**Article:**

Mohd Hazir, MH, Gloor, E and Galbraith, D (2022) Hydraulic traits predict stem growth across Hevea brasiliensis clones in a Malaysian climatically marginal area. Forest Ecology and Management, 504. 119864. ISSN 0378-1127

https://doi.org/10.1016/j.foreco.2021.119864

# Hydraulic traits predict stem growth across *Hevea brasiliensis* clones in a Malaysian climatically marginal area

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## Highlights

i. Xylem embolism resistance, *$P_{50}$,* and minimum leaf water potential, *$P_{min}$,* vary substantially across nine studied *H. brasiliensis* clones.
ii. Across clones there is a growth-hydraulic safety trade-off such that fast-growing clones have lower hydraulic safety margins.
iii. Hydraulic traits are important predictors of clone growth rate.

## Abstract

Competition for land resources is forcing rubber (*Hevea brasiliensis Müll. Arg.)* production into more agroclimatically vulnerable zones, which are more likely to be affected by drought. It is therefore of interest to determine whether there are particularly drought resistant rubber genotypes. Established plant drought-resistance indicators include xylem resistance to embolism under water stress ($P_{50}$, water potential at which 50% xylem conductivity is lost), and hydraulic safety margins ($HSM_{50}$), defined as the difference between $P_{50}$ and minimum leaf water potential ($P_{min}$) under driest conditions in the year. We report here on measurements of in-situ growth performance of nine mature rubber clones at an agro-climatically marginal site in North-Western Malaysia and their hydraulic, leaf and stem traits to investigate inter-clonal variation in drought resistance and growth rate. We find that $P_{50}$ varies substantially across clones, between -3.05 and -1.37 MPa, while $HSM_{50}$ varied within the range of -0.11 MPa to 1.37 MPa. Similar to what has been reported across species, we find a growth-hydraulic safety trade-off between rubber clones with faster growth rates associated with a lower $HSM_{50}$ and less negative $P_{50}$, with one exception. Based on hierarchic linear regression we find that almost all of the best growth models include hydraulic traits, besides morphological traits, indicating that hydraulic traits are important to predict growth accurately. Furthermore, rubber genotypes with high growth rate and low hydraulic safety margin ($HSM_{50}$) were associated with lower wood density, higher leaf to sapwood area and larger leaf area. Overall while there are clones that are more drought resistant and are thus suited for plantation in marginal areas, they tend to be less productive.

**Keyword: rubber clones; hydraulic traits; growth; rubber; *Hevea brasiliensis*; drought resistance**

## 1.0 Introduction

Anthropogenic climate change has led to substantial increases in global temperature and is altering hydrological regimes, with important functional consequences for woody species **(IPCC 2021)**. In many regions of the Earth, continued climate change is predicted to increase the frequency, duration and intensity of drought events **(Chiang et al. 2021)** that lead to reduced tree growth and increased risk of drought mortality **(Criado et al., 2020; McDowell et al., 2018; Panchen et al., 2014)**. Plant hydraulic properties that describe the ability of the xylem to transport water under soil water stress are fundamentally important for understanding the impacts of drought on growth. Xylem sap is transported under tension (negative pressure), and this tension intensifies under progressive soil water depletion. Very high tensions (very negative pressures) lead to air formation in the xylem (cavitation), disrupting the water column and restricting water transport to the leaves **(Li et al., 2018; Choat et al., 2012)**.

Species with high assimilation rates are known to have more efficient water transport systems (higher hydraulic conductivity in the xylem)**.** However, high water transport efficiency may also be associated with reduced ability to resist cavitation in the xylem under water stress conditions **(e.g. Yan et al. 2020)** and thus may be more susceptible to drought-induced mortality **(e.g. Rowland et al. 2015)**. The metric most often used to characterise xylem resistance to embolism is the water potential associated with a 50% reduction in xylem hydraulic conductance ($P_{50}$). Plants can regulate their stomates to avoid low water potentials, and thus a further important hydraulic property is the hydraulic safety margin which how close plant water potential drops relative to critical cavitation thresholds such as $P_{50}$. HSM integrates soil water status with plant properties including rooting depth and stomatal regulation strategies. In recent years, a number of studies have focused on *interspecies* vulnerability in xylem resistance to embolism formation **(Feng et al., 2021; Chen et al., 2021; Savi et al., 2019; Zhu et al., 2017; Saiki et al., 2017; Anderegg et al., 2016; Li et al., 2015)**. Only a relatively small number of studies **(e.g. Yáñez et al. 2021; Jinagool et al. 2018)** have focus on *intraspecific* variation in hydraulic attributes. An understanding of intra-specific heterogeneity is vital for considering the adaptive potential of a given species. Such variability may result from genetic distinctions between individuals or maybe the expression of phenotypic plasticity **(Aitken et al., 2008)**.

It was recently proposed that a fundamental trade-off exists between hydraulic safety margins and plant growth rates such that plants with acquisitive strategies (high growth rates) take more hydraulic risks (i.e. have lower safety margins) than those with more conservative strategies **(Oliveira et al., 2021)**. Such a trade-off has important implications for carbon storage as it suggests that those plants that accumulate carbon most rapidly and contribute more to ecosystem woody productivity are also the most vulnerable. This framework has received some support at the species level **(e.g. Eller et al., 2018)** but has, to the best of our knowledge, never been evaluated at the *intraspecific* level. In this study, we provide an explicit test of the HSM-growth trade-off across clones of a single species, *Hevea brasiliensis* (rubber), considering nine clones planted in a climatically marginal region of Malaysia.

*H. brasiliensis* was chosen for our study not only to test ecological theory but also because of its important place in the Malaysian economy. Rubber is Malaysia's second most important crop, covering a planted area of over one million hectares (~3% of Malaysia's area) and providing substantial income and employment. In 2015, the entire rubber production was 722,122 tonnes, and the rubber industry contributed 7.2% of the national agriculture GDP **(MESTECC, 2018)**. The optimal climate window for rubber production consists of annual rainfall between 1,500 and 2,500 mm and mean annual temperatures of 23°C to 30°C **(MRB, 2009; Priyadarshan and Goncalves, 2003; Subramaniam, 1987)**. An increase in annual temperatures above 30°C, together with a reduction in rainfall below 1,500 mm, has been predicted to prolong the immature period and reduce rubber yield by up to 10 per cent. Thus an understanding of the drought sensitivity of Malaysian rubber clones is crucial in the context of a changing climate.

Given competing demands for other land uses, rubber plantations now occupy increasingly marginal lands in Malaysia. Indeed, only 35% of Malaysian rubber plantations are in areas with a suitable or highly suitable climate and soil, with the remainder considered marginal with regards to soil, climate or both factors combined (**Hazir et al., 2020)**. Climate change is expected to affect production disproportionately in marginal areas as even relatively small climate-induced reductions in growth could mean that they will become economically unviable. In Malaysia, climate change may be expected to have the highest impact on agro-climatically marginal lands in the more drought-prone North-Western states. It is therefore of interest to determine how climate-resilient rubber trees are in general and whether there are particularly well-suited clones regarding resistance and productivity for expected future climate conditions.

Although inter-clonal variation in xylem vulnerability to cavitation has not been studied in rubber clones mainly used in Malaysia, it has been studied at other locations. **Jinagool et al., 2015** found that in Thailand vulnerability to cavitation in branches in *H. brasiliensis* did not vary among clones, despite differences in growth and latex yield. A recent study conducted by **Waite, 2020** in Indonesia also found no significant difference in xylem embolism resistance between mature rubber trees from the same clone planted in a well-drained *vs.* a riparian environment. However, none of these studies have considered how hydraulic safety margins, considered to be the strongest predictor of drought-induced tree mortality **(Anderegg and Meinzer, 2015)** vary across clones. Our study thus provides the first examination of how this critical property varies across clones.

We specifically consider the following questions: 1) Do Malaysian rubber clones vary in $P_{50}$ and HSM? 2) Is there evidence that HSM-growth trade-off applies across clones of *H. brasiliensis*? 3) Are hydraulic traits related to commonly measured leaf/wood traits? and 4) How important are hydraulic traits relative to other functional traits in determining growth of *H. brasiliensis*? To address these questions, we integrate measurements of hydraulic traits with measurements of stem growth and of commonly measured leaf/stem traits including leaf area (LA), leaf mass per area (LMA), leaf dry matter content (LDMC), leaf thickness (LT), leaf area to sapwood area (LA: SA), wood density (WD), tree height and bark thickness were measured **(Bhusal et al., 2021; McGregor et al., 2020, Chen and Cao, 2015; Chaturvedi et al., 2011; Kitajima and Poorter, 2010)**. Attributes such as wood density are much easier to sample than hydraulic traits and the existence of strong bivariate relationships between such traits and hydraulic properties could facilitate the assessment of sensitivity to drought.

## 2.0 Methodology

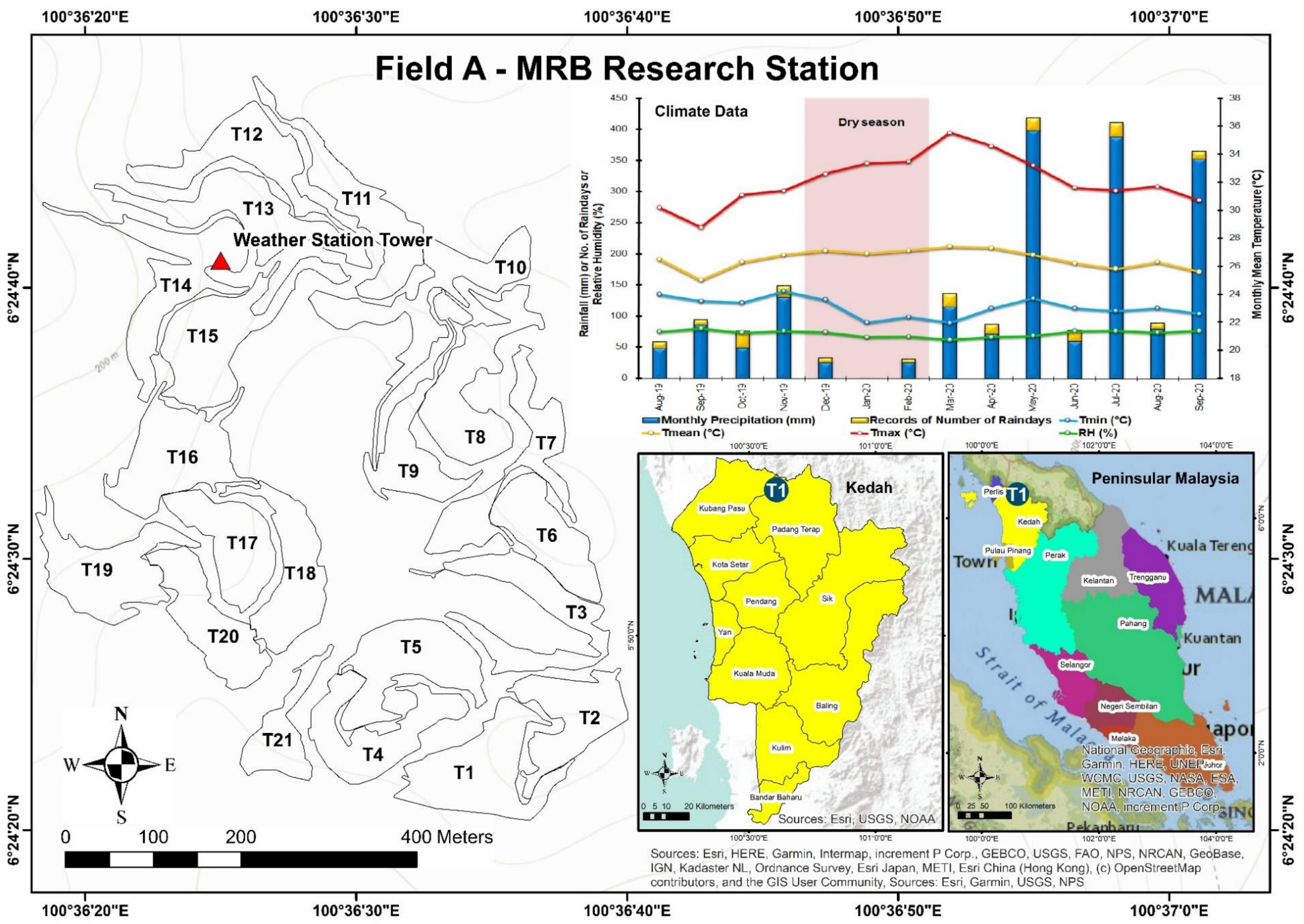
### 2.1 Site

The study was performed inside a 40 ha area at Sungai Sari Research Station which is part of a 640-ha plantation operated by the Malaysian Rubber Board in Kedah, Malaysia (6° 24' 41" N, 100° 36' 25" E; altitude 166 m). Sungai Sari is located in the Northern region of Peninsular Malaysia in the Padang Terap and Kubang Pasu district of Kedah **(Figure 1)**. The main economic activities are agriculture and trading. The climate is tropical monsoonal (Am in the Köppen and Geiger classification). Climatic seasonality is more pronounced at the study site compared to other rubber-planting areas of Malaysia, with marked reductions in rainfall (< 50mm $month^{-1}$) in the Northeast monsoon season (December 2019 until February 2020). Sungai Sari is also characterised by higher maximum air temperatures compared to other rubber plantations in Malaysia, with daily maximum temperatures close to or exceeding 32 degrees in most months of the year. It is located in hilly terrain and considered an agro-climatically marginal area. The soil falls under the Bungor series based on the Malaysian Soil Taxonomy or Ultisol under US Soil Taxonomy and subgroups of Typic Paleudult according to the USDA Soil Taxonomy or Haplic Acrisol under FAO Unesco Legend classification. The texture of Bungor soils is the result of these soils developing over mixed sedimentary rocks and shale with brown colour (hue 7.5-10 YR in the Munsell system), while the subsoil (15-30 cm) is sandy clay to clay **(Shamshuddin and Darus, 1976; Zainol, 1985; De Dapper and Debaveye, 1986; DOA, 2010; DSM, 2015)**. The area initially was primary forest before the Malaysian Rubber Board (MRB) developed it as a rubber research station.

We focus here on 20 different stands (called 'tasks'), with each task covering an area between 0.8 and 1.3 hectares. Each task was planted on an 8 m wide terrace with individuals belonging to a single *H. brasiliensis* clone or a mix of two to three rubber clones. Trees were planted at 2.3 m distance from each other, resulting in a planting density of 550 trees per hectare. All nine rubber clones investigated in this study are known as Latex-Timber Clones **(Aris, 2005)** and are listed in the MRB Clone Recommendation 2021 **(MRB, 2021)** except for RRIM 929 and RRIM 2025. All trees were planted in 2010 and are thus of the same age **(Supplementary Table A.1)**. Hired rubber tappers tap the trees for latex on the lowest tapping level (1.5 m above ground) where the bark had been removed to harvest latex (so-called 'first basal virgin panel') once every three days. This sampling protocol is known as the d/3 tapping system and had been applied for four to five years prior to the data collection undertaken in this study.

We randomly sampled twenty healthy trees from each of the nine rubber clones. Thus, in total, 180 trees were selected. Each selected tree was marked and tagged. We generally chose trees close to each other to reduce soil and topographic variability. Maximum temperature ($T_{max}$, °C), mean temperature ($T_{min}$, °C), minimum temperature ($T_{mean}$, °C), rainfall (mm), and relative humidity (RH, %) were measured by an *in-situ* weather station (Davis Instruments WeatherLink, Vantage Pro) as well as by a weather station owned by the Malaysian Department of Irrigation and Drainage located approximately 5 km from the study site (as a backup) **(Figure 1)**.

Our measurements were made from August 2019 until September 2020. This period includes the dry season from December 2019 to February 2020 with low rainfall (less than 50 mm month$^{-1}$) and high temperatures (above 30°C) which are followed by the wet season. During the dry season, rubber trees lose their leaves, with leaf flush occurring between March and May. Total rainfall during our study period of 1,427 mm is lower than the national annual average rainfall for Peninsular Malaysia (about 2,000 mm) and lower than the historical average annual rainfall for the North-Western region of Peninsular Malaysia (2,213 mm) **(MESTECC, 2018)**. It is also slightly below the recommended minimum total annual rainfall for rubber plantation of 1,500 mm **(MRB, 2009)**.



Sources: Esri, HERE, Garmin, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), (c) OpenStreetMap contributors, and the GIS User Community, Sources: Esri, Garmin, USGS, NPS

Figure 1 Study site and climate data within the study period.

## 2.2 Tree height and stem growth rate

We measured tree height using a laser rangefinder embedded with a hypsometer (Nikon Forestry Pro II, Tokyo, Japan). Growth was measured monthly at the end of the month, starting in August 2019 until September 2020, except for the total national lockdown period because of the Covid-19 pandemic (March 2020 until May 2020). The dendrometer bands, built by ourselves based on the design of **Kho et al. (2013)**, were installed at 160 cm height or slightly above the tapping panel, usually at 165 cm height. Circumference increments (mm month$^{-1}$) were determined from the bands using a high precision digital Vernier calliper from which diameter growth rates was calculated (dividing by $\pi$).

## 2.3 Hydraulic traits

### 2.3.1 Xylem vulnerability curves

The measurement of branch xylem embolism vulnerability was made using the recently-developed pneumatic method **(Pereira et al., 2016; Bittencourt et al., 2018)** combined with the bench dehydration technique used to induce cavitation **(Sperry et al., 1988)**. The pneumatic method measures xylem air discharge which can be translated into a quantitative measurement of embolism formation. The pneumatic method has now been widely tested, and embolism resistance metrics derived from this method have been found to agree well with those derived from traditional hydraulic methods **(Tavares 2019; Bittencourt et al., 2020; Zhang et al., 2018; Pereira et al., 2020; Wu et al., 2020; Brum et al., 2019; Oliveira et al., 2019; Barros et al., 2019)**, as well as with a new non-hydraulic optical method **(Guan et al., 2021)** although some recent studies suggest it may overestimate vulnerability to embolism in relation to other methods **(Sergent et al. 2020, Chen et al. 2021)**. The pneumatic method is ideally suited to deployment in the field due to its low cost **(Paligi et al., 2021)**, rapid accessibility of the methodology during the study period (during Covid 19 pandemic), easy setup and applicability in a remote location. Simultaneous measurements of air discharge and water potential were made repeatedly for each sampled branch over three to four days while the branch was dried to construct xylem vulnerability curves.

In total, we measured vulnerability curves for 30 branches. We harvested three branches from three individuals for all rubber clones except RRIM 2007, RRIM 2025 and RRIM 3001, where we harvested four branches from three individuals. Branches of approximately 1 m in length were cut using a long telescopic pruner, selecting only sunlit branches, and sampling before dawn under non-transpiring conditions. After cutting, samples were immediately wrapped in wet tissue and covered with thick black plastic before transporting the branches from the plantation to a small field laboratory (~10 minutes by four-wheel drive). Upon arrival in the laboratory and before connection to the air discharge apparatus, branches were recut under water to preserve full hydraulic conductivity and covered with an opaque black plastic bag for at least one hour to allow equilibration of leaf and xylem water potentials.

Before attachment to the pneumatic apparatus, a small amount of bark was cut from the branch to ensure that latex exudation did not block the xylem vessels during the measurement. After that, the branch end was fixed inside a rubber tube. To obtain an airtight seal between the rubber tube and the branch, the branch was wrapped with plastic film before being inserted into the rubber tube. A plastic clamp was fastened around the rubber tube where the branch had been inserted.

The vacuum reservoir's partial vacuum (2L conical glass flask) was created using an electric pump (35-40 kPa). After opening the vacuum reservoir to the branch, air was discharged from the branch for 2.5 minutes, after which the absolute pressure was measured again ($P_f$, kPa). The sample was then disconnected from the pneumatic system. From the pressure change, the air discharge volume is calculated. Immediately after air discharge determination, a random leaf was cut from the measured branch to determine its leaf water potential using a Scholander pressure chamber (Model 1505D, PMS Instrument, Oregon, USA) coupled to a portable microscope to capture precisely the pressure at which liquid starts to exude from the leaf petiole. Glue was applied to the leaf cut to prevent the entry of air into the branch. The branch was then left to dry (bench dehydrated) for an hour before placing it inside a black plastic for equilibration between leaf and xylem water potentials. The above steps (joint determination of air discharge and water potential) were repeated throughout the bench dehydration process. We did not establish *a priori* a terminal water potential value at which to conclude the measurements. Instead, we followed protocols in other studies where measurements were continued until a plateau in air discharge values was reached **(Pereira et al. 2016; Barros et al. 2019)**. We note that for two clones (RRIM 2002 and 2024), leaves fell from the branches prior to clear plateaus being reached **(Supplementary Figure A.2)**.

Data processing and analysis were done using RStudio (R Core Team, 2016 [version 1.1.463.0]). To estimate $P_{50}$, the leaf water potential at which 50% of conductivity is lost, we followed **Pammenter and Willigen (1998)** and fitted the model using **Equation 1** to the air discharge versus leaf water potential data. Here *PAD* is percentage of air discharged from the branch relative to the maximal discharge (%); *S* is the slope of the curve; $P_x$ is xylem leaf water potential (MPa).

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

$P_{50}$ represents the steepest part of the vulnerability curve **(Choat et al., 2012)**, where small changes in xylem tension result in large changes in conductivity. $P_{12}$ and $P_{88}$ were also estimated based on **Sparks and Black (1999)** and **Domec and Gartner (2001),** respectively as **Equation 2** and **Equation 3.**

$$P_{12} = P_{50} + \frac{2}{(\frac{S}{25})}$$ **Equation 2**

$$P_{88} = P_{50} - \frac{2}{(\frac{S}{25})}$$ **Equation 3**

Curves were fitted for each clone in turn, combining all individuals of each rubber clone.

### 2.3.2 Determining hydraulic safety margins

Predawn (before sunrise) and midday (12 AM to 14 PM local time) leaf water potential from five individuals was measured *in situ* for top of canopy sun-exposed fully expanded branches (two leaves per branch, a branch per individual) for five individuals for each of the nine rubber clones in both the wet and the dry seasons using a Scholander pressure chamber (Model 1505D, PMS Instrument, Oregon, USA). The minimum leaf water potential, $P_{min}$ is the midday leaf water potential during the peak of the dry season. As all *H. brasiliensis* clones evaluated in this study lose their leaves in February (the final month of the 3-month dry season – see **Figure 1**), $P_{min}$ was measured in January 2020 as this corresponded to the driest time of the year before leaf senescence ensued. Combining independently measured leaf water potentials measured over the year, $P_{min}$ and $P_{50}$, the hydraulic safety margin ($HSM_{50}$), can be calculated:

$$HSM_{50} = P_{min} - P_{50} \quad . \qquad \textbf{Equation 4}$$

### 2.4 Leaf and stem traits

We measured the following leaf and stem traits: leaf area (LA), leaf mass per area (LMA), leaf dry-matter content (LDMC), leaf area to sapwood area ($L_A$: $S_A$), leaf thickness (LT), wood density (WD) and bark thickness. Leaf traits were measured using the same branches samples from hydraulics traits measurement. We measured these traits during the wet season and avoided the dry season and the leaf flushing period. Only fully expanded mature leaves were used. Fresh leaves were collected from five individuals for each rubber clone **(Supplementary Table A.6)**. In total 494 leaves were scanned (LiDE, Canon, Japan) and processed using ImageJ v1.52p **(Schneider et al., 2012)** to measured its leaf area ($cm^2$) **(Supplementary Table A.6)**. Leaf mass (g) per area ($m^{-2}$) (LMA) and leaf oven-dry mass (mg) per unit leaf fresh mass ($g^{-1}$) (LDMC) were determined following standard protocols (**Wilson et al., 1999; Vendramini et al., 2002; Cornelissen et al., 2003**).

The fresh mass of an individual leaf was measured using a precision balance (Jadever - 0.01 g, Taipei, Taiwan). Then, samples were wrapped in moist paper and kept in sealed plastic bags to promote rehydration. All samples were kept inside a closed polystyrene cooling box filled partially with ice to maintain the temperature below 6°C. We measured the leaf's water-saturated fresh and dry mass using an analytical balance (Ohaus Pioneer, 0.0001g). Samples were oven-dried (Memmert B40, Germany) at 70 °C for at least two days before measuring dry mass. Fresh leaf thickness was measured using a digital thickness gauge (Mitutoyo - 0.001 mm, Kanagawa, Japan) at least four points of each leaf. The sapwood area (*n=90*) was measured on sunlit terminal branches after bark removal using a high precision Vernier calliper.

To measure stem bark thickness and wood density we extracted cores from 10 individuals for each rubber clone using an increment borer (Haglöf 3, Ø 5.15 mm, Långsele, Sweden) at a height of 1.5 m above ground. Bark thickness was then measured using a thickness gauge. After removing the bark, the remaining tree cores (of 6-9 cm length) were also used to determine wood density (via the fixed volume of cores). The fresh weight and length of core samples were weighed and measured before they were oven-dried until a constant weight was achieved (105°C, ~72 hours) **(Farias et al., 2020; Schuldt et al., 2013)**.

## 2.5 Statistical analysis

We tested for normality of measurements using the Shapiro-Wilks test (rejection level p > 0.05). We used one-way analysis of variance (ANOVA) followed by post-hoc Tukey tests to test for differences among clones in $P_{50}$, hydraulic safety margins and leaf/stem functional traits. Linear regressions were used to test for significant relationships between traits and growth rates using York's method **(York et al., 2004; Pieter, 2018),** which accounts for errors in x and y **(York, 1968;)**. Significance of linear relationships was assessed using the reduced chi-square test, with relationships considered significant at $p< 0.05$. Bivariate regressions were repeated excluding the two clones where a clear plateau was not reached to assess the influence of these values on the overall relationships.

Linear mixed-effects models of the relationship between rubber growth rate and the total rainfall were constructed using the "lme4" function **(Bates et al., 2012)**, with rainfall treated as fixed effect, and rubber clone included as a random effect.

We applied backward stepwise regression **(Chatterjee and Hadi, 2015; Yan and Su, 2009)** to determine which combinations of hydraulic, leaf and stem traits best explain *H. brasiliensis* growth, and separately height, and retained only those traits with the highest partial correlation with the growth. We measured multicollinearity using the variance inflation factor (VIF), adopting as a rule of thumb that VIF must be less than 10 **(Kalnins, 2018; O'brien, 2007; Kutner et al., 2005)**. We removed variables from the models if they were highly correlated with other variables and led to VIF higher than five. Model performance was assessed using Akaike's Information Criterion (AIC) to distinguish among a set of possible models describing the relationship between hydraulic traits, tree traits, and growth. The best-fit model was selected based on fewer traits, VIF less than five and had the lowest AIC. All of the tests were executed using SPSS v25 (IBM Corp., Armonk, New York) and RStudio (version 1.4.1103, PBC).

## 3.0 Results

At the starting point of the stem growth measurements in August 2019, all nine rubber clones had a diameter-at-breast-height (DBH) between 16.8±1.8 cm and 22.1±3.7 cm ($F(8,171)= 8.042$, $p= 0.00$) **(Supplementary Table A.2)**. In general, all rubber clones followed a similar growth pattern with a slow stem growth rate and shrinking phase during the first 6 months of data collection (September 2019 to February 2020) and a high growth rate in the last 6 months (March 2020 to August 2020) **(Figure 2 and Supplementary Figure A.1)**.

Mean (±standard deviation) growth rate from September to November 2019 varied from 0.17±0.27 mm month$^{-1}$ (RRIM 2007) and 2.2±1.53 mm month$^{-1}$ (RRIM 2023) across clones ($F$(8, 170)= 16.062, $p$= 0.00) **(Supplementary Table A.2)**. From March to May 2020, stem growth rates of all rubber clones increased substantially with the highest and the lowest recorded growth rate for RRIM 928 and RRIM 2007 of 6.91±2.54 mm month$^{-1}$ and 2.77±1.27 mm month$^{-1}$, respectively **(Figure 2)**. Growth rates continued to increase until September 2020. During June to September, a period with high rainfall **(Supplementary Table A.3)**, the leaves were in a mature stage. Over the entire study period, the highest mean growth rate was 4.07±1.39 mm month$^{-1}$ (RRIM 928) and the lowest growth rate was 1.17±0.45 mm month$^{-1}$ (RRIM 2007) **(Supplementary Table A.2)**.

The stem growth rate was not related to tree height ($p$= 0.587). The tree height for the same age trees varied between 13.4±1.7 m for two rubber clones of RRIM 2007 and RRIM 2025 and 8.4±1.4 m (RRIM 2001) **(Supplementary Table A.2)**.

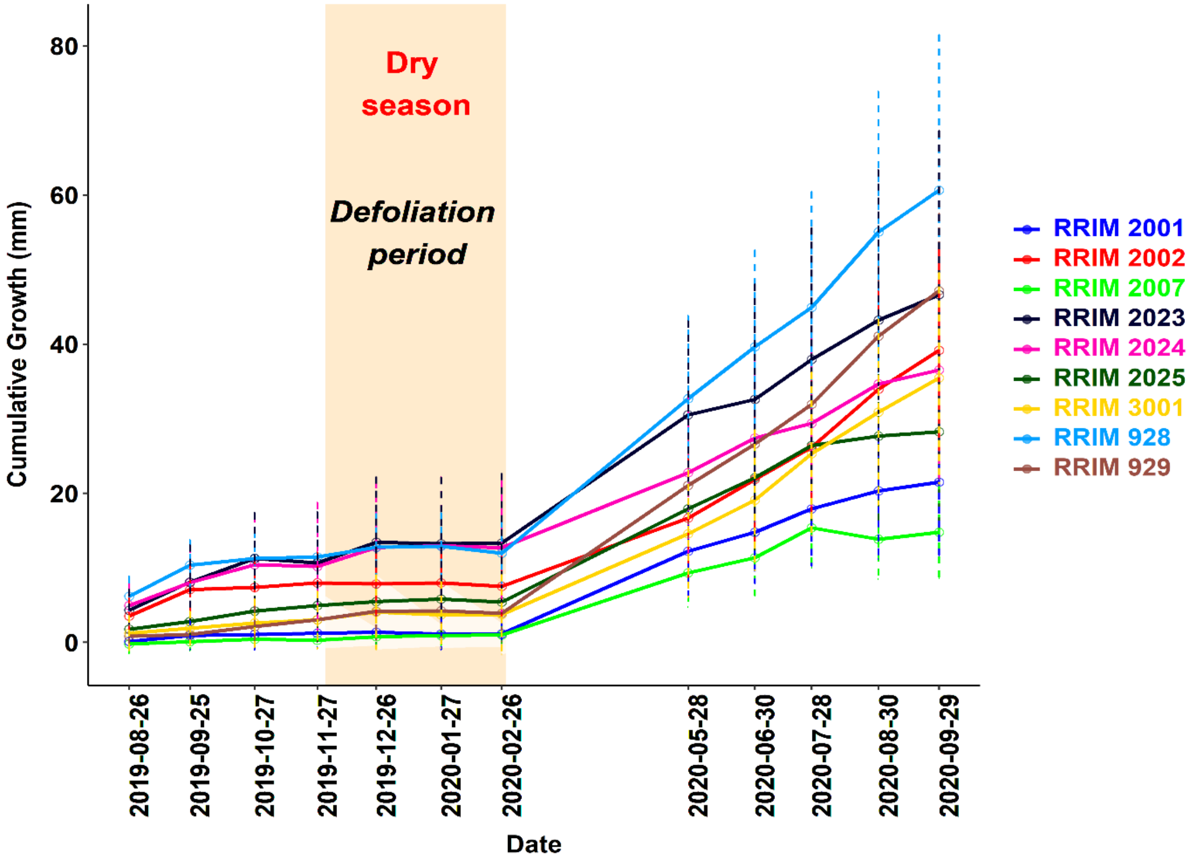


Figure 2 Cumulative stem growth (mean±sd) of nine rubber clones ($n$=180) during the study period (August 2019 – September 2020).

## 3.1 Leaf water potential daily and seasonal cycle

Daily leaf water potential cycles follow the familiar pattern of lower leaf water potentials at midday compared to predawn **(Figure 3a),** both during the wet and dry season. During the dry season, mean leaf water potentials are more negative for both predawn and midday (dry season: -0.70±0.25 MPa and -1.37±0.30 MPa; wet season: -0.42±0.14 MPa and -0.90±0.23 MPa). There are some inter-clonal differences: midday leaf water potentials varied between -1.87±0.18 MPa (RRIM 2002) and -0.94±0.08 MPa (RRIM 2025) during the dry season and -1.27±0.04 MPa (RRIM 2007) and -0.64±0.02 MPa (RRIM 2025) during the wet season, respectively **(Supplementary Table A.4)**. Midday leaf water potentials were strongly associated with predawn leaf water potential regardless of the wet or dry season ($r$= 0.88, $p$< 0.01 and $r$= 0.90, $p$< 0.01) but were not significantly related to tree height ($r$= -0.21, $p$= 0.596 and $r$= -0.29, $p$= 0.444) **(Supplementary Figure A.3)**.

## 3.2 Interclonal hydraulic trait variation

### 3.2.1 Xylem embolism resistance and hydraulic safety margin

Xylem resistance to embolism, $P_{50}$, of nine *H. brasiliensis* genotypes ranged between -3.05±0.83 MPa (RRIM 2007) and -1.37±0.23 MPa (RRIM 928) **(Figure 3b)**. $P_{88}$, varied between -4.16±0.85 MPa to -2.29±0.4 MPa **(Supplementary Figure A.2)** and $P_{12}$ varied between -1.58±1.05 MPa and -0.54±0.02 MPa **(Supplementary Table A.4)**. $P_{50}$ was strongly positively associated with the minimum leaf water potential observed in the dry season ($P_{min}$) ($r$= 0.68, $p$< 0.05) and also with pre-dawn leaf water potential in the wet season ($r$= 0.68, $p$< 0.05) and the dry season $P_{50}$ ($r$= 0.64, $p$< 0.05) **(Supplementary Table A.5)**.

Hydraulic safety margins, *$HSM_{50}$*, were positive for most clones with one exception (RRIM 3001) (**Figure 3b)**. For almost all rubber clones (except RRIM 2007 and RRIM 929) safety margins were smaller during the dry season than during the wet season. For a few clones, the safety margin during the dry season was close to 0 (RRIM 2002 and RRIM 928). Only two clones were found to have statistically different dry season *$HSM_{50}$*, with RRIM 2007 having a significantly higher safety margin than RRIM 3001 **(Supplementary Table A.4)**. The diurnal range of midday and predawn leaf water potential during the wet and dry season were -0.33 to -0.92 MPa and -0.34 to -1.2 MPa, respectively **(Supplementary Table A.4)**.

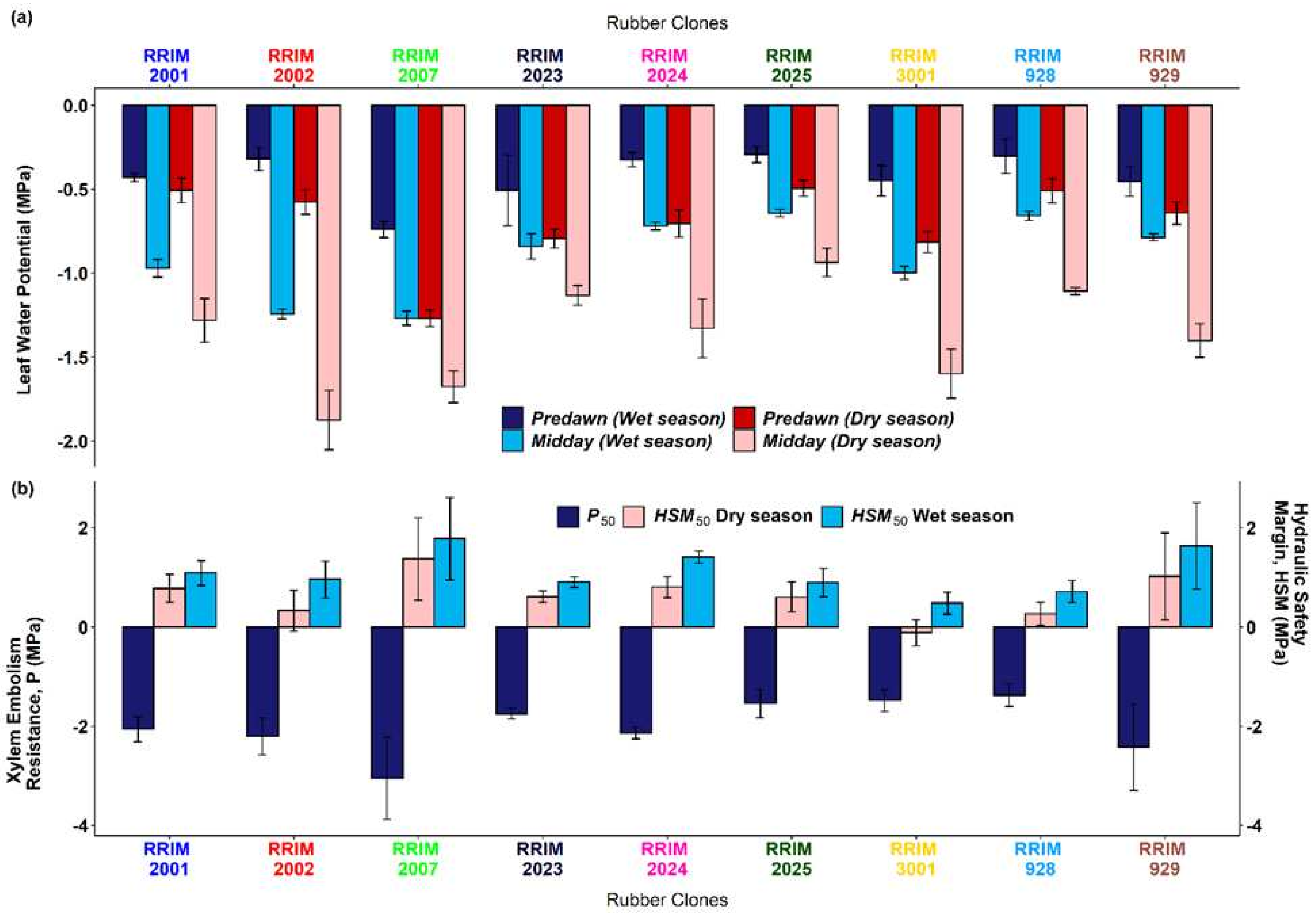


Figure 3 Variability in hydraulic traits of nine rubber clones: a) leaf water potential in predawn and midday during the dry season and wet season (mean±sd) b) xylem embolism resistance ($P_{50}$) and hydraulic safety margin in the wet ($HSM_{50}$ Wet season) and dry season ($HSM_{50}$ Dry season) (mean±sd)

## 3.3 Interclonal variability in leaf and stem traits

Leaf area across the nine rubber clones varied between 26.1±5.1 cm$^2$ (RRIM 2001) and 70.50±26.7 cm$^2$ (RRIM 3001) with an average of 49.2±20.7 cm$^2$ **(Supplementary Table A.6)**. The average leaf thickness of *H. brasiliensis* was 0.24±0.04 mm, with thinnest and thickest leaf thickness of 0.17±0.03 mm and 0.28±0.04 mm, respectively. The average LMA, LDMC, wood density and leaf density for nine rubber genotypes were 84.7±15.5 g m$^{-2}$, 433.6±17.4 mg g$^{-1}$, 0.53±0.02 g cm$^{-3}$ and 0.37±1.2 g cm$^{-3}$, respectively. RRIM 2001 had the highest LMA, LDMC, wood density and leaf density of all clones investigated.

## 3.4 Relationship between stem growth rate and studied traits

We find that faster-growing rubber clones are associated with lower (less negative) xylem embolism resistance ($R^2$= 0.30, $p$= 0.04) **(Figure 4a)** and higher minimum (less negative) leaf water potentials ($R^2$= 0.12, $p$= 0.05) **(Figure 4b)**. Moreover, we find a trade-off between stem growth rate and hydraulic safety margin ($R^2$= 0.19, $p$= 0.03) **(Figure 4c)**. Rubber clones with a lower stem growth rate tend to have a lower vulnerability (more negative $P_{50}$) to cavitation and a higher (more positive) hydraulic safety margin ($HSM_{50}$). Exclusion of the two clones where a clear plateau in the vulnerability curves was not reached had very little impact on the relationships between hydraulic traits and growth and between hydraulic traits and other traits **(Supplementary Table A.7)**. Clone-level growth rates are also correlated with the leaf area to sapwood area ratio (Huber value) ($R^2$= 0.41, $p$= 0.04 when using all clones **(Figure 4d)**. However, if RRIM 928 is removed from the analysis, the relationship between the growth rate and inverse Huber value is not strong anymore ($R^2$= 0.08, $p$= 0.5). Leaf area to sapwood area ratio varied between 44.74 cm$^2$ cm$^{-2}$ (RRIM 2001) to 294.21 cm$^2$ cm$^{-2}$ (RRIM 928) **(Supplementary Table A.6)**.

There was no significant relationship between stem growth rate and other studied traits at 0.05 significance level **(Supplementary Table A.8)**. The stem growth rate had a weak negative association with wood density, with genotypes with faster growth rate having lower wood density ($R^2=0.10$, $p$=0.06) **(Figure 4e)**. There is also a very weak relationship between growth rate and leaf density ($R^2$= 0.02, $p$=0.08) **(Figure 4f)**. Furthermore, we also found that higher tree height is associated with lower wood density ($F$(1, 7)= 7.669, $R^2$= 0.52, $p$= 0.03) **(Supplementary Figure A.4a)** and lower leaf density ($F$(1, 7)= 7.215, $R^2$= 0.50, $p$= 0.03) **(Supplementary Figure A.4b)**.

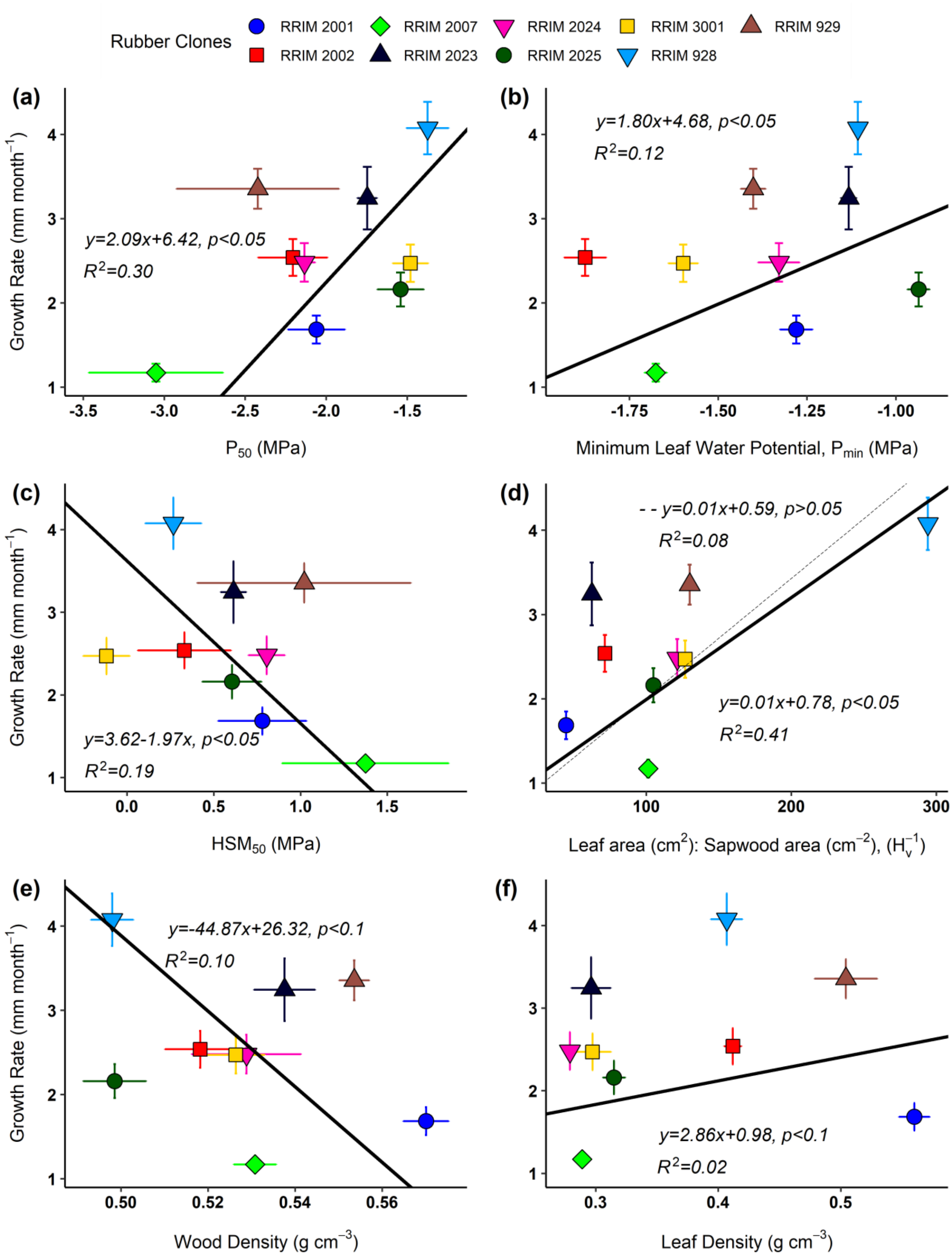

Rubber Clones
RRIM 2001
RRIM 2002
RRIM 2007
RRIM 2023
RRIM 2024
RRIM 2025
RRIM 3001
RRIM 928
RRIM 929
(a)
Growth Rate (mm month$^{-1}$)
y=2.09x+6.42, p<0.05
R$^2$=0.30
-3.5 -3.0 -2.5 -2.0 -1.5
P$_{50}$ (MPa)
(b)
y=1.80x+4.68, p<0.05
R$^2$=0.12
-1.75 -1.50 -1.25 -1.00
Minimum Leaf Water Potential, P$_{min}$ (MPa)
(c)
Growth Rate (mm month$^{-1}$)
y=3.62-1.97x, p<0.05
R$^2$=0.19
0.0 0.5 1.0 1.5
HSM$_{50}$ (MPa)
(d)
- - y=0.01x+0.59, p>0.05
R$^2$=0.08
y=0.01x+0.78, p<0.05
R$^2$=0.41
100 200 300
Leaf area (cm$^2$): Sapwood area (cm$^{-2}$), (H$_v^{-1}$)
(e)
Growth Rate (mm month$^{-1}$)
y=-44.87x+26.32, p<0.1
R$^2$=0.10
0.50 0.52 0.54 0.56
Wood Density (g cm$^{-3}$)
(f)
y=2.86x+0.98, p<0.1
R$^2$=0.02
0.3 0.4 0.5
Leaf Density (g cm$^{-3}$)
1 2 3 4

Figure 4 Relationship between stem growth rate and studied traits (mean±se): a) Growth rate vs $P_{50}$ b) Growth rate *vs* minimum leaf water potential c) Growth rate *vs* $HSM_{50}$ d) Growth rate *vs* leaf area to sapwood area (inverse Huber value) e) Growth rate *vs* wood density f) Growth rate *vs* leaf density (stripping line indicate without RRIM 928). Solid black and dotted lines depict the best-fit slopes from York's regression.

### 3.5 Coordination of hydraulic traits and tree traits

High (more negative) xylem embolism resistance, $P_{50}$, *is* associated with high wood density ($p < 0.01$) **(Figure 5a)** and there is a weak positive correlation with LMA ($p < 0.01$) **(Figure 5b)**. There are strong correlations between hydraulic traits ($P_{50}$, $P_{88}$, $HSM_{50}$ and $HSM_{88}$) and leaf area **(Supplementary Table A.9)**. Moreover, predawn leaf water potential in the dry season and LMA were positively correlated ($R^2$=0.20, $p < 0.05$).

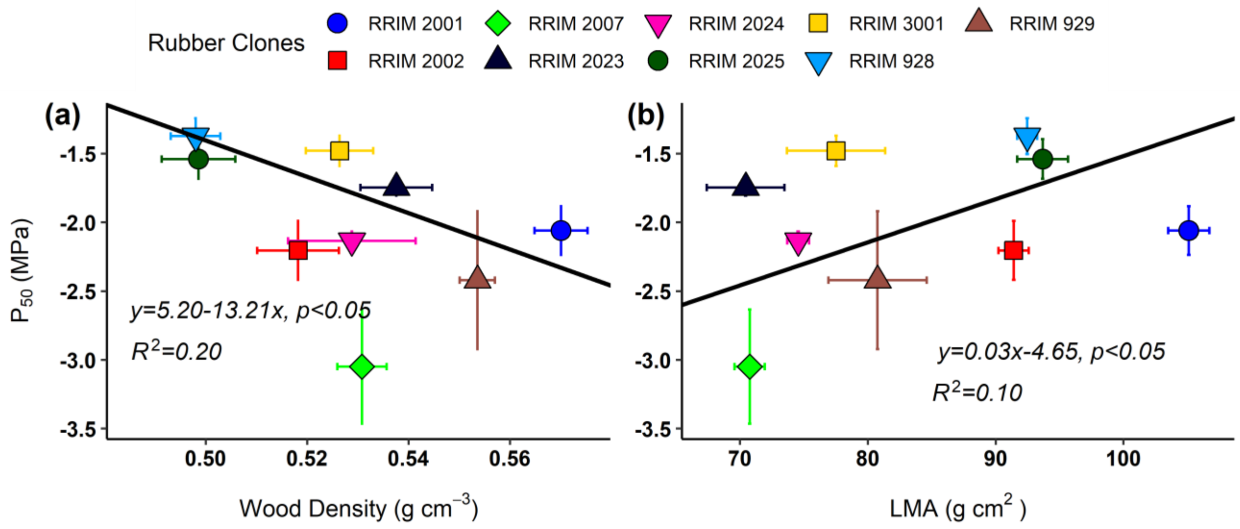


Figure 5 Relationship between xylem embolism resistance and tree traits (mean±se): a) $P_{50}$ *vs* wood density b) $P_{50}$ *vs* LMA. Solid black lines depict the best-fit slopes from York's regression.

### 3.6 Multiple regression analysis of growth and tree height

For the regression analysis we included the following traits: $P_{50}$, $HSM_{50}$, ∆LWP, LA:SA, Wood density, leaf thickness, leaf area. The results are shown in **Table 1 and Supplementary Table A.11**.

The best model identified by the AIC criteria for stem growth **(Equation 5)** is

$$\text{Stem growth (mm month}^{-1}) = 2.176 \times \Delta\text{LWP}_{\text{wet season}}\text{ (MPa)} - 1.197 \times HSM_{50,\text{dry season}}\text{ (MPa)} - 25.893 \times \text{Wood density (g cm}^{-3}) - 20.015 \times \text{Leaf thickness (mm)} + 123.157 \qquad \textbf{Equation 5}$$

Given the observed ranges of each of these variables **(Supplementary Table A.4 and Table A.6)** all terms are of similar importance to predict observed growth variation across clones.

We similarly examined determinants of tree height. The best model in this case is

$$\text{Tree height (m)} = -1.166 \times \Delta\text{LWP}_{\text{wet season}}\text{ (MPa)} - 1.553 \times P_{50}\text{ (MPa)} - 41.599 \times \text{Wood density (g cm}^{-3}) + 20.050 \times \text{Leaf thickness (mm)} + 25.167 \qquad \textbf{Equation 6}$$

**Table 1.** Models of stem growth, coefficient of determination and their ranking according to the Akaike Information Criterion (AIC)

| Stem Growth Model Predictors | | Stem growth (mm month$^{-1}$) | | |
|---|---|---|---|---|
| | | $R^2$ | *Adjusted* $R^2$ | ∆AIC |
| 1. | -$HSM_{50}$, +∆LWP, -Wood density, -Leaf thickness | 0.86 | 0.73 | 16.39 |
| 2. | +∆LWP, -Wood density, -Leaf thickness, +Leaf area | 0.81 | 0.63 | 19.12 |
| 3. | +$P_{50}$, +∆LWP, -Wood density, -Leaf thickness | 0.77 | 0.55 | 20.89 |
| 4. | -Wood density, -Leaf thickness, +Leaf area | 0.69 | 0.50 | 21.76 |
| 5. | +LA:SA | 0.45 | 0.37 | 22.86 |

|  |  |  |  |  |
|---|---|---|---|---|
| 6. | +$P_{50}$, +LA:SA | 0.53 | 0.37 | 23.57 |
| 7. | -$HSM_{50}$, +LA:SA | 0.50 | 0.33 | 24.03 |
| 8. | -$HSM_{50}$, +ΔLWP, +LA:SA, +Leaf area | 0.67 | 0.35 | 24.19 |
| 9. | +$P_{50}$, +LA:SA, +Leaf area | 0.58 | 0.33 | 24.51 |
| 10. | -$HSM_{50}$, +LA:SA, -Wood density, -Leaf thickness | 0.65 | 0.30 | 24.89 |

* we included sign of the coefficients in the models to indicate direction of covariation but for readability we report the values of the coefficients only in the supplementary materials.

**Table 2.** Models of tree height, coefficient of determination and their ranking according to the Akaike Information Criterion (AIC)

|  | Tree Height Model Predictors | Tree height (m) |  |  |
|---|---|---|---|---|
|  |  | $R^2$ | *Adjusted* $R^2$ | ΔAIC |
| 1. | -$P_{50}$, -Wood density, -ΔLWP, +Leaf thickness | 0.88 | 0.75 | 26.39 |
| 2. | -$P_{50}$, -Wood density, +Leaf area | 0.82 | 0.71 | 27.78 |
| 3. | -$P_{50}$, -Wood density, -LMA, -LA:SA | 0.84 | 0.69 | 28.61 |
| 4. | -$P_{50}$, -Wood density, -LA:SA | 0.80 | 0.68 | 28.65 |
| 5. | -$P_{50}$, -Wood density, -ΔLWP, +Leaf area | 0.83 | 0.66 | 29.19 |
| 6. | -$P_{50}$, -Wood density, -LMA | 0.78 | 0.65 | 29.59 |
| 7. | +$HSM_{50}$, -ΔLWP, -Wood density, +Leaf thickness | 0.79 | 0.59 | 31.03 |
| 8. | +$HSM_{50}$, -Wood density, -LMA, -LA:SA | 0.78 | 0.55 | 31.81 |
| 9. | +$HSM_{50}$, -ΔLWP, -Wood density, +Leaf area | 0.78 | 0.55 | 31.82 |
| 10. | +$HSM_{50}$, -Wood density, -LA:SA | 0.70 | 0.51 | 32.51 |

## 4. Discussion

### 4.1 Inter clonal trait variation and coordination

In general, the $P_{50}$ and $P_{88}$ values for *H. brasiliensis* clones investigated here are within the range of observed values for deciduous angiosperm species **(Scoffoni and Sack, 2017; Choat et al., 2012)**. Deciduous species such as *H. brasiliensis* tend to operate closer to the point of hydraulic failure than ever-green species as shown by **Choat et al., 2012** and **Markesteijn et al., 2011**.

Compared to other studies of *H. brasiliensis,* $P_{50}$ values measured at our site are generally more negative and the variation of $P_{50}$ across clones is comparably large. Various possibilities may explain these results but existing data are not sufficient to decide unambiguously which explanation is correct.

Firstly, it could reflect true genetically determined variation across clones with clones at our site characterised by comparably negative $P_{50}$'s. Secondly, the more negative $P_{50}$ could be an indication of acclimation as the clones we measured have been grown in comparably dry conditions. Unfortunately, there are no $P_{50}$ measurements at other sites of the clones grown at our site. Nonetheless some studies measured $P_{50}$'s on the same juvenile clones of RRIM 600 and RRIT 251 but grown in different climates in Bangkok and Nong Khai, Thailand **(Sangsing et al., 2004; Jinagool et al., 2015).** Bangkok which is located in the central of Thailand had a climate of Tropical Monsoon Climate while Nong Khai location in the north-eastern of Thailand experienced Tropical Savanna Climate. The $P_{50}$ at the drier study site (Nong Khai) was more negative compared to the wetter site (Bangkok) for both RRIM 600 and RRIT 251 **(Supplementary Table A.10)** consistent with this explanation.

Another explanation could be that $P_{50}$ varies with life stage and that different studies have measured rubber at different life stages (seedling and sapling stage versus adult trees). Saplings/ juveniles of the clone PB 260 had indeed a higher $P_{50}$ (less negative) compared to adult 260 **(Waite, 2020; Jinagool et al., 2015)**. Across rubber clones measured by the studies compiled in **Supplementary Table A.10** $P_{50}$ decreases with height which is closely related to age **(Figure 6)** consistent with this explanation ($R^2$= 0.28, $p$< 0.05 with estimation height values included and $R^2$= 0.18, $p$< 0.05 without the estimation height values included). This association is similar to the results of a study of tropical rainforest trees in Sulawesi, Indonesia **(Zach et al., 2010)**. However, it differs from the studies on Amazonian trees, *M. oleifera, C. edulis, P. ayacahuite* and Norway spruce trees, which find that $P_{50}$ increases with height **(e.g. Rowland et al. 2015; Olson et al. 2018; Prendin et al., 2018)**. Recently, **Bittencourt et al., 2020** suggested that changes in embolism resistance with tree size exist, but are highly dependent on tree taxonomic identity.

Lastly, the variability of $P_{50}$ may be influenced by methodological differences across studies. Ours is the first study to use the pneumatic method to determine embolism resistance in *H. brasiliensis* while other studies have used a range of other approaches **(Supplementary Table A.10)**. The $P_{50}$ values we report are of a similar magnitude to those determined using centrifugation methods **(e.g. Jinagool *et al.* 2015, Waite 2020)** and air-injection methods **(Jinagool *et al.* 2015)**. The least resistant $P_{50}$ values reported for *H. brasiliensis* are actually for bench dehydration approaches, but these were also for very young plants **(Supplementary Table A.10)** . We find no evidence in our compilation of data from across studies to support the assertion of **Sergent *et al.* (2020)** that the pneumatic method results in $P_{50}$ values that are less resistant than other methods for long-vessel species such as *H. brasiliensis*.

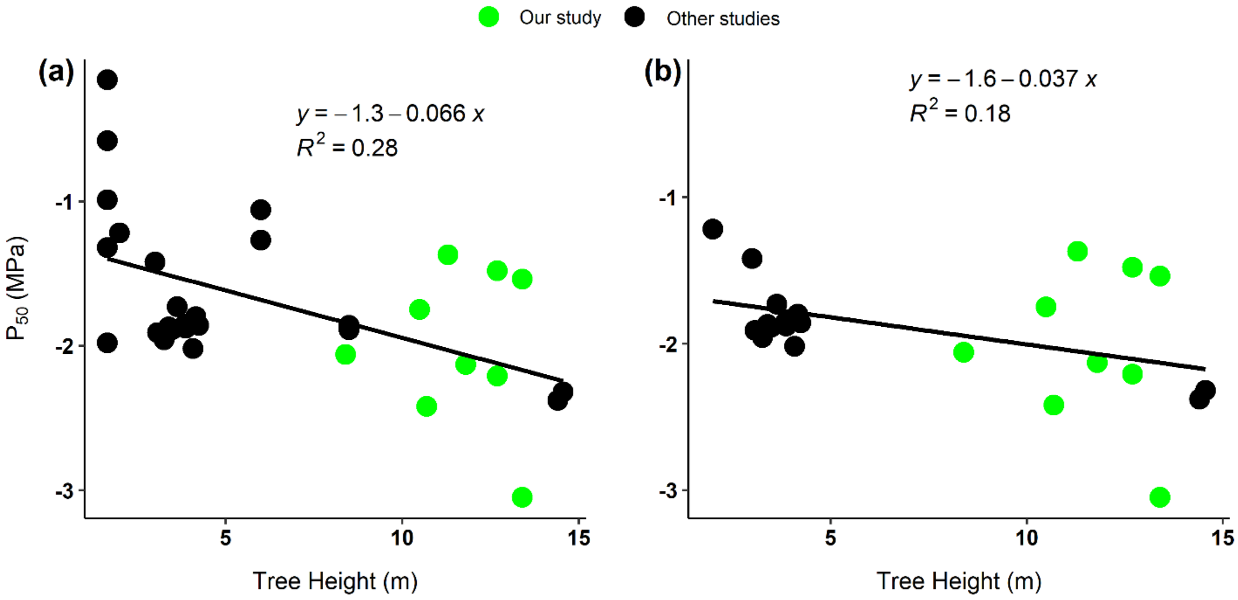


Figure 6 The relationship between $P_{50}$ and tree height (a) Included other study with estimation height based on provided tree age information or the range of tree height (b) Only data from other studies which provide with clear height information were included.

For most of the clones we studied there was a strong leaf water potential pre-dawn mid-day difference both during the dry and wet season **(Supplementary Table A.4)**. Thus at our site these clones function anisohydrically. In some studies, rubber has also been found to be anisohydric **(Chandrashekar et al., 1990; Kumagai et al., 2015; Wu and Chen, 2016)** while in other studies, mature rubber trees showed relative stability of midday leaf water potential on sunny days, i.e. isohydric behaviour (**Isarangkool Na Ayutthaya et al., 2011 and Liu et al., 2014).** The observed differences in water regulation may have several causes. They may arise because climate and soil characteristics differ, because different rubber clones were studied, or they may be an artefact of different experimental setup. For example, the Thailand and China study sites experience low annual rainfall and rubber is exposed to dry spells during the dry and wet season **(Isarangkool Na Ayutthaya et al., 2011 and Liu et al., 2014).** Both study sites use the same rubber clone (RRIM 600) and both find isohydric behaviour. In contrast, the same rubber clone was found to behave in an anisohydric manner at a tropical savanna climate study site in Thailand, where water availability was greater **(Kumagai et al, 2015; Kunjet et al., 2013)**. **Kumagai et al., 2015** indicated that the RRIC-100 rubber clone in Cambodia could alternate between isohydric behaviour in dry conditions and anisohydric behaviour during a moist period. With regards to inter-clonal variability, **Rao et al., 1990** found that different rubber clones have their own water use requirements and that water-regulation strategies can vary across clones.

We observed a significant linear relationship between the minimum measured leaf water potential ($P_{min}$) and $P_{50}$ for rubber clones, indicating a link between regulation of leaf water potential via stomatal control and embolism resistance. This result is consistent with **Choat et al.'s 2012** finding based on angiosperm and gymnosperm species data across forest biomes that embolism resistance is linked to maximum experienced drought stress.

In line with previous studies, (e.g. **Markesteijn et al. 2011, Christoffersen et al. 2016),** we found that vulnerability to cavitation ($P_{50}$) is negatively related to wood density, despite the range of wood density sampled in our study being much narrower than in other studies (wood density in our study ranged from 0.50 to 0.57 g cm$^{-3}$ compared to a range of 0.2 – 1.1 g cm$^{-3}$ in **Christoffersen et al. 2016**). Low wood density clones generally have higher growth rates than more densely-wooded clones **(Figure 5)** and this is aligned with lower resistance to embolism. Across tropical forest species, high growth has been shown to be underpinned by higher hydraulic conductivity at the expense of lower resistance to embolism **(Markesteijn et al. 2011)**. Our results suggest that such a trade-off between xylem safety and efficiency may also operate across genotypes of a species (although we did not measure xylem conductivity directly.

Our LMA values for all nine rubber clones fall within the range of 40–120 g m$^{-2}$ reported for global deciduous woody species functional groups **(Poorter et al., 2009)**. Rubber clones with high drought tolerance (low $P_{50}$) had low LMA and vice versa **(Figure 6)**. Our finding is in agreement with interspecies results for the genera Acer and Quercus by **Nardini et al.'s 2012**. They suggested that the $P_{50}$ and LMA correlation might be driven by vein density, as high vein density implies high carbon investment in venation and results in high LMA values. This is also supported by the results of **Blonder et al. 2011**.

## 4.2 Growth rate trait relationships

Even though planted in the same year, experiencing the same environmental condition and receiving the same plantation management treatment, each of nine rubber clone's growth pattern differed substantially. Growth rates varied between 1.17 mm month$^{-1}$ and 4.07 mm month$^{-1}$ **(Supplementary Table A.2)**. The trees height of the ten-year-old rubber also varied substantially between 8.4 m and 13.4 m.

The outcome of our multiple regression analysis aiming to identify the traits which best describe variation in stem growth is summarised in **Table 1** and **Supplementary Table A.11**. Most of the high-ranked growth models include tree hydraulic traits such as $HSM_{50}$,

$P_{50}$, ∆LWP (defined as (midday - predawn leaf water potential) measured during the wet season), leaf area to sapwood area ratio **(Table 1)**. The six best models all include $P_{50}$ and the next four best models $HSM_{50}$. Thus tree hydraulics is important in explaining inter-clonal rubber stem growth performance. The best model **(Equation 5)** specifically suggests that $\Delta LWP_{\text{wet season}}$, $HSM_{50}$, wood density and leaf thickness are important controls on stem growth.

Firstly ∆LWP ($\Delta LWP \equiv P_{\text{midday}} - P_{\text{predawn}}$ where P is leaf water potential measured during the wet season) is negatively related to growth and the larger the absolute value of ∆LWP the higher stem growth. A large absolute value of ∆LWP is indicative of large water transport during the day. Within species and across species large water transport is associated with large $CO_2$ gain **(e.g. Oliveira et al., 2021)**. Large water transport suggests non-conservative stomatal control permitting leaf water potential to reach large negative values possibly causing water potential in xylem reaching levels close to embolism resistance thresholds. Thus overall this first term is an indicator of conservative versus non-conservative water use during the growing season.

The second determinant is the hydraulic safety margin ($HSM_{50}$). The nine clones exhibited a broad range of hydraulic safety margins (ranging from close to -1.5 MPa to > 0). This corresponded to a large range of *in natura* dry season percentage conductivity loss, ranging from a 5.6% loss in RRIM 2007 to a 57.7% loss in RRIM 3001. High overall growth of stem diameter and tree height are associated with low dry season safety margins or i.e. operation at comparably high risk of embolism (less negative $P_{50}$) and vice versa. Thus this determinant indicates a hydraulic safety-growth trade-off. This is in line with results found for Poplar Hybrid species, for which fast-growing genotypes are more vulnerable to xylem embolism **(Zhang et al., 2020)**. The same trade-off has been observed at the species level **(Rowland et al., 2015; Eller et al., 2018; Liu et al., 2019)**. **Eller et al., 2018** suggested that the growth rate-HSM trade-off can be attributed to xylem vessels of fast-growing trees being less resistant to cavitation, and is thus in agreement with the findings of **Oliveira et al. (2021)**.

The third determinant identified by the model is wood density. High wood density is associated with low growth and vice versa. At the species level for tropical trees, a negative correlation between growth and wood density has been reported in several studies **(Enquist, 1999; Burslem and Whitmore, 2003; Muller-Landau, 2004; Martínez-Vilalta et al., 2010; Francis et al., 2017; Gray et al., 2019)**. According to **King et al. 2006** and **Eller et al. 2018** one factor contributing to this negative correlation is the costs of high density, structurally strong wood and embolism resistant vessels.

The final determinant is leaf thickness. Rubber leaves are covered by waxy cuticle and trichomes on the outer surface which help prevent the loss of water and its thickness varies among clones **(Martins and Zieri, 2003; MRB 2009; Kulshreshtha and Ahmed, 1993)**. We find that leaf thickness is also a significant control on growth as clones with thinner leaves have higher growth rates. This result is consistent with the results of **Poorter and Bongers (2006)** who analysed growth of 53 tropical rainforest species and its relation to a wide range of traits. It also had similar pattern with **Bai et al., 2020** results where they found negative association between relative growth rate and leaf thickness for the deciduous lianas. In contrast, they found opposite correlation for evergreen lianas suggesting that deciduous or evergreen lianas may employ some differentiated strategies to adapt to the cloud forest environment. Across species they found strong anti-correlations between tree growth rate and leaf life-span which tends to be correlated with leaf thickness **(Mediavilla et al., 2008)**, as well as a strong correlation between tree growth rate and specific leaf area, which is inversely related to leaf thickness. Furthermore, thicker leaves are more sturdy and store more water in a cell, contributing also to drought tolerance but can reduce the transpiration rate **(Wright et al., 2004; Poorter et al., 2009)**. This may reflect the negative relationship between leaf thickness and photosynthetic rates that has been observed in previous studies. However, we note that the strength of this relationship is weak and this may be an outcome of the poor coordination between leaf and wood traits **(Richardson et al., 2013; Wright et al., 2010)**.

Altogether we find substantial inter-clonal variation of hydraulic and morphological traits across rubber clones while trade-offs between growth and traits are similar across species.

A similar analysis for tree height **(Equation 6)** reveals that $P_{50}$ and wood density are strong predictors of tree height. Clones with comparably greater height are associated with strongly negative $P_{50}$ values and low wood density. Strongly negative $P_{50}$'s indicate high embolism resistance while low density wood is known to be associated with rapid growth at the species level (pioneers) **(Kiorapostolou et al., 2019; Fajardo, 2018; Trueba et al., 2017; Urli et al., 2013; Iida et al., 2012; King et al., 2005)**. Clones which grow taller will be exposed to increased water potential differences from canopy to soil. Strongly negative $P_{50}$ values will counteract this risk **(Falster and Westoby, 2003)** and this is indeed an attribute of the clones which grow rapidly in height.

### 4.3 Implications for future rubber cultivation

From an economic point of view, rubber clones best suited for planting in agro-climatically marginal areas are clones with a high stem growth rate and which are also drought tolerant (a high hydraulic safety margin). A median-quadrant analysis for growth and hydraulic safety margin thus summarizes suitability **(Figure 7a)**. Consistent with the results of the growth model analysis - and specifically the growth safety trade-off -most clones do not fulfil both criteria. The drought-tolerance clones with high vertical growth are RRIM 2007 and RRIM 2002 in Quadrant I **(Supplementary Figure A.5)**. Indeed, for the wood production, tree height and stem growth are both important and we found that only RRIM 2002 had higher than average for both characteristics **(Figure 7b)**. Nonetheless one clone deviates some from this main axis falling both into the quadrant with higher than average stem growth rate and higher than average hydraulic safety margin (RRIM 929).

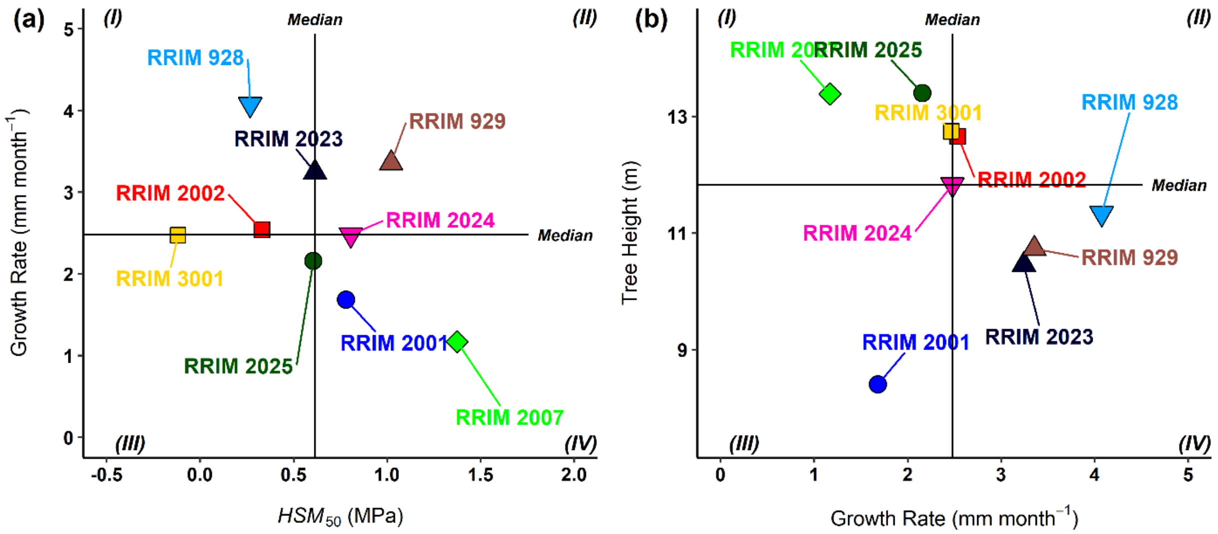


Figure 7 Quadrant panel diagram of (a) stem growth *vs* $HSM_{50}$ and (b) tree height *vs* stem growth. Both best selected clone located in Quadrant **II**.

4.4 Broader implications

Our results not only have implications for management of *H. brasiliensis* but also have broader ecological implications as they provide evidence to support recently proposed frameworks that link ecological strategies and plant hydraulic function **(Oliveira et al. 2021)**. Our work suggests that a growth-HSM trade-off operates not only at the species level but also across genetic variants of the same species. This trade-off has yet to be explicitly included into ecosystem modelling frameworks but could have important implications for simulations of how forest taxonomic composition may be affected by climate change.

## 5.0 Summary and Conclusions

We were interested in the vulnerability and growth-vulnerability trade-offs across rubber clones and how these relate to morphological traits in a climatically marginal area of Malaysia. To achieve this goal, we took advantage of clones planted in the same year, experiencing the same environmental condition and receiving the same plantation management treatment on which we studied growth trait relationships. Our results have implications for rubber management and also for broader understanding of the relationship between hydraulic properties and tree function. From a management perspective, we find that there is no clone with high growth and high hydraulic safety, although RRIM 929 appears most suited for planting in climatically marginal areas. More broadly, we find similar relationships between growth and hydraulic strategies exist between clones as observed within and across species, further supporting the generality of a growth-HSM trade-off by demonstrating that plants with higher growth rates take greater hydraulic risks (i.e. have lower safety margins).

## Acknowledgement

We want to heartily acknowledge the University of Leeds, the Malaysian Rubber Board, the Malaysian Department of Irrigation and Drainage, the Malaysian Meteorological Department, the Malaysian Agricultural Ministry and the Malaysian Ministry of Plantation Industries and Commodities for sharing their valuable data and expert collaboration. We appreciate the Sungai Sari Research Centre Manager, Mr Shaardan bin Shariff and all his staff for their valuable support. We heartily thank Mr Hadzlee bin Mat Noor and Mr Mohamad Amirulhisham bin Mohamad Akhir, contributing to the *in-situ* monthly data collection. Many thanks to Dr Julia Valentim Tavares and Mr Martin B Gilpin for their guidance on technical aspect in measuring branch xylem vulnerability to embolism. We very much appreciated positive comments and suggestions from the reviewers. This study was funded by the Malaysian Rubber Board (RMK11-P20110010620001), the University of Leeds (RSTG 95551730) and the Climate Research Bursary Fund (95535048).

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## Supplementary Materials

**Table A.1** List of rubber clones, parents and the total numbers of samples.

| Clones | Parents | Number of samples (trees) |
|---|---|---|
| **RRIM 2007** | GT 1 x PB 260 | 20 |
| **RRIM 2025** | IAN 873 x RRIM 803 | 20 |
| **RRIM 2001** | RRIM 600 x PB 260 | 20 |
| **RRIM 2024** | IAN 873 x PB 235 | 20 |
| **RRIM 929** | RRIM 605 x RRIM 725 | 20 |
| **RRIM 928** | RRIM 605 x RRIM 725 | 20 |
| **RRIM 2002** | PB 5/51 x FORD 351 | 20 |
| **RRIM 2023** | IAN 873 x PB 260 | 20 |
| **RRIM 3001** | IAN 873 x PB 235 | 20 |
| TOTAL | | **180** |

**Table A.2** Tree girth, height, bark thickness and growth rate variability of nine rubber clones. The different letter indicates a statistically significant difference ($p \leq 0.05$) among rubber clones by Tukey's test.

| Rubber clone | Tree girth in Aug 2019 (cm) Mean±SD | Tree height (m) Mean±SD | Bark thickness (mm) Mean±SD | Growth rate Sep 2019 - Aug 2020 (mm month$^{-1}$) |
|---|---|---|---|---|
| RRIM 2001 | $52.7\pm5.7^{a}$ | $8.4\pm1.4^{a}$ | $8.95\pm1.8^{abc}$ | $1.68\pm0.74^{bc}$ |
| RRIM 2002 | $60.6\pm6.5^{b}$ | $12.7\pm1.3^{cd}$ | $10.1\pm0.88^{bc}$ | $2.54\pm0.98^{bcd}$ |
| RRIM 2007 | $55.3\pm7^{ab}$ | $13.4\pm1.7^{d}$ | $8.85\pm0.82^{ab}$ | $1.17\pm0.45^{a}$ |
| RRIM 2023 | $60.4\pm6^{b}$ | $10.5\pm1.5^{b}$ | $10.2\pm0.92^{bc}$ | $3.26\pm1.53^{de}$ |
| RRIM 2024 | $69.5\pm11.7^{c}$ | $11.8\pm1.5^{bc}$ | $9.75\pm1.06^{abc}$ | $2.48\pm1^{bcd}$ |

| | | | | |
|---|---|---|---|---|
| RRIM 2025 | $61.1\pm6.1^{b}$ | $13.4\pm1.7^{d}$ | $8.35\pm0.53^{a}$ | $2.16\pm0.9^{abc}$ |
| RRIM 3001 | $59.4\pm8.6^{ab}$ | $12.7\pm1.5^{cd}$ | $9.7\pm1.64^{abc}$ | $2.47\pm0.99^{bcd}$ |
| RRIM 928 | $62.3\pm6.8^{bc}$ | $11.3\pm1.2^{bc}$ | $9.45\pm0.86^{abc}$ | $4.07\pm1.39^{e}$ |
| RRIM 929 | $62\pm6.2^{b}$ | $10.7\pm0.7^{b}$ | $10.45\pm0.76^{c}$ | $3.35\pm1.06^{cde}$ |

**Table A.3** Result of linear mixed-effect model between rainfall and growth rate. Rubber clones was added as random effect.

| | **Growth Rate (mm month$^{-1}$)** | | | | |
|---|---|---|---|---|---|
| *Predictors* | *Estimates* | *std. Beta* | *CI* | *standardised CI* | *p* |
| (Intercept) | -0.49 | 0 | -1.34 – 0.36 | -0.25 – 0.25 | 0.26 |
| Rainfall | 0.01 | 0.82 | 0.01 – 0.01 | 0.65 – 0.99 | **<0.001** |
| **Random Effects** | | | | | |
| $\sigma^2$ | 1.32 | | | | |
| $\tau_{00\ \text{Rubber clone}}$ | 0.45 | | | | |
| ICC | 0.25 | | | | |
| $N_{\text{Rubber clone}}$ | 9 | | | | |
| Observations | 36 | | | | |
| Marginal R$^2$ / Conditional R$^2$ | 0.661 / 0.747 | | | | |

**Table A.4** Hydraulic traits variability of nine rubber clones. The different letter indicates a statistically significant difference ($p \leq 0.05$) among rubber clones by Tukey's test

| Rubber clone | Predawn LWP (MPa) (Dry Season) Mean±SD | Midday LWP (MPa) (Dry Season) Mean±SD | Predawn LWP (MPa) (Wet Season) Mean±SD | Midday LWP (MPa) (Wet Season) Mean±SD | $P_{12}$ (MPa) Mean±SD | $P_{50}$ (MPa) Mean±SD | $P_{88}$ (MPa) Mean±SD |
|---|---|---|---|---|---|---|---|
| RRIM 2001 | -0.51±0.07$^{f}$ | -1.28±0.13$^{de}$f | -0.43±0.03$^{bc}$ | -0.97±0.05$^{b}$ | -1.21±0.14$^{a}$ | -2.06±0.25$^{ab}$ | -2.91±0.64$^{a}$ |
| RRIM 2002 | -0.58±0.07$^{ef}$ | -1.87±0.18$^{a}$ | -0.32±0.07$^{cd}$ | -1.24±0.03$^{a}$ | -1.24±0.19$^{a}$ | -2.21±0.37$^{ab}$ | -3.50±0.23$^{a}$ |
| RRIM 2007 | -1.27±0.05$^{a}$ | -1.68±0.10$^{ab}$ | -0.74±0.05$^{a}$ | -1.27±0.04$^{a}$ | -1.58±1.05$^{a}$ | -3.05±0.83$^{a}$ | -4.16±0.85$^{a}$ |
| RRIM 2023 | -0.79±0.06$^{bc}$ | -1.13±0.06$^{ef}$ | -0.51±0.21$^{b}$ | -0.84±0.08$^{c}$ | -0.75±0.07$^{a}$ | -1.75±0.1$^{ab}$ | -2.94±0.15$^{a}$ |
| RRIM 2024 | -0.70±0.08$^{cd}$ | -1.33±0.18$^{ef}$ | -0.32±0.04$^{cd}$ | -0.72±0.02$^{de}$ | -1.33±0.15$^{a}$ | -2.13±0.12$^{ab}$ | -2.93±0.15$^{a}$ |
| RRIM 2025 | -0.49±0.05$^{f}$ | -0.94±0.08$^{g}$ | -0.29±0.05$^{d}$ | -0.64±0.02$^{f}$ | -0.64±0.23$^{a}$ | -1.54±0.29$^{b}$ | -2.40±0.43$^{a}$ |
| RRIM 3001 | -0.82±0.06$^{b}$ | -1.6±0.15b$^{c}$ | -0.45±0.09$^{b}$ | -1.00±0.04$^{b}$ | -0.66±0.18$^{a}$ | -1.48±0.22$^{b}$ | -2.29±0.4$^{a}$ |
| RRIM 928 | -0.51±0.07$^{f}$ | -1.11±0.02f$^{g}$ | -0.30±0.1$^{d}$ | -0.66±0.03$^{ef}$ | -0.54±0.02$^{a}$ | -1.37±0.23$^{b}$ | -2.30±0.62$^{a}$ |
| RRIM 929 | -0.64±0.07$^{de}$ | -1.40±0.10$^{cd}$ | -0.45±0.09$^{b}$ | -0.79±0.02$^{cd}$ | -1.11±0.3$^{a}$ | -2.42±0.87$^{ab}$ | -3.78±1.71$^{a}$ |

| Rubber clone | $HSM_{50}$ Dry Season | $HSM_{88}$ Dry Season | $HSM_{50}$ Wet Season | $HSM_{88}$ Wet Season | LWP Deficit Wet Season | LWP Deficit Dry Season |
|---|---|---|---|---|---|---|
| RRIM 2001 | 0.82±0.25$^{ab}$ | 1.67±0.64$^{a}$ | 1.09±0.25$^{a}$ | 1.94±0.64$^{a}$ | -0.54 | -0.77 |
| RRIM 2002 | 0.33±0.37$^{ab}$ | 1.62±0.23$^{a}$ | 0.96±0.37$^{a}$ | 2.25±0.23$^{a}$ | -0.92 | -1.30 |
| RRIM 2007 | 1.37±0.83$^{b}$ | 2.48±0.85$^{a}$ | 1.78±0.83$^{a}$ | 2.89±0.85$^{a}$ | -0.53 | -0.41 |

| | | | | | | |
|---|---|---|---|---|---|---|
| RRIM 2023 | 0.86±0.10$^{ab}$ | 2.06±0.15$^{a}$ | 0.91±0.10$^{a}$ | 2.10±0.15$^{a}$ | -0.33 | -0.34 |
| RRIM 2024 | 0.81±0.12$^{ab}$ | 1.60±0.15$^{a}$ | 1.41±0.12$^{a}$ | 2.21±0.15$^{a}$ | -0.40 | -0.62 |
| RRIM 2025 | 0.61±0.29$^{ab}$ | 1.46±0.43$^{a}$ | 0.90±0.29$^{a}$ | 1.76±0.43$^{a}$ | -0.35 | -0.44 |
| RRIM 3001 | -0.12±0.22$^{a}$ | 0.69±0.40$^{a}$ | 0.48±0.22$^{a}$ | 1.29±0.40$^{a}$ | -0.55 | -0.78 |
| RRIM 928 | 0.27±0.23$^{ab}$ | 1.19±0.62$^{a}$ | 0.72±0.23a | 1.64±0.62$^{a}$ | -0.36 | -0.60 |
| RRIM 929 | 1.02±0.87$^{ab}$ | 2.38±1.71$^{a}$ | 1.64±0.87$^{a}$ | 2.99±1.71$^{a}$ | -0.33 | -0.76 |

**Table A.5** Pearson correlation coefficients for linear relationships among hydraulic traits of nine studied rubber clones

| | $HSM_{50}$ (MPa) | $HSM_{88}$ (MPa) | $P_{50}$ (MPa) | $P_{88}$ (MPa) |
|---|---|---|---|---|
| $HSM_{88}$ (MPa) | **0.926**$^{**}$ | | | |
| $P_{50}$ (MPa) | **-0.826**$^{**}$ | **-0.851**$^{**}$ | | |
| $P_{88}$ (MPa) | **-0.765**$^{*}$ | **-0.896**$^{**}$ | **0.957**$^{**}$ | |
| Midday LWP in the dry season (MPa) | -0.007 | -0.160 | 0.569 | 0.582 |
| Midday LWP in the wet season (MPa) | -0.156 | -0.269 | 0.621 | 0.616 |
| Predawn LWP in the dry season (MPa) | -0.460 | -0.435 | **0.637**$^{*}$ | 0.565 |
| Predawn LWP in the wet season (MPa) | -0.580 | -0.580 | **0.680**$^{*}$ | 0.640 |

**. Correlation is significant at the 0.01 level (2-tailed).

*. Correlation is significant at the 0.05 level (2-tailed).

**Table A.6** Tree traits variability of nine studied rubber clones. The different letter indicates a statistically significant difference ($p \leq 0.05$) among rubber clones by Tukey's test.

| Rubber clone | Total number of leaves | Leaf area (cm$^2$) Mean±SD | Leaf thickness (mm) Mean±SD | LMA (g m$^{-2}$) Mean±SD | LDMC (mg g$^{-1}$) Mean±SD | Leaf density (g cm$^{-3}$) Mean±SD | $L_A$ (cm$^2$): $S_A$ (cm$^2$) ($H_v$) |
|---|---|---|---|---|---|---|---|
| RRIM 2001 | 53 | 26.1±5.1$^{a}$ | 0.19±0.03$^{b}$ | 105.11±11.74$^{d}$ | 489.27±20.61$^{g}$ | 0.56±0.1$^{c}$ | 44.74 |
| RRIM 2002 | 62 | 42.8±10.6$^{bc}$ | 0.23±0.04$^{c}$ | 91.29±9.37$^{c}$ | 446.8±10.28$^{e}$ | 0.41±1.3$^{b}$ | 71.51 |
| RRIM 2007 | 54 | 43.7±11.3$^{bc}$ | 0.25±0.04$^{e}$ | 71.73±8.64$^{a}$ | 414.05±24.71$^{c}$ | 0.29±1.7$^{a}$ | 101.37 |
| RRIM 2023 | 44 | 37.1±12.9$^{b}$ | 0.24±0.06$^{d}$ | 69.82±7.65$^{a}$ | 401.81±25.36$^{b}$ | 0.3±1.5$^{a}$ | 62.44 |
| RRIM 2024 | 61 | 69.4±20.3$^{e}$ | 0.27±0.04$^{f}$ | 74.20±4.51$^{ab}$ | 383±15.25$^{a}$ | 0.28±1.5$^{a}$ | 121.38 |
| RRIM 2025 | 54 | 52.1±13.9$^{cd}$ | 0.3±0.04$^{h}$ | 93.68±14.65$^{c}$ | 449.33±20.59$^{e}$ | 0.32±1.7$^{a}$ | 104.91 |
| RRIM 3001 | 60 | 70.5±26.7$^{e}$ | 0.28±0.04$^{g}$ | 83.38±15.5$^{b}$ | 415.24±19.08$^{c}$ | 0.3±1.5$^{a}$ | 126.86 |
| RRIM 928 | 54 | 61.6±21.2d$^{e}$ | 0.24±0.04$^{d}$ | 93.09±4.91$^{c}$ | 469.29±9.84$^{f}$ | 0.41±1.2$^{b}$ | 294.21 |
| RRIM 929 | 52 | 41.1±12.6$^{b}$ | 0.17±0.03$^{a}$ | 86.33±16.62$^{b}$ | 434.17±10.68$^{d}$ | 0.5±0.7$^{c}$ | 129.91 |

| Rubber clone | Total number of wood cores | Wood density (g cm$^{-3}$) Mean±SD |
|---|---|---|
| RRIM 2001 | 10 | 0.57±0.02$^{d}$ |
| RRIM 2002 | 10 | 0.52±0.03$^{ab}$ |
| RRIM 2007 | 10 | 0.53±0.02$^{bc}$ |

|  |  |  |
|---|---|---|
| RRIM 2023 | 10 | $0.54\pm0.02^{bc}$ |
| RRIM 2024 | 10 | $0.53\pm0.04^{abc}$ |
| RRIM 2025 | 10 | $0.50\pm0.02^{a}$ |
| RRIM 3001 | 10 | $0.53\pm0.02^{abc}$ |
| RRIM 928 | 10 | $0.50\pm0.02^{a}$ |
| RRIM 929 | 10 | $0.55\pm0.01^{cd}$ |

**Table A.7** Comparison traits relationship results using all nine clones, removed RRIM 2024, removed RRIM 2002 or both using York's regression.

| **Traits** |  | **Relationship, $R^2$** |  |  |  |
|---|---|---|---|---|---|
| **x** | **y** | **Original with all 9 clones** | **Removed RRIM 2024 and RRIM 2002** | **Removed only RRIM 2024** | **Removed only RRIM 2002** |
| $P_{50}$ | Growth rate | 0.30 | 0.31 | 0.30 | 0.31 |
| $P_{min}$ | Growth rate | 0.12 | 0.18 | 0.12 | 0.19 |
| $HSM_{50}$ | Growth rate | 0.19 | 0.20 | 0.19 | 0.20 |
| La:Sa | Growth rate | 0.41 | 0.43 | 0.41 | 0.43 |
| Wood density | Growth rate | 0.08 | 0.09 | 0.08 | 0.09 |
| Leaf density | Growth rate | 0.02 | 0.02 | 0.01 | 0.02 |
| Wood density | Tree height | 0.52 | 0.51 | 0.52 | 0.51 |
| Leaf density | Tree height | 0.50 | 0.63 | 0.55 | 0.59 |

| | | | | | |
|---|---|---|---|---|---|
| Wood density | P$_{50}$ | 0.20 | 0.25 | 0.21 | 0.24 |
| LMA | P$_{50}$ | 0.10 | 0.13 | 0.10 | 0.14 |

**Table A.8:** Pearson's correlation between growth rate and tree traits

| | Wood density (g cm$^{-3}$) | Leaf density (g cm$^{-3}$) | Leaf thickness (mm) | Leaf Area (cm$^{2}$) | LMA (g cm$^{-2}$) | LDMC (mg g$^{-1}$) |
|---|---|---|---|---|---|---|
| Growth rate (mm month$^{-1}$) | -0.288 | 0.129 | -0.213 | 0.279 | -0.021 | 0.043 |
| Tree height (m) | **-0.723*** | **-0.712*** | **0.726*** | 0.404 | -0.377 | -0.403 |

**. Correlation is significant at the 0.01 level (2-tailed).

*. Correlation is significant at the 0.05 level (2-tailed).

**Table A.9** Pearson correlation coefficients for linear relationships between hydraulic traits and tree traits of nine studied rubber clones

| | Leaf thickness (mm) | Leaf Area (cm$^{2}$) | LMA (g cm$^{-2}$) | LDMC (mg g$^{-1}$) | Leaf density (g cm$^{-3}$) | Wood density (g cm$^{-3}$) |
|---|---|---|---|---|---|---|
| HSM$_{50}$ (Mpa) | -0.325 | **-0.692**$^{*}$ | -0.238 | -0.151 | 0.090 | 0.415 |
| HSM$_{88}$ (Mpa) | -0.491 | **-0.811**$^{**}$ | -0.285 | -0.145 | 0.166 | 0.414 |
| P$_{50}$ (Mpa) | 0.370 | **0.653*** | 0.323 | 0.229 | -0.070 | -0.450 |
| P$_{88}$ (Mpa) | 0.487 | **0.735**$^{*}$ | 0.337 | 0.203 | -0.134 | -0.428 |

|  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|
| Midday LWP in the dry season | 0.184 | 0.149 | 0.227 | 0.186 | 0.007 | -0.194 |
| Midday wet season | 0.162 | 0.392 | 0.139 | 0.036 | 0.002 | -0.265 |
| Predawn LWP in the dry season | -0.191 | 0.113 | **0.760**$^*$ | 0.589 | 0.537 | -0.123 |
| Predawn LWP in the wet season | 0.132 | 0.424 | 0.552 | 0.304 | 0.185 | -0.417 |
| La:Sa | 0.076 | 0.467 | 0.119 | 0.245 | 0.024 | -0.551 |

**. Correlation is significant at the 0.01 level (2-tailed).

*. Correlation is significant at the 0.05 level (2-tailed).

**Table A.10** *H. Brasiliensis* inter-clonal variation of $P_{50}$

|  | Study site | Climate information | Methods to assess embolism resistance | Rubber Clone | Tree height/ DBH/ Age | *N* | $P_{50}$ (SE) | Reference |
|---|---|---|---|---|---|---|---|---|
| 1. | Nursery, Kasetsart University, Bangkok, | Using pot for drought treatment | Air pressure dehydration technique | RRIM 600 | 1.5 years, 2 m | - | -1.22 | Sangsing et al., 2004 |

|  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|
|  | Thailand |  |  |  |  |  |  |  |
| 2. | Nursery, Kasetsart University, Bangkok, Thailand | Using pot for drought treatment | Air pressure dehydration technique | RRIT 251 | 1.5 years, 3 m | - | -1.42 | Sangsing et al., 2004 |
| 3. | Xishuangbanna Tropical Botanical Garden, south-western Yunnan, China | 1,560 mm yr$^{-1}$ and dry season of five to six months | Bench drying method | Unknown | 5–7 m, DBH 15–20 cm | 3-5 | -1.27 | Chen et al., 2009a |
| 4. | Xishuangbanna Tropical Botanical Garden, south- | 1,560 mm yr$^{-1}$ and dry season of five to six months | Bench drying method | Unknown | 5–7 m height, DBH 15–20 cm | 3-5 | -1.06 | Chen et al., 2009b |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | western Yunnan, China | | | | | | | |
| 5. | Rubber Research Institute of the Chinese Academy of Tropical Agricultural Sciences. Danzhou, Hai8.nan, China | 1,566 mm yr$^{-1}$, dry season of four to five months | Air pressure dehydration technique | GT1 | 1-year-old | - | -0.58 | Weifu & Qiubo, 2011 |
| | | | | Reyan 7-33-97 | 1-year-old | | -1.98 | |
| | | | | PR107 | 1-year-old | | -0.99 | |
| | | | | Renken 525 | 1-year-old | | -1.32 | |
| | | | | Reken 523 | 1-year-old | | -0.16 | |
| 6. | Nong Khai, northeastern region of Thailand | 1,600 mm yr$^{-1}$, dry season of five to six months | Cavitron | BPM 24 | 3.86 m | 3 | -1.85 (0.04) | Jinagool et al., 2015 |
| | | | | PB 217 | 3.07 m | 3 | -1.91 (0.04) | |
| | | | | PB 235 | 3.87 m | 3 | -1.88 (0.07) | |
| | | | | PB 260 | 3.26 m | 3 | -1.96 (0.08) | |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | PB 5/51 | 3.39 m | 3 | -1.87 (0.05) | |
| | | | | RRII 105 | 4.08 m | 3 | -2.02 (0.11) | |
| | | | | RRII 118 | 3.49 m | 3 | -1.89 (0.15) | |
| | | | | RRIM 600 | 4.24 m | 3 | -1.86 (0.06) | |
| | | | | RRIT 251 | 4.16 m | 3 | -1.80 (0.12) | |
| | | | | RRIT 408 | 3.63 m | 3 | -1.73 (0.14) | |
| 7. | Xishuangbanna Tropical Botanical Garden, south-western Yunnan, China | 1,560 mm $yr^{-1}$ and dry season of five to six months | Bench drying method | Unknown | 5–7 m, 15–20 cm DBH | 3-5 | -1.06 | Chen & Cao, 2015 |
| 8. | Surat Thani, southern region of Thailand | 1,800 mm $yr^{-1}$ rainfall and dry conditions of | Cavitron | Mix of PB 235, RRIM 600 and RRIT 251 | 7-10 years | 5 | -1.86 (0.05) | Jinagool et al., 2015 |

|  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|
|  |  | only one to two months per year |  |  |  |  |  |  |
| 9. | Surat Thani, southern region of Thailand | 1,800 mm $yr^{-1}$ rainfall and dry conditions of only one to two months per year | Air-injection | Mix of PB 235, RRIM 600 and RRIT 251 | 7-10 years | 4 | -1.89 (0.15) | Jinagool et al., 2015 |
| 10. | Jambi province in Sumatra, Indonesia | 2,235 mm $yr^{-1}$, dry conditions of only one to two months per year (Well drained) | Modified centrifuge flow technique | PB260 | 14.56 m, 23.24 cm DBH | 17 | -2.32 | Waite, 2020 |
| 11. | Jambi province in Sumatra, Indonesia | 2,235 mm $yr^{-1}$, dry conditions of only one to two months per year (Riparian) | Modified centrifuge flow technique | PB260 | 14.41 m, 16.07 cm DBH | 18 | -2.38 | Waite, 2020 |

|  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|
| 12. | Rubber Research Institute of Malaysia, northwestern region of Malaysia | 1,427 mm yr$^{-1}$, dry spell of three to four months | Recently-developed pneumatic method | RRIM 2001 | 8.4 m | 3 | -2.06(0.18) | Our study |
|  |  |  |  | RRIM 2002 | 12.7 m | 3 | -2.21(0.21) |  |
|  |  |  |  | RRIM 2007 | 13.4 m | 4 | -3.05(0.41) |  |
|  |  |  |  | RRIM 2023 | 10.5 m | 3 | -1.75(0.06) |  |
|  |  |  |  | RRIM 2024 | 11.8 m | 3 | -2.13(0.07) |  |
|  |  |  |  | RRIM 2025 | 13.4 m | 4 | -1.54(0.14) |  |
|  |  |  |  | RRIM 3001 | 12.7 m | 4 | -1.48(0.11) |  |
|  |  |  |  | RRIM 928 | 11.3 m | 3 | -1.37(0.13) |  |
|  |  |  |  | RRIM 929 | 10.7 m | 3 | -2.42(0.50) |  |

**Table A.11** Growth Model Summary

| | Growth Model | Stem growth (mm month$^{-1}$) | | | Tree height (m) | | |
|---|---|---|---|---|---|---|---|
| | | $R^2$ | Adjusted $R^2$ | ΔAIC | $R^2$ | Adjusted $R^2$ | ΔAIC |
| **1.** | $HSM_{50}$, LWP deficit, Wood density, Leaf thickness | 0.86 | 0.73 | 16.39 | 0.79 | 0.59 | 31.03 |
| **2.** | $P_{50}$, LWP deficit, Wood density, Leaf thickness | 0.77 | 0.55 | 20.89 | 0.88 | 0.75 | 26.39 |
| **3.** | $HSM_{50}$, LA:SA, Wood density, Leaf thickness | 0.65 | 0.30 | 24.89 | 0.72 | 0.45 | 33.69 |
| **4.** | LWP deficit, Wood density, Leaf thickness, Leaf area | 0.81 | 0.63 | 19.12 | 0.71 | 0.43 | 34.00 |
| **5.** | Wood density, Leaf thickness, Leaf area | 0.69 | 0.50 | 21.76 | 0.66 | 0.45 | 33.56 |
| **6.** | $HSM_{50}$, LWP deficit, LA:SA, Leaf area | 0.67 | 0.35 | 24.19 | 0.45 | -0.09 | 39.81 |
| **7.** | $HSM_{50}$, LA:SA, Leaf area | 0.56 | 0.29 | 24.97 | 0.24 | -0.21 | 40.75 |
| **8.** | $HSM_{50}$, LA:SA | 0.50 | 0.33 | 24.03 | 0.01 | -0.32 | 41.13 |
| **9.** | LA:SA | 0.45 | 0.37 | 22.86 | 0.01 | -0.14 | 39.18 |
| **10.** | $P_{50}$, LWP deficit, LA:SA, Leaf area | 0.58 | 0.17 | 26.40 | 0.42 | -0.17 | 40.42 |
| **11.** | $P_{50}$, LA:SA, Leaf area | 0.58 | 0.33 | 24.51 | 0.38 | 0.00 | 38.98 |
| **12.** | $P_{50}$, LA:SA | 0.53 | 0.37 | 23.57 | 0.03 | -0.30 | 41.00 |
| **13.** | $HSM_{50}$, LWP deficit, Wood density, Leaf area | 0.53 | 0.07 | 27.40 | 0.78 | 0.55 | 31.82 |
| **14.** | $P_{50}$, LWP deficit, Wood density, Leaf area | 0.38 | -0.24 | 29.99 | 0.83 | 0.66 | 29.19 |
| **15.** | $HSM_{50}$, Wood density, Leaf area | 0.21 | -0.27 | 30.17 | 0.60 | 0.36 | 34.98 |
| **16.** | $P_{50}$, Wood density, Leaf area | 0.32 | -0.08 | 28.77 | 0.82 | 0.71 | 27.78 |
| **17.** | $HSM_{50}$, Wood density, LA:SA | 0.53 | 0.25 | 25.48 | 0.70 | 0.51 | 32.51 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| **18.** | $P_{50}$, Wood density, LA:SA | 0.56 | 0.29 | 24.93 | 0.80 | 0.68 | 28.65 |
| **19.** | $P_{50}$, Wood density, LMA | 0.35 | -0.04 | 28.43 | 0.78 | 0.65 | 29.59 |
| **20.** | $HSM_{50}$, Wood density, LMA | 0.21 | -0.26 | 30.11 | 0.68 | 0.48 | 33.12 |
| **21.** | $P_{50}$, Wood density, LMA, LA:SA | 0.61 | 0.22 | 25.76 | 0.84 | 0.69 | 28.61 |
| **22.** | $HSM_{50}$, Wood density, LMA, LA:SA | 0.56 | 0.13 | 26.81 | 0.78 | 0.55 | 31.81 |

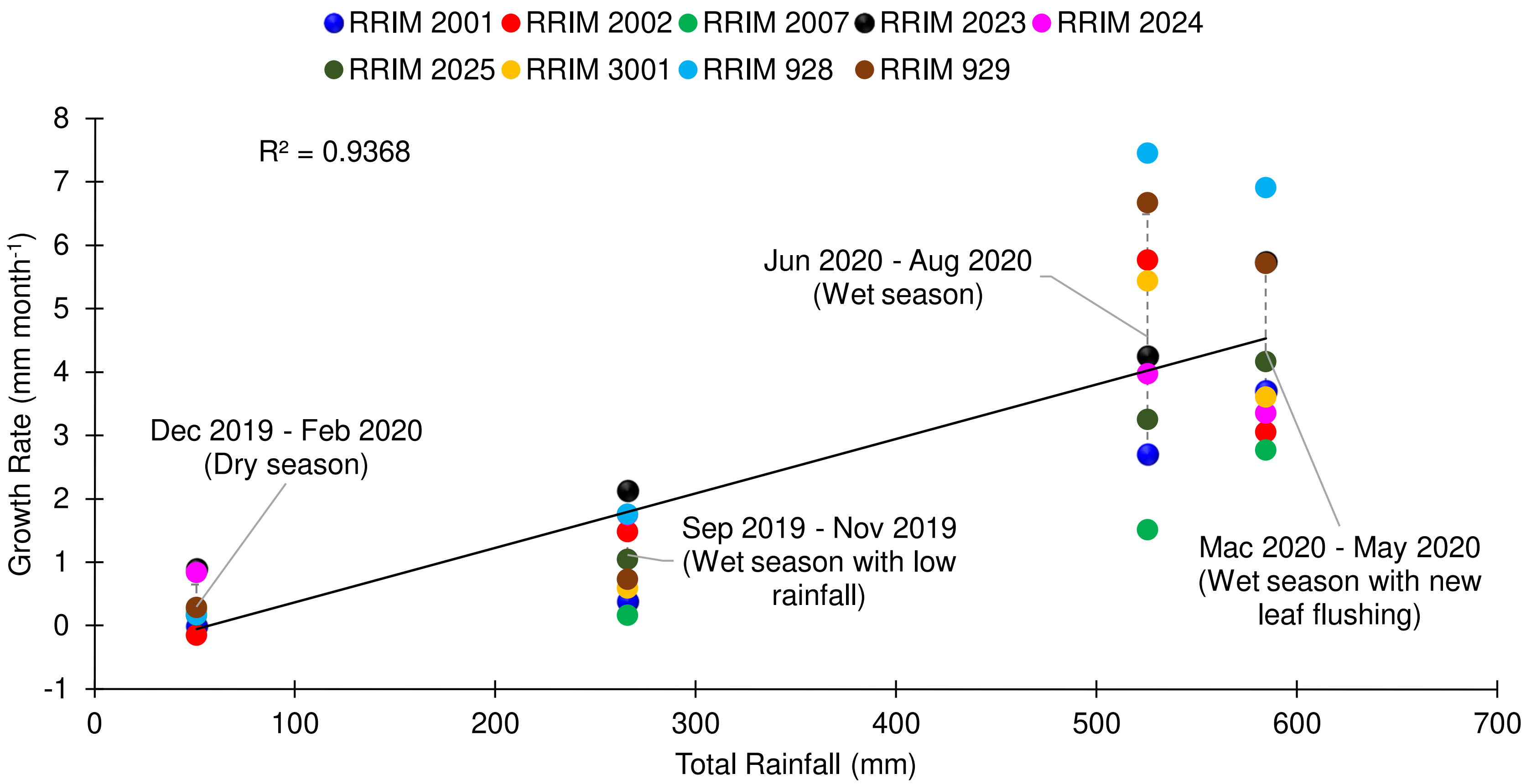

**Figure A.1** Variability of rubber clone's growth rate coupled with climate data based on 3-months interval

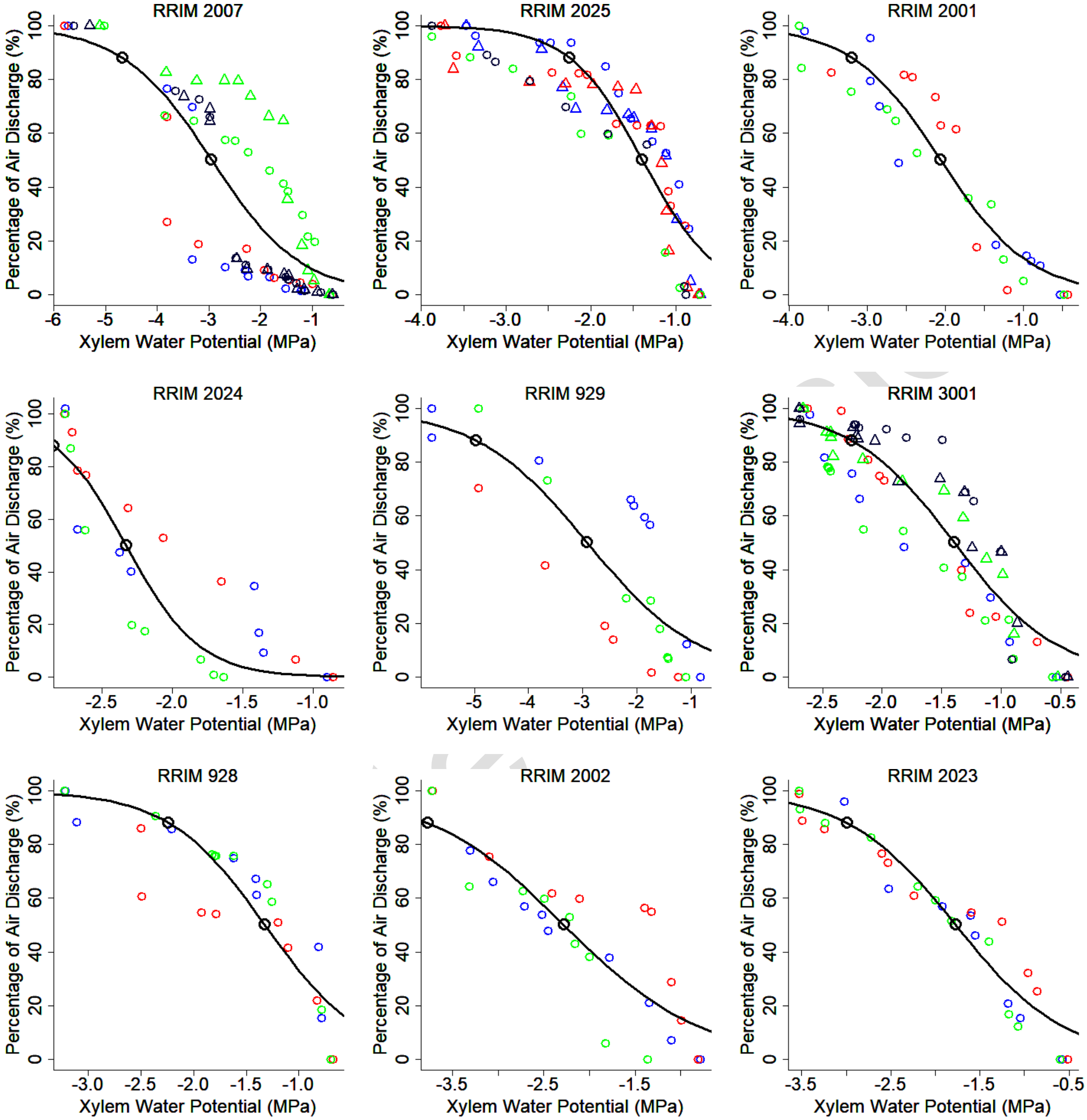

**Figure A.2** Xylem vulnerability curves for nine rubber clones. Different colours represent different individuals while different symbol with the same colour indicates replicate from the same individual. Black open circles show the xylem water potential on which 50% and 88% of the conductance is lost (*$P_{50}$* and *$P_{88}$*).

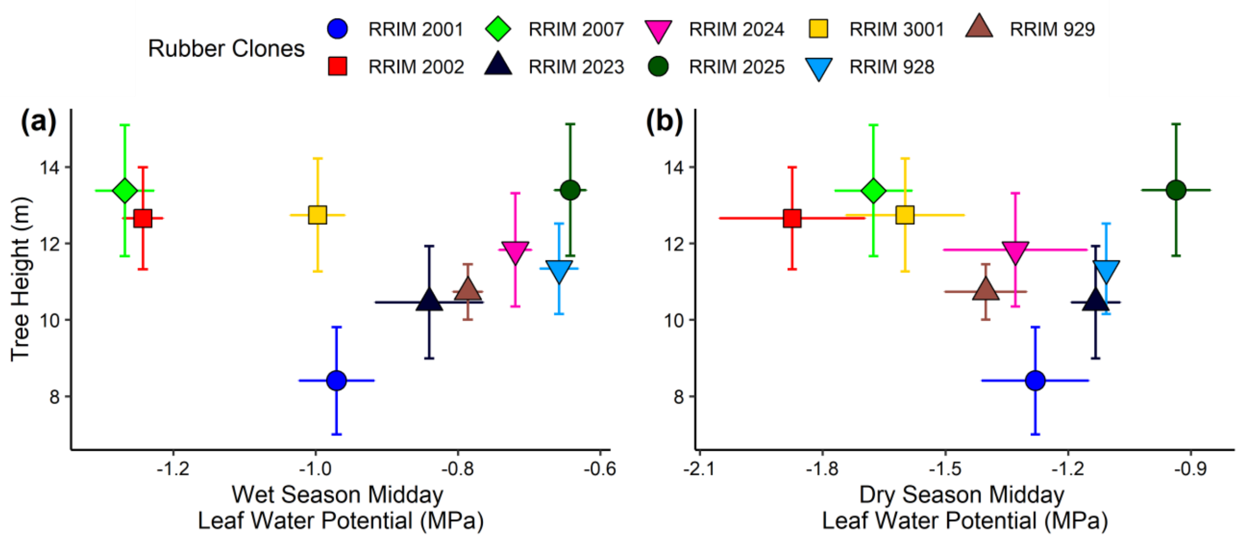

**Figure A.3** No relationship between rubber growth and midday leaf water potential (mean±se): a) Tree height *vs* wet season midday leaf water potential b) Tree height *vs* dry season midday leaf water potential.

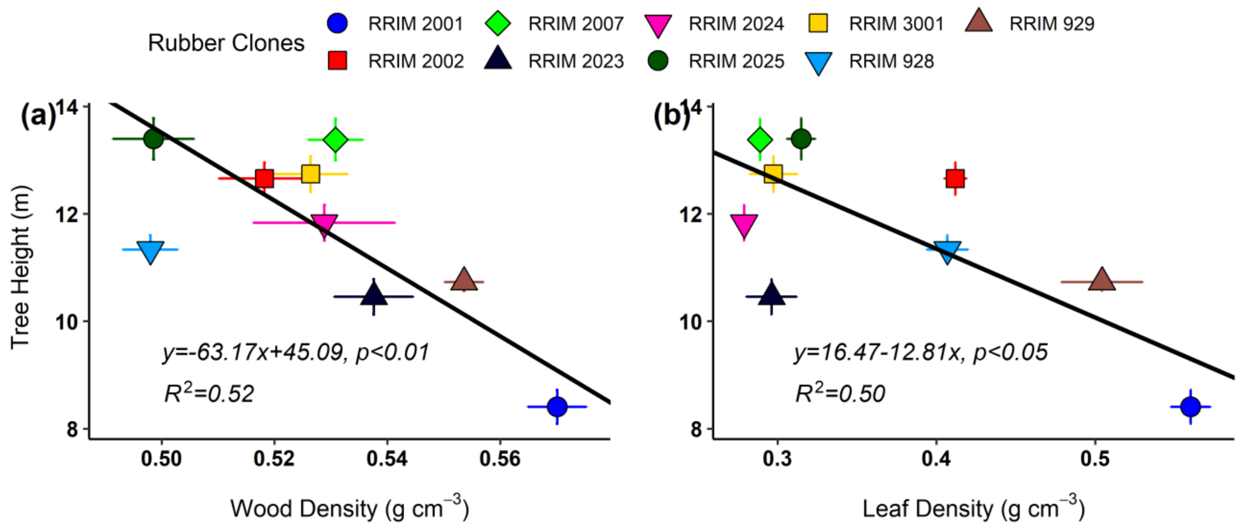

**Figure A.4** Relationship between rubber growth and other traits (mean±se): a) Tree height *vs* wood density b) Tree height *vs* leaf density. Solid black lines depict the best-fit slopes from York's regression.

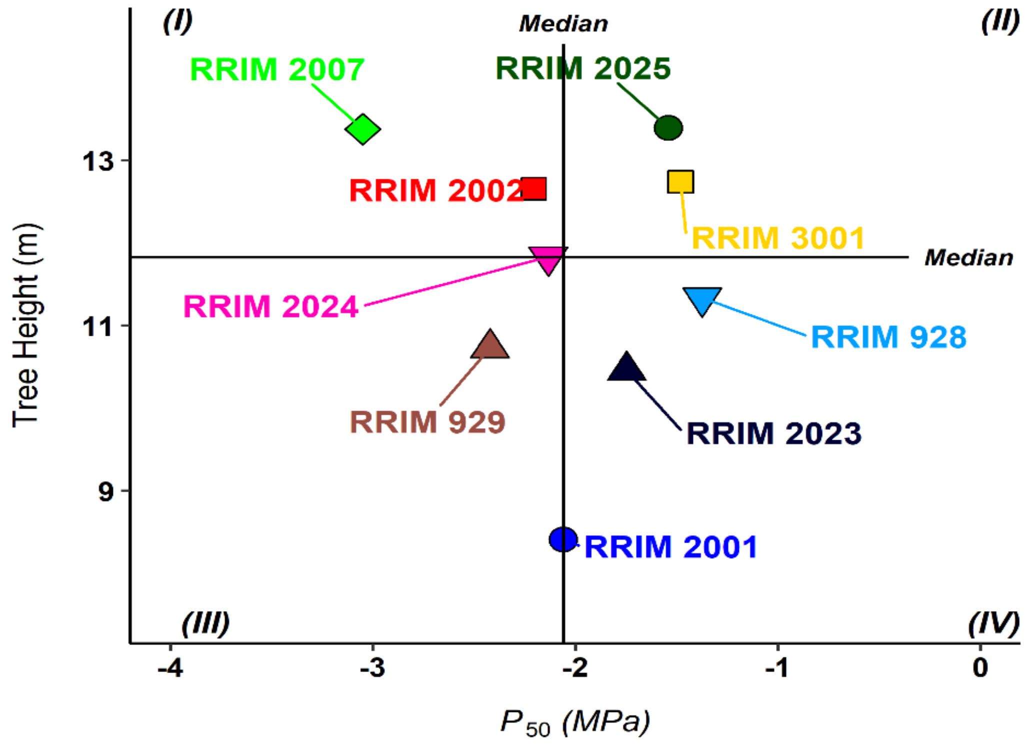

**Figure A.5** Quadrant panel diagram between tree height and $P_{50}$. The drought-tolerance clones with high vertical growth located in Quadrant I

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