

RESEARCH PAPER

Local hydrological gradients structure high intraspecific variability in plant hydraulic traits in two dominant central Amazonian tree species

Maquella N. Garcia^{1, }, Jia Hu², Tomas F. Domingues³, Peter Groenendijk⁴, Rafael S. Oliveira⁴, and Flávia R. C. Costa^{5,*}

¹ Tropical Forest Science Program, National Institute of Amazon Researches, Manaus, AM, Brazil

² School of Natural Resources and the Environment, University of Arizona, Tucson, AZ, USA

³ Department of Biology, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto, SP, Brazil

⁴ Department of Plant Biology, Institute of Biology, P.O. Box: 6109, University of Campinas – UNICAMP, 13083-970, Campinas, SP, Brazil

⁵ Coordenação de Pesquisas em Biodiversidade, Instituto Nacional de Pesquisas da Amazônia, Caixa Postal 2223, CEP 69008-971, Manaus, AM, Brazil

* Correspondence: flavia.costa@inpa.gov.br

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Abstract

Addressing the intraspecific variability of functional traits helps understand how climate change might influence the distribution of organismal traits across environments, but this is notably understudied in the Amazon, especially for plant hydraulic traits commonly used to project drought responses. We quantified the intraspecific trait variability of leaf mass per area, wood density, and xylem embolism resistance for two dominant central Amazonian tree species, along gradients of water and light availability, while accounting for tree age and height. Intraspecific variability in hydraulic traits was high, with within-species variability comparable to the whole-community variation. Hydraulic trait variation was modulated mostly by the hydrological environment, with higher embolism resistance of trees growing on deep-water-table plateaus compared with shallow-water-table valleys. Intraspecific variability of leaf mass per area and wood density was mostly modulated by intrinsic factors and light. The different environmental and intrinsic drivers of variation among and within individuals lead to an uncoupled coordination among carbon acquisition/conservation and water-use traits. Our findings suggest multivariate ecological strategies driving tropical tree distributions even within species, and reflect differential within-population sensitivities along environmental gradients. Therefore, intraspecific trait variability must be considered for accurate predictions of the responses of tropical forests to climate change.

Keywords: Central Amazon, environmental gradients, hydraulic, hydrological environment, light environment, niche partitioning, tree rings, wood traits.

Introduction

The Amazon is renowned for containing the world's largest rainforest, which exhibits exceptional species diversity (Cardoso *et al.*, 2017; Ter Steege *et al.*, 2020) and high functional diversity (Asner *et al.*, 2014). Functional traits can link ecophysiology to community via trade-offs that define life-history strategies and performance, thus influencing population demographic rates (Poorter *et al.*, 2018; Schmitt *et al.*, 2020; Westerland *et al.*, 2021). This high trait diversity arises from a combination of genetic variation and phenotypic plasticity, and results in adaptations to a range of environmental conditions across space and time. However, the functional variability of plants has been frequently collapsed at the species level by using mean values, thus ignoring intraspecific trait variability (ITV). There is evidence that ITV is the effective level when making predictions about plant community assembly and ecosystem functioning (Violle *et al.*, 2012; Siefert *et al.*, 2015), improving predictions of vegetation responses to environmental change. This is particularly the case when we move from global to more regional scales (Siefert *et al.*, 2015; Pritzkow *et al.*, 2020) and from organ-level traits to integrative traits involving whole-tree responses (Maseda and Fernández, 2006), as the latter tend to be more sensitive to the environment and show higher ITV as a result of local genetic adaptation and phenotypic plasticity.

Tropical forests have high heterogeneity of plant-relevant environmental factors, such as light, water availability and soil nutrients, even at local scales (Oliveira *et al.*, 2021). This heterogeneity can lead to multiple strategies and trait adjustments to deal with changing conditions along ontogeny and across the landscape. In addition to variation due to local genetic adaptation and plastic phenotypic adjustment to environmental variation, functional traits can vary in response to intrinsic factors, such as plant size or age (Domec *et al.*, 2005; Santiago *et al.*, 2018; Skelton *et al.*, 2019). However, few studies have tried to tease apart the intrinsic and environmental influences on plant functional traits in tropical forests. Theoretically, environmental selection is expected to be a stronger driver of the phenotype of traits that are more integrative than of organ-level traits (Marks and Lechowicz, 2006a, b; Dias *et al.*, 2020).

Previous studies show that hydraulic traits can vary among species along global-scale climatic gradients, and across local-scale soil hydrological gradients (Cosme *et al.*, 2017; Oliveira *et al.*, 2019; Fontes *et al.*, 2020). Valley-growing species with close proximity to groundwater tend to be more vulnerable to embolism (i.e. they have a less negative P_{50} , the water potential at which 50% of conductivity is lost) than trees growing on plateaus. In addition, there is evidence demonstrating that hydraulic traits can change with tree size, depending on taxonomic identity (Bittencourt *et al.*, 2020). However, it is unknown whether such differences only occur primarily at the interspecific level and higher-order taxonomic ranks, or whether variation can also be high at the within-species level. Unlike hydraulic traits, leaf mass per area (LMA) among species

tends to respond to tree height following the light gradient and nutrient availability (Domingues *et al.*, 2005; Cavaleri *et al.*, 2010; Kenzo *et al.*, 2015). At the local scale, high light levels can usually induce interspecific variability in LMA by the development of thicker mesophyll layers in leaves, resulting in higher LMA in top-canopy leaves (Coble and Cavaleri, 2014; Kenzo *et al.*, 2015). Conversely, shade-tolerant tree species confined to the understory are expected to have low LMA, as investments in larger leaf areas improve light interception. Thus, along the vertical profile of the forest, the gradient of light availability can be expected to induce high ITV in LMA (Rosas *et al.*, 2019), but primarily in species that grow across a range of light intensities. Another important functional trait, wood density (WD), is also sensitive to both extrinsic and intrinsic factors, and at local scales, WD can vary within species (Cosme *et al.*, 2017; Rosas *et al.*, 2019). WD is generally positively related to resistance to hydraulic failure and survival (Hacke *et al.*, 2001; Maherali *et al.*, 2004), but negatively related to radial growth rates (King *et al.*, 2005; Poorter *et al.*, 2008; Wright *et al.*, 2010), which makes WD a more integrative trait. WD can also respond to age variation (Domec and Gartner, 2003), with older trees having an increased proportion of large-diameter vessels and hence lower WD (Mencuccini *et al.*, 1997; Domec and Gartner, 2001). However, how WD relates to tree age has so far not been studied within species in tropical environments. Although some sources of intraspecific variation of traits related to water and carbon acquisition/conservation have been studied, a more thorough and integrated evaluation of the intrinsic and extrinsic drivers of trait variation is clearly needed.

Recent studies have highlighted the important role of hydraulic traits in understanding plant responses to climate change (Anderegg *et al.*, 2016; Blackman *et al.*, 2019). Plant hydraulic traits may integrate plant strategies, driven by trade-offs related to plant water stress and carbon uptake (Adams *et al.*, 2017; McDowell *et al.*, 2018). A widely used perspective contrasts expensive short-lived leaves (with low LMA and low WD) with rapid returns on carbon and nutrient investments versus costly long-lived leaves (with high LMA and WD) with slow returns on investments (Wright *et al.*, 2005; Díaz *et al.*, 2016). Plants lose water to capture CO₂, and thus some integration is expected between traits related to limiting water loss and traits related to CO₂ capture and conservation in response to environmental changes (Wright *et al.*, 2005; Reich, 2014). However, there is also some evidence of a decoupling of leaf and wood traits across species (Baraloto *et al.*, 2010; Laughlin *et al.*, 2017; Umaña and Swenson, 2019), which leads to the alternative expectation that if functional traits at different organizational levels are subject to different environmental pressures, there may not be a strict coordination between them, both among and within species.

Here, we study the ITV associated with water use and carbon acquisition/conservation to understand whether they

respond to the same or different pressures and, if so, whether environmental or intrinsic adjustments occur at the organ/trait level or at the integrated individual level. We focus on two dominant tree species widely distributed in central Amazonian forests with contrasting ecological strategies: *Protium hebetatum*, a shade-tolerant species confined to the understory, and *Scleronema micranthum*, a partially shade-tolerant species that can reach the canopy during its lifetime. Specifically, we posit the following three questions and hypotheses. First, what is the degree of intraspecific variation of LMA, WD, and hydraulic traits (e.g. P_{50} and P_{88} , the water potential at which 88% of conductivity is lost) in these two species, and does this differ between the species? We hypothesize that the amount of trait variation is a function of the range of environmental variation. Thus, we predict large variations in LMA in the partially shade-tolerant species because it experiences greater variation in height and light environments through ontogeny. We predict that WD and hydraulic trait variations will be large in both species because they are well distributed along the local hydrological gradient. Second, how do environmental gradients (in light and the hydrological environment) and intrinsic gradients (in age and height) drive functional traits within these two species? We hypothesize that trait adjustments along environmental variation will be driven by the environmental or intrinsic gradient more directly relevant to the acquisition/conservation of the resource performed by each trait. We predict that within species, hydraulic traits will be mainly driven by the hydrological environment, while LMA will be driven by factors associated with light and height. WD is harder to predict because it integrates several functions. Third, is there a coordination between leaf functional traits (i.e. LMA) and branch functional traits (e.g. WD, P_{50} , and P_{88}), even when these traits are driven by different environmental and intrinsic factors? We hypothesize that a coordination of trait adjustments depends on common selection pressures among them. Given the expected differences in the drivers of variation for each trait described above, we predict no coordination in the variation among them.

Materials and methods

Study site

The study was conducted at Ducke Reserve, located in the central Amazon region (2° 55' 47.80" S; 59° 58' 30.34" W) and covering 10 000 ha (10 km × 10 km) of the primary *terra firme* rainforest. The climate has a small seasonal variation in air temperature, with monthly average temperatures ranging from 24°C to 27 °C. The total annual precipitation is 2600 mm, with a dry season (<100 mm month⁻¹) occurring typically between July and September. Relative humidity reaches a minimum monthly average value of 75% in August, and a maximum average of 92% in April, during the period of high precipitation (Costa et al., 2020). The landscape is characterized by a topography of alternating plateaus and valleys, with plateau elevation of 90–120 m above sea level and valley elevation of 40–65 m above sea level. Soils in the plateau regions have a high clay fraction (90%), dominated by clay yellow latosol soils with a 20–40 m deep water table (Chauvel et al., 1987). In valleys, soils are sandy

and hydromorphic, where the water table is close to the surface (<2 m deep) and soils are nearly permanently saturated during the rainy season (Hodnett et al., 1997). The average height of the canopy in the plateaus is 30 m and in the valleys it is 25 m (Stark et al., 2012). Emergent trees reach 40–45 m height (Guillaumet, 1987).

Experimental design and species

We focused the study on two common species of central Amazon trees: *Scleronema micranthum* (Malvaceae), a partially shade-tolerant species that reaches the canopy, and *Protium hebetatum* (Burseraceae), a shade-tolerant species found primarily in the sub-canopy (see Supplementary Fig. S1). These species are dominant in terms of both stem number and basal area (Fauset et al., 2015). Between the two species, we sampled a total of 45 healthy individuals without liana infestation, distributed to cover the extremes of the local soil hydrologic gradient (i.e. plateaus and valleys). We covered the range of heights achieved by each species (from the maximum height to the minimum height that still allowed the collection of material for physiological analysis without severely affecting the individual): these ranges were 3.24–24.8 m for *P. hebetatum* and 4.1–35.14 m for *S. micranthum*. This scheme allowed us to sample a range of tree sizes and ages within each hydrological environment. We discarded some individual measurements as they were unreliable or overly noisy: these were the age data for two individuals of each species due to unclear and problematic ring structures, and vulnerability curves for six trees. The final number of sampled trees comprised nine trees on plateaus and 11 trees in valleys for *S. micranthum*, and nine trees on plateaus and 10 trees in valleys for *P. hebetatum*, totaling 39 analyzed individuals. We have focused on variation among individuals, which should be driven by phenotypic plasticity in response to the environment and/or genetic variation. Although we did not quantify the genetic variability, we expect it to be low given the small area sampled (~6 km²).

Environmental measurements

To contrast the hydrological environments of the plateau and valley areas, we used the Height Above the Nearest Drainage (HAND) as a proxy for the vertical distance of the soil surface to the groundwater (Rennó et al., 2008). Plants were sampled at sites with HAND ~1–7.3 m in the valleys (i.e. shallow water tables) and 32–37.5 m on plateaus (i.e. deep water tables).

We measured an index of the light position of a tree crown relative to its neighbors following the protocol proposed by Dawkins and Field (1978), in which three different observers assign a score for the exposure of each individual crown to light, and the average score is then computed. Light levels that were scored included crowns with their top fully exposed to light (light exposure index of 5) to crowns in full shade (light exposure index of 1), according to the illustrations and the respective scores in the protocol (Dawkins and Field, 1978).

Functional traits

We sampled trees in September 2019. For tall trees, a climber collected branches from the middle of the canopy. To standardize the height of the sampled branch in relation to the total height of the tree, branches were collected from the middle portion of the crown, using a pruner. In the tallest trees, the collected branches were exposed to partial solar radiation; the smaller trees were shaded by the forest canopy. Branches were collected at pre-dawn, immediately wrapped in a moist paper towel, and placed in a dark plastic bag. The samples were brought back to the laboratory within 1 h of branch collection.

In the laboratory, we used the pneumatic method (Pereira et al., 2016; Zhang et al., 2018), which measures air discharged from embolized xylem vessels during bench-top dehydration of branches, to obtain percentage

loss of conductivity (PLC) curves in relation to declines of xylem water potential (Ψ_x). This method allows the collection of data on many samples over a short period of time, which was imperative given the study design and execution under field conditions. This method performs well for a large range of species ((Pereira *et al.*, 2016; Zhang *et al.*, 2018). To avoid potential artifacts due to leakage from open vessels, we sampled branches that were longer (>81cm) than the maximum vessel lengths measured at this site (75.6 cm; Supplementary Fig. S2). Measurements were made on two branches per individual tree (Supplementary Fig. S3). Before each measurement, we bagged branches for 40 min to equilibrate. At full hydration, we took the first branch water potential measurement using a pressure chamber (Pressure Chamber Instrument model 1505D, PMS, Albany, OR, USA), followed by measurements of air discharge. We used the bench-top dehydration method to decrease branch water potential values (Sperry and Saliendra, 1994), drying the branches while measuring leaf Ψ_x and the corresponding air discharge values until full dehydration was reached. We used the standardized air discharge measurements for each branch, considering minimum and maximum values following the protocol in Pereira *et al.* (2016). We computed the PLC for each branch using these minimum and maximum values. To calculate the water potential points at which 12%, 50%, and 88% of conductivity is lost (i.e. P_{12} , P_{50} , and P_{88} values), we pooled the data from the two branch replicates from the same tree and fitted a non-linear two-parameter Weibull equation (Eq. 1):

$$PLC = 1 - e^{-(\Psi_x/b)^K} \quad (1)$$

where Ψ_x is the xylem water potential, b is the scale parameter, and K is the shape parameter to be estimated. The coefficients were estimated by using non-linear least-squares fitting in the `optimx` function of the `optimx` package of R (R Development Core Team, 2011).

In general, vulnerability to cavitation can be inferred by three distinct points extracted from the PLC curves: P_{12} , the xylem tension at which pit membranes within the conducting xylem are overcome with air, thereby indicating the start of cavitation (Crombie *et al.*, 1985; Sparks and Black, 1999); P_{50} , the water potential at which 50% of conductivity is lost, which represents a point of incipient damage to plant functionality (Skelton *et al.*, 2015); and P_{88} , the water potential point associated with canopy dieback in angiosperms (Urli *et al.*, 2013). Another potentially useful metric is the difference between P_{12} and P_{50} , because it corresponds to the time period during which plants are actively regulating leaf stomata to reduce water loss and prevent continuing cavitation (Bartlett *et al.*, 2016). A large difference between P_{12} and P_{50} indicates lower hydraulic resistance to embolism, whereas a smaller difference between P_{12} and P_{50} suggests higher hydraulic resistance, or a higher hydraulic sensitivity to embolism.

To evaluate the water status before the transpiration process starts, we measured pre-dawn water potentials on six leaves per individual tree from an extra branch collected from the same crown position as those used for generating the PLC curves. The branches were kept in a black plastic bag to stop transpiration and to equilibrate the leaf and branch. The water potential measurement was made upon arrival at the laboratory 1–1.5 hours after sampling, following the protocol of Turner (1981).

LMA was calculated for three to five leaves per individual tree from the same branches used for the water potential measurements and PLC curves. Whole leaves without petioles were scanned to calculate the leaf area and subsequently dried at 60 °C to calculate the leaf dry mass. LMA was determined as the ratio between the dry mass (g) and the leaf area (m²).

WD was calculated from branch segments using the dry mass to saturated volume ratio (Williamson and Wiemann, 2010). To ensure complete saturation, three branch segments per individual (2–4 cm in diameter) were immersed in distilled water for 12 h after removal of the outer bark. The saturated volume was measured by the water displacement method (Pérez-Harguindeguy *et al.*, 2016). Dry mass was measured after the samples had been dried at 105 °C until constant mass was obtained.

Intrinsic factors

Tree height was determined trigonometrically using the distance from the observer to the tree (measured with a measuring tape) and the angle from the observer's eye to the canopy top (the highest visible leaf), as well as the angle to the base of the trunk (measured with a clinometer and kept under 50° to minimize errors). On sloping terrain, the slope of the ground in relation to the base of the tree was also measured and the distance was corrected. All height measurements were taken by the same observer. Tree diameter at breast height was measured at 1.30 m above ground level using a 5 m diametric tape.

To estimate tree age, we sampled two 5.15 mm diameter radial wood cores from opposite sides of the trunk using an increment borer. The cores were collected at 1.50 m above the ground. In the laboratory, each core was glued to a support and polished with progressively finer sandpaper (from 80 to 600 grains mm⁻²) until xylem tissues (and growth rings) became visible. Subsequently, all tree rings were identified with the aid of a stereomicroscope, using the descriptions of anatomical markers to distinguish annual rings (Worbes, 2011; Schöngart *et al.*, 2017). Previous studies had already reported the formation of annual rings for these species and provided recommendations on how to identify the anatomical pattern of an annual ring (Schöngart *et al.*, 2017). For *S. micranthum*, we focused primarily on whether or not the radially oriented parenchyma cells bisected ray cells (Albiero-Júnior *et al.*, 2019) and marginal parenchyma (Supplementary Fig. S4). For *P. hebetatum*, we focused on intra-annual variation in WD (Supplementary Fig. S4). After identifying growth rings, samples were scanned at a resolution of 2400 dpi (Epson scanner 1640SU) and ring widths were measured using WinDENDRO software (WinDENDRO 6.11, Regent Instruments Inc., Québec, Canada). Cross-dating within trees was usually high, but we were unable to cross-date growth curves between trees (i.e. we found no common growth signal). We acknowledge that dating of the rings is not absolute and that dating errors will occur. However, these species have been proven to form annual rings in locations nearby (Ohashi *et al.*, 2016; Albiero-Júnior *et al.*, 2019), errors may be relatively small even when cross-dating between trees is weak or absent (dating errors <10%; Groenendijk *et al.*, 2014), and small dating errors do not strongly affect the results of experiments designed to answer ecological questions (Van Der Sleen *et al.*, 2015).

Statistical analysis

To address our first research question, evaluating the degree of ITV (of LMA, WD, and P_{50}), we computed the ratio of the maximum to the minimum value for each trait. We also compared the ranges of ITV of our studied species with the ranges reported previously in interspecific studies conducted at the same site (Cosme *et al.* 2017, Oliveira *et al.* 2019).

To address our second question, in which we evaluated how LMA, WD, and hydraulic traits (P_{50} , P_{88} , and $P_{12} - P_{50}$) were associated with multivariate species strategies, we ran a principal component analysis (PCA). Pairwise trait relationships were subsequently analyzed with Pearson's correlations and regression analyses.

To address our third question, we used generalized linear models to examine the effects of environmental factors (crown exposure to light and hydrological environment) and intrinsic factors (age and height) on LMA, WD, and hydraulic traits (P_{50} , P_{88} , and $P_{12} - P_{50}$). Data distributions were selected to the best fit in each analysis: for the hydraulic traits P_{50} and P_{88} , the best-fitting distribution was the Gumbel distribution, while for $[P_{12} - P_{50}]$, LMA and WD, a gamma distribution provided the best fit. Generalized linear model analyses were run with the R package `gamlss` (Stasinopoulos and Rigby, 2007). For all the models described above, we applied the Akaike Information Criterion (AIC) to identify the best-fitting subset models, and to avoid the risk of overfitting (Burnham and Anderson, 2002), we used unsupervised model selection [`dredge` function, `MuMIn` package (Bartón, 2016)]. We established a correlation rule excluding fixed-effects variable pairs whose correlation

was greater than 0.5. Because the number of observations was low with respect to the number of parameters, we chose the bias-corrected form, AICc, which adds a greater penalty on the number of parameters. All models within two units of the model with the lowest AICc were considered as having strong support, and the model with the lowest AICc value was assigned as the 'best model' (Burnham and Anderson, 2004). Nonetheless, we report the results of all models with high support. The relative importance of each predictor was evaluated by summing model weights across all the models in the full set in which the respective predictor occurred (Supplementary Table S1). All analyses were performed in R (R Development Core Team 2011).

Results

Comparison of intraspecific variation

There was substantial intraspecific variability in WD, LMA, and hydraulic traits in both species (Table 1). In the shade-tolerant species *P. hebetatum*, WD varied 1.6-fold (from 0.49 to 0.79 g cm⁻³), LMA varied 1.5-fold (from 71.35 to 111.58 g m⁻²), and P_{50} varied 20.7-fold (from -0.14 to -2.90 MPa) considering trees growing in valleys with seasonal flooding to plateaus with a deep water table. ITV of *S. micranthum* was similarly high; WD varied 1.6-fold (from 0.46 to 0.72 g cm⁻³), LMA varied 2.8-fold (from 38.4 to 106.11 g m⁻²), and P_{50} varied 26.3-fold (from -0.14 to -3.68 MPa).

We compared the intraspecific ranges from our study against interspecific ranges from previously published studies conducted at the same site (Cosme et al., 2017; Oliveira et al., 2019). For the interspecific range of hydraulic traits in the previously published studies, the range of variation of P_{50} was -3.64 MPa (-0.56 to -4.2 MPa); in this study, the intraspecific range of P_{50} for *S. micranthum* was -3.54 MPa (-0.14 to -3.68 MPa, i.e. 97% of the interspecific range), and for *P. hebetatum* it was -2.76 MPa (-0.14 to -2.9 MPa, 76% of the interspecific range). For the interspecific variation of LMA

reported in the previously published studies, the range was 123.12 g m⁻² (59.17 to 182.29 g m⁻²); in this study, the intraspecific range of LMA was lower for *S. micranthum* at 67.7 g m⁻² (38.4 to 106.1 g m⁻², 55% of the interspecific range) and for *P. hebetatum* at 40.2 g m⁻² (71.35 to 111.58 g m⁻², 32% of the interspecific range). For the interspecific range of WD, Cosme et al. (2017) reported a range of 0.47 g cm⁻³ (0.48 to 0.95 g cm⁻³). In this study, the WD intraspecific range for *S. micranthum* was 0.26 g cm⁻³ (0.46 to 0.72 g cm⁻³, 55% of the interspecific range), and for *P. hebetatum* it was 0.3 (0.49 to 0.79 g cm⁻³, 63% of the interspecific range).

Variation of hydraulic traits across intrinsic and environmental factors

The local hydrological environment was the strongest explanatory variable of the variation in hydraulic traits for both species (Table 2), and ranked highest across all models (Supplementary Table S1). Trees located in valleys were more hydraulically vulnerable; specifically, *P. hebetatum* trees growing in valleys did not differ from trees on plateaus in their P_{50} values (Fig. 1A), but they had less negative P_{88} (Fig. 1B) and a larger [$P_{12} - P_{50}$] value (Fig. 1C) than trees on plateaus. The crown exposure to light did not affect the P_{50} of this species (Fig. 1D). *S. micranthum* trees growing in valleys had less negative P_{50} than trees on plateaus (Fig. 1E), but we did not find differences for P_{88} (Fig. 1F) or for [$P_{12} - P_{50}$] (Fig. 1G) between valley and plateau trees of this species. However, P_{50} was affected by an interaction between crown exposure to light and the hydrological environment in the second-ranked model (Table 2, $\Delta\text{AICc}=1.70$). By examining this interaction in partial regressions for P_{50} , we found that *S. micranthum* trees growing on plateaus showed reduced embolism resistance when their crowns were exposed to higher light levels, compared with trees growing in valleys

Table 1. Overview of the intraspecific variability of embolism resistance (P_{50} , P_{88} , and [$P_{12} - P_{50}$]), LMA, and WD in *P. hebetatum* and *S. micranthum*

Species	Trait	Unit	Median	Range (max-min)	CV (%)	Percentiles		
						5th	95th	Range 5th-95th
<i>P. hebetatum</i>	P_{50}	MPa	-0.45	-2.76	-95.3	-2.41	-0.2	2.2
	P_{88}	MPa	-2.06	-5.02	-71.6s	-5.17	-0.47	4.71
	[$P_{12} - P_{50}$]	MPa	0.3	1.64	92.7	0.08	1.68	1.6
	WD	g cm ⁻³	0.62	0.3	12.0	0.51	0.72	0.21
	LMA	g m ⁻²	89.1	40.2	13.5	76.0	111.4	35.4
<i>S. micranthum</i>	P_{50}	MPa	-0.99	-3.54	-65.7	-2.26	-0.38	1.88
	P_{88}	MPa	-4.27	-7.51	-51.2	-7.68	-1.11	6.57
	[$P_{12} - P_{50}$]	MPa	0.75	1.78	56.3	0.34	1.72	1.38
	WD	g cm ⁻³	0.65	0.26	11.5	0.53	0.72	0.19
	LMA	g m ⁻²	76.2	67.7	26.0	40.2	104.9	64.7

CV, Coefficient of variation.

Table 2. Selected statistical models based on AICc criteria ($\Delta < 2$) considering tree height (H), age (A), crown exposure to light (L), and hydrologic environment (Hy) to predict embolism resistance (P_{50} , P_{88} , and $[P_{12} - P_{50}]$), LMA, and WD in *P. hebetatum* and *S. micranthum*

Species	Independent variable	Response variable	var1	var2	var3	R ²	AICc	Δ AICc
<i>P. hebetatum</i>	Hy, L, A, H	P_{50}	Null	Null	Null	–	–	–
	Hy, L, A, H	P_{88}	-Hy ^a	–	–	0.17	72.4	0
	Hy, L, A, H	$[P_{12} - P_{50}]$	+Hy*	–	–	0.26	15.2	0
	Hy, L, A, H	WD	Null	Null	Null	–	–	–
	Hy, L, A, H	LMA	+H**	–	–	0.36	139.2	0
	Hy, L, A, H	LMA	+Hy*	+L**	–	0.42	140.7	1.48
	Hy, L, A, H	LMA	+Hy (ns)	+H**	–	0.42	140.7	1.48
<i>S. micranthum</i>	Hy, L, A, H	P_{50}	-Hy*	–	–	0.25	35.8	0
	Hy, L, A, H	P_{50}	-Hy*	-L(ns)	+Hy:L*	0.43	37.5	1.7
	Hy, L, A, H	P_{88}	Null	Null	Null	–	–	–
	Hy, L, A, H	$[P_{12} - P_{50}]$	Null	Null	Null	–	–	–
	Hy, L, A, H	WD	+A**	–	–	0.32	-44.2	0
	Hy, L, A, H	WD	+H*	–	–	0.27	-42.9	1.27
	Hy, L, A, H	WD	+A**	+Hy*	-A:Hy*	0.49	-42.7	1.46
	Hy, L, A, H	WD	+L*	–	–	0.24	-42.2	1.98
	Hy, L, A, H	LMA	+H***	–	–	0.51	170.1	0
	Hy, L, A, H	LMA	-Hy(ns)	+H***	–	0.54	171.7	0.31

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ^a $P < 0.1$; ns, not significant; +, positive effect; –, negative effect; –, variable not included in the model.

AICc, Bias-corrected Akaike information criterion; Null, null model; R², likelihood-ratio based.

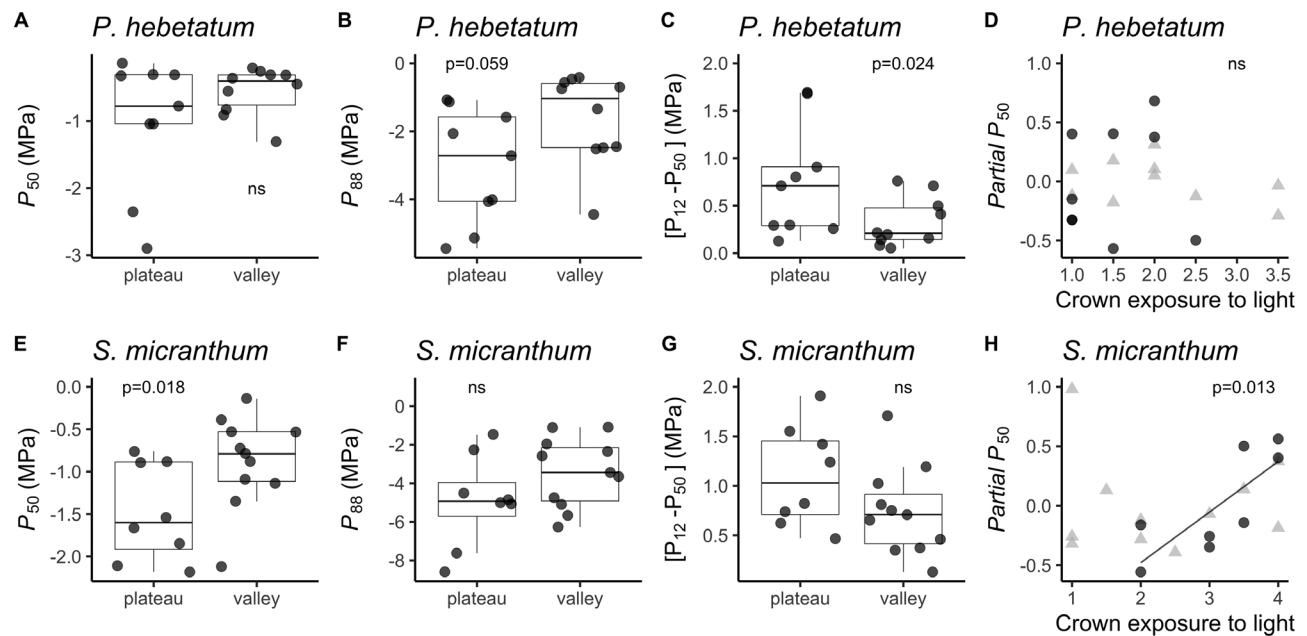


Fig. 1. Plots of the best statistical models for how intrinsic and environmental factors modulate variations in hydraulic characteristics for *P. hebetatum* (A–D) and *S. micranthum* (E–H). The plots show differences in the water potential at which 50% of hydraulic conductivity is lost (P_{50}) for (A) *P. hebetatum* and (E) *S. micranthum*, differences in the water potential at which 88% of conductivity is lost (P_{88}) for (B) *P. hebetatum* and (F) *S. micranthum*, and differences in the proxy for hydraulic resistance to embolism associated with stomatal regulation $[P_{12} - P_{50}]$ for (C) *P. hebetatum* and (G) *S. micranthum*, between trees growing in valleys and on plateaus. (D, F) Partial effects derived from the multiple regression of models considering the interaction between crown exposure to light and hydrological environment on P_{50} for (D) *P. hebetatum* and (H) *S. micranthum*; black circles indicate data for plateau-growing trees, and gray triangles indicate data for valley-growing trees.

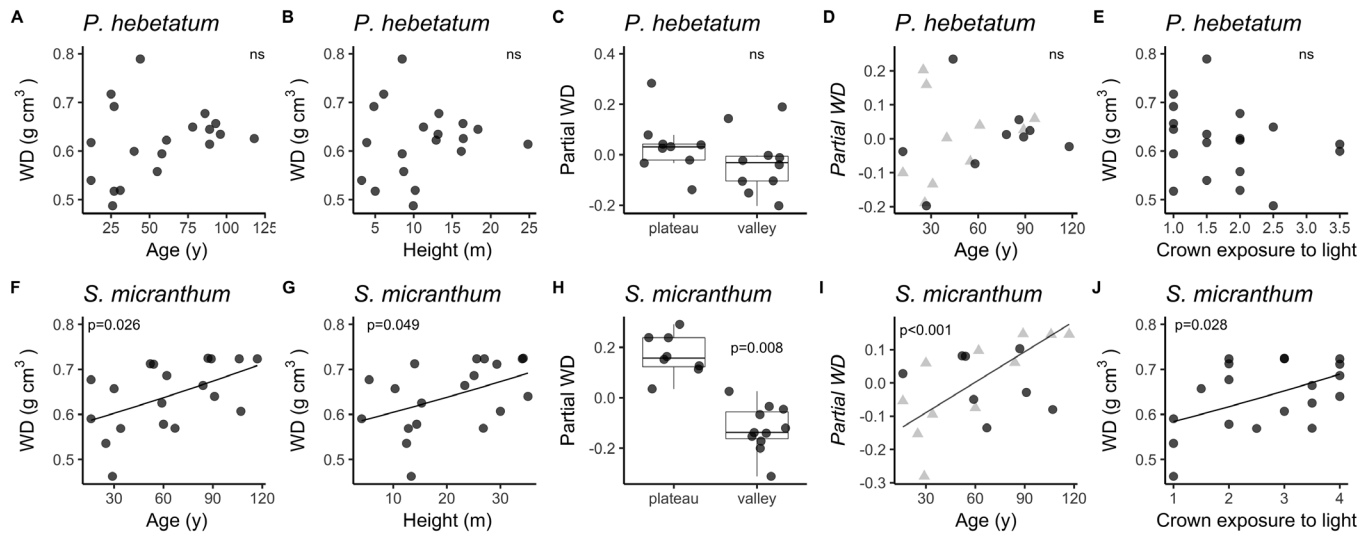


Fig. 2. Plots of the best statistical models for how intrinsic and environmental factors modulate variations in WD for *P. hebetatum* (A–E) and *S. micranthum* (F–J). (A, F) Relationship between age and branch WD for (A) *P. hebetatum* and (F) *S. micranthum*. (B, G) Relationship between tree height and WD for (B) *P. hebetatum* and (G) *S. micranthum*. Panels (C, D) and (H, I) are the partial regressions derived from the multiple regression models: the partial effect of the hydrological environment on WD for (C) *P. hebetatum* and (H) *S. micranthum*, and the partial effect of the interaction between age and the hydrological environment on WD for (D) *P. hebetatum* and (I) *S. micranthum*. In (D) and (I), black circles indicate data for plateau-growing trees, and gray triangles indicate data for valley-growing trees. (E, J) Relationship between crown exposure to light and WD for (E) *P. hebetatum* and (J) *S. micranthum*.

(Fig. 1H). The intrinsic factors (age and height) of the two species did not affect any of the hydraulic traits (Table 2).

For the shade-tolerant species *P. hebetatum*, WD was not associated with either intrinsic or environmental factors (Table 2, Fig. 2A–E). However, for the partial shade-tolerant species *S. micranthum*, WD increased with tree age (the best AICc model is shown in Fig. 2F). Age was the variable with higher relative importance across the full set of models to predict WD (Supplementary Table S1). Models that ranked high also include height (second-ranked model, $\Delta\text{AICc}=1.27$, Fig. 2G). We found the third-ranked model to include an interaction between tree age and hydrological environment ($\Delta\text{AICc}=1.46$). To expand on this interaction, we examined the partial regression relationships. We found that *S. micranthum* growing on plateaus consistently had higher WD compared with trees growing in valleys (Fig. 2H). However, the lower WD in trees growing in valleys was largely driven by younger trees (Fig. 2I). Finally, the light environment had a positive effect on WD (fourth-ranked model, $\Delta\text{AICc}=1.98$, Fig. 2J).

Height and light were the variables with higher relative importance in determining the variability of LMA of both species (Supplementary Table S1). For *P. hebetatum*, tree height was the best predictor of LMA (Table 2, Fig. 3A), and the second-ranked model ($\Delta\text{AICc}=1.48$) included crown exposure to light (Fig. 3B) and hydrological environment (Fig. 3C). For *S. micranthum*, tree height was the best predictor of LMA (Fig. 3D). We also found models that had high support including LMA (Table 2) increasing with crown exposure to light (Fig. 3E), and LMA tended to decrease on plateaus (Fig. 3F).

Trait coordination within the two species

Considering hydraulic and economic traits, 76.6% of the variance was explained by the first two axes of the PCA (Fig. 4). The within-species correlation between hydraulic and economic traits was low, creating orthogonal axes; PC1 was related to embolism resistance and PC2 to plant acquisition/conservation traits. The hydraulic trait axis segregated trees with lower tolerance to embolism and high hydraulic sensitivity to embolism to the left (Fig. 4), and higher tolerance to embolism and less sensitivity to embolism to the right. The grouping of most *P. hebetatum* individuals and the valley-growing individuals of *S. micranthum* to the left side of the PC1 axis demonstrates a convergence of individuals growing in the understory and in wetter soils, suggesting a common strategy of lower embolism resistance. This is further supported through the pairwise correlation analysis that showed significant but weak ($P<0.1$) correlations between economic and hydraulic traits, and only in *P. hebetatum*, where embolism resistance was positively related to WD and LMA (Table 3).

Discussion

Evaluating the ITV of Amazonian trees is important to understand whether species have the capacity to adjust to environmental changes, especially in the context of climate change. However, there is uncertainty regarding the degree of ITV in many tropical tree species and whether ITV is

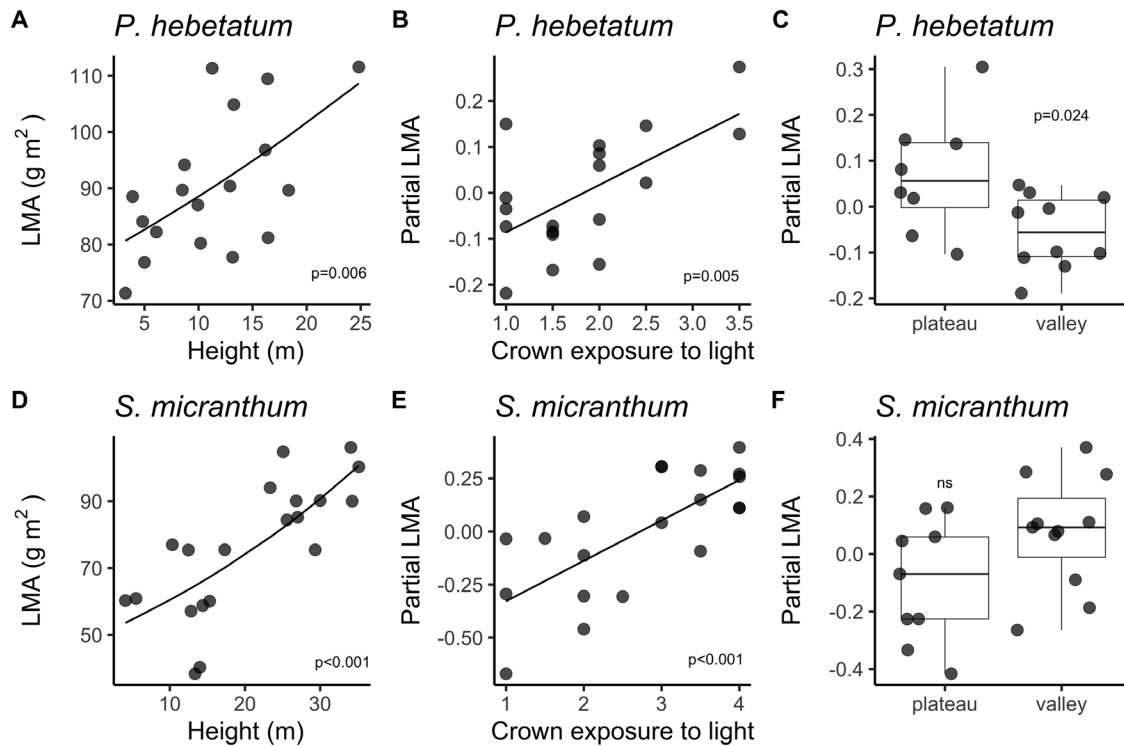


Fig. 3. Plots of the best statistical models for how intrinsic and environmental factors modulate variations in LMA for *P. hebetatum* (A–C) and *S. micranthum* (D–F). (A, D) Relationship between height and LMA for (A) *P. hebetatum* and (D) *S. micranthum*. The partial regressions derived from the multiple regression models are presented in panels (B, C) and (E, F). (B, E) Partial effect of crown exposure to light for (B) *P. hebetatum* and (E) *S. micranthum*. (C, F) Partial effect of the hydrological environment on LMA for (C) *P. hebetatum* and (F) *S. micranthum*.

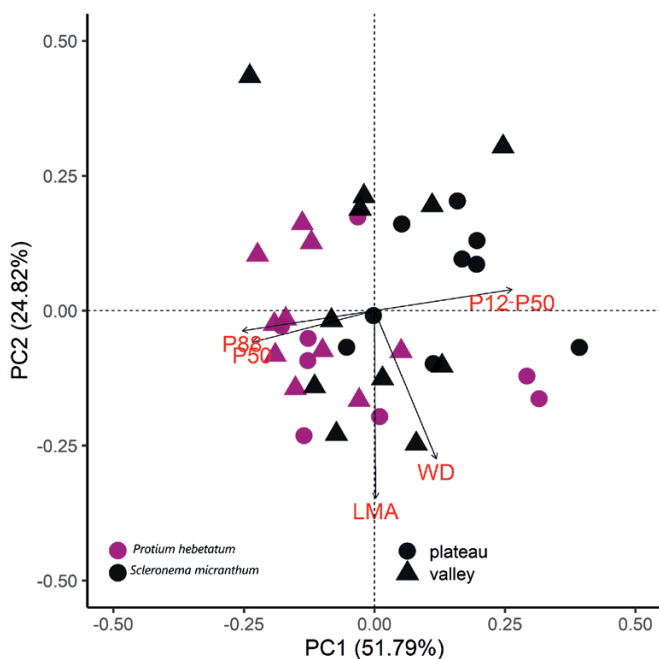


Fig. 4. PCA of embolism resistance (P_{50} , P_{88} , and $[P_{12} - P_{50}]$), LMA, and WD for *P. hebetatum* and *S. micranthum* growing in two distinct hydrological environments, plateau (circles) and valley (triangles).

driven by environmental variation or primarily governed by individual intrinsic variations (e.g. due to size or age). Here, we highlight three main findings that advance knowledge about these uncertainties in tropical forests. First, the ITV of hydraulic traits (e.g. P_{50}) was as large as the interspecific variation previously reported for the site. Interspecific patterns of niche diversity have long been recognized as mechanisms allowing the high species diversity within tropical forests (Leibold, 1995; Tilman *et al.*, 1997); however, our study highlights that the same degree of niche diversity can also occur within a species. Second, local hydrological environments, not intrinsic factors, were a central filter of the ITV of hydraulic traits for both species, and the tallest and oldest trees were not more hydraulically vulnerable. However, crown exposure to light unexpectedly played a role in modulating within-species hydraulic trait responses. Third, the ITV of LMA and WD was modulated mostly by intrinsic factors, whereas hydraulic traits were modulated by the environment, suggesting an uncoupling of the coordination between carbon-uptake and water-use traits. This uncoupling suggests that accounting for the effects of intrinsic and environmental factors on ITV is critical in predicting forest responses to future climate change.

Table 3. Correlation matrix between the functional traits embolism resistance (P_{50} , P_{88} , and $[P_{12} - P_{50}]$), LMA, and WD in *P. hebetatum* and *S. micranthum*

Species	Trait	Unit	P_{50}	P_{88}	$[P_{12} - P_{50}]$	WD	LMA
<i>P. hebetatum</i>	P_{50}	MPa		0.79***	-0.89***	-0.33	-0.34
	P_{88}	MPa	<0.001		-0.92***	-0.3	-0.27
	$[P_{12} - P_{50}]$	MPa	<0.001	<0.001		0.43 ^a	0.46 ^a
	WD	g cm ⁻³	0.178	0.227	0.078		0.28
	LMA	g m ⁻²	0.162	0.276	0.054	0.26	
<i>S. micranthum</i>	P_{50}	MPa		0.61**	-0.92***	-0.04	0.06
	P_{88}	MPa	0.006		-0.80***	-0.16	-0.16
	$[P_{12} - P_{50}]$	MPa	<0.001	<0.001		0.1	-0.07
	WD	g cm ⁻³	0.862	0.515	0.682		0.45 ^a
	LMA	g m ⁻²	0.813	0.509	0.766	0.054	

The upper right diagonals show correlation coefficients, and the lower left diagonals with bold text show the P -values: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ^a $P < 0.1$.

Intraspecific variation of functional traits

To understand community functioning and the dynamics of forest water use and carbon acquisition/conservation along local water and light gradients, it is just as important to quantify intraspecific changes as interspecific changes (Sperry and Saliendra, 1994; Albert *et al.*, 2012; Kang *et al.*, 2014; Laforest-Lapointe *et al.*, 2014; Siefert *et al.*, 2015; Laughlin *et al.*, 2017; Read *et al.*, 2017; Ahrens *et al.*, 2020; Westerband *et al.*, 2021). Our results confirmed our hypothesis that LMA variations would be higher in the partially shade-tolerant species, *S. micranthum*, because this species experiences greater variations in height and light environments while growing to reach the canopy. We also found variation in WD and hydraulic traits in both species because they are widely distributed along the hydrological gradient (Table 1, Supplementary Fig. S5). Our data add to the growing evidence of relatively high (e.g. ~40%) variation in LMA and WD within tropical species (Poorter *et al.*, 2018). However, for the first time, we show that the ITV for hydraulic traits in tropical species can be as high as in temperate tree species (Skelton *et al.*, 2019). Additionally, hydraulic traits had higher variability than LMA and WD, suggesting that trees of these species may be able to adjust their physiological responses under future droughts.

Intrinsic and environmental controls on tree hydraulic traits

The local hydrological environment was a central filter of the ITV of hydraulic traits across individuals widely distributed in the landscape (Fig. 1, Table 2). For both *P. hebetatum* and *S. micranthum*, trees growing in valleys had more vulnerable hydraulic systems than trees growing on plateaus. Previous studies reported that species growing in valleys (Oliveira *et al.*, 2019) and in seasonally inundated forests (Fontes *et al.*, 2020) were more vulnerable to embolism than those on plateaus. Our results confirmed these previous findings that local soil water availability within the same microclimate influences embolism resistance through interspecific differences; however, our results also expand the knowledge to include intraspecific variation. This adds to the growing body of evidence that local hydrological conditions created by topography are critical filters of Amazonian tree hydraulic traits among species (Oliveira *et al.*, 2019) and within species across a precipitation gradient in Central America (Choat *et al.*, 2007), creating a mosaic of landscape functional structures (Kraft *et al.*, 2008) with consequences for forest functioning (Toledo *et al.*, 2017).

Although we found that individuals of the partially shade-tolerant species *S. micranthum* growing on plateaus had more negative P_{50} than trees growing in valleys, we also found that the higher exposure of the crown to light on the plateaus led to a less resistant hydraulic system (less negative P_{50}) (Fig. 1H). We reason that this seemingly contradictory finding is likely due to the fact that, during the wet season of central Amazonia, water may not be the major growth-limiting factor for trees on plateaus, whereas light is always very limited in this dense forest (Poorter *et al.*, 2018), and that trees therefore prioritize light capture over hydraulic safety. Throughout the lifetime of a tree, the strategy of this light-requiring species is to increase water transport efficiency in response to increases in light availability (Herbette *et al.*, 2010), with subsequent increased hydraulic vulnerability. Thus, building branches that have higher hydraulic conductances (and therefore less negative P_{50} values) should allow this species to maintain high leaf water potentials, stomatal conductance rates, and, consequently, high photosynthetic carbon assimilation rates (Kenzo *et al.*, 2006). This strategy seems to work well in the mild conditions of normal years of this region with two to three dry months per year

(<100 mm, between July and September), but experiencing a more prolonged water deficit during drought years could increase the hydraulic vulnerability and mortality of this species (Aleixo *et al.*, 2019).

While recent studies have suggested that taller trees are more vulnerable to water-stress-related mortality (Bennett *et al.*, 2015; Giardina *et al.*, 2018; Liu *et al.*, 2019; Stovall *et al.*, 2019), our study did not find a direct link between embolism resistance and tree height or tree age that could provide a mechanistic explanation for those observations. The variability in age and height that describes hydraulic relationships can be quite difficult to untangle, given the physiological, developmental, and mechanical interactions within the plant's xylem. As a plant grows it experiences changes in both its external environment and its internal physiology. Thus, a constant straightforward set of rules orchestrating the development of all species' adaptive patterns under all environmental conditions should not be expected. We also did not find changes in pre-dawn water potentials across individuals varying in height, or even among the tallest trees (Supplementary Fig. S6). In fact, we found a nearly zero pre-dawn water potential, which implies that soil water was readily available for trees in this forest, and that this water availability may be enough to supply the demand in the leaves. In a more seasonal forest, however, these relationships could be different (Bittencourt *et al.*, 2020), since soil-water availability decreases sharply in the dry season.

Changes in age can potentially induce higher vulnerability to embolism; for example, studies have recognized age-related changes in other species, such as conifers (Domec and Gartner, 2002; Domec *et al.*, 2005), in which the water transport resistances increased along the path as they became taller, suggesting that older trees could decrease the hydraulic resistance to improve water transport (Koch *et al.*, 2004; Giardina *et al.*, 2018). However, in our study, neither species had a direct relationship between age and hydraulic traits. We found that both species generally increased in height and age simultaneously (Supplementary Fig. S7). While the age of *S. micranthum* was positively associated with exposure of the canopy to light, this pattern was less clear in *P. hebetatum* (Supplementary Fig. S8). Therefore, environmental factors played a more important role in embolism responses than age and height.

Intrinsic and environmental controls on LMA and WD

Our study also highlights the differential responses of LMA, WD, and hydraulic factors to intrinsic and environmental factors. We found that ITV in LMA and WD were more affected by intrinsic plant factors than by the environment (Figs 2, 3), whereas hydraulic traits were more affected by the environment (Fig. 1). The gradients in LMA variation were associated with height and light exposure in both species (Fig. 3), potentially due to adjustments of leaf morphology along vertical

gradients of water stress. Decreasing water potential with height imposes constraints on leaf turgor pressure (Scoffoni *et al.*, 2012), which is required for leaf cell expansion and division. Reduced turgor pressure could result in smaller, denser leaves with more densely packed cells and, subsequently, greater LMA (Coble and Cavaleri, 2014). Increasing leaf thickness also allows a higher density of photosynthetic cells in more developed palisade parenchyma to capitalize on the high-light environments higher up in the canopy (Kenzo *et al.*, 2015). Therefore, the morphological adjustments on LMA seem to respond to light availability and might result in increases in the rate of photosynthesis.

The differential influence of intrinsic or environmental factors on WD was less clear between the two species (Fig. 2). In the shade-tolerant species, *P. hebetatum*, WD was not influenced by tree age, height, light level, or hydrological environment. By contrast, in the partially shade-tolerant species *S. micranthum*, both intrinsic and environmental factors influenced variation in WD, but the significant interactions between these terms made it challenging to untangle mechanistic reasons. WD increased with tree age and height in *S. micranthum* (Fig. 2F, G), but this was mediated by the fact that older trees growing in the valleys tended to have a higher WD (Fig. 2I), which is consistent with the need for stronger structural support as trees become taller with age (Domec and Gartner, 2002). However, more generally, we found that trees on the plateaus had denser wood than trees in the valleys (Fig. 2H), indicating that soil water availability was also important in modulating this trait (Cosme *et al.*, 2017; Rocha *et al.*, 2020). More research examining the impacts of water availability on WD as trees age (or grow taller) and how WD patterns vary within trees (from patterns at breast height to canopy branches) is needed to further untangle these results.

Trade-offs between functional traits

The divergent strategies among LMA and WD (mostly modulated by intrinsic factors and light exposure) and hydraulic traits (mostly modulated by the hydrological environment) led to low coordination of these two groups of traits in *P. hebetatum*, and a lack of coordination in *S. micranthum*. We also observed that *P. hebetatum* individuals were mostly associated with the lower-resistance side of the hydraulic axis, indicating that *P. hebetatum* is more vulnerable to embolism than *S. micranthum* (Fig. 4). The different strategies indicate that varying severities of drought in central Amazonia will likely impact the two species in different ways.

We did not find clear support for the hypothesis of a strong selection along trait trade-off axes for either tree species (Reich, 2014). Orthogonal axes among leaf and wood properties, indicating poor coordination, have also been found for many other Amazonian species (Baraloto *et al.*, 2010), indicating that the constraints to growth and survival do not always lead to coordinated traits within tropical wet forests. This might suggest

that in the absence of strong environmental stress, the favorable environments of tropical wet forests select for a more variable set of traits. The implication would be that these species can be expected to have high ITV (as we found here) and a higher capacity to adjust to environmental changes than is accepted today (Westerband *et al.*, 2021).

In many cases, the interactions between intrinsic and environmental factors complicated the assessment of trade-offs between economic and hydraulic traits. Theoretically, a tree species confined to the light-limited understory environment during its entire life would likely coordinate hydraulic and economic traits with a low potential growth rate and thus a conservative strategy of resource use (Ouedraogo *et al.*, 2013). However, in our study, *P. hebetatum*, a shade-tolerant species, was more vulnerable to embolism and showed weak coordination between hydraulic traits and LMA and WD. This weak coordination may be associated with the fact that despite the shallow rooting nature of this understory species (Brum *et al.*, 2019), the *P. hebetatum* individuals at our study site may not have experienced sufficient hydraulic stress for the trade-offs to be significant.

The partially shade-tolerant species *S. micranthum*, on the other hand, had a more hydraulically resistant strategy despite being able to reach full sunlight and thus theoretically being expected to be more acquisitive and less hydraulically resistant. Moreover, the hydraulic strategy was decoupled from LMA and WD. One potential explanation for this decoupling may be leaf phenology, since *S. micranthum* is brevi-deciduous. Replacing old leaves with young leaves can provide better stomatal control (Reich and Borchert, 1988; Albert *et al.*, 2018), so hydraulic adjustments may not necessarily depend on anatomical changes such as adjustments of LMA. Another reason for the lack of correlation among LMA, WD, and hydraulic traits for this species resides in the different pressures experienced both between individuals, and within individuals along their lifespan (Table 1). Because of the large variation in height and crown exposure to light experienced by this species, other factors could be shaping LMA and WD that are unrelated to hydraulic adjustments. For example, WD can increase with tree height to provide biomechanical support for taller trees reaching the canopy (Borchert and Pockman, 2005). Additionally, canopy leaves that experience high light, temperature, wind speed, and vapor pressure deficit can also respond by adjusting the elasticity modulus, causing sclerophylly and elastic adjustments to maintain water content at turgor loss point, thus increasing LMA. This can help prevent cell dehydration but does not play a direct role in drought tolerance (Bartlett *et al.*, 2012). LMA adjustments can also be a response to nutrient, mechanical, and herbivory stresses (Mody *et al.*, 2009), which are also independent of drought tolerance. The uncoupling of hydraulic and carbon acquisition/conservation traits observed here apparently violates the principles of optimization of resource acquisition and conservation expected in plants (Reich, 2014).

However, the trait values of our study species still fit well in the global-scale patterns of the plant economic spectrum (Wright *et al.*, 2005; Díaz *et al.*, 2016; Oliveira *et al.*, 2021). Thus, our results suggest that optimization of resource acquisition and conservation is not perfect at the local scale, where variation in the functional design may be selected according to pressures that vary among habitats and life phases. Therefore, the biophysical constraints indicated by Reich (2014) and Oliveira *et al.*, (2021) seem to be reasonably flexible after the large-scale environmental filters (e.g. climate) have selected the range of trait values allowing local survivorship.

Despite some differing strategies between the two species, the hydrological environment played an important role in regulating embolism resistance in both species. The lower embolism resistance of valley-growing trees found in both species suggests that trees in valleys may be more vulnerable to mortality during intense and prolonged droughts (Zuleta *et al.*, 2017). Even the controversial tree-height mortality study (Stovall *et al.*, 2019, 2020, response by Stephenson and Das, 2020) found that taller trees that experience higher mortality tend to grow in more convergent landscape positions (valleys), that is, the hydrological environment may be more relevant to the drought response than the tree's height. During intense but short droughts, the conditions of valleys with more shallow access to groundwater can supply tree roots with water, and even hydraulically vulnerable trees growing in valleys can thus be protected from droughts by the high availability of water (Sousa *et al.*, 2020; Esteban *et al.*, 2021). However, this scenario could change if prolonged and intense droughts in the future caused water table levels to be out of reach, placing valley-growing trees of both species in increased danger of hydraulic failure and mortality.

Supplementary data

The following supplementary data are available at [JXB online](#).

Fig. S1. Sample distributions of tree age, crown exposure to light, and height, and tree occurrence in sampled plots.

Fig. S2. Size of branches collected in this study versus maximum vessel size distribution for nine different species on the same site.

Fig. S3. Vulnerability curves for shade-tolerant *P. hebetatum* and partially shade-tolerant *S. micranthum*.

Fig. S4. Anatomical visualization of growth tree rings.

Fig. S5. Functional trait distributions by species.

Fig. S6. Relationships between height and predawn water potential.

Fig. S7. Relationships between age and diameter at breast height.

Fig. S8. Relationships between tree canopy height and crown light exposure.

Table S1. Relative AICc weights of variables.

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Author contributions

MNG, FRCC, TFD, RSO, and JH designed the research; MNG collected the data; MNG, JH, and FRCC analyzed the data; MNG, JH, and PG interpreted the tree-ring data; all authors interpreted the results; MNG wrote the first draft, and all authors contributed to the writing of the manuscript.

Conflict of interest

The authors declare that there is no conflict of interest.

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Data availability

The data supporting the findings of this study are available from the corresponding author, Maquella N. Garcia, upon request.

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