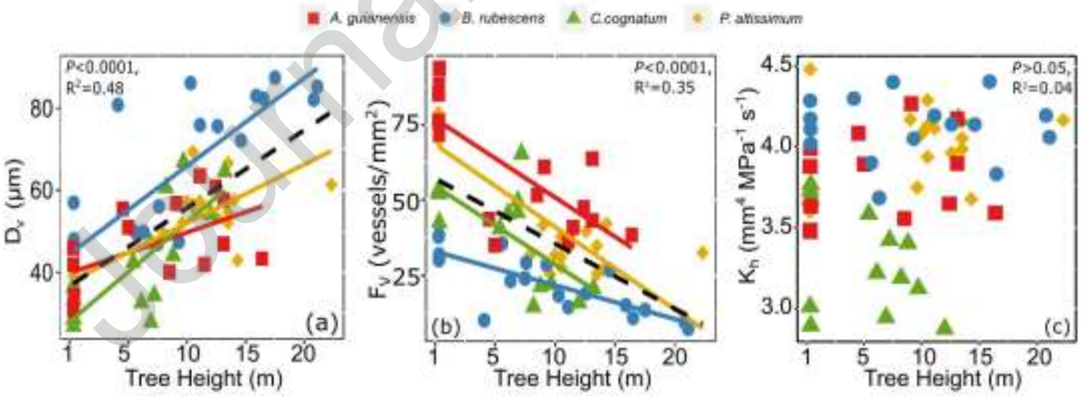

Fig. 2 Relationships between tree height and xylem anatomical traits. (a) vessel lumen diameter - D_V, (b) vessel frequency - F_V and (c) theoretical hydraulic conductivity - K_h. The solid lines provide the predicted linear regression for each species. The bold dashed black line provides the general linear regression best-fit line for all species together (The R^2 in the figure and P value refers to the general linear regression best-fit line for all species together, extended data Tables **S4** to **S6**).

4.3 Xylem functional traits and hydraulic vulnerability

In general, xylem functional traits are related to hydraulic vulnerability, however the magnitude of the relationships varies between species (Fig. **3a, b**). While vessel lumen diameter is positively related to embolism resistance (P <0.0001, R^2 = 0.37, Fig. **3a**), vessel frequency is negatively associated with hydraulic vulnerability (P = 0.0004, R^2 = 0.19, Fig. **3b**). We did not find a relationship between embolism resistance and theoretical hydraulic conductivity for tree species (Fig. **3c**). Furthermore, the overall relationship between embolism resistance and hydraulically weighted vessel diameter was much weaker than that between embolism resistance and mean vessel diameter (Fig. **S2a**) and driven by one species, *B. rubescens* (Fig. **S2a**, Table **S11**). We also observed that the xylem vulnerability index (VI) derived from anatomical measurements (D_V/F_V) exhibited an overall positive relationship to P_{50}, but that the variation in VI was often much lower than that in P_{50} (Fig. **S2b**, Table **S12**).

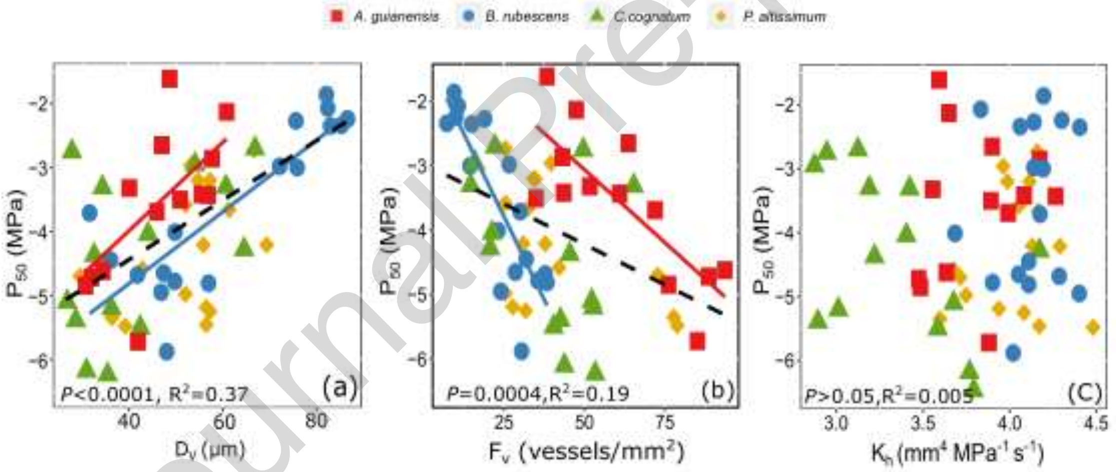

Fig. 3 Relationships between xylem anatomical traits and theoretical hydraulic conductivity with the resistance to xylem embolism P_{50}: (a) vessel lumen diameter – D_V, (b) vessel frequency -F_V and (c) theoretical hydraulic conductivity - K_h. The solid lines provide the predicted linear regression for each species. The bold dashed black line provides the general linear regression best-fit line for all species together (The R^2 in the figure and P value refers to the general linear regression best-fit line for all species together, extended data Tables **S7** to **S9**).

5. Discussion

5.1 Variation of hydraulic safety and efficiency with tree height

Our results show that for all four species tested in a southern Amazon Forest, the canopy branches of taller trees have lower (more negative) hydraulic safety margins than equivalent branches of shorter conspecifics. These results are qualitatively consistent with the results of Giles *et al.,* (2022), who found that smaller trees (1-10 cm in diameter) in the northeastern Amazon site of Caxiuanã had higher hydraulic safety margins than larger trees of the same genera, although no clear patterns in HSM_{50} were observed at the same site, in relation to diameter for adults trees with DBH >10 cm (Bittencourt *et al.,* 2020). We are aware of no other studies that have specifically evaluated how hydraulic safety margins (integrating both resistance to embolism and leaf water potentials observed *in situ*) vary with tree height in Amazon forests. Although HSM_{50} declined with height for almost all species evaluated (Fig. 1c), we note that the steepest declines in HSM_{50} with height were for those species that attained lower maximum height (*A. guianensis and C. cognatum*). In these species, HSM_{50} of larger individuals was invariably negative but was positive in all instances for *B. rubescens* and *P. altissimum*. Negative HSM_{50} values have been widely reported both in Amazonian forests (e.g., Tavares *et al*. 2023) and in global syntheses (e.g., Choat *et al*. 2012) and their occurrence indicates that at least some species are able to survive exposure to negative HSM_{50}. Indeed, lethal water potentials, although still unknown for tropical forest trees but have been found be well beyond P_{50} values in experimental studies on temperate trees (Li *et al.,* 2016; Liang *et al.,* 2020).

We find that in our study site, the relationship between tree height and HSM_{50} is driven by marked reductions in P_{50} with increasing height and not by changes in P_{MIN}. Rather, P_{MIN} displayed strong species-specific signatures that were independent of height. These results contrast with other studies in tropical forests that have reported lower P_{MIN} in larger trees than in smaller trees (e.g., Kenzo *et al.,* 2015; Giles *et al.,* 2022). The lack of a height effect on P_{MIN} may be associated with the specific characteristics of our study site, which is transitional in nature and has a more open canopy than tropical forests in core biome areas. Thus, the light and evaporative demand gradients between taller and smaller trees are less pronounced. Any differences in evaporative demand in our study site may also be offset by differential access to water by smaller plants. The soil in the study site has a layer of semi-concretionary hydromorphic laterite (Marimon-Junior *et al.,* 2020) at a depth of approximately two metres which may restrict deeper access to water by roots of smaller trees. Although we do not have direct observations of rooting depth at our sites, recent studies have shown that large trees tend to have long roots that help reduce water stress and competition during extreme drought compared to short tree species with shallow roots (Brum *et al.,* 2019; Giles *et al.,* 2022). Differences in access to soil water (e.g., rooting depth) and possibly in stomatal regulation may also explain the interspecific differences we observed whereby individuals of the two shorter species (*Amaioua guianensis* and *Cheiloclinium cogantum*) had lower P_{MIN} and HSM_{50} values. The low HSM_{50} observed for taller individuals of these species suggests that hydraulics may limit the height attainment of these species.

The decline in embolism resistance (i.e., the tendency towards less negative P_{50}) with tree height is a consistent feature across all four species considered. The observed pattern is in agreement with other studies that report an interspecific relationship between maximum tree height and embolism resistance (e.g., Liu *et al.,* 2019), decline in embolism resistance with height in experimental plantations (Olson *et al.,* 2018) and reduced embolism resistance in taller trees compared to shorter trees of the same genera in the northeastern Amazon (Rowland *et al.,* 2015; but see Bittencourt *et al.,* 2020; Giles *et al.,* 2022) or the same species in temperate systems (e.g., Prendin *et al.,* 2018). This relationship has been previously explained by: 1) small trees developing more resistant xylem to compensate for shallow rooting profiles (Brum *et al.,* 2019; Giles *et al.,* 2022), and 2) a vessel conduit diameter-vulnerability link whereby taller trees with larger vessels face greater embolism risk than shorter conspecifics. In line with a large number of other studies, we observe an increase in apical vessel lumen diameter with increasing tree height (e.g., Zach *et al.,* 2010; Prendin *et al.,* 2018). Taller trees face the challenge of transporting water to the canopy against increasing resistance due to increasing path length. Wider apical vessels in taller trees provide a mechanism for overcoming the effects of longer path length on hydraulic resistance (Prendin *et al.,* 2018) but this may come at the expense of increased vulnerability to drought (e.g., Isasa *et al.,* 2023; Olson *et al.,* 2023).

We find a moderately strong relationship (Fig. **3a**) between embolism resistance and mean vessel lumen diameter of apical branches, such that branches with wider mean apical diameters (generally from taller trees) are less resistant to embolism. This is consistent with previous work on temperate species where the same general pattern has been observed at the interspecific level (e.g., Maherali *et al.,* 2006; Levionnois *et al.,* 2021; Isasa *et al.,* 2023). Our study finds that the vessel lumen diameter – P_{50} linkage also holds true across individuals of different sizes of the same species. The causal basis of this relationship remains unclear but possible mechanisms include: 1) Increased likelihood of spontaneous embolism formation in larger vessels: embolism formations are discrete events and are more likely to happen at least once in vessels with larger xylem sap volumes (Isasa *et al.,* 2021) and 2) Increased potential for transmission of embolism to other vessels: wider vessels may have larger pores in their pit membranes and a higher amount of intervessel pitting, thus increasing their vulnerability to water-stress-induced embolism (Hargrave *et al.,* 1994). A large intervessel pit fraction or number would increase the probability to have one to few disproportionately large pit membrane pores leading to embolism propagation (Wheeler *et al.,* 2005). Recently, a study with temperate tree species (Isasa *et al.,* 2023), provided clear evidence that vessel dimensions have an effect on embolism resistance, and that this relationship cannot be explained by pit membrane thickness only. Interestingly, we found that relationships between hydraulic diameter and P_{50} were weaker than between mean vessel diameter and P_{50} (Fig. **S2**), reflecting differences in vessel diameter distributions between species and within species across different sizes (Fig. **S3**).

Beyond vessel diameter, other anatomical traits may also be related to embolism resistance. In our study, we found that the vessel frequency – P_{50} linkage also holds in trees of different sizes within the same species. as plants with greater vessel frequency are more embolism resistant (have more negative P_{50}). Concomitant decreases in vessel density with height have been reported alongside increases in apical vessel diameter in several studies (e.g., Echeverria *et al.,* 2019; Chambers-Ostler *et al.,* 2022). This has been attributed to carbon economics as plants optimise carbon investment to maintain leaf-specific conductance by investing more in fewer wider conduits (Echeverria *et al.,* 2019). The relationships observed between P_{50} and F_v may simply reflect this. On the other hand, a greater number of vessels has independently been proposed to increase redundancy, providing alternative pathways for water transport in plants and thereby increase hydraulic safety (Ewers *et al.,* 2007). As well as vessel number per se, vessel grouping may be important too. For example, Levionnois *et al*. (2021) found that greater vessel grouping increased embolism resistance across rainforest species in French Guiana and also attributed this to redundancy in the vessel network as connections with other vessels allow embolised vessels to be bypassed more easily. Finally, xylem ultrastructural properties, especially pit membrane thickness and architecture, have been shown to correlate well with P_{50} (e.g., Levionnois *et al.,* 2021; Isasa *et al.,* 2023) but were beyond the scope of this study.

5.2 Trade-off between K_h and P_{50}

Our results showed that total theoretical hydraulic conductivity - K_h does not change with tree height, suggesting no direct role for a trade-off between K_h and P_{50} in explaining increased xylem vulnerability with height. Furthermore, we found no general cross-species relationship between branch P_{50} and total theoretical hydraulic conductivity. The observed pattern is in line with other studies that either report no trade-off between P_{50} and K_h in enclaves of the Amazonian savannah (Simioni *et al.,* 2023) or found a weak trade-off between K_h and hydraulic safety - P_{50} for woody plants at a global scale (e.g., Gleason *et al.,* 2016). In contrast, studies in two Panamanian forests (van der Sande *et al.,* 2019) and Norwegian spruce forests in Italy (Prendin *et al.,* 2018) have identified stronger relationships between K_h and P_{50}. In our study, the lack of an overall relationship with total theoretical hydraulic conductivity likely reflects the compensating effects of diameter and vessel frequency – vessel frequency decreases as vessel diameter increases. The relationship between hydraulic vulnerability and vessel diameter may ultimately be more important than that between vulnerability and total theoretical conductivity, as it suggests that, on average, vessels in taller trees may be more vulnerable due to their larger diameters.

5.3 Conclusions and implications for southern Amazon forests

Our study evaluates the variation in the hydraulic properties of trees with height within species in one of the southernmost Amazon forests. This region has faced substantial recent climate changes (Nobre *et al.,* 2016; Marengo *et al.,* 2018) and its trees have the lowest hydraulic safety margins of all Amazon forests evaluated to date (Tavares *et al.,* 2023). Our results provide a possible mechanism behind the increased mortality of tallest trees: the decrease in HSM_{50} with height, driven by declining resistance to embolism with height (less negative P_{50} in taller trees). As forest biomass is concentrated in the largest trees in these forests, continuing trends in increasing vapour pressure deficit and reduced rainfall in this region have the potential to further accentuate hydraulic stress in larger trees and to markedly alter forest structure and carbon storage. Our study further finds a linkage between vulnerability and vessel diameter size that may potentially explain the declines in P_{50} with height. However, a deeper understanding of the biophysical processes that determine embolism formation and spread at the nanoscale level is crucial to fully comprehend the observed diameter-vulnerability link.

Finally, the results presented here have clear implications for modelling, as we find that height-related declines are consistent across all species evaluated (i.e., the slopes of the height-P_{50} relationships were not found to vary statistically). This facilitates inclusion of such a relationship in ecosystem models and may help to improve predictions of drought-induced tree mortality in this region.

6. References

Adams HD, Guardiola-Claramonte M, Barron-Gafford GA, Villegas JC, Breshears DD, Zo CB, Huxman TE. 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *Proceedings of the national academy of sciences*, **106**(17): 7063-7066.

Adams HD, Zeppel MJ, Anderegg WR, Hartmann H, Landhäusser SM, Tissue DT, McDowell NG et al. 2017. A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. *Nature ecology & evolution*, **1**(9): 1285-1291.

Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Cobb N et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest ecology and management*, **259**(4): 660-684.

Alvares CA, Stape JL, Sentelhas PC, Gonçalves JDM, Sparovek G. 2013. Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift*, **22**(6): 711-728.

Anfodillo T, Olson ME. 2021. Tree mortality: testing the link between drought, embolism vulnerability, and xylem conduit diameter remains a priority. *Frontiers in Forests and Global Change*, **4**(1): 704670.

Anderegg WR, Klein T, Bartlett M, Sack L, Pellegrini AF, Choat B, Jansen S. 2016. Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. *Proceedings of the National Academy of Sciences*, **113**(18): 5024-5029.

Araújo I, Marimon BS, Scalon MC, Fauset S, Junior BHM, Tiwari R, Gloor MU et al. 2021. Trees at the Amazonia-Cerrado transition are approaching high temperature thresholds. *Environmental Research Letters*, **16**(3): 034047.

Araújo I, Morandi PS, Müller AO, Mariano LH, Alvarez F, da Silva IV, Marimon BS et al. 2022. Leaf functional traits and monodominance in Southern Amazonia tropical forests. *Plant Ecology*, 223: 185-200.

Araújo I, Scalon MC, Amorim I, Menor IO, Cruz WJ, Reis SM, Marimon BS et al. 2023. Morpho-anatomical traits and leaf nutrient concentrations vary between plant communities in the Cerrado-Amazonia transition?. *Flora*, 306: 152366.

Bennett AC, McDowell NG, Allen CD, Anderson-Teixeira KJ. 2015. Larger trees suffer most during drought in forests worldwide. *Nature Plants*, **1**(10): 1-5.

Berlyn GP, Miksche JP, Sass JE. 1976. Botanical microtechnique and cytochemistry. *Iowa State University Press*, **1**(2):200.

Becker P, Gribben, RJ. 2001. Estimation of conduit taper for the hydraulic resistance model of West et al. *Tree Physiology*, **21**(10): 697-700.

Becker P, Gribben RJ, Lim CM. 2000a. Tapered conduits can buffer hydraulic conductance from path-length effects. *Tree Physiology*, **20**(14): 965-967.

Becker P, Meinzer FC, Wullschleger SD, 2000b. Hydraulic limitation of tree height: a critique. *Functional Ecology*, **14**(1): 4-11.

Bittencourt PR, Oliveira RS, da Costa AC, Giles AL, Coughlin I, Costa PB, Rowland L et al. 2020. Amazonia trees have limited capacity to acclimate plant hydraulic properties in response to long-term drought. *Global change biology*, **26**(6): 3569-3584.

Brodribb TJ, Carriqui M, Delzon S, Lucani C. 2017. Optical measurement of stem xylem vulnerability. *Plant Physiology*, **174**(4): 2054-2061.

Brodribb TJ, Cochard H. 2009. Hydraulic failure defines the recovery and point of death in water-stressed conifers. *Plant physiology*, **149**(1): 575-584.

Brum M, Vadeboncoeur MA, Ivanov V, Asbjornsen H, Saleska S, Alves LF, Oliveira RS et al. 2019. Hydrological niche segregation defines forest structure and drought tolerance strategies in a seasonal Amazon forest. *Journal of Ecology*, **107**(1): 318-333.

Carlquist S. 1977. Ecological factors in wood evolution: a floristic approach. *American journal of botany*, **64**(7): 887-896.

Castelar JVS, Da Cunha M, Simioni PF, Castilhori MF, Lira-Martins D, Giles AL, Callado CH. 2023. Functional traits and water-transport strategies of woody species in an insular environment in a tropical forest. *American journal of botany*, **110**(9), e16214.

Chambers-Ostler A, Gloor E, Galbraith D, Groenendijk P, Brienen R. 2022. Vessel tapering is conserved along a precipitation gradient in tropical trees of the genus *Cedrela*. *Trees*, **37**(2): 269-284.

da Costa ACL, Galbraith D, Almeida S, Portela BTT, da Costa M, Junior JDAS, Meir P et al. 2010. Effect of 7 yr of experimental drought on vegetation dynamics and biomass storage of an eastern Amazonian rainforest. *New Phytologist*, **187**(3): 579-591.

Duffy PB, Brando P, Asner GP, Field CB. 2015. Projections of future meteorological drought and wet periods in the Amazon. *Proceedings of the National Academy of Sciences*, **112**(43): 13172-13177.

Echeverría A, Anfodillo T, Soriano D, Rosell JA, Olson ME. 2019. Constant theoretical conductance via changes in vessel diameter and number with height growth in *Moringa oleifera*. *Journal of Experimental Botany*, **70**(20): 5765-5772.

Esquivel-Muelbert A, Phillips OL, Brienen RJ, Fauset S, Sullivan MJ, Baker TR, Galbraith D et al. 2020. Tree mode of death and mortality risk factors across Amazon forests. *Nature communications*, **11**(1): 1-11.

Ewers FW, Ewers JM, Jacobsen A, López-Portillo J. 2007. Vessel redundancy: modeling safety in numbers. *Iawa Journal*, **28**(4): 373-388.

Ferrell GT, Otrosina WJ, Demars Jr CJ. 1994. Predicting susceptibility of white fir during a drought-associated outbreak of the fir engraver, *Scolytus ventralis*, in California. *Canadian Journal of Forest Research*, **24**(2): 302-305.

Fortunel C, Ruelle J, Beauchêne J, Fine PV, Baraloto C. 2014. Wood specific gravity and anatomy of branches and roots in 113 A mazonian rainforest tree species across environmental gradients. *New Phytologist*, **202**(1): 79-94.

Freitas GV, Silva JLA, Ribeiro DR, Simioni P, Campbell G, Pireda S, Vitória AP. 2024. Functional trait patterns: investigating variation-covariation relationships and the importance of intraspecific variability along distinct vegetation types. *Community Ecology*, **25**(2): 221-236.

Gatti LV, Basso LS, Miller JB, Gloor M, Gatti Domingues L, Cassol HL, Neves RA et al. 2021. Amazonia as a carbon source linked to deforestation and climate change. *Nature*, **595**(7867): 388-393.

Givnish TJ. 1982. On the adaptive significance of leaf height in forest herbs. *The American Naturalist*, **120**(3): 353-381.

Giles AL, Rowland L, Bittencourt PRL, Bartholomew DC, Coughlin I, Costa PB, Oliveira RS et al. 2022. Small understorey trees have greater capacity than canopy trees to adjust hydraulic traits following prolonged experimental drought in a tropical forest. *Tree physiology*, **42**(3): 537-556.

Gleason SM, Westoby M, Jansen S, Choat B, Hacke UG, Pratt RB, Zanne AE et al. 2016. Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant species. *New Phytologist*, **209**(1): 123-136.

Guimberteau M, Ronchail J, Espinoza JC, Lengaigne M, Sultan B, Polcher J, Ciais P et al. 2013. Future changes in precipitation and impacts on extreme streamflow over Amazonian sub-basins. *Environmental Research Letters*, **8**(1): 014035.

Haghtalab N, Moore N, Heerspink BP, Hyndman DW. 2020. Evaluating spatial patterns in precipitation trends across the Amazon basin driven by land cover and global scale forcings. *Theoretical and Applied Climatology*, **140**(1) 411-427.

Hargrave KR, Kolb KJ, Ewers FW, Davis SD. 1994. Conduit diameter and drought-induced embolism in *Salvia mellifera* Greene (Labiatae). *New Phytologist*, **126**(4): 695-705.

Holbrook NM, Burns MJ, Field CB. 1995. Negative xylem pressures in plants: a test of the balancing pressure technique. *Science*, **270**(5239): 1193-1194.

Iawa Committee. 1989. IAWA list of microscopic features for hardwood identification. *IAWA Bull*, **10**(1): 219-332.

Isasa E, Link RM, Jansen S, Tezeh FR, Kaack L, Sarmento Cabral J, Schuldt B. 2023. Addressing controversies in the xylem embolism resistance–vessel diameter relationship. *New Phytologist*, **238**(1): 283-296.

Jancoski HS, Marimon BS, Scalon MC, Barros FV, Marimon-Junior BH, Carvalho E, Oliveira RS, Oliveras Menor I. 2022. Distinct leaf water potential regulation of tree species and vegetation types across the Cerrado-Amazonia transition. *Biotropica*, **54**(2): 431-443.

Janssen TA, Hölttä T, Fleischer K, Naudts K, Dolman H. 2020. Wood allocation trade-offs between fiber wall, fiber lumen, and axial parenchyma drive drought resistance in neotropical trees. *Plant, cell & environment*, **43**(4): 965-980.

Jacobsen AL, Pratt RB, Venturas MD, Hacke UG. 2019. Large volume vessels are vulnerable to water-stress-induced embolism in stems of poplar. *Iawa Journal,* **40**(1): 4-S4.

Jiménez-Muñoz JC, Sobrino JA, Mattar C, Malhi Y. 2013. Spatial and temporal patterns of the recent warming of the Amazon forest. *Journal of Geophysical Research: Atmospheres*, **118**(11): 5204-5215.

Johansen DA. 1940. Plant microtechnique. *Plant microtechnique.*, 530p.

Johnson DJ, Needham J, Xu CG, Massoud EC, Davies SJ, Anderson-Teixeira KJ, McMahon SM et al. 2018. Climate sensitive size-dependent survival in tropical trees. *Nature ecology & evolution*, **2**(9): 1436–1442.

Kenzo T, Inoue Y, Yoshimura M, Yamashita M, Tanaka-Oda A, Ichie T. 2015. Height-related changes in leaf photosynthetic traits in diverse Bornean tropical rain forest trees. *Oecologia*, **177**(1): 191-202.

Koch GW, Sillett SC, Jennings GM, Davis SD. 2004. The limits to tree height. *Nature*, **428**(6985): 851-854.

Levene H. 1961. Robust Tests for the equality of variance. Contributions to Probability and Statistics, California.

Levionnois S, Jansen S, Wandji RT, Beauchêne J, Ziegler C, Coste S, Heuret P et al. 2021. Linking drought-induced xylem embolism resistance to wood anatomical traits in Neotropical trees. *New Phytologist*, **229**(3): 1453-1466.

Lewis SL, Brando PM, Phillips OL, van der Heijden GM, Nepstad D. 2011. The 2010 amazon drought. *Science*, **331**(6017): 554-554.

Liu H, Gleason SM, Hao G, Hua L, He P, Goldstein G, Ye Q. 2019. Hydraulic traits are coordinated with maximum plant height at the global scale. *Science Advances*, **5**(2): eaav1332.

Li S, Feifel M, Karimi Z, Schuldt B, Choat B, Jansen S. 2016. Leaf gas exchange performance and the lethal water potential of five European species during drought. Tree physiology, **36**(2): 179-192.

Liang X, Ye Q, Liu H, Brodribb TJ. 2021. Wood density predicts mortality threshold for diverse trees. *New Phytologist*, **229**(6): 3053-3057.

Lobo A, Torres-Ruiz JM, Burlett R, Lemaire C, Parise C, Francioni C, Delzon S et al. 2018. Assessing inter-and intraspecific variability of xylem vulnerability to embolism in oaks. *Forest Ecology and Management*, **424**(1): 53-61.

Marimon BS, Marimon-Junior BH, Feldpausch TR, Oliveira-Santos C, Mews HA, Lopez-Gonzalez G, Phillips OL et al. 2014. Disequilibrium and hyperdynamic tree turnover at the forest-cerrado transition zone in southern Amazonia. *Plant Ecology & Diversity*, **7**(2): 281-292.

Marimon-Junior BH, Hay JDV, Oliveras I, Halina Jancoski H, Umetsu RK, Feldpausch TR, Galbraith DR, Gloor EU, Phillips OL, Marimon BS. 2020. Soil water-holding capacity and monodominance in Southern Amazon tropical forests. *Plant and Soil*, **450**(1): 65–79.

Marques EQ, Marimon-Junior BH, Marimon BS, Matricardi EA, Mews HA, Colli GR. 2020. Redefining the Cerrado–Amazonia transition: implications for conservation. *Biodiversity and conservation*, **29**(5): 1501-1517.

Marengo JA, Souza Jr CM, Thonicke K, Burton C, Halladay K, Betts RA, Soares WR et al. 2018. Changes in climate and land use over the Amazon region: current and future variability and trends. *Frontiers in Earth Science*, **6**(1): 1-21.

Maherali H, Moura CF, Caldeira MC, Willson CJ, Jackson RB et al. 2006. Functional coordination between leaf gas exchange and vulnerability to xylem cavitation in temperate forest trees. *Plant, Cell & Environment*, **29**(4): 571-583.

McDowell NG, Allen CD. 2015. Darcy's law predicts widespread forest mortality under climate warming. *Nature Climate Change*, **5**(7): 669-672.

Meinzer FC, Johnson DM, Lachenbruch B, McCulloh KA, Woodruff DR. 2009. Xylem hydraulic safety margins in woody plants: coordination of stomatal control of xylem tension with hydraulic capacitance. *Functional Ecology*, **23**(5): 922-930.

Meir P, Mencuccini M, Dewar RC. 2015. Drought-related tree mortality: addressing the gaps in understanding and prediction. *New Phytologist*, **207**(1): 28-33.

Mews HA, Marimon BS, Pinto JRR, Silvério DV. 2011. Dinâmica estrutural da comunidade lenhosa em floresta estacional semidecidual na transição cerrado-floresta amazônica, Mato Grosso, Brasil. *Acta Botanica Brasilica*, **25**(4): 845-857.

Mews HA, Marimon BS, Ratter JA. 2012. Observations on the vegetation of Mato Grosso, Brazil. V. Changes in the woody species diversity of a forest in the Cerrado–Amazonian Forest transition zone and notes on the forests of the region. *Edinburgh Journal of Botany*, **69**(2): 239-253.

Morandi PS, Marimon BS, Eisenlohr PV, Marimon-Junior BH, Oliveira-Santos C, Feldpausch TR, Phillips OL et al. 2016. Patterns of tree species composition at watershed-scale in the Amazon ‘arc of deforestation’: implications for conservation. *Environmental Conservation*, **43**(4): 317-326.

Nobre CA, Sampaio G, Borma LS, Castilla-Rubio JC, Silva JS, Cardoso M. 2016. Land-use and climate change risks in the Amazon and the need of a novel sustainable development paradigm. *Proceedings of the National Academy of Sciences*, **113**(39): 10759-10768.

Olson ME, Soriano D, Rosell JA, Anfodillo T, Donoghue MJ, Edwards EJ, Méndez-Alonzo R et al. 2018. Plant height and hydraulic vulnerability to drought and cold. *Proceedings of the National Academy of Sciences*, **115**(29): 7551-7556.

Olson ME, Pace MR, Anfodillo T. 2023. The vulnerability to drought-induced embolism-conduit diameter link: breaching the anatomy-physiology divide. *IAWA Journal*, **1**(aop): 1-20.

Pammenter NV, Van der Willigen C. 1998. A mathematical and statistical analysis of the curves illustrating vulnerability of xylem to cavitation. *Tree physiology*, **18**(8): 589-593.

Panisset JS, Libonati R, Gouveia CMP, Machado-Silva F, França DA, França JRA, Peres LF. 2018. Contrasting patterns of the extreme drought episodes of 2005, 2010 and 2015 in the Amazon Basin. *International Journal of Climatology*, **38**(2): 1096-1104.

Pereira L, Bittencourt PR, Oliveira RS, Junior MB, Barros FV, Ribeiro RV, Mazzafera P. 2016. Plant pneumatics: stem air flow is related to embolism–new perspectives on methods in plant hydraulics. *New Phytologist*, **211**(1): 357-370.

Phillips OL, Van Der Heijden G, Lewis SL, López-González G, Aragão LE, Lloyd J, Vilanova E et al. 2010. Drought–mortality relationships for tropical forests. *New Phytologist*, **187**(3): 631-646.

Prendin AL, Mayr S, Beikircher B, von Arx G, Petit G. 2018. Xylem anatomical adjustments prioritize hydraulic efficiency over safety as Norway spruce trees grow taller. *Tree Physiology*, **38**(8): 1088-1097.

R Core Team 2022. A Language and Environment for Statistical Computing: version 4.2.1, R Foundation for Statistical Computing, Vienna, Austria. There is no corresponding record for this reference.

Ratter JA, Richards PW, Argent G, Gifford DR. 1973. Observations on the vegetation of the northeastern Mato Grosso. I. The woody vegetation types of the XavantinaCachimbo expedition area. *Philosophical Transactions of the Royal Society of London* **226**(880): 449–492.

Reis SM, Marimon BS, Esquivel-Muelbert A, Marimon Jr BH, Morandi PS, Elias F, Phillips OL et al. 2022. Climate and crown damage drive tree mortality in southern Amazonian edge forests. *Journal of Ecology*, **110**(4): 876-888.

Rowland L, da Costa ACL, Galbraith DR, Oliveira RS, Binks OJ, Oliveira AAR, Meir P et al. 2015. Death from drought in tropical forests is triggered by hydraulics not carbon starvation. *Nature*, **528**(7580): 119-122.

Ryan MG, Yoder BJ. 1997. Hydraulic limits to tree height and tree growth. *Bioscience*, **47**(4): 235-242.

Scholander PF, Bradstreet ED, Hemmingsen EA, Hammel HT. 1965. Sap Pressure in Vascular Plants: Negative hydrostatic pressure can be measured in plants. *Science*, **148**(3668): 339-346.

Scholz A, Klepsch M, Karimi Z, Jansen S. 2013. How to quantify conduits in wood?. *Frontiers in plant science*, **4**(56): 1-11.

Shapiro SS, Wilk MB. 1965. An analysis of variance test for normality (complete samples). *Biometrika*, **52**(1): 591-611.

Simioni PF, Emilio T, Giles AL, de Freitas GV, Oliveira RS, Setime L, Da Cunha M et al. 2023. Anatomical traits related to leaf and branch hydraulic functioning on Amazonian savanna plants. *AoB PLANTS*, **15**(3): plad018.

Sperry JS, Donnelly JR, Tyree MT. 1988. A method for measuring hydraulic conductivity and embolism in xylem. *Plant, Cell & Environment*, **11**(1): 35-40.

Tardieu F. 1996. Drought perception by plants do cells of droughted plants experience water stress?. *Plant growth regulation*, **20**(2): 93-104.

Tavares JV, Oliveira RS, Mencuccini M, Signori-Müller C, Pereira L, Diniz FC, Galbraith DR et al. 2023. Basin-wide variation in tree hydraulic safety margins predicts the carbon balance of Amazon forests. *Nature*, **617**(1): 111–117.

Tiwari R, Gloor E, da Cruz WJA, Schwantes Marimon B, Marimon-Junior BH, Reis SM, Galbraith D et al. 2020. Photosynthetic quantum efficiency in south-eastern Amazonian trees may be already affected by climate change. *Plant, cell & environment*, **44**(7): 2428-2439.

Tyree MT, Zimmermann MH. 2002. Hydraulic architecture of whole plants and plant performance. In Xylem structure and the ascent of sap (pp. 175-214). *Springer*, Berlin, Heidelberg.

Tyree MT, Sperry JS. 1988. Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress?: answers from a model. *Plant physiology*, **88**(3): 574-580.

van der Sande MT, Poorter L, Schnitzer SA, Engelbrecht BM, Markesteijn L et al. 2019. The hydraulic efficiency–safety trade-off differs between lianas and trees. *Ecology*, **100**(5): e02666.

Wheeler JK, Sperry JS, Hacke UG, Hoang N. 2005. Inter-vessel pitting and cavitation in woody Rosaceae and other vesselled plants: a basis for a safety versus efficiency trade-off in xylem transport. *Plant, Cell & Environment*, **28**(6): 800-812.

Williamson GB, Wiemann MC. 2010. Measuring wood specific gravity correctly. *American Journal of Botany*, **97**(3): 519-524.

Wickham, H. 2011. ggplot2: Wiley interdisciplinary reviews: computational statistics, **3**(2): 180-185.

Zach A, Schuldt B, Brix S, Horna V, Culmsee H, Leuschner C. 2010. Vessel diameter and xylem hydraulic conductivity increase with tree height in tropical rainforest trees in Sulawesi, Indonesia. *Flora-Morphology, Distribution, Functional Ecology of Plants*, **205**(8): 506-512.

Zaehle S. 2005. Effect of height on tree hydraulic conductance incompletely compensated by xylem tapering. *Functional Ecology*, **19**(2): 359-364.

Zwieniecki MA, Holbrook NM. 1998. Diurnal variation in xylem hydraulic conductivity in white ash (*Fraxinus americana* L.), red maple (*Acer rubrum* L.) and red spruce (*Picea rubens* Sarg.). *Plant, Cell & Environment*, **21**(11): 1173-1180.

Acknowledgements

Coordination for the Improvement of Higher Education Personnel (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - CAPES Proc. Da Conservação da Biodiversidade a Biotecnologia: uma proposta para o fortalecimento da ciência na UNEMAT e uso sustentável da terra em Mato Grosso - 88887.586792/2020-00) and from the National Council for Scientific and Technological Development (Conselho Nacional de Desenvolvimento Científico e Tecnológico - CNPq Proc. SWE - 200576/2022-4) grant to Igor Araújo. This research received financial support from the (For a Climate Resilient Amazon - FORAMA - Royal Society ICA/R1/180100). We thank Programa de Pós-Graduação em Ecologia e Conservação, Universidade do Estado de Mato Grosso - UNEMAT.

Competing interests

The authors declare that they have no conflict of interest.

Funding

CAPES Proc. 88887.586792/2020-00

CNPq Proc. SWE - 200576/2022-4

FORAMA - Royal Society ICA/R1/180100

Author contributions

IA, MUG and DRG: Conceptualization, Methodology, Formal analysis, Investigation, Writing - Original Draft. **BSM and BHMJ:** Conceptualization, Writing - Review & Editing. **CHLO, JWSS, RGB and JVT:** Investigation, Methodology and writing - Review & Editing. **OLP, IVS and PFS:** Writing - Review & Editing.

Data availability

The data that support the findings of this study are available in the Supporting Information of this publication.

Highlights

- Potential increases in drought frequency and vapour pressure deficit pose a risk to the future function of tropical trees;
- The greater hydraulic vulnerability of larger trees provides a potential explanation for the higher drought-induced mortality observed in taller tropical trees;

- The consistency of the height-P_{50} relationship across species opens the door to a more accurate prediction of southern Amazon forest responses to future droughts;