

Research paper

Plasticity of wood and leaf traits related to hydraulic efficiency and safety is linked to evaporative demand and not soil moisture in rubber (*Hevea brasiliensis*)

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The predicted increase of drought intensity in South-East Asia has raised concern about the sustainability of rubber (*Hevea brasiliensis* Müll. Arg.) cultivation. In order to quantify the degree of phenotypic plasticity in this important tree crop species, we analysed a set of wood and leaf traits related to the hydraulic safety and efficiency in PB260 clones from eight small-holder plantations in Jambi province, Indonesia, representing a gradient in local microclimatic and edaphic conditions. Across plots, branch embolism resistance (P_{50}) ranged from -2.14 to -2.58 MPa. The P_{50} and P_{88} values declined, and the hydraulic safety margin increased, with an increase in the mean annual vapour pressure deficit (VPD). Among leaf traits, only the changes in specific leaf area were related to the differences in evaporative demand. These variations of hydraulic trait values were not related to soil moisture levels. We did not find a trade-off between hydraulic safety and efficiency, but vessel density (VD) emerged as a major trait associated with both safety and efficiency. The VD, and not vessel diameter, was closely related to P_{50} and P_{88} as well as to specific hydraulic conductivity, the lumen-to-sapwood area ratio and the vessel grouping index. In conclusion, our results demonstrate some degree of phenotypic plasticity in wood traits related to hydraulic safety in this tropical tree species, but this is only in response to the local changes in evaporative demand and not soil moisture. Given that VPD may increasingly limit plant growth in a warmer world, our results provide evidence of hydraulic trait changes in response to a rising evaporative demand.

Keywords: embolism resistance, leaf turgor loss point, phenotypic plasticity, vapour pressure deficit, vulnerability curve, wood anatomy.

Introduction

In South-East Asia, rubber (*Hevea brasiliensis* Müll. Arg.) plantations are one of the economically most important cash crops. Indonesia, the second largest latex producer worldwide, produced, in 2017, 3.6 million tons of latex on an area of 3.7 million hectares (FAO 2017). Rubber, a tree species originally introduced from the Amazon basin, is traditionally cultivated under ample water supply on well-drained soils in the equatorial belt

under humid tropical and monsoon climates (Raj et al. 2005, Priyadarshan 2017). The increasing intensity of El Niño–Southern Oscillation events during the last decades, however, might threaten the growth and yield potential of this important crop in part of its current distribution range (Wichichonchai and Manmeun 1992, Chandrashekar et al. 1998, Irawan 2003). To explore the likely agronomic consequences of increasing drought exposure in Indonesia (Susilo et al. 2013), evaluating

the plasticity of functional traits related to the growth and drought resistance of rubber is of great interest.

As a consequence of global climate warming, the drought response of tropical trees has been intensively studied during the past decades (Moser et al. 2014, Rowland et al. 2015, Santiago et al. 2016, McDowell et al. 2018). As the involved drought response mechanisms are complex (Aroca 2012), there is a need to understand and identify the key factors or traits linked to the mechanisms of drought avoidance and tolerance (Rungwattana et al. 2018, Pritzkow et al. 2020). Because plant hydraulic strategies are multidimensional, several interdependent and coordinated functional traits associated with drought-induced mortality have been identified in the recent past (Adams et al. 2017, Choat et al. 2018). At the wood level, xylem hydraulic safety from embolism formation as a direct measure of the functionality of the water transport system has emerged as a major trait related to drought resistance (Rowland et al. 2015, Anderegg et al. 2016, Adams et al. 2017, Laginha Pinto Correia et al. 2019). Hydraulic efficiency (i.e., the rate of water conductance per sapwood area across a given pressure gradient), on the other hand, is closely related to growth (Hajek et al. 2014, Kotowska et al. 2015, Schumann et al. 2019), while the wood density (WD) as an integrative trait has been associated with both growth (Hoeber et al. 2014, Finegan et al. 2015) and drought survival (Phillips et al. 2010, Poorter et al. 2019, Janssen et al. 2020). At the leaf level, the water potential at the leaf turgor loss point (π_{tlp}) emerged as a good predictor of drought tolerance (Oppenheimer 1963, Bartlett et al. 2012a). The π_{tlp} is generally interrelated with embolism resistance due to the relationship between the onset of embolism formation and full stomatal closure that depends on leaf turgor-induced abscisic acid synthesis (e.g., Brodribb et al. 2003, McAdam and Brodribb 2016, Rodriguez-Dominguez et al. 2016).

In angiosperms, most current research has examined the inter-specific variability of hydraulic-related functional traits, while much less is known about trait variation at the intra-specific level (Anderegg and Meinzer 2015). However, understanding the intra-specific variability is mandatory in order to understand the adaptive capacity of a given species. Such a variability can result from the genetic differences between individuals or it could be an expression of phenotypic plasticity (Aitken et al. 2008). In temperate forests, for example, branch hydraulic safety increased in *Fagus sylvatica* with climatic aridity (Schuldt et al. 2016, Stojnic et al. 2018). A similar dependence on aridity was observed in this species for the water potential at the turgor loss point and the sapwood-to-leaf area ratio (Rosas et al. 2019), while this study could not detect a relationship between embolism resistance and climatic aridity. Likewise, no effect of water availability on embolism resistance was observed in *Quercus ilex* (Martin-StPaul et al. 2012, Rosas et al. 2019). In fact, several factors other than precipitation rates may influence

embolism resistance across climatic gradients, which could lead to contradicting results. These include soil physical properties related to water-holding capacity (Hultine et al. 2006, Waite et al. 2019) and sampling height in the tree (Burgess et al. 2006, Rowland et al. 2015). Sapling studies with variable soil water availability have shown that hydraulic safety generally increases with decreasing water availability (Plavcová and Hacke 2012, Lübbe et al. 2017, Knipfer et al. 2018) due to vascular adjustment. When grown in drier soil, tree saplings typically form narrower vessels, while the vessel density (VD) increases (Fonti et al. 2013, Lübbe et al. 2017).

Other than in temperate forests, intra-specific variation in hydraulic safety-related traits has rarely been studied in tropical tree species along environmental gradients. The only study that we are aware of has been carried out on oil palm (*Elaeis guineensis*), a tropical monocot that responded sensitively, in its hydraulic architecture, to the changes in soil moisture (Waite et al. 2019). It therefore remains an open question whether embolism resistance in rubber is a more conservative or a plastic trait that responds sensitively to local environmental conditions. This tree crop has been widely distributed across the tropics and is currently grown under a broad range of climates outside its native range. In some regions, it is tolerating a certain level of drought at the cost of reduced yield (Rao et al. 1998, Cahyo et al. 2016). Because the photosynthetic activity, growth and yield of rubber are sensitive to the atmospheric evaporative demand and soil water availability (Devakumar et al. 1998, Clermont-Dauphin et al. 2013, Falqueto et al. 2017), at least some degree of phenotypic variability, as a result of either genetic variation and/or phenotypic plasticity, is to be expected (Valladares et al. 2007). In fact, Rungwattana et al. (2018) observed, for some drought-related wood and leaf traits, a high degree of intra-specific genetic variability in a rubber provenance trial. Because leaf traits were more closely related to the climate at the place of origin than wood traits, the latter seems to be more plastic, while the former may contain a stronger phylogenetic signal (Rungwattana et al. 2018).

The main objective of the present study was to investigate the phenotypic plasticity of several morphological, anatomical and physiological leaf and wood traits associated with drought tolerance in rubber (*H. brasiliensis*). We focused on traits linked to hydraulic safety (i.e., the ability of plants to maintain the integrity of their conductive system during water stress) and efficiency (i.e., the ability of the plants to conduct water efficiently) that might respond sensitively to the local environment (see Table 1). We compared clonal trees of similar height across eight plantations differing in mean local microclimatic and edaphic conditions. As all trees belonged to the same clone, we could attribute all trait variations to phenotypic plasticity. From the existing knowledge about acclimation of hydraulic-related traits to water deficits, we hypothesized that (i) hydraulic

Table 1. List of studied variables with abbreviations, units, and definitions.

Abbreviation	Unit	Definition
Environmental characteristics		
VWC	vol. %	Volumetric soil water content at 0.3 m depth
VPD	kPa	Annual average vapor pressure deficit calculated from relative humidity and air temperature for 2018
VPD _{dry}	kPa	Annual average vapor pressure deficit calculated from relative humidity and air temperature for the 20% driest days in 2018
Plot parameters		
SD	n ha ⁻¹	Stem density per hectare
A	year	Plantation age
% sand	%	Percentage of sand in the soil top 30 cm
% clay	%	Percentage of clay in the soil top 30 cm
Yield	kg	Total amount of latex harvested in 2017
Stand structural parameters		
DBH	cm	Tree diameter at 1.7 m height
H	m	Tree height
WD	g cm ⁻³	Stem wood density
Hydraulic traits		
<i>Efficiency</i>		
K _p	kg m ⁻¹ MPa ⁻¹ s ⁻¹	Potential hydraulic conductivity
K _s	kg m ⁻¹ MPa ⁻¹ s ⁻¹	Branch xylem-specific hydraulic conductivity
K _l	kg m ⁻¹ MPa ⁻¹ s ⁻¹	Leaf-specific hydraulic conductivity
<i>Safety</i>		
P ₁₂	MPa	Xylem pressure at 12% loss of hydraulic conductance
P ₅₀	MPa	Xylem pressure at 50% loss of hydraulic conductance
P ₈₈	MPa	Xylem pressure at 88% loss of hydraulic conductance
HSM	MPa	Hydraulic safety margin calculated as $\pi_{\text{tlp}} - P_{88}$
Anatomical traits		
<i>Efficiency/safety</i>		
A _{lumen} :A _{xylem}	cm ² mm ⁻²	Lumen-to-sapwood area ratio
<i>Efficiency</i>		
D	μm	Vessel diameter
<i>Safety</i>		
VD	n mm ⁻²	Vessel density
V _g	n group ⁻¹	Vessel grouping index: mean number of cells per group
Leaf traits		
<i>Efficiency/safety</i>		
SLA	m ² kg ⁻¹	Specific leaf area
HV	m ² m ⁻²	Huber value as the ratio of branch xylem area and total leaf area distal to the branch
<i>Safety</i>		
π _{tlp}	MPa	Leaf turgor loss point
<i>Efficiency</i>		
δ ¹³ C	‰	Carbon isotope signature

safety increases and hydraulic efficiency declines with increasing evaporative demand and soil water scarcity; (ii) wood traits are more plastic than leaf traits with regard to microclimatic and edaphic conditions; and (iii) changes in embolism resistance can be attributed to wood anatomical adjustments.

Materials and methods

Study site, plot and soil characteristics

The study was carried out in eight smallholder rubber (*H. brasiliensis*) plantations in the province of Jambi, Sumatra (Indonesia), at elevations of 39–79 m a.s.l. The region has a moist equatorial climate with a mean annual precipitation

(MAP) of 2235 mm, a mean annual temperature of 26.7 °C (Drescher et al. 2016) and a distinct dry season between May and September. The plantations are located in a homogeneous landscape, which is best defined by its dominant soil type and texture, i.e., clayey Acrisol (Allen et al. 2016). In every plantation, a 50 × 50 m plot was demarcated. Soil texture was determined in all plots, except for P1 which was not included in the survey of Allen et al. (2016) in 0- to 30-cm soil depth by means of the pipette method of Köhn (DIN ISO 11277:2002-08 2002). The clay and sand contents varied considerably among the plots (Table 2). All eight plots were situated in the same region (maximum distance: 10 km; see Table S1 available as Supplementary data at *Tree Physiology*

Online for plot details). Plantation age ranged from 9 to 29 years, with trees planted at densities ranging from 300 to 732 trees per hectare (Table 2), which is within the common range for latex production (Carr 2012). Such differences were inherent to our experimental design which focused on structurally variable small-holder plantations, representing a gradient in water availability and evaporative demand. We sampled only mature trees with similar height across plots to account for size-related anatomical adjustments. The stem density in rubber plantations can vary, with literature citing densities ranging between 300 and 1000 stems per hectare (Carr 2012, Blagodatsky et al. 2016). However, it is essential to acknowledge that, for optimal productivity, typical densities are more confined. Densities below 400 or above 800 stems ha^{-1} can significantly influence the productivity per land area. In the context of our study, the densities reflect common small-holder practices, contrasting with large-scale plantations where density is typically maintained closer to optimal. Nonetheless, age- and density-related differences were always accounted for throughout the statistical analyses. Please further note that, because of latex-harvesting scars on the trees, diameter at breast height (DBH) given here refers to the diameter taken at 1.7 m throughout the manuscript. Latex was harvested by tapping the tree trunk and was recorded by the plot owners, in 2017, two to three times a month (Tables 1 and 2).

Microclimatic and hydrologic conditions

On every plot, a climate station was installed in the centre below the canopy and was operated throughout 2017 and 2018, which were representative years for the area in terms of climatic conditions (based on WorldClim climatic data from 2010 to 2018; Figure S1 available as Supplementary data at *Tree Physiology* Online). A meteorological station was installed in the centre of each 50 × 50 m plantation (for details, refer to Meijide et al. 2018). Volumetric soil water content (VWC, %) at 30-cm soil depth was measured with three Trime-Pico32 sensors (IMKO, Ettlingen, Germany), and from this, the mean was estimated. Air temperature (T , °C) and relative air humidity (RH, %) at 2 m height were recorded with a thermohygrometer (Galltec Mela, Bondorf, Germany). Data were logged every hour using a UIT LogTrans 16-GPRS data logger (UIT, Dresden, Germany). Atmospheric vapour pressure deficit (VPD) was calculated from T and RH according to Allen et al. (1998). Air and soil humidity in the stands were high throughout the year, with a monthly mean daytime VPD (06:00 to 18:00 h) ranging from 0.3 to 1.4 kPa and with a monthly mean VWC varying between 25 and 65% across plots (Figure 1). Likewise, the annual mean VPD in 2017 and 2018 ranged from 0.49 to 0.86 kPa across plots (Table 2). In 2017 and 2018, a distinct dry season between July and September was observed, which we used to calculate VPD for the 20% driest days of the year (VPD_{dry}; Table 2). Because the plantation structure remained

Table 2. Plot characteristics of the eight studied *H. brasiliensis* plantations in Jambi, Sumatra (Indonesia).

Plot	α	SD	Yield	% sand	% clay	VWC	VPD	VPD _{dry}	DBH	H	n_{tree}	n_{cavitron}
P1	19	316	508	—	—	32.47 ± 0.05 ^h	0.49 ± 0.02 ^e	0.78 ± 0.02 ^f	24.44 ± 0.71 ^a	14.58 ± 0.24 ^a	15	3
P2	26	300	358	3.64 ± 0.04 ^g	37.90 ± 0.95 ^d	35.36 ± 0.03 ^f	0.62 ± 0.01 ^c	1.03 ± 0.01 ^c	21.10 ± 1.16 ^{ab}	14.57 ± 0.25 ^a	15	3
P3	22	420	936	48.8 ± 1.39 ^a	14.40 ± 3.60 ⁱ	44.49 ± 0.12 ^c	0.61 ± 0.01 ^c	1.00 ± 0.02 ^c	24.25 ± 1.52 ^a	14.56 ± 0.23 ^a	15	5
P4	23	652	441	21.87 ± 0.89 ^{bc}	54.88 ± 5.43 ^a	38.68 ± 0.05 ^d	0.75 ± 0.01 ^b	1.31 ± 0.03 ^a	23.26 ± 1.56 ^a	14.51 ± 0.18 ^a	15	6
P5	29	668	338	14.81 ± 1.32 ^{de}	41.50 ± 2.81 ^{bc}	56.86 ± 0.10 ^a	0.74 ± 0.01 ^b	1.19 ± 0.01 ^b	15.29 ± 0.71 ^{cd}	14.21 ± 0.19 ^a	15	6
P6	21	448	402	18.02 ± 0.44 ^{cd}	30.57 ± 0.49 ^{ef}	33.94 ± 0.06 ^g	0.49 ± 0.01 ^e	0.83 ± 0.02 ^e	15.79 ± 0.86 ^{cd}	14.49 ± 0.22 ^a	15	3
P7	18	404	545	13.56 ± 1.80 ^{ef}	29.08 ± 1.58 ^g	47.28 ± 0.11 ^b	0.57 ± 0.01 ^d	0.94 ± 0.01 ^d	19.68 ± 2.22 ^{bc}	14.57 ± 0.24 ^a	15	5
P8	9	732	721	32.58 ± 9.57 ^{ab}	28.16 ± 9.30 ^g	35.89 ± 0.03 ^e	0.86 ± 0.01 ^a	1.31 ± 0.02 ^a	13.54 ± 0.29 ^d	14.39 ± 0.21 ^a	15	4

Given are tree age (α , year), stem density (SD, n ha^{-1}), total latex yield in 2017 (kg), percent of sand and clay in the top 30 cm of the soil, average soil VWC in 2018 (vol. %), daily average VPD (kPa) in 2018, mean VPD of the 20% driest days (VPD_{dry}, kPa), average tree DBH (cm), tree height (H, m) and number of investigated trees (n_{tree}) and branches (n_{cavitron}) for xylem safety measurements. Values are means ± SE. Different small letters indicate significant differences across the eight plots (Kruskal–Wallis test or one-way analysis of variance).

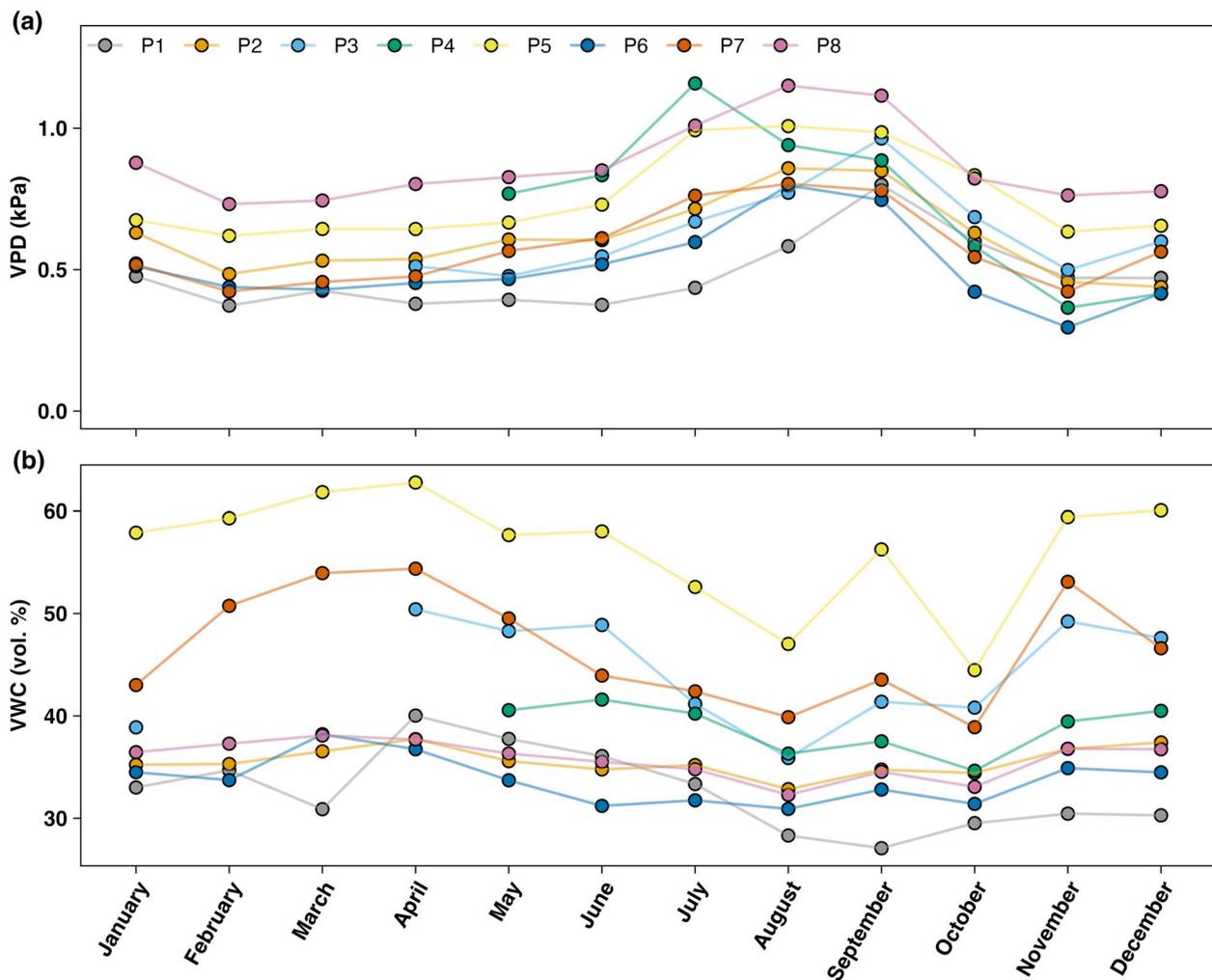


Figure 1. Annual course of (a) atmospheric VPD and (b) volumetric soil moisture (VWC) for the years 2017 and 2018 at eight *H. brasiliensis* plantation sites in Jambi province, Sumatra, Indonesia. Each point represents the monthly average calculated from daily values measured every 10 min between 06:00 h and 18:00 h. Each line represents one of the eight plots.

stable across the years (i.e., within plots, canopy structure, tree space and density remained the same and understorey vegetation was always well controlled), we assume that the atmospheric and edaphic conditions measured in 2017 and 2018 reflect fairly well the past growing conditions of the trees throughout the study. Indeed, both years were not extreme with regards to their climate conditions (Figure S1 available as Supplementary data at *Tree Physiology Online*).

Tree selection and plant material

In each plot, 15 mature rubber trees of similar height and canopy position were selected. According to the plot owners and collaborators, all sampled rubber trees are PB260 clones, a widely planted clone in Indonesia and Malaysia from where it originates (Hoong 1997, Pereira et al. 2018). The PB260 clone is suitable for areas with low MAP and is one of the best-studied clones of the Sumbawa Research Centre in South Sumatra (Ardika et al. 2017). In an initial collection campaign

between September and November 2017, we collected samples from the same preselected 120 trees (15 trees \times 8 plots). We sampled one wood core on each tree (c. 7 cm length) at 1.7 m stem height above the rubber tapping scars using an increment corer (Hagl f, L ngsele, Sweden). From the upper canopy of these trees, we took branches (about 60 cm long) using a long-reaching branch cutter. These branches were dedicated to measuring the leaf morphology and hydraulic efficiency ($n = 1$ branch \times 15 trees \times 8 plots = 120). We also extracted small adjacent leafy branch segments, around 20 cm long, and immediately stored them in humidified bags for subsequent analyses of the leaf water potential at turgor loss point (π_{tlp} ; $n = 120$). In the field, all leaves distal to the branch segments to be used for measuring hydraulic efficiency were collected, and branches were immediately transferred to polyethylene tubes filled with deionized water containing a sodium-silver-chloride complex ($16 \mu\text{g L}^{-1}$ Ag and 8mg L^{-1} NaCl; Micropur katadyn, Wallisellen, Switzerland) to prevent microbial growth.

After harvest, all samples were transported to the University of Jambi (UNJA) and were stored in a fridge until being possessed.

A second collection campaign in March 2018 aimed at determining the hydraulic safety. We initially took branch samples from 64 trees (8 trees \times 8 plots), a subset from the previous 120 trees. From these, 35 vulnerability curves (VCs) were included in further analyses (for details, refer to the subsequent sections). Special care was taken during the transfer of these branches to the Phenobois facility at the University of Bordeaux to ensure they remained hydrated throughout. This transfer, which included necessary storage precautions, spanned 3–4 days.

Tree height and WD

Tree height (H) was measured with a Vertex III height metre in 2016 (Haglöf). Stem WD (g cm^{-3}), defined as the oven-dry mass over wet volume, was measured for 119 trees after removing the bark. The fresh volume of each previously sampled c. 7-cm long and c. 5-mm wide core was calculated based on means of 2 length and 10 diameter measurements using a digital calliper (cf. Schüller et al. 2013). Subsequently, cores were oven-dried at 105 °C for 72 h to obtain dry mass.

Leaf morphology

All leaves distal to the twig segments used for hydraulic conductivity measurements were scanned in order to determine the leaf areas (WinFolia 2005; Régent Instruments, Quebec, Canada). Per branch segment and tree, 5–52 leaves were scanned, yielding 2313 leaves in total. We calculated the Huber value (HV) as the ratio of branch sapwood area to the total leaf area ($A_{\text{xylem}}:A_{\text{leaf}}$; $10^{-4} \text{ m}^2 \text{ m}^{-2}$). Subsequently, leaves were oven-dried at 70 °C for 48 h and specific leaf area (SLA; $\text{cm}^2 \text{ g}^{-1}$) calculated. Dried and grinded leaf samples were shipped to the University of Göttingen, Germany, and were analysed for the leaf mass carbon isotope signature ($\delta^{13}\text{C}$) by mass-ratio spectroscopy (Deltaplus; ThermoFinnigan, Bremen, Germany) at the Center for Stable Isotope Research and Analysis (KOSI). We used $\delta^{13}\text{C}$ for inferring on the leaf intrinsic water-use efficiency and stomatal limitation of leaf gas exchange (Bchir et al. 2016).

Water potential at turgor loss point

A vapour pressure osmometer (VAPRO 5600, Wescor, Logan, USA) was used to measure the osmolality of apoplastic and symplastic liquid fractions inside the sampled leaves. Osmolality (mmol kg^{-1}) was then derived into osmotic potential (π_{osm} ; MPa) using the Van't Hoff equation. Finally, water potential at turgor loss point (π_{tlp} ; MPa) was derived from π_{osm} according to the equation given by Bartlett et al. (2012b). We used fully hydrated leaves from branches re-cut under water, stored overnight at 4 °C with their basipetal ends submerged in water and covered with an opaque plastic bag. Prior to measurement, two leaves per branch segment were stored in

humidified, air-blown and refrigerated plastic bags in order to avoid dehydration. For each leaf, one 8-mm diameter disc was stamped out between the midrib and the margin of one of the leaflets, thereby avoiding minor veins. Following the method described in Bartlett et al. (2012b), we wrapped each disc in an aluminium foil and submerged it into liquid nitrogen (LN_2) for 2 min. After the LN_2 treatment, the disc was punctured with sharp pliers in order to facilitate evaporation and were placed in the osmometer chamber within 30 s. The apparatus subsequently measured osmolality until equilibrium was reached, i.e., two following readings differed by less than $0.05 \text{ mmol kg}^{-1}$ from each other. Subsequently, leaf π_{tlp} was calculated according to Bartlett et al. (2012b) as follows:

$$\pi_{\text{tlp}} = 0.832 \cdot \pi_{\text{osm}} - 0.631. \quad (1)$$

Hydraulic efficiency and safety

Axial hydraulic conductivity was measured on branch segments (mean diameter \pm SE: $7.81 \pm 0.09 \text{ mm}$) from 14 to 15 trees per plot, yielding 115 samples in total. After harvest, each branch was processed in the laboratory within a week. Before measurements, branch segments were shortened (mean length \pm SE: $39.73 \pm 4.16 \text{ cm}$), branch diameter was measured twice at the basal and distal ends and at four positions along the segment, lateral branches cut-off and scars sealed with a quick-drying glue (Loctite 431, Henkel, Düsseldorf, Germany). Subsequently, segments were connected to the Xyl'em apparatus (Bronkhorst, Montigny les Cormeilles, France) and were flushed three times for 10 min at a pressure of 120–180 kPa and the hydraulic conductivity (K_h , $\text{kg m MPa}^{-1} \text{ s}^{-1}$) was measured at 25 °C at a pressure head of 5 kPa. For the conductivity measurements, a degassed and filtered ($0.22 \mu\text{m}$) 10 mM KCl and 1 mM CaCl_2 solution was used. Sapwood-specific hydraulic conductivity (K_s , $\text{kg m}^{-1} \text{ MPa}^{-1} \text{ s}^{-1}$) was calculated by dividing K_h by the average xylem cross-sectional area (cf. Schuldt et al. 2016). We used anatomical images taken at the base of the same branches to quantify the proportion of xylem tissue (A_{xylem} , mm^2) per cross-section area (A_{cross} , mm^2) for each segment. The following regression coefficients were used to calculate the sapwood area without pith and bark for a given segment diameter: $A_{\text{xylem}} = -6.02 + 0.54 \times A_{\text{cross}}$ ($P < 0.001$, $r^2 = 0.81$; $n = 90$). Leaf-specific hydraulic conductivity (K_l , $\text{kg m}^{-1} \text{ MPa}^{-1} \text{ s}^{-1}$) was calculated by dividing K_h by the total supported leaf area distal to the branch segment.

Branch xylem VCs were measured according to the standard protocols (Delzon et al. 2010) at the Phenobois platform of the University of Bordeaux (France) using a modified centrifuge flow technique (Cochard et al. 2005) and the Cavisoft software (Cavisoft v1.5, University of Bordeaux). Per plot, branch samples from three to six trees were processed, yielding 35 constructed VCs. To exclude possible bias caused by the open-vessel artefact (Torres-Ruiz et al. 2014, 2017), additional

branch material was used to guarantee that the maximum vessel length (MVL) was shorter than the centrifuge rotor diameter (c. 27 cm). To measure the MVL, we injected air with a syringe at low pressure (0.10 MPa) into the open-cut distal branch end. The proximal end was submerged in water and was cut successively until bubbles, i.e., air flowing in from the syringe, became visible. We assumed that the remaining length of the branch corresponds to the longest open-cut vessel. We found a MVL of 13.86 ± 1.31 cm (mean \pm SE; $n = 30$; Table S2 available as Supplementary data at *Tree Physiology Online*). However, MVL remained highly variable across segments (range = 5–28 cm), indicating that an open-vessel artefact could have been present in some of the samples used for the construction of xylem VCs. We reduced this risk by selecting curves based on their shape. The R-shaped curves, likely resulting from open vessels, were therefore dismissed from the analyses. This selection process reduced our initial sample size from 64 to 35.

Branches were shortened to 27 cm length and the bark was removed at both ends. Segments were subsequently placed in a custom-made honeycomb rotor mounted on a commercially available centrifuge (HS18; MSE Scientific, London, UK). Conductivity measurements with a degassed and filtered (0.22 μm) 10 mM KCl and 1 mM CaCl_2 solution started at -0.8 MPa and were repeated stepwise at intervals of 0.2–0.3 MPa until c. 85% loss of hydraulic conductance was recorded. The xylem pressures at 12, 50 and 88% loss of hydraulic conductance (P_{12} , P_{50} and P_{88}) were calculated according to a Weibull function (see the Statistical analysis section). We further calculated the hydraulic safety margin (HSM) as the difference between π_{tip} and P_{50} (Martin-StPaul et al. 2017, Berry et al. 2019, Ziegler et al. 2019).

Wood anatomy and potential conductivity

Semi-thin branch transversal sections were cut with a sliding microtome (G.S.L.1; Schenkung Dapples, Zurich, Switzerland) on the 120 branches collected for measuring hydraulic efficiency-related traits. Transversal sections were dyed with alcian blue and safranin, embedded in Euparal (Carl Roth, Karlsruhe, Germany) and the complete cross-section was digitalized at $\times 100$ magnification using a stereomicroscope equipped with a digital camera (SteREOV20; Carl Zeiss MicroImaging GmbH, Göttingen, Germany). Image processing was done with the add-on ROXAS (von Arx and Carrer 2014) for the software Image-Pro Plus v7.0 (Media Cybernetics, Rockville, MD, USA). For every section, total cross-sectional (A_{cross} , m^2), xylem (A_{xylem} , m^2) and lumen area, average vessel lumen area (A_{lumen} , μm^2), relative vessel lumen area, i.e., the lumen-to-sapwood area ratio ($A_{\text{lumen}}:A_{\text{xylem}}$, %), VD (n mm^{-2}), vessel group index (V_g), i.e., mean number of cells per group (Carlquist 2001), and the radial and tangential vessel diameters were estimated. The latter were used to calculate the average vessel diameter (D , μm) according to Lewis and Boose (1995). Potential conductivity

(K_p ; $\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$) was calculated according to the Hagen–Poiseuille equation as follows:

$$K_p = \frac{\pi \rho \cdot \sum D^4}{128 \eta \cdot A_{\text{xylem}}}, \quad (2)$$

where η is the viscosity ($1.002 \cdot 10^{-9} \text{MPa s}^{-1}$) and ρ the density of water (998.2kg m^{-3}), both at 20°C .

Statistical analysis

Statistical analyses were conducted with R version 4.2.2 (R Development Core Team 2022). All investigated variables are summarized in Table 1.

To proceed with the analyses, we first built the VCs with the cumulative function of the Weibull distribution. We fitted them to the data with non-linear hierarchical models using R package nlme (Pinheiro et al. 2018) to account for the plot effects in parameter estimates. Effects of the major sources of variability in our plots (i.e., stem density, age and DBH) were also tested, but they did not improve the explanatory power of the model (measured through Akaike's information criterion, AIC, in the ANOVAs). We used a nested study design and investigated one branch i per tree j and three to six trees per plot k . Model equations were re-parameterized with P_{50} and slope at P_{50} (Ogle et al. 2009) to build Eq. (3), where PLC indicates the percent loss of hydraulic conductivity and Ψ_x indicates the measured xylem water potential.

$$\text{PLC}_{ijk} = 100 \times \left(0.5 \left(\frac{\Psi_{xijk}}{P_{50jk}} \right)^{\left(\frac{-P_{50jk} \times \text{slope}_{jk}}{50 \times \ln(0.5)} \right)} \right). \quad (3)$$

From this expression, we estimated the parameters P_{50} and slope as the linear functions of plot-aggregated VPD, with trees and plots as random effects (Table S3 available as Supplementary data at *Tree Physiology Online*). The model which includes VPD was the best-fitting model according to the ANOVA analysis. As a natural variable, VPD was centred around the mean before implementation in the model to avoid impossible values (i.e., negative VPD values). We estimated P_{12} , P_{50} and P_{88} (water potential at 12, 50 and 88% loss of hydraulic conductivity) for each plot and tree from the predictions of the model (Table S3 available as Supplementary data at *Tree Physiology Online*). Due to some differences in stand structure across plots (Table 2), we considered stem diameter, plot age and density as either fixed or random effects, but none of them improved the different models, allowing us to keep the initial hierarchical structure of trees nested in plots.

We then explored the relationships between different functional traits and the relationships between traits and mean local environmental factors. Inter-relationships among traits were first

analysed by constructing a pair-wise Pearson's correlation table using the R package *corrormorant* (<https://github.com/r-link/corrormorant/>) at the tree level. To complement the correlation analyses, we employed the linear mixed effects models (R package *lme4*; Bates et al. 2015) to take into account the plot, tree diameter, plantation age and density as random effects, selecting the best model based on AIC. We used the same linear mixed effect model approach to analyse the relationships between traits and the local environment. This was done by investigating the relation of hydraulic conductivity (K_s and K_l), branch embolism resistance (P_{12} , P_{50} and P_{88}), anatomical traits (WD , $A_{\text{lumen}}:A_{\text{xylem}}$, VD , D and V_g), leaf traits (i.e., SLA , π_{tlp} , $\delta^{13}\text{C}$ and HV), and HSM with VPD, VPD_{dry} and VWC. Further models were developed to describe the variation of P_{88} as a function of VD and V_g and the variation of P_{50} as a function of VD , SLA , their interaction, the mean D per cut and V_g . We always introduced tree and plot as random effects and tested the importance of the stem density, tree age and DBH in our models.

To estimate the goodness of fit of nonlinear VC models, we calculated equivalent r^2 values as the ratio of residual and total variance of the model, following Nakagawa and Schielzeth (2013). For linear mixed effects models, we calculated generalized r^2 values after Jaeger et al. (2016) using the standardized generalized variance approach and calculated marginal r^2 values as per Nakagawa and Schielzeth (2013).

Results

Soil moisture status and microclimatic gradient

The selected sites presented a clear microclimatic gradient with respect to the atmospheric evaporative demand and soil moisture levels (Figure 1 and Table 2). In 2017 and 2018, VWC ranged from 32.47 ± 0.05 to $56.86 \pm 0.10\%$ across plots. Likewise, both the 2-year VPD average and the mean VPD of extreme days (VPD_{dry}) differed significantly across plots (VPD range: 0.49 ± 0.01 to 0.86 ± 0.02 kPa, VPD_{dry} range: 0.78 ± 0.01 to 1.31 ± 0.01 , respectively).

Embolism resistance variation across plots

The shape of the predicted tree-level xylem VCs was sigmoidal in all cases, as indicated by the shape parameter k of the Weibull distribution, which reached values well above 1 (Figure S2 available as Supplementary data at *Tree Physiology* Online). We estimated the overall means of xylem pressures causing 12, 50 and 88% loss of conductivity (P_{12} , P_{50} and P_{88}) of -1.67 ± 0.05 , -2.36 ± 0.05 and -4.00 ± 0.13 MPa (mean \pm SE, $n = 35$), respectively (Figure 2 and Table S4 available as Supplementary data at *Tree Physiology* Online). Across plots, we found a variation in embolism resistance thresholds, with mean P_{50} ranging from -2.01 to -2.51 MPa (Figure 2 and Table S4 available as Supplementary data at *Tree Physiology* Online).

Trait variation in response to the mean local site-specific environment

All investigated plant traits exhibited some degree of plasticity across trees and plots (Figure 2). We found a strong relationship between the mean local microclimatic conditions and branch hydraulic safety (Figure 3 and Table 3): plot-level VPD was a good predictor for P_{50} ($r^2 = 0.39$, $P < 0.01$, $b = -1.53$ MPa kPa^{-1}), P_{88} ($r^2 = 0.28$, $P < 0.05$, $b = -3.62$ MPa kPa^{-1}) and the HSM ($r^2 = 0.28$, $P < 0.01$) (Figure 3 and Table 3). By contrast, the mean local VWC had no influence on the branch embolism resistance. Including VPD as a predictor improved the model estimates for the tree-level VCs. The model for the VCs had a marginal r^2 of 0.83 and a conditional r^2 of 0.94 (including plot and tree effects; Table S3 available as Supplementary data at *Tree Physiology* Online).

Other than for hydraulic safety, no effect of the mean local evaporative demand on hydraulic efficiency was observed (Table 3). Likewise, differences in VPD did not affect the vessel diameter (Table 3). However, the lumen-to-sapwood area ratio ($A_{\text{lumen}}:A_{\text{xylem}}$) increased significantly with an increase in VPD_{dry} ($P < 0.04$; Table 3). The VPD_{dry} also tended to explain the variation of VD ($P < 0.08$), although at marginal significance only (Table 3). At the leaf level, SLA declined with an increase in VPD ($r^2 = 0.36$, $P < 0.05$; Figure 3 and Table 3), indicating that leaves become smaller and thicker with an increase in atmospheric evaporative demand.

Relationships across leaf and wood traits

Relationships among traits as revealed by the tree-level Pearson's correlation analyses (Figure 4) were in good agreement with the output of our linear mixed effects models with plot, tree diameter, plantation age or density added as random effects (Table S5 available as Supplementary data at *Tree Physiology* Online). According to the Pearson's correlation analyses, VD ($r = -0.57$, $P < 0.001$), $A_{\text{lumen}}:A_{\text{xylem}}$ ($r = -0.55$, $P = 0.002$) and the vessel grouping index (V_g ; $r = -0.38$, $P < 0.01$) were closely related to P_{88} . The VD was also related to P_{50} , but only at marginal significance (VD : $r = -0.35$, $P = 0.054$) (Figure 4). When accounting for random plot effects, however, the relationship between VD and P_{50} became significant according to the LME output (effect $r^2 = 0.33$; Figure 5 and Table S5 available as Supplementary data at *Tree Physiology* Online). By contrast, vessel diameter (D) and the three measures of hydraulic efficiency (K_p , K_s and K_l) were all unrelated to embolism resistance (Figure 4 and Table S5 available as Supplementary data at *Tree Physiology* Online). In addition to the three anatomical measures related to the number of vessels, i.e., VD , V_g and $A_{\text{lumen}}:A_{\text{xylem}}$, SLA was also associated with the P_{50} value according to the LME (Figure S3 available as Supplementary data at *Tree Physiology* Online; Table 3).

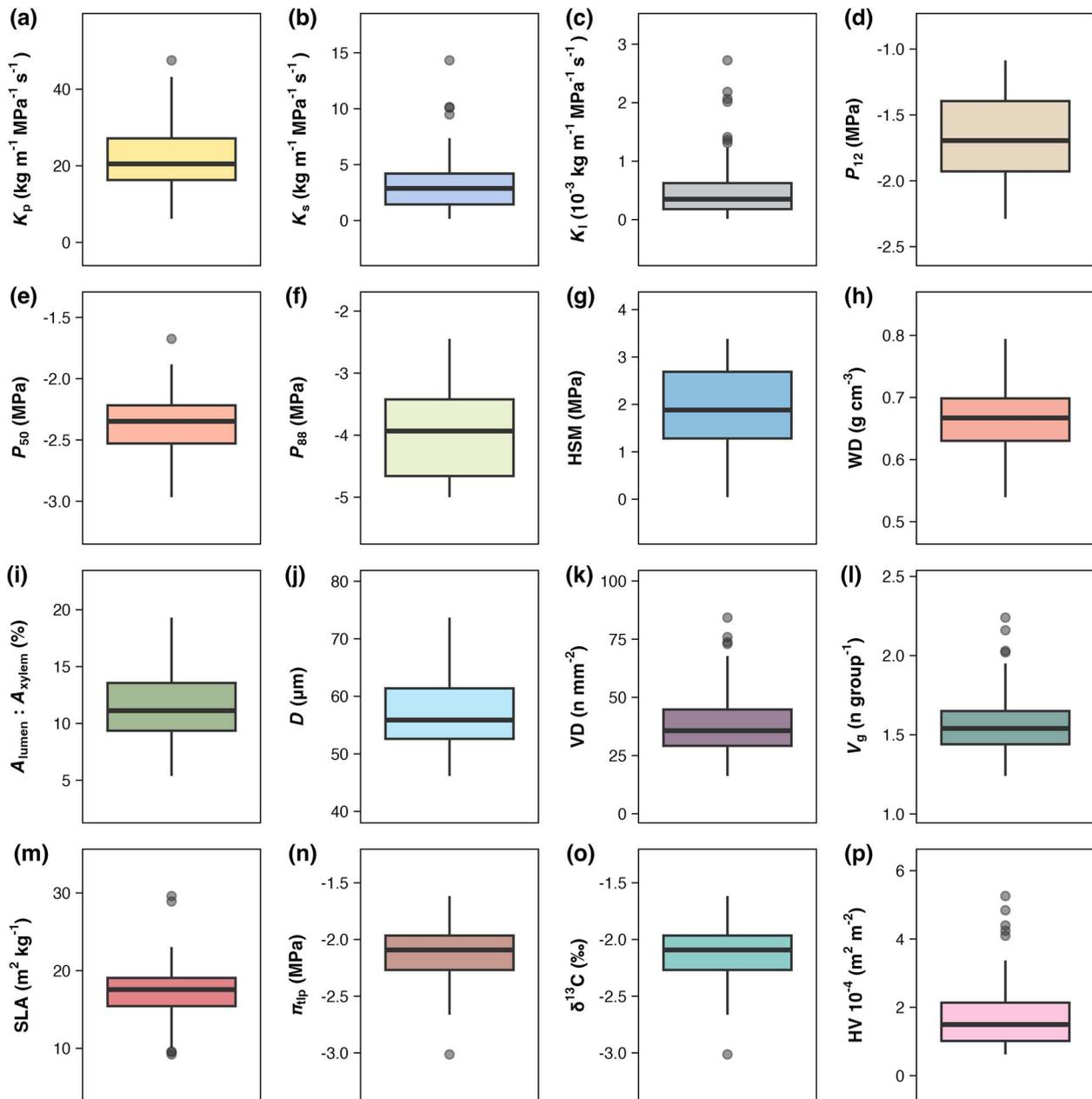


Figure 2. Boxplots of all functional wood and leaf traits in *H. brasiliensis* from eight plantation sites in Jambi province, Sumatra, Indonesia. Given are the (a) potential conductivity (K_p), (b) specific conductivity (K_s), (c) leaf-specific conductivity (K_l), (d) xylem pressures at 12% (P_{12}), at (e) 50% (P_{50}) and at (f) 88% loss of hydraulic conductance (P_{88}), (g) HSM ($\pi_{\text{tip}} - P_{88}$), (h) WD, (i) percentage of lumen area per xylem area ($A_{\text{lumen}} : A_{\text{xylem}}$), (j) vessel diameter (D), (k) VD, (l) vessel grouping index (V_g), (m) SLA, (n) leaf water potential at turgor loss point (π_{tip}), (o) carbon isotope signature ($\delta^{13}\text{C}$) and (p) the HV.

At the wood level, VD emerged as a major trait, responding sensitively to the changes in VPD. The VD was positively associated with hydraulic efficiency (K_s ; $r = 0.31$, $P = 0.003$) and was negatively associated with hydraulic safety (P_{50} and P_{88}) (Figure 3 and Table S5 available as Supplementary data at *Tree Physiology Online*), and it showed a close relation to V_g ($r = 0.59$, $P < 0.001$) and $A_{\text{lumen}} : A_{\text{xylem}}$ ($r = 0.77$, $P < 0.001$), but not to D (Figure 4). At the leaf level, VD was closely negatively related to HV, i.e., sapwood-to-leaf area ratio (HV; $r = -0.44$, $P < 0.001$). However, no relationship was observed

between VD and turgor loss point (π_{tip} ; $r = 0.11$, $P = \text{n.s.}$), and π_{tip} was also unrelated to P_{50} ($r = 0.04$, $P = \text{n.s.}$) or P_{88} ($r = -0.01$, $P = \text{n.s.}$) (Figure 4). Overall, SLA emerged as one of the most influential traits at the leaf level. This widely studied functional leaf trait did not only tend to respond to changes in VPD ($P < 0.07$), but it was also positively related to WD ($r = 0.39$, $P < 0.001$) and to P_{50} at marginal significance ($r = 0.32$, $P = 0.088$) (Figure 4). Similar to the relationship between VD and P_{50} , however, random plot effects had to be accounted for in order to observe a significant relationship

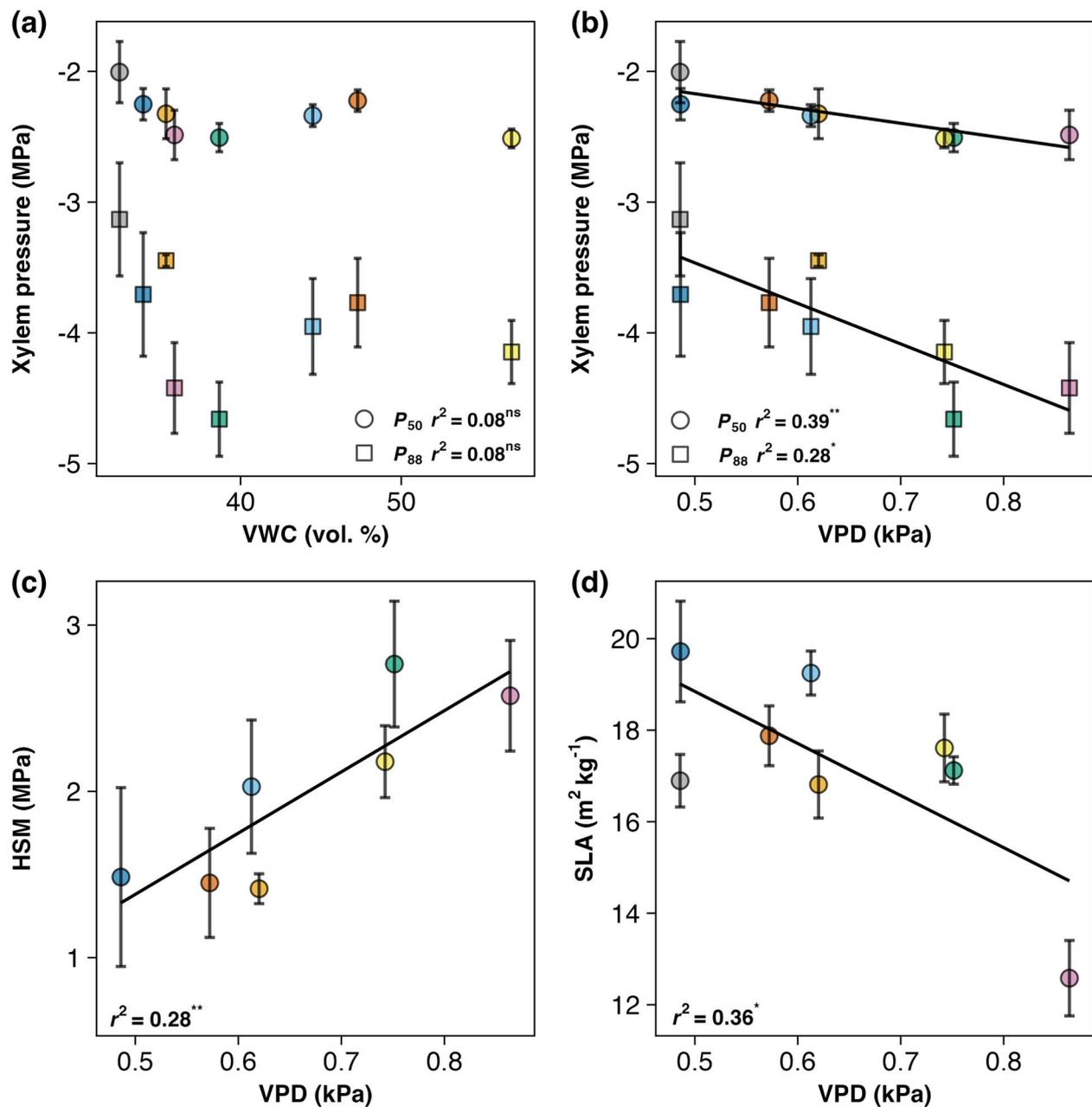


Figure 3. Xylem pressures inducing 50 or 88% loss of hydraulic conductance (circle = P_{50} ; square = P_{88}) of *H. brasiliensis* branches in relation to (a) VWC and (b) VPD. Further shown are (c) HSM and (d) SLA in dependence on VPD. Values are mean \pm SE per site. Given are the conditional r^2 of the LME models (including plot and stem density as random effects), and asterisks indicate the level of significance (ns, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$). Each plot is represented by one colour.

between SLA and P_{50} (effect $r^2 = 0.14$; Table S5 available as Supplementary data at *Tree Physiology Online*; Figure S3 available as Supplementary data at *Tree Physiology Online*).

Discussion

Hydraulic strategy of *H. brasiliensis*

As a consequence of an increasing global demand for latex, rubber plantations are expanding into drought-prone and thus climatically suboptimal regions. This indicates that this

economically important tree crop species must tolerate a certain extent of drought intensity even though it originates from a humid tropical environment. Our data on the xylem pressure at 50% loss of hydraulic conductance are indeed the lowest P_{50} values documented for *H. brasiliensis* so far (-2.33 MPa; clone PB260). While Hazir et al. (2022) found an average P_{50} of -2.0 MPa across nine rubber clones using the pneumatic method, Jinagool et al. (2016) reported P_{50} values for the PB260 clone of -1.96 MPa using the same methodology as we did. By contrast, Sangsing et al. (2004a)

Table 3. Summary of mixed effects models on the influence of VWC, mean annual VPD and mean VPD of the 20% driest days (VPD_{dry}) on the 16 wood and leaf traits related to hydraulic efficiency and safety.

Variable	VWC			VPD			VPD _{dry}		
	Marginal r^2	Conditional r^2	P	Marginal r^2	Conditional r^2	P	Marginal r^2	Conditional r^2	P
K_p	0.02	0.24	0.83	0.00	0.24	0.83	0.00	0.24	0.81
K_s	0.03	0.30	0.44	0.00	0.30	0.90	0.01	0.30	0.65
K_l	0.02	0.23	0.27	0.00	0.28	0.91	0.00	0.28	0.76
P_{12}	0.04	0.04	0.30	0.03	0.03	0.38	0.03	0.03	0.36
P_{50}	0.08	0.51	0.35	0.39	0.39	0.005	0.41	0.41	0.004
P_{88}	0.01	0.28	0.72	0.29	0.29	0.01	0.31	0.31	0.01
HSM	0.02	0.33	0.57	0.31	0.31	0.01	0.36	0.36	0.007
WD	0.00	0.59	0.88	0.21	0.56	0.08	0.16	0.57	0.14
$A_{\text{lumen}}:A_{\text{xylem}}$	0.02	0.33	0.49	0.08	0.33	0.20	0.13	0.32	0.04
D	0.00	0.24	0.99	0.03	0.24	0.40	0.05	0.24	0.25
VD	0.02	0.52	0.65	0.11	0.51	0.21	0.19	0.50	0.08
V_g	0.06	0.29	0.23	0.05	0.30	0.29	0.07	0.28	0.18
SLA	0.02	0.39	0.59	0.17	0.36	0.05	0.12	0.37	0.13
π_{tip}	0.00	0.26	0.90	0.01	0.26	0.66	0.02	0.26	0.47
$\delta^{13}\text{C}$	0.04	0.12	0.21	0.01	0.12	0.54	0.01	0.13	0.60
HV	0.01	0.13	0.45	0.01	0.13	0.47	0.12	0.13	0.50

For abbreviations, see Table 1. Given are the marginal r^2 , conditional r^2 and P -values of the models, including plot and stem density as random effects. Details are shown in Table S4 available as Supplementary data at *Tree Physiology Online*. Significant relationships ($P < 0.05$) are marked in bold, marginally significant relationships ($P < 0.10$) in bold and italics.

and Chen and Cao (2015) found less negative values using the bench dehydration method on different clones (-1.22 and -1.42 MPa for Sangsing et al. 2004a and -1.06 MPa for Chen and Cao 2015). This collection of P_{50} values indicates that the xylem of this tropical deciduous tree species is fairly vulnerable to drought-induced embolism even though the sensitivity may vary according to environmental conditions or genotype. In agreement herewith, several studies have reported a tight stomatal control of transpiration in rubber which may help to avoid hydraulic failure (Isarangkool Na Ayutthaya et al. 2011, Sopharat et al. 2015, Kumagai et al. 2015). Such risk-avoiding behaviour is confirmed by the fairly high water potential at turgor loss point (π_{tip}) and a large HSM (-2.12 and 1.97 MPa, respectively). Because of its relationship with the water potential at stomatal closure, π_{tip} reflects the ability of plants to regulate their stomata under water stress (Brodrribb et al. 2003, Farrell et al. 2017). Our findings are generally in agreement with the notion that rubber regulates its stomata sensitively (cf. Rodriguez-Dominguez et al. 2016, Berry et al. 2019). Interestingly, π_{tip} was in general more negative or equivalent to P_{12} . Such an unusual result might mean that rubber is closing its stomata after the onset of embolism formation in its xylem, albeit before a major hydraulic failure. This may allow rubber to be highly productive and competitive in a particularly humid environment (Carr 2012), highlighting the threat of increasing drought events on rubber plantations.

Overall, we confirm the drought-avoiding strategy of rubber. Supporting our observations, several studies have reported

other drought-avoidance characteristics, such as a deep rooting pattern (Zeng et al. 2022), which could explain why rubber is viable in drought-prone areas despite its significant water demand (Tan et al. 2011). The high acclimation potential and versatility of rubber is well illustrated by its leaf shedding behaviour, especially when cultivated in varied climatic conditions. In regions with pronounced climatic seasonality, like Northern Thailand, a distinct dry period causes rubber trees to rapidly shed their leaves. This behaviour effectively mitigates potential drought impacts on the hydraulic system of rubber (Li et al. 2016, Zhai et al. 2019). However, in regions with milder seasonality, such as Jambi province in Sumatra, our study location, the leaf shedding process appears more staggered and may not be strictly related to water availability (Yeang 2007). Notably, our observations in Jambi highlighted a lack of complete canopy shedding in the studied plantations. This staggered shedding ensures a consistent photosynthetic activity, with new leaves emerging in certain canopy parts, while older leaves start falling in others. It is this nuanced shedding pattern that has led some authors to classify rubber with contrasted definitions, either as an evergreen species with opportunistic deciduous tendencies (Chen and Cao 2015, Li et al. 2016) or as a deciduous species with diffuse behaviour (Yeang 2007). This remarkable flexibility in leaf phenology, corroborated by studies emphasizing the petiole as the organ with the least hydraulic resistance in rubber hydraulic pathway (Sangsing et al. 2004b), might reflect rubber's intrinsic plasticity in hydraulic traits, especially in climatically diverse habitats.

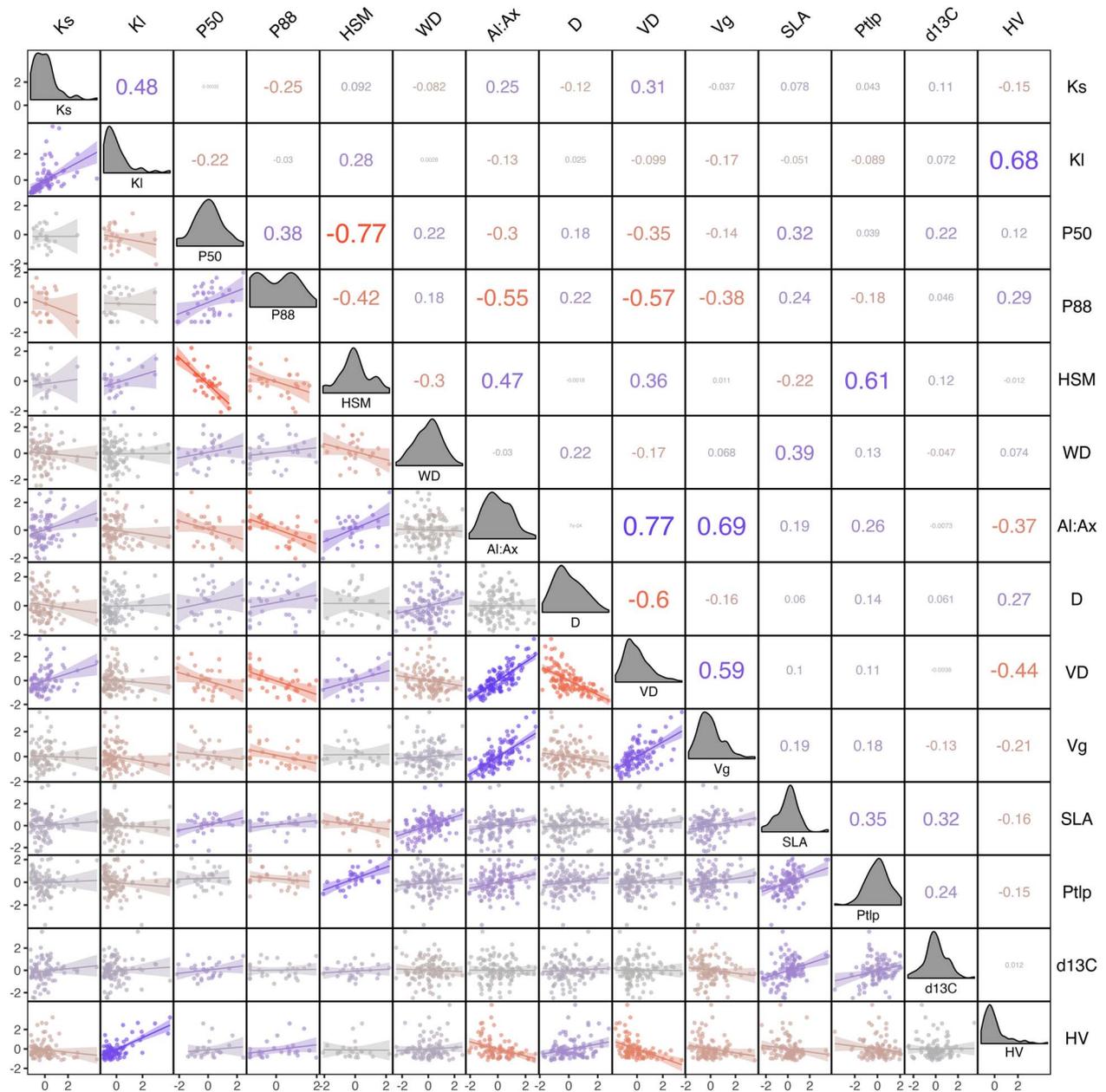


Figure 4. Pair-wise Pearson's correlation table (upper triangle), scatter plot (lower triangle) and density plot (diagonal panels) for the relationships between 14 functional traits of *H. brasiliensis*. Shown are the data on tree level ($n = 125$), including trend lines from linear regressions with 95% confidence intervals. Embolism resistance was only quantified for a subset of tree individuals ($n = 35$). Colour and size indicate the strength of the correlation.

Trait plasticity in response to soil water availability

We observed a very limited impact of soil moisture on the wood and leaf traits related to hydraulic efficiency or safety, partly contradicting our first hypothesis. Because all studied trees belong to the same clone (PB260), we were able to quantify the degree of phenotypic plasticity in response to water availability. In a provenance trial with 15 rubber provenances located in Northern Thailand, Rungwattana et al. (2018) observed a strong correlation between the leaf traits and the climate at the place of origin, while wood-related traits were only weakly

related. We therefore assumed that wood-related traits might respond more plastically to the local water content, while leaf traits are under stronger genetic control. However, all wood and leaf traits were unrelated to the variations in volumetric water content (VWC).

It is reasonable to assume that modification of a tree's anatomy, morphology and physiology is related to the leaf habit, i.e., drought-deciduous or evergreen. The xylem of tropical evergreen or semi-deciduous tree species (e.g., with refoliation patterns during dry periods as is rubber in Jambi plantations)

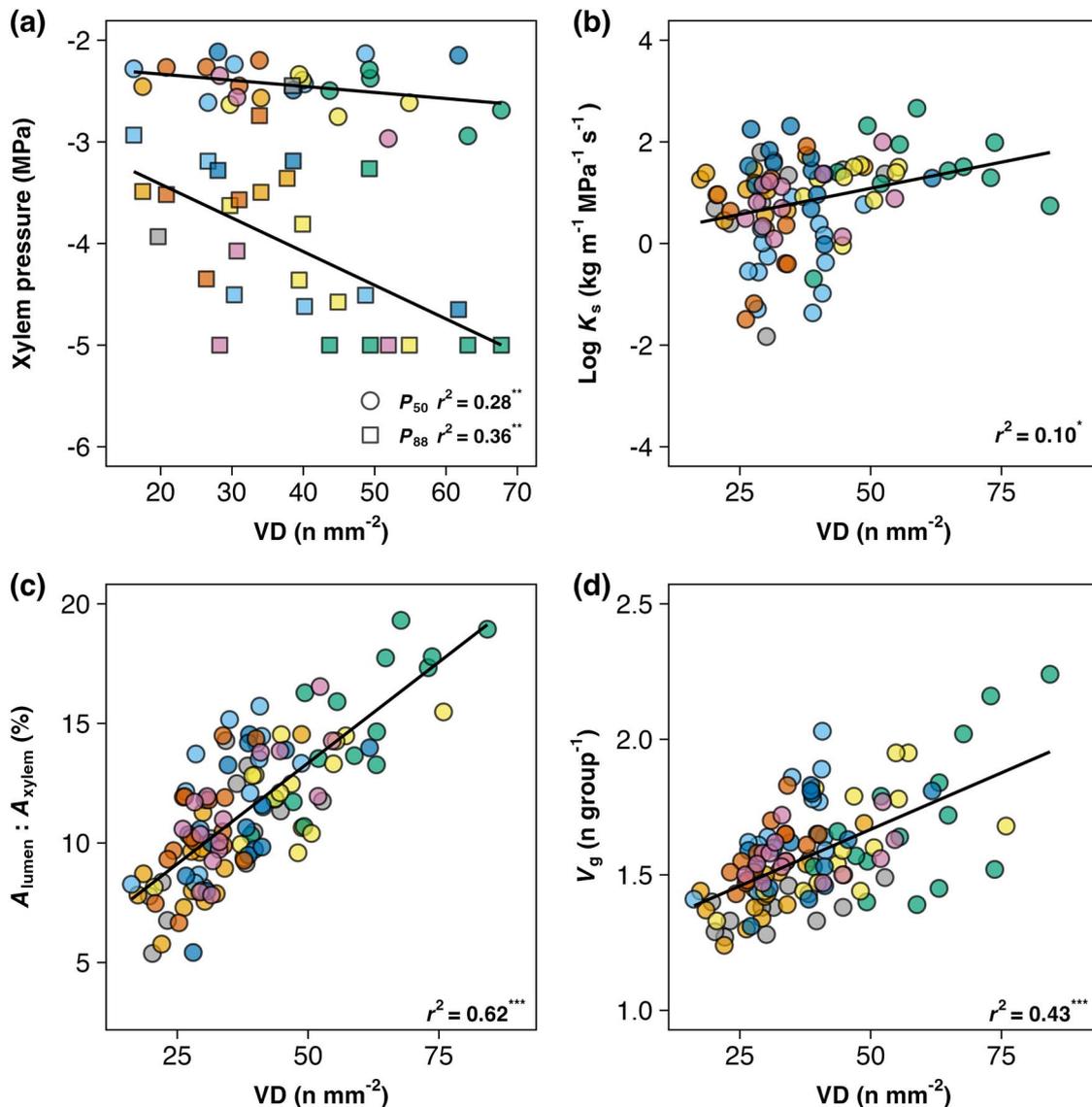


Figure 5. (a) Xylem pressures inducing 50 or 88% loss of hydraulic conductance (circle = P_{50} ; square = P_{88}), (b) specific conductivity (K_s), (c) lumen-to-sapwood-area ratio ($A_{\text{lumen}}:A_{\text{xylem}}$) and the (d) vessel grouping index (V_g) in dependence on VD. Given are the conditional r^2 based on the LME models, and asterisks indicate the level of significance (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.01$). Different colours indicate different plots.

must withstand greater xylem pressure gradients during the dry season than that of drought-deciduous species (Choat et al. 2005, Fu et al. 2012). While species retaining their foliage during dry spells might need higher adjustments in their xylem properties to support water transport under shifting water availability, we did not find such a result in rubber. The limited impact of soil water availability on hydraulic traits could be attributed to its potential access to deep water reserves (Vijayakumar et al. 1998, Wu et al. 2016, Zeng et al. 2022), especially in regions like Jambi province, where we did not observe complete deciduousness during drier periods. Yet, we had anticipated variations in xylem anatomy in line with available literature, such as a decrease in conduit diameters and increases in conduit density (Fonti et al. 2013, Schuldt et al. 2016,

Lübbe et al. 2017). Rubber's distinctive hydraulic strategy and its potential access to deeper water might be one reason for the lack of effects of VWC fluctuations. Furthermore, water availability likely does not affect vascular differentiation directly. Its primary effect may manifest through growth modulation, impacting the tree size and shoot elongation rates (Olson et al. 2014, Dória et al. 2019, Lechthaler et al. 2019). Given that rubber trees in our study exhibited consistent height and branch diameters, we do not expect variances in flow path length or cambial age between plots (cf. Li et al. 2019).

An alternative explanation for the absence of an effect of VWC on the hydraulic safety and efficiency in rubber may be the lack of spatial representativeness of the soil moisture measurements. Soil moisture usually shows a high spatial variation, and the

three sensors per plot that were used may not be sufficient when comparing plantation types (Western et al. 2003). This may have masked any relationship between the hydraulic traits and soil moisture in our study. Moreover, VWC remained relatively high in all plots, which could explain why soil water availability did not affect the safety- and efficiency-related traits. In comparison, VWC ranged between 20 and 40% in seasonal flooded forest and between 20 and 35% in well-drained areas in an Amazonian tropical forest (Stahl et al. 2011). At our sites, VWC remained above 30%, which suggests that the trees of our study rarely experience stress due to soil drought. Given the intriguing results from our current study location, there is a clear need to further study rubber in areas with more pronounced dry conditions. Assessing rubber's comprehensive hydraulic behaviours and unique phenological traits in regions with strong seasonal variations could provide more information on its ability to adapt and acclimate, which is crucial, given the tree's economic importance.

Trait plasticity in response to the evaporative demand

Across the eight sites, a close relationship of the mean local evaporative demand and hydraulic safety was observed, but not with xylem efficiency. With an increase in VPD, the xylem pressures at 50 and 88% loss of hydraulic conductance (P_{50} and P_{88} , respectively) both declined, while the HSM increased. In contrast to the wood-related traits, the water potential at turgor loss point (π_{tlp}) was unaffected by the differences in VPD. The increase in hydraulic safety was accompanied by an increase in VD, but not vessel diameter. This is in line with a recent study that highlighted the importance of vessel grouping and density for hydraulic safety across species (Levionnois et al. 2021). Traditionally, the atmospheric water status has been viewed as the factor driving water transport and influencing stomatal aperture, but its role as a factor influencing tree water status, growth and vitality has only rarely been considered (but, see Köcher et al. 2012, Brodribb et al. 2017, Amitrano et al. 2019). However, rising global temperatures have resulted in an increase in the frequency and intensity of 'hotter droughts' (Allen et al. 2015), which has increased the awareness to consider VPD as a driving factor of drought-induced tree mortality (Eamus et al. 2013, Grossiord et al. 2020a). While Blackman et al. (2017) related VPD to leaf embolism resistance in *Corymbia calophylla*, a direct link between the VPD level at a site and branch xylem P_{50} has, to our knowledge, not yet been shown. Because the annual mean VPD has strongly increased since the late 1990s, both regionally and globally (Barkhordarian et al. 2019, Yuan et al. 2019, Schuldt et al. 2020), our finding of an apparent adaptive response of hydraulic safety in rubber to a VPD increase is of high interest. Rubber trees growing in an environment with higher mean VPD had lower P_{50} , and especially P_{88} , values and a higher HSM than trees exposed to lower VPD. The HSM, calculated here as the

difference between π_{tlp} and P_{88} , increased from plots with lower to higher evaporative demand due to the decrease in P_{50}/P_{88} , while π_{tlp} remained constant. With respect to climate warming, this is a promising result, as it may indicate that certain species are able to counteract the increases in the evaporative demand to a certain extent by increasing the xylem hydraulic safety. In the absence of electron microscopic data, we can only speculate that higher VPD may have triggered the development of thicker and thus more embolism-resistant pit membranes in the xylem since structural modification of inter-vessel pits can reduce the spread of embolism (Li et al. 2016, Isasa et al. 2023).

At the leaf level, we observed a decline in SLA with an increasing VPD level. A decrease in leaf area per dry mass is caused by anatomical changes in the lamina, and this has been linked to a reduced drought-induced mortality of trees (Greenwood et al. 2017). Both adjustments, the increase in hydraulic safety and the development of smaller and/or thicker leaves, have frequently been observed with inter-specific trait variation along climatic gradients, but these were rarely confirmed for intra-specific trait variation within a species (e.g., Schuldt et al. 2016, Rosas et al. 2019). In our research, there was no notable difference in the leaf carbon isotope signature ($\delta^{13}\text{C}$) across plots, a proxy for plant water-use efficiency (Petrik et al. 2023). This suggests that the vascular modifications resulting in higher hydraulic safety in combination with the development of leaves capable of tolerating more negative water potentials were sufficient to avoid reductions in stomatal conductance under higher VPD conditions. Interestingly, this contrasts with previous studies that identified strong stomatal responses under elevated VPD even in well-watered scenarios (Isarangkool Na Ayutthaya et al. 2011, Sopharat et al. 2015). The absence of $\delta^{13}\text{C}$ changes that we observed could also be attributed to the milder seasonal droughts in our study area as opposed to North-East Thailand. Other factors, such as the specific clone varieties (PB260 vs RRIM 600) and whether the trees were tapped for latex, may also play roles in these differences, as indicated by Kunjet et al. (2013). Nonetheless, our results show that this economically important tropical tree species has a sufficiently high phenotypic plasticity to adjust its xylem structure in response to a higher evaporative demand in agreement with our first hypothesis. A high degree of phenotypic plasticity in traits related to hydraulic safety might be more advantageous for coping with the anticipated increase in drought intensity than genetic adaptation (Grossiord et al. 2020b). The tight relationship between P_{50} and VPD clearly demonstrates the magnitude of phenotypic plasticity in rubber. While we do not believe that the VPD level experienced in 2017 and 2018 had a distinct effect on the anatomy of the xylem formed in 2018, weather data show that climatic conditions in the region changed only little during the last 8 years prior to the measurements. Thus, the 2017 and 2018 VPD levels can be assumed to be representative of the

growth conditions in the near past and may therefore serve as a proxy for the evaporative demand experienced by the trees during the period of branch xylem and leaf formation of our samples.

Relationships among traits

In agreement with a growing body of intra-specific studies, we could not confirm any trade-off between hydraulic safety and efficiency (e.g., Hajek et al. 2016, Schuldt et al. 2016, Pritzkow et al. 2020). Our results support the assumption that this trade-off is generally weak and that safety and efficiency might largely be decoupled (Gleason et al. 2016). In intra-specific data sets, the variation in either hydraulic safety or efficiency might simply be too small to observe this trade-off, as speculated by Schuldt et al. (2016). In fact, most recent studies confirming this classic plant hydraulic paradigm (cf. Tyree et al. 1994) were inter-specific studies (e.g., Maherali et al. 2006, Fan et al. 2011, Markesteijn et al. 2011, Schumann et al. 2019, van der Sande et al. 2019). In contrast to vessel diameter (D) and hydraulic efficiency, a close relationship between VD and embolism resistance was observed. While the often-observed relationship between D and P_{50} (e.g., Wheeler et al. 2005, Domec et al. 2010, Hajek et al. 2014) is most likely related to the changes in pit properties (Li et al. 2016, Isasa et al. 2023), the observed relationship between VD and embolism resistance has been attributed to pathway redundancy (Schuldt et al. 2016, Levionnois et al. 2021). In rubber, VD is further associated with the lumen-to-sapwood area ratio ($A_{\text{lumen}}:A_{\text{xylem}}$), and consequently, hydraulic efficiency, while D is not. Supporting our results, a growing body of recent studies observed a close relationship between $A_{\text{lumen}}:A_{\text{xylem}}$ and P_{50} (e.g., Lübbe et al. 2022, Avila et al. 2023). However, one would expect D to be the principal determinant of hydraulic conductivity according to Hagen-Poiseuille's law. One explanation for our finding could be that the branch xylem of rubber is composed of very large vessels of c. 60 μm in diameter, resulting in a high specific conductivity (K_s ; mean \pm SE: $3.22 \pm 0.40 \text{ kg m}^{-1} \text{ MPa}^{-1} \text{ s}^{-1}$). Because hydraulic efficiency is already high, it might be favourable to increase the vessel numbers and not vessel diameter. In rubber, the high degree of trait plasticity of VD and $A_{\text{lumen}}:A_{\text{xylem}}$ in relation to other functional wood traits has also been observed by Rungwattana et al. (2018). In their provenance trial, both traits were related to the climate at the place of origin even though a much closer relationship was observed for SLA. In our study, we likewise observed that VD and SLA were not only reacting sensitively to changes in evaporative demand, but both were also related to the P_{50} value. At the leaf level, significant relationships between hydraulic safety and leaf scleromorphy have mainly been observed across species (Willson et al. 2008, Fan et al. 2011; but, see Schumann et al. 2019) but not within species. While *H. brasiliensis* seems to increase its hydraulic safety mostly through vascular adjustments, leaf morphological

modifications also seem to contribute to its hydraulic safety to some extent.

Conclusions

A main motivation of the present study in Indonesian rubber plantations was to analyse the effect of soil moisture regime and evaporative demand on 16 wood and leaf traits related to hydraulic safety and efficiency. Because all trees belonged to the same clone (PB260), we were able to quantify the degree of phenotypic plasticity in response to the variation in edaphic and atmospheric water statuses across an environmental gradient. Mean local evaporative demand, and not VWC, impacted on the branch hydraulic safety and efficiency and leaf morphological traits. In light of the general VPD increase with global warming during the past 30 years, our results are, to our knowledge, the first evidence that trees may be able to modify their woody and foliar tissues to acclimatize to an increasing evaporative demand. Due to its drought-avoiding strategy in conjunction with a high degree of phenotypic plasticity, rubber might be able to acclimatize successfully to more intensive droughts. This may even not be at the cost of a yield reduction as rubber is a secondary metabolite and therefore is not directly related to the general metabolism of the tree. Future experimental studies have to show which atmospheric and soil moisture conditions will drive rubber beyond its drought limit.

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Supplementary data

Supplementary data for this article are available at *Tree Physiology* Online.

Conflict of interest

None declared.

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Data availability statement

All functional traits data as well as vulnerability to cavitation data have been uploaded to the Göttingen Research Online CRC990 Dataverse (<https://data.goettingen-research-online.de/dataverse/crc990>). DOI: <https://doi.org/10.25625/FP7P6K>.

References

- Adams HD, Zeppel MJB, Anderegg WRL et al. (2017) A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. *Nat Ecol Evol* 1:1285–1291.
- Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evol Appl* 1:95–111.
- Allen CD, Breshears DD, McDowell NG (2015) On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 6:art129.
- Allen K, Corre MD, Kurniawan S, Utami SR, Veldkamp E (2016) Spatial variability surpasses land-use change effects on soil biochemical properties of converted lowland landscapes in Sumatra, Indonesia. *Geoderma* 284:42–50.
- Allen RG, Pereira LS, Raes D, Smith M (1998) FAO irrigation and drainage paper no. 56: Crop evapotranspiration. Guidelines for computing crop water requirements, p 326.
- Amitrano C, Arena C, Rouphael Y, de Pascale S, de Micco V (2019) Vapour pressure deficit: the hidden driver behind plant morphofunctional traits in controlled environments. *Ann Appl Biol* 152:688.
- Anderegg WRL, Meinzer FC (2015) Wood anatomy and plant hydraulics in a changing climate. In: Hacke UG (ed) *Functional and ecological xylem anatomy*. Springer International Publishing, Cham, pp. 235–253.
- Anderegg WRL, Klein T, Bartlett MK, 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.
- Ardika R, Sanchez PB, Badayos RB, Cruz PCS (2017) Growth of PB 260 clone (*Hevea brasiliensis* (Willd. ex A. Juss.) Muell-Arg.) in different potting media and fertilization scheme. *Agrivita J Agr Sci* 39:182–191.
- Aroca R (ed) (2012) *Plant responses to drought stress: from morphological to molecular features*. Springer, Berlin, Heidelberg, p 18.
- Avila RT, Kane CN, Batz TA, Trabi C, Damatta FM, Jansen S, McAdam SAM (2023) The relative area of vessels in xylem correlates with stem embolism resistance within and between genera. *Tree Physiol* 43:75–87.
- Barkhordarian A, Saatchi SS, Behrangi A, Loikith PC, Mechoso CR (2019) A recent systematic increase in vapor pressure deficit over tropical South America. *Sci Rep* 9:15331.
- Bartlett MK, Scoffoni C, Sack L (2012a) The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: a global meta-analysis. *Ecol Lett* 15:393–405.
- Bartlett MK, Scoffoni C, Ardy R, Zhang Y, Sun S, Cao K-F, Sack L (2012b) Rapid determination of comparative drought tolerance traits: using an osmometer to predict turgor loss point. *Methods Ecol Evol* 3:880–888.
- Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48.
- Bchir A, Escalona J, Galle A, Hernández-Montes E, Tortosa I, Braham M, Medrano H (2016) Carbon isotope discrimination ($\delta^{13}C$) as an indicator of vine water status and water use efficiency (WUE): looking for the most representative sample and sampling time. *Agric Water Manag* 167:11–20.
- Berry ZC, Espejel X, Williams-Linera G, Asbjornsen H (2019) Linking coordinated hydraulic traits to drought and recovery responses in a tropical montane cloud forest. *Am J Bot* 106:1316–1326.
- Blackman CJ, Aspinwall MJ, Tissue DT, Rymer PD (2017) Genetic adaptation and phenotypic plasticity contribute to greater leaf hydraulic tolerance in response to drought in warmer climates. *Tree Physiol* 37:583–592.
- Blagodatsky S, Xu J, Cadisch G (2016) Carbon balance of rubber (*Hevea brasiliensis*) plantations: a review of uncertainties at plot, landscape and production level. *Agric Ecosyst Environ* 221: 8–19.
- Brodribb TJ, Holbrook NM, Edwards EJ, Gutiérrez MV (2003) Relations between stomatal closure, leaf turgor and xylem vulnerability in eight tropical dry forest trees. *Plant Cell Environ* 26: 443–450.
- Brodribb TJ, Am McAdam S, Carins Murphy MR (2017) Xylem and stomata, coordinated through time and space. *Plant Cell Environ* 40:872–880.
- Burgess O, Pittermann J, Dawson TE (2006) Hydraulic efficiency and safety of branch xylem increases with height in *Sequoia sempervirens* (D. Don) crowns. *Plant Cell Environ* 29:229–239.
- Cahyo AN, Babel MS, Datta A, Prasad KC, Clemente R (2016) Evaluation of land and water management options to enhance productivity of rubber plantation using Wanulcas model. *Agrivita J Agric Sci* 38:93–103.
- Carlquist S (2001) *Comparative wood anatomy: systematic, ecological, and evolutionary aspects of dicotyledon wood*. Springer, Berlin Heidelberg, p 449.
- Carr MKV (2012) The water relations of rubber (*Hevea Brasiliensis*): a review. *Exp Agric* 48:176–193.
- Chandrashekar TR, Nazeer MA, Marattukalam JG, Prakash GP, Annamalaiathan K, Thomas J (1998) An analysis of growth and drought tolerance in rubber during the immature phase in a dry subhumid climate. *Exp Agric* 34:287–300.
- Chen J-W, Cao K-F (2015) A possible link between hydraulic properties and leaf habits in *Hevea brasiliensis*. *Funct Plant Biol* 42:718.
- Choat B, Ball MC, Lully JG, Holtum JAM (2005) Hydraulic architecture of deciduous and evergreen dry rainforest tree species from north-eastern Australia. *Trees* 19:305–311.
- Choat B, Brodribb TJ, Brodersen CR, Duursma RA, López R, Medlyn BE (2018) Triggers of tree mortality under drought. *Nature* 558:531–539.
- Clermont-Dauphin C, Suvannang N, Hammecker C, Cheylan V, Pongwichian P, Do FC (2013) Unexpected absence of control of rubber tree growth by soil water shortage in dry subhumid climate. *Agron Sustain Dev* 33:531–538.
- 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.
- 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.
- Devakumar AS, Mohamed Sathik MB, Jacob J, Annamalaiathan K, Gawai Prakash P, Vijayakumar KR (1998) Effects of atmospheric

- and soil drought on growth and development of *Hevea brasiliensis*. *J Rubber Res (Malaysia)* 1:190–198.
- Din Iso 11277:2002-08 (2002) Bodenbeschaffenheit - Bestimmung der Partikelgrößenverteilung in Mineralböden - Verfahren mittels Siebung und Sedimentation, ISO 11277: 1998/Cor.1:2002. Beuth Verlag, Berlin, Germany.
- Domec J-C, Schäfer K, Oren R, Kim HS, McCarthy HR (2010) Variable conductivity and embolism in roots and branches of four contrasting tree species and their impacts on whole-plant hydraulic performance under future atmospheric CO₂ concentration. *Tree Physiol* 30:1001–1015.
- Dória LC, Podadera DS, Lima RS, Lens F, Marcatti CR (2019) Axial sampling height outperforms site as predictor of wood trait variation. *IAWA J* 40:191–S3.
- Drescher J, Rembold K, Allen K et al. (2016) Ecological and socio-economic functions across tropical land use systems after rainforest conversion. *Philos Trans R Soc Lond Ser B Biol Sci* 371:20150275. <https://doi.org/10.1098/rstb.2015.0275>.
- Eamus D, Boulain N, Cleverly J, Breshears DD (2013) Global change-type drought-induced tree mortality: vapor pressure deficit is more important than temperature per se in causing decline in tree health. *Ecol Evol* 3:2711–2729.
- Falqueto AR, da Silva Júnior RA, Gomes MTG, Martins JPR, Silva DM, Partelli FL (2017) Effects of drought stress on chlorophyll a fluorescence in two rubber tree clones. *Sci Hortic* 224:238–243.
- Fan D-Y, Jie S-L, Liu C-C, Zhang X-Y, Xu X-W, Zhang S-R, Xie Z-Q (2011) The trade-off between safety and efficiency in hydraulic architecture in 31 woody species in a karst area. *Tree Physiol* 31:865–877.
- FAO (2017) UN Food and Agricultural Organisation statistic database. <http://faostat3.fao.org/browse/Q/QC/E> (8 May 2020, date last accessed).
- Farrell C, Szota C, Arndt SK (2017) Does the turgor loss point characterize drought response in dryland plants? *Plant Cell Environ* 40:1500–1511.
- Finegan B, Peña-Claros M, de Oliveira A et al. (2015) Does functional trait diversity predict above-ground biomass and productivity of tropical forests? Testing three alternative hypotheses. *J Ecol* 103:191–201.
- Fonti P, Heller O, Cherubini P, Rigling A, Arend M (2013) Wood anatomical responses of oak saplings exposed to air warming and soil drought. *Plant Biol (Stuttg)* 15:210–219.
- Fu P-L, Jiang Y-J, Wang A-Y, Brodribb TJ, Zhang J-L, Zhu S-D, Cao K-F (2012) Stem hydraulic traits and leaf water-stress tolerance are co-ordinated with the leaf phenology of angiosperm trees in an Asian tropical dry karst forest. *Ann Bot* 110:189–199.
- Gleason SM, Westoby M, Jansen S et al. (2016) Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant species. *New Phytol* 209:123–136.
- Greenwood S, Ruiz-Benito P, Martínez-Vilalta J et al. (2017) Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. *Ecol Lett* 20:539–553.
- Grossiord C, Buckley TN, Cernusak LA, Novick KA, Poulter B, Siegwolf RTW, Sperry JS, McDowell NG (2020a) Plant responses to rising vapor pressure deficit. *New Phytol* 226:1550–1566.
- Grossiord C, Ulrich DEM, Vilagrosa A (2020b) Controls of the hydraulic safety–efficiency trade-off. *Tree Physiol* 40:573–576.
- Hajek P, Leuschner C, Hertel D, Delzon S, Schuldt B (2014) Trade-offs between xylem hydraulic properties, wood anatomy and yield in *Populus*. *Tree Physiol* 34:744–756.
- Hajek P, Kurjak D, von Wühlisch G, Delzon S, Schuldt B (2016) Intraspecific variation in wood anatomical, hydraulic, and foliar traits in ten European beech provenances differing in growth yield. *Front Plant Sci* 7:791.
- Hazir MHM, Gloor E, Galbraith D (2022) Hydraulic traits predict stem growth across *Hevea brasiliensis* clones in a Malaysian climatically marginal area. *For Ecol Manag* 504:119864.
- Hoeber S, Leuschner C, Köhler L, Arias-Aguilar D, Schuldt B (2014) The importance of hydraulic conductivity and wood density to growth performance in eight tree species from a tropical semi-dry climate. *For Ecol Manage* 330:126–136.
- Hoong CW (1997) Performance of clone PB260 in a large plantation group in peninsular Malaysia. *The planter, Kuala Lumpur* 73:403–418.
- Hultine KR, Koepke DF, Pockman WT, Fravolini A, Sperry JS, Williams DG (2006) Influence of soil texture on hydraulic properties and water relations of a dominant warm-desert phreatophyte. *Tree Physiol* 26:313–323.
- Irawan B (2003) Multilevel impact assessment and coping strategies against El Nino: case of food crops in Indonesia: multilevel impact assessment and coping strategies against El Nino: case of food crops in Indonesia. Working Paper number 32714, United Nations Centre for Alleviation of Poverty Through Secondary Crops' Development in Asia and the Pacific (CAPSA).
- Isarangkool Na Ayutthaya S, Do FC, Pannangpetch K, Junjittakarn J, Maeght J-L, Rocheteau A, Cochard H (2011) Water loss regulation in mature *Hevea brasiliensis*: effects of intermittent drought in the rainy season and hydraulic regulation. *Tree Physiol* 31:751–762.
- Isasa E, Link RM, Jansen S, Tezeh FR, Kaack L, Sarmiento Cabral J, Schuldt B (2023) Addressing controversies in the xylem embolism resistance–vessel diameter relationship. *New Phytol* 238:283–296.
- Jaeger B, Edwards L, Das K, Sen P (2016) An R² statistic for fixed effects in the generalized linear mixed model. *J Appl Stat* 44:1086–1105.
- Janssen TAJ, 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 Environ* 43:965–980.
- Jinagool W, Rattanawong R, Sangsing K, Barigah TS, Gay F, Cochard H, Kasemsap P, Herbette S (2016) Clonal variability for vulnerability to cavitation and other drought-related traits *Hevea brasiliensis* Müll. *Arg. J Plant Hydraul* 2:1–12.
- Knipfer T, Barrios-Masias FH, Cuneo IF, Bouda M, Albuquerque CP, Brodersen CR, Kluepfel DA, McElrone AJ (2018) Variations in xylem embolism susceptibility under drought between intact saplings of three walnut species. *Tree Physiol* 38:1180–1192.
- Köcher P, Horna V, Leuschner C (2012) Environmental control of daily stem growth patterns in five temperate broad-leaved tree species. *Tree Physiol* 32:1021–1032.
- Kotowska MM, Leuschner C, Triadiati T, Meriem S, Hertel D (2015) Quantifying above- and belowground biomass carbon loss with forest conversion in tropical lowlands of Sumatra (Indonesia). *Glob Chang Biol* 21:3620–3634.
- Kumagai T'O, Mudd RG, Giambelluca TW et al. (2015) How do rubber (*Hevea brasiliensis*) plantations behave under seasonal water stress in northeastern Thailand and central Cambodia? *Agric For Meteorol* 213:10–22.
- Kunjet S, Thaler P, Gay F, Chuntuma P, Sangkhasila K, Kasemsap P (2013) Effects of drought and tapping for latex production on water relations of *Hevea brasiliensis* trees. *Kasetsart J (Nat Sci)* 47:506–515.
- Laginha Pinto Correia D, Bouchard M, Filotas É, Raulier F (2019) Disentangling the effect of drought on stand mortality and productivity in northern temperate and boreal forests. *J Appl Ecol* 56:758–768.
- Lechthaler S, Turnbull TL, Gelmini Y, Pirotti F, Anfodillo T, Adams MA, Petit G (2019) A standardization method to disentangle environmental information from axial trends of xylem anatomical traits. *Tree Physiol* 39:495–502.

- Levionnois S, Jansen S, Wandji RT et al. (2021) Linking drought-induced xylem embolism resistance to wood anatomical traits in neotropical trees. *New Phytol* 229:1453–1466.
- Lewis AM, Boose ER (1995) Estimating volume flow rates through xylem conduits. *Am J Bot* 82:1112–1116.
- Li S, Klepsch M, Jansen S, Schmitt M, Lens F, Karimi Z, Schuldt B, Espino S, Schenk HJ (2016) Intervessel pit membrane thickness as a key determinant of embolism resistance in angiosperm xylem. *IAWA J* 37:152–171.
- Li S, Li X, Link R et al. (2019) Influence of cambial age and axial height on the spatial patterns of xylem traits in *Catalpa bungei*, a ring-porous tree species native to China. *Forests* 10:662.
- Lübbe T, Schuldt B, Leuschner C (2017) Acclimation of leaf water status and stem hydraulics to drought and tree neighbourhood: alternative strategies among the saplings of five temperate deciduous tree species. *Tree Physiol* 37:456–468.
- Lübbe T, Lamarque LJ, Delzon S, Torres Ruiz JM, Burrett R, Leuschner C, Schuldt B (2022) High variation in hydraulic efficiency but not xylem safety between roots and branches in four temperate broad-leaved tree species. *Funct Ecol* 36:699–712.
- Maherali H, Moura CE, Caldeira MC, Willson CJ, Jackson RB (2006) Functional coordination between leaf gas exchange and vulnerability to xylem cavitation in temperate forest trees. *Plant Cell Environ* 29:571–583.
- Markesteyn L, Poorter L, Paz H, Sack L, Bongers F (2011) Ecological differentiation in xylem cavitation resistance is associated with stem and leaf structural traits. *Plant Cell Environ* 34:137–148.
- Martin-StPaul NK, Limousin J-M, Rodríguez-Calcerrada J, Ruffault J, Rambal S, Letts MG, Misson L (2012) Photosynthetic sensitivity to drought varies among populations of *Quercus ilex* along a rainfall gradient. *Funct Plant Biol* 39:25.
- Martin-StPaul NK, Delzon S, Cochard H (2017) Plants resistance to drought relies on early stomata closure. *Ecol Lett* 20:1437–1447.
- McAdam SAM, Brodribb TJ (2016) Linking turgor with ABA biosynthesis: implications for stomatal responses to vapor pressure deficit across land plants. *Plant Physiol* 171:2008–2016.
- McDowell NG, Allen CD, Anderson-Teixeira K et al. (2018) Drivers and mechanisms of tree mortality in moist tropical forests. *New Phytol* 219:851–869.
- Meijide A, Badu CS, Moyano F, Tiralla N, Gunawan D, Knohl A (2018) Impact of forest conversion to oil palm and rubber plantations on microclimate and the role of the 2015 ENSO event. *Agric For Meteorol* 252:208–219.
- Moser G, Schuldt B, Hertel D, Horna V, Coners H, Barus H, Leuschner C (2014) Replicated throughfall exclusion experiment in an Indonesian perhumid rainforest: wood production, litter fall and fine root growth under simulated drought. *Glob Chang Biol* 20:1481–1497.
- Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods Ecol Evol* 4:133–142.
- Ogle K, Barber JJ, Willson C, Thompson B (2009) Hierarchical statistical modeling of xylem vulnerability to cavitation. *New Phytol* 182:541–554.
- Olson ME, Anfodillo T, Rosell JA, Petit G, Crivellaro A, Isnard S, León-Gómez C, Alvarado-Cárdenas LO, Castorena M (2014) Universal hydraulics of the flowering plants: vessel diameter scales with stem length across angiosperm lineages, habits and climates. *Ecol Lett* 17:988–997.
- Oppenheimer HR (1963) Zur Kenntnis kritischer Wasser-Sättigungsdefizite in Blättern und Ihrer Bestimmung. *Planta* 60:51–69.
- Pereira JDP, Leal AC, Ramos ALM (2018) Evaluation of rubber tree clones under different tapping systems in Northwestern Paraná State. *Brazil Braz Arch Biol Technol* 61:430.
- Petrik P, Petek-Petrik A, Mukarram M, Schuldt B, Lamarque LJ (2023) Leaf physiological and morphological constraints of water-use efficiency in C3 plants. *AoB Plants* 15:plad047.
- Phillips OL, van der Heijden G, Lewis SL et al. (2010) Drought-mortality relationships for tropical forests. *New Phytol* 187:631–646.
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2018) {nlme}: linear and nonlinear mixed effects models. R package version 3.1-137.
- Plavcová L, Hacke UG (2012) Phenotypic and developmental plasticity of xylem in hybrid poplar saplings subjected to experimental drought, nitrogen fertilization, and shading. *J Exp Bot* 63:6481–6491.
- Poorter L, Rozendaal DMA, Bongers F et al. (2019) Wet and dry tropical forests show opposite successional pathways in wood density but converge over time. *Nat Ecol Evol* 3:928–934.
- Pritzkow C, Williamson V, Szota C, Trouvé R, Arndt SK (2020) Phenotypic plasticity and genetic adaptation of functional traits influences intra-specific variation in hydraulic efficiency and safety. *Tree Physiol* 40:215–229.
- Priyadarshan PM (2017) *Biology of Hevea rubber*. Springer International Publishing, Cham, p 252.
- R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Raj S, Das G, Pothen J, Dey SK (2005) Relationship between latex yield of *Hevea brasiliensis* and antecedent environmental parameters. *Int J Biometeorol* 49:189–196.
- Rao PS, Saraswathyamma CK, Sethuraj MR (1998) Studies on the relationship between yield and meteorological parameters of para rubber tree (*Hevea brasiliensis*). *Agric For Meteorol* 90:235–245.
- Rodríguez-Domínguez CM, Buckley TN, Egea G, de Cires A, Hernández-Santana V, Martorell S, Díaz-Espejo A (2016) Most stomatal closure in woody species under moderate drought can be explained by stomatal responses to leaf turgor. *Plant Cell Environ* 39:2014–2026.
- Rosas T, Mencuccini M, Barba J, Cochard H, Saura-Mas S, Martínez-Vilalta J (2019) Adjustments and coordination of hydraulic, leaf and stem traits along a water availability gradient. *New Phytol* 223:632–646.
- Rowland L, da Costa ACL, Galbraith DR et al. (2015) Death from drought in tropical forests is triggered by hydraulics not carbon starvation. *Nature* 528:119–122.
- Rungwattana K, Kasemsap P, Phumichai T, Kanpanon N, Rattanawong R, Hietz P (2018) Trait evolution in tropical rubber (*Hevea brasiliensis*) trees is related to dry season intensity. *Funct Ecol* 32:2638–2651.
- Sangsing K, Kasemsap P, Thanisawanyangkura S, Sangkhasila K, Gohet E, Thaler P, Cochard H (2004a) Xylem embolism and stomatal regulation in two rubber clones (*Hevea brasiliensis* Muell. Arg.). *Trees* 18:109–114.
- Sangsing K, Cochard H, Kasemsap P, Thanisawanyangkura S, Sangkhasila K, Gohet E, Thaler P (2004b) Is growth performance in rubber (*Hevea brasiliensis*) clones related to xylem hydraulic efficiency? *Can J Bot* 82:886–891.
- Santiago LS, Bonal D, Guzman ME, de Ávila-Lovera E (2016) Drought survival strategies of tropical trees. In: Goldstein G, Santiago LS (eds) *Tropical tree physiology*, Vol. 6. Springer International Publishing, Cham, pp. 243–258.
- Schuldt B, Knutzen F, Delzon S, Jansen S, Müller-Haubold H, Burrett R, Clough Y, Leuschner C (2016) How adaptable is the hydraulic system of European beech in the face of climate change-related precipitation reduction? *New Phytol* 210:443–458.

- Schuldt B, Buras A, Arend M et al. (2020) A first assessment of the impact of the extreme 2018 summer drought on Central European forests. *Basic Appl Ecol* 45:86–103.
- Schüller E, Martínez-Ramos M, Hietz P (2013) Radial gradients in wood specific gravity, water and gas content in trees of a Mexican tropical rain forest. *Biotropica* 45:280–287.
- Schumann K, Leuschner C, Schuldt B (2019) Xylem hydraulic safety and efficiency in relation to leaf and wood traits in three temperate *Acer* species differing in habitat preferences. *Trees* 33:1475–1490.
- Sopharat J, Gay F, Thaler P, Sdoodee S, Isarangkool Na Ayuthaya S, Tanavud C, Hammecker C, Do FC (2015) A simple framework to analyze water constraints on seasonal transpiration in rubber tree (*Hevea brasiliensis*) plantations. *Front Plant Sci* 5:753.
- Stahl C, Burban B, Goret JY, Bonal D (2011) Seasonal variations in stem CO₂ efflux in the neotropical rainforest of French Guiana. *Ann For Sci* 68:771–782.
- Stojnic S, Suchocka M, Benito-Garzón M et al. (2018) Variation in xylem vulnerability to embolism in European beech from geographically marginal populations. *Tree Physiol* 38:173–185.
- Susilo GE, Yamamoto K, Imai T (2013) Modeling groundwater level fluctuation in the tropical peatland areas under the effect of El Niño. *Procedia Environ Sci* 17:119–128.
- Tan Z-H, Zhang Y-P, Song Q-H et al. (2011) Rubber plantations act as water pumps in tropical China. *Geophys Res Lett* 38:1–3.
- Torres-Ruiz JM, Cochard H, Choat B et al. (2017) Xylem resistance to embolism: presenting a simple diagnostic test for the open vessel artefact. *New Phytol* 215:489–499.
- Torres-Ruiz JM, Cochard H, Mayr S, Beikircher B, Diaz-Espejo A, Rodriguez-Dominguez CM, Badel E, Fernández JE (2014) Vulnerability to cavitation in *Olea europaea* current-year shoots: further evidence of an open-vessel artifact associated with centrifuge and air-injection techniques. *Physiol Plant* 152:465–474.
- Tyree MT, Cochard H, Davis SD (1994) Biophysical perspectives of xylem evolution: Is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction? *IAWA J* 15:335–360.
- Valladares F, Gianoli E, Gómez JM (2007) Ecological limits to plant phenotypic plasticity. *New Phytol* 176:749–763.
- van der Sande MT, Poorter L, Schnitzer SA, Engelbrecht BMJ, Markesteijn L (2019) The hydraulic efficiency-safety trade-off differs between lianas and trees. *Ecology* 100:e02666.
- Vijayakumar KR, Dey SK, Chandrasekhar TR, Devakumar AS, Mohankrishna T, Sanjeeva Rao P, Sethuraj MR (1998) Irrigation requirement of rubber trees (*Hevea brasiliensis*) in the subhumid tropics. *Agric Water Manag* 35:245–259.
- von Arx G, Carrer M (2014) ROXAS – a new tool to build centuries-long tracheid-lumen chronologies in conifers. *Dendrochronologia* 32:290–293.
- Waite P-A, Schuldt B, Link R, Breidenbach N, Triadiati T, Hennings N, Saad A, Leuschner C (2019) Soil moisture regime and palm height influence embolism resistance in oil palm. *Tree Physiol* 39:1696–1712.
- Western A, Grayson RB, Blöschl G, Wilson DJ (2003) Spatial Variability of Soil Moisture and Its Implications for Scaling. *Scaling Methods in Soil Physics*:119–142.
- 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 Environ* 28:800–812.
- Wichichonchai N, Manmeun S (1992) Yield of rubber in the northeastern province. *Para Rubber Bull Thailand* 12:101.
- Willson CJ, Manos PS, Jackson RB (2008) Hydraulic traits are influenced by phylogenetic history in the drought-resistant, invasive genus *Juniperus* (Cupressaceae). *Am J Bot* 95:299–314.
- Wu J, Liu W, Chen C (2016) Below-ground interspecific competition for water in a rubber agroforestry system may enhance water utilization in plants. *Sci Rep* 6:19502.
- Yeang H-Y (2007) Synchronous flowering of the rubber tree (*Hevea brasiliensis*) induced by high solar radiation intensity. *New Phytol* 175:283–289.
- Yuan W, Zheng Y, Piao S et al. (2019) Increased atmospheric vapor pressure deficit reduces global vegetation growth. *Sci Adv* 5:eaax1396.
- Zeng H, Wu J, Singh AK, Zhu X, Zhang W, Hahn P, Hölscher D, Liu W (2022) Effect of intercrops complexity on water uptake patterns in rubber plantations: evidence from stable isotopes (C-H-O) analysis. *Agric Ecosyst Environ* 338:108086.
- Zhai D-L, Yu H, Chen S-C, Ranjitkar S, Xu J (2019) Responses of rubber leaf phenology to climatic variations in Southwest China. *Int J Biometeorol* 63:607–616.
- Ziegler C, Coste S, Stahl C et al. (2019) Large hydraulic safety margins protect neotropical canopy rainforest tree species against hydraulic failure during drought. *Ann For Sci* 76:1285.