HAL open science

Seasonal variation of leaf thickness: An overlooked component of functional trait variability

S. Schmitt, S. Trueba, S. Coste, É. Ducouret, Niklas Tysklind, M. Heuertz, D. Bonal, B. Burban, B. Hérault, Géraldine Derroire

► **To cite this version:**

S. Schmitt, S. Trueba, S. Coste, É. Ducouret, Niklas Tysklind, et al.. Seasonal variation of leaf thickness: An overlooked component of functional trait variability. Plant Biology, 2022, 24 (3), pp.458-463. 10.1111/plb.13395 . hal-03772046

HAL Id: hal-03772046

https://hal.inrae.fr/hal-03772046v1

Submitted on 18 Sep 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Distributed under a Creative Commons Attribution 4.0 International License

plant biology

Plant Biology ISSN 1435-8603

RESEARCH PAPER

Seasonal variation of leaf thickness: An overlooked component of functional trait variability

S. Schmitt[1,2], S. Trueba[3], S. Coste[4], É. Ducouret[4], N. Tysklind[5], M. Heuertz[2], D. Bonal[6], B. Burban[5], B. Hérault[7,8] & G. Derroire[9]

1 CNRS, UMR EcoFoG (Agroparistech, Cirad, INRAE, Université des Antilles, Université de la Guyane), Campus Agronomique, Kourou, French Guiana
2 Université de Bordeaux, INRAE, BIOGECO, Pessac, France
3 Université de Bordeaux, INRAE, BIOGECO, Allée Geoffroy St-Hilaire, Pessac, France
4 Université de la Guyane, UMR EcoFoG (Agroparistech, Cirad, CNRS, INRAE, Université des Antilles), Campus Agronomique, Kourou, French Guiana
5 INRAE, UMR EcoFoG (Agroparistech, CNRS, Cirad, Université des Antilles, Université de la Guyane), Campus Agronomique, Kourou, French Guiana
6 Université de Lorraine, AgroParisTech, INRAE, UMR Silva, Nancy, France
7 Forêts et Sociétés, Université de Montpellier, CIRAD, Montpellier, France
8 Institut National Polytechnique Félix Houphouët-Boigny, INP-HB, Yamoussoukro, Côte d'Ivoire
9 Cirad, UMR EcoFoG (Agroparistech, CNRS, INRAE, Université des Antilles, Université de la Guyane), Campus Agronomique, Kourou, French Guiana

Keywords
Dry season; leaf thickness; leaf traits; seasonal variation; trait variability; tropical forests.

Correspondence
S. Schmitt, CNRS, UMR EcoFoG (Agroparistech, Cirad, INRAE, Université des Antilles, Université de la Guyane), Campus Agronomique, Kourou, French Guiana.
E-mail: sylvain.m.schmitt@gmail.com

Editor
J.F. Scheepens

Received: 28 July 2021; Accepted: 7 January 2022

doi:10.1111/plb.13395

ABSTRACT

- The dry and wet seasons in the Neotropics have strong effects on soil water and nutrient availability, as well as on forest dynamics. Despite these major effects on forest ecology, little is known on how leaf traits vary throughout the seasons in tropical rainforest trees.
- Here, we investigated the influence of seasonal variations in climate and soil characteristics on leaf trait variation in two tropical tree species. We measured two leaf traits, thickness and water mass per area, in 401 individuals of two species of *Symphonia* (Clusiaceae) in the Paracou research station in French Guiana tropical lowland rainforest.
- We found a significant effect of seasonal variation on these two leaf traits. Soil relative extractable water was a strong environmental predictor of leaf trait variation in response to seasonal variation. Reduced soil water availability during the dry season was associated with increased leaf thickness and water mass per area, possibly as a result of stomatal closure.
- Our findings advocate the need to account for environmental seasonality when studying leaf traits in seasonal ecosystems such as tropical forests.

INTRODUCTION

Strong seasonal variations in precipitation determine soil water availability in tropical forests (Wagner *et al.* 2011; Bonal *et al.* 2016), leading to shifts in soil nutrient availability (Van Langenhove *et al.* 2021) and, ultimately, to variation in tree growth (Wagner *et al.* 2011) and survival (Aubry-Kientz *et al.* 2015). However, to date few studies have investigated seasonal variation of leaf functional traits in tropical forests, including leaf thickness. Gotsch *et al.* (2010) found that 26.7% of leaf trait variation was linked to seasons in Costa Rican dry and wet forests but, conversely, they found that most species had little variation in leaf thickness across seasons in both forest types. Such studies are needed to ascertain whether the seasonal variation in leaf traits must be considered for trait-based ecological research.

Leaf thickness is a functional trait, *i.e.* a phenotypic trait that impacts fitness through its effect on individual performance (Violle *et al.* 2007). Leaf thickness is part of the leaf economics spectrum in which there are two opposite ecological strategies: an acquisitive strategy with high photosynthetic carbon assimilation, or a conservative strategy with high investment in leaf defence and durability, observed among communities (Bruelheide *et al.* 2018), species (Wright *et al.* 2004), and individuals (Schmitt *et al.* 2020). For instance, leaf thickness was shown to vary with topography within and among species (Schmitt *et al.* 2020). Within individuals, studies have revealed variation in leaf traits with irradiance between shade and sun leaves (Hulshof & Swenson 2010; Osnas *et al.* 2018), which may be confounded or independent of leaf variation associated with tree height (Oldham *et al.* 2010).

A strong correlation between leaf thickness and leaf water content has been found since the early 20th century (Bachmann 1922). One of the most conspicuous metrics of water status at the leaf scale is indeed the water mass per leaf area (Tucker 1980; Seelig *et al.* 2008), which is positively linked with leaf thickness. Further, it has been shown that leaf thickness has a strong correlation with leaf relative water content (Meidner 1952; Búrquez, 1987). During the dry season, soil water shortages and high vapour pressure deficit (VPD) can lead to embolism formation in the hydraulic system (Brodribb 2017). To avoid such stressful water deficits and to prevent drought-induced damage, tree species that follow an isohydric strategy close their stomata in dry conditions to prevent dehydration and to reduce significant declines in water potential (Fisher *et al.* 2006). In contrast, anisohydric species keep their stomata open during drought. In addition, stomatal closure, induced by high VPD to prevent water loss, contributes to increasing leaf relative water content (Schulze *et al.* 1972), consequently leading to

14388677, 2022, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/plb.13395 by Cochrane France, Wiley Online Library on [22/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

14388677, 2022, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/plb.13395 by Cochrane France, Wiley Online Library on [22/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

increases in leaf thickness. In this context, experimental studies have shown that increased leaf thickness is observed under induced atmospheric or soil drought across species (Schulze *et al.* 1972; Nautiyal *et al.* 1994; Guerfel *et al.* 2009; Ennajeh *et al.* 2010).

Here, we addressed the effects of seasonal variations in climate and soil characteristics on leaf thickness and related leaf water content per area. We controlled for the effect of tree diameter, as a proxy of tree size and access to light, two factors known for their effects on leaf trait variation within individuals (Hulshof & Swenson 2010; Osnas *et al.* 2018). We measured leaf traits in a large number of individuals (401 trees, > 10 cm diameter at breast height, DBH) belonging to two Neotropical tree species in a rainforest site located in the Guiana Shield that experience marked seasonal variations in precipitation (Bonal *et al.* 2008; Aguilos *et al.* 2018), and hence in soil water availability (Bonal *et al.* 2008; Wagner et al., 2011). For instance, in 2017 the mean precipitation per month was 364 mm in the rainy season as compared to 47 mm in the dry season (months with < 100 mm precipitation *sensu* Bonal *et al.* 2008). By combining tree inventories, meteorological data and functional leaf traits, we used Bayesian modelling to study the influence of season on the variation in leaf thickness of the two tropical tree species studied. We expected seasonal effects on leaf thickness, with thicker leaves during the dry season, potentially resulting from stomatal closure to prevent water loss, thus increasing leaf water content.

MATERIAL AND METHODS

Study site

The study was conducted in the northernmost part of the Guiana Plateau region, at the Paracou field station in French Guiana. The site is characterized by average annual precipitation of 3,102 mm and average air temperature of 25.7°C (Aguilos *et al.* 2018). An ancient tropical forest grows in this area through a succession of small hills reaching 10 to 40 m in elevation (Gourlet-Fleury *et al.* 2004). We used 16 permanent inventory plots at Paracou (*i.e.* fifteen 6.25-ha plots and one 25-ha plot) where tree growth (*i.e.* DBH > 10 cm) has been surveyed every 1–2 years since 1984.

Climate data

Microclimate data for the year 2017 were extracted from the long-term climate database of the Guyaflux eddyflux site (Bonal *et al.* 2008; Aguilos *et al.* 2018). Global radiation (CNR1, Kipp and Zonen, Bohemia, NY, USA), air temperature and humidity (HMP45; Vaisala, Helsinki, Finland), rainfall (ARG100; EM, Sunderland, UK) and wind direction and speed (A05103-5; R.M. Young, Traverse City, MI, USA) were measured above the canopy on top of a 55-m high tower or at 30-m height. Vapour pressure deficit above the canopy (VPD, kPa) and Penman evapotranspiration (PET, mm) were calculated based on these measurements. A datalogger (CR23X; Campbell Scientific, Logan, UT, USA) was used to collect meteorological data at 1-min intervals and to compile data as 30-min averages or sums. Rainfall data were incorporated into a soil water balance model (Wagner *et al.* 2011) to estimate relative extractable water (REW) for trees from the soil surface down to 3 m depth.

Plant material

The genus *Symphonia* (Clusiaceae) includes the evergreen tropical rainforest trees of the botanically described species *Symphonia globulifera* L.f., which contains two locally recognized morphotypes in French Guiana, *S. globulifera sensu stricto* and *Symphonia sp. 1* (Molino & Sabatier 2001). These two morphotypes occur in sympatry but in different habitats, with *S. globulifera* preferentially growing in valley bottoms and *S. sp. 1* preferentially exploiting a variety of drier habitats (Schmitt 2020; Allié *et al.* 2015). We sampled 401 individuals of the *Symphonia* genus, 232 *S. sp. 1* and 169 *S. globulifera sensu stricto*. In 2017, the dry season (months with < 100 mm precipitation; *sensu* Bonal *et al.* 2008) lasted 3 months, from August to October. We sampled the 401 individuals (each individual sampled once) over an 8-week time period from October (dry period) to December (wet period) 2017, overlapping both the dry and rainy seasons (Fig. 1). Trees with DBH > 10 cm were randomly selected across all plots, spanning the natural distribution of tree diameters and topographic habitats. For each tree, five mature and healthy leaves were sampled at the top of the crown using a slingshot sampling device (BIG SHOT; SherillTree, Greensboro, NC, USA). To avoid desiccation, leaves were kept in darkness in humidified ziplock bags containing CO_2-enriched air. Leaf trait measurements were carried out within 6 h after sampling. Access to light for each sampled tree was visually assessed using the Dawkins index (Dawkins 1958). The sampling protocol is further described in Schmitt *et al.* (2020).

Measurement of leaf traits

We measured leaf thickness (LT, μm) on fresh leaves using a micrometer with precision of 1 μm. The average thickness of each leaf was calculated from three measurements taken on both sides of the blade, avoiding the midrib. Leaves were then oven-dried for at least 72 h and water mass per leaf area (WMA, g m^{-2}) calculated as leaf fresh weight minus dry weight divided by leaf area. Leaf fresh and dry weights were measured on an analytical balance with precision 0.001 g (Denver Instruments, New York, USA), and leaf area was quantified using the ImageJ software (Schneider *et al.* 2012) on scanned images of fresh leaves with a precision of 0.01 cm^2. The petiole was removed for all measurements.

Descriptors of leaf traits

Relative extractable water (REW; Wagner *et al.* 2011), which is the daily available soil water standardized by the potentially available water in soil, was selected from the many correlated weather descriptors (Fig. 1; Fig. S1) given its ecological significance. REW captures soil water filling and root water extraction, which are important factors in soil water dynamics and hence might represent the response of tropical forests to rainfall.

The DBH (cm) was chosen to control for tree size (O'Brien *et al.* 1995; Zhang *et al.* 2004). DBH values of sampled individuals were retrieved from the 2017 inventory of the Paracou permanent plots. Average DBH was 35.2 ± 19.0 cm for *S. globulifera* and 26.0 ± 11.0 cm for *S. sp. 1*. Given that leaf thickness has been shown to increase toward a plateau with tree

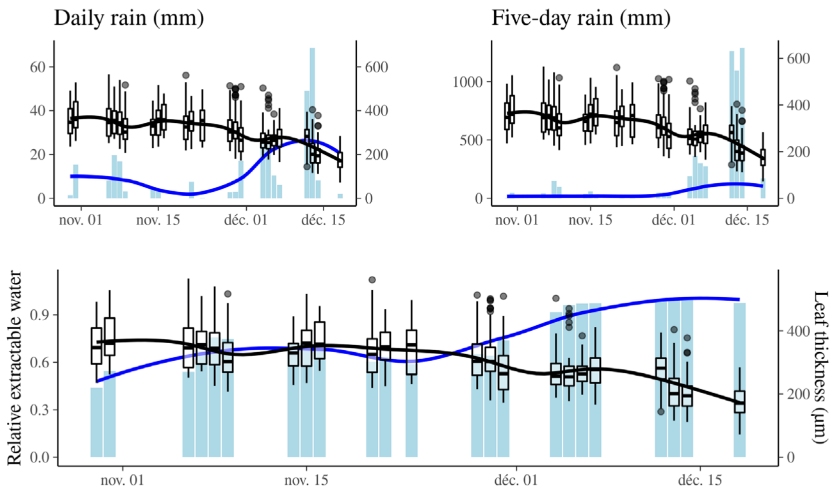

Fig. 1. Leaf thickness (µm) variation with daily and five-day rainfall (mm) and with relative extractable water between October and December 2017. Bars represent observed daily and five-day rainfall (mm) and relative extractable water between October and December, respectively from left to right and top to bottom. Black box plots represent daily and five-day distribution of measured leaf thickness among *Symphonia* individuals. Blue and black lines represent polynomial regressions for weather data and leaf thickness data, respectively.

size, we log-transformed DBH to obtain a linear effect of DBH on leaf thickness (Schmitt *et al.* 2020).

Analyses

We used linear mixed models with REW, the logarithm of DBH, and species fixed effects on the intercept and the slope of REW, combined with a random effect of individuals on the intercept, to explain functional traits (FT), *i.e.* leaf thickness (LT) and water mass per area (WMA). This was the model with better likelihood among the tested models without interaction (Fig. S2), and the interaction was not significant for this model (Fig. S3).

Functional trait $FT_{l,i,s}$ for leaf l belonging to individual $i \in [1;I]$ in species $s \in [1;S]$ was inferred with a log-normal distribution using the following formula:

$$FT_{l,i,s} \sim logN\left(\log\left[\alpha_s + \gamma_i + \beta_{REW,S}.REW_i + \beta_{DBH}.logDBH_i\right], \sigma\right)$$

With $\gamma_i \sim N(0, \sigma_I)$where α_s is the mean functional trait value of species s, γ_i is the individual random effect centred on 0 variance σ_I, and $\beta_{REW,S}$ and β_{DBH} are the slopes of REW for each species and for logDBH effects, respectively. REW and the logarithm of DBH were normalized to improve model inference and enable comparison of covariates. A Bayesian method was used to infer parameters using 'stan' language (Carpenter *et al.* 2017; stan code available in Model S1) and the 'rstan' package (Stan Development Team 2018) in the R environment (R Core Team 2020).

RESULTS

Leaf thickness (LT) and water per mass area (WMA) showed a high and significant positive correlation in *Symphonia* species in French Guiana (Pearson's R = 0.56, $P < 10^{-15}$; Fig. S1). Relative extractable water (REW) and DBH both had a significant effect on leaf thickness and WMA (Table 1, Figs 1 and 2). REW had a significant negative effect on LT (Figs 1 and 2) for both *S. globulifera* (−45 µm; Table 1) and *S. sp. 1* (−45 µm; Table 1), and a negative effect on WMA that was significant for *S. globulifera* (−15 gm^{-2}; Table 1) but was not significant for *S. sp. 1* (−4 gm^{-2}; Table 1). DBH had a significant positive effect

Table 1. Parameter estimates for the model for functional trait variation, *i.e.* leaf thickness (LT) and water mass per area, with relative extractable water (REW) and log-transformed diameter at breast height (DBH). The table includes the median ± SE of the posteriors of parameters: mean leaf trait value (α_S) for *S. globulifera* and *S. sp.1*, the slope of REW effect (β_{REW}) for *S. globulifera* and *S. sp.1*, the slope of logDBH effects on both species (β_{DBH}) and individual (σ_I) and residual (σ) variations. Significant parameters at a level of 5% are given in bold.

Parameter	Species	Leaf thickness (LT µm)	Water mass per area (WMA g m^{-2})
α_S	*S. globulifera*	**316 ± 5**	**208 ± 3**
α_S	*S. sp.1*	**284 ± 4**	**185 ± 3**
β_{REW}	*S. globulifera*	**−45 ± 5**	**−15 ± 3**
β_{REW}	*S. sp.1*	**−41 + 4**	−4 ± 2
β_{DBH}		**31 ± 3**	**11 ± 2**
σ_I		**55 ± 2**	**33 ± 1**
σ		**0.09 ± 0**	**0.19 ± 0.03**

on both LT (31 µm; Table 1, Fig. 2) and WMA (11 gm^{-2}; Table 1). To summarize, an increase in REW drove a decrease in LT and a decrease in leaf water content, while an increase in tree size drove an increase in LT and in leaf water content. Note that the addition of an interaction between REW and DBH was negative, although slightly insignificant for LT (Fig. S3), indicating that, for example, an increase in LT at low REW might be stronger for large trees than for small ones (Fig. S5).

DISCUSSION

The dry and wet seasons in the Neotropics have strong effects on soil water and nutrient availability, as well as on forest tree dynamics. Despite these major effects on forest ecology, little is known about how leaf traits vary throughout the seasons in tropical rainforest trees. In our study, we evidenced a significant effect of season through the effect of REW on two leaf traits, thickness and WMA (Fig. 1). Relative extractible water captures the most important factors in soil water dynamics in response to rainfall. We found that reduced soil water availability during the dry season increases LT and WMA. This increase in leaf thickness and water content might result from stomatal closure during the dry season (Schulze *et al.* 1972; Maroco

14388677, 2022, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/plb.13395 by Cochrane France, Wiley Online Library on [22/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

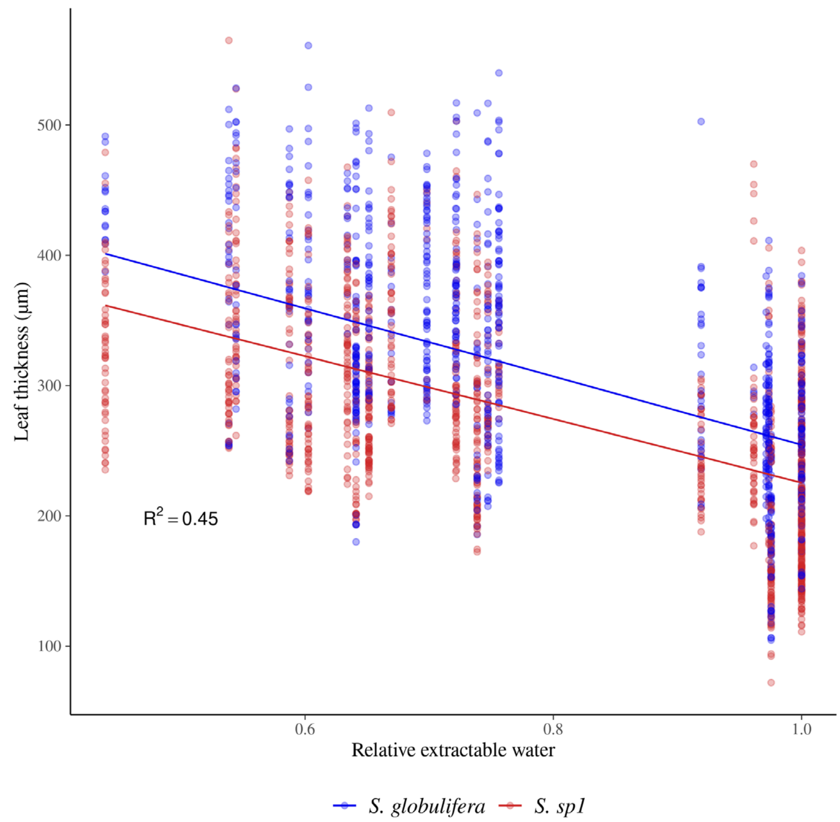

Fig. 2. Leaf thickness variation with relative extractable water. Predicted leaf thickness of species with points indicating observed leaf thickness in Paracou, and solid line leaf thickness variation with relative extractable water for a diameter at breast height fixed to the mean. The colour indicates the species, with *S. globulifera* in blue and *S. sp*.1 in red.

et al. 1997) in *Symphonia* individuals. Our results illustrate that accounting for environmental seasonality improves our understanding of the variations in leaf traits in seasonally variable ecosystems, such as tropical forests, and should therefore be carefully considered in the measurement protocols for leaf functional traits.

Thickening of leaves during the dry season

We found a strong and significant effect of season on LT and WMA, with a thickening of leaves during the dry season as a result of reduced seasonal water availability. During the dry season, plants are exposed to reduced soil water availability, which, together with increased VPD, places the plant hydraulic system under significant strain (Choat *et al*. 2018; Grossiord *et al*. 2020). Such increases in water deficit and VPD can lead to stomatal closure of isohydric species, a physiological reaction to prevent dehydration and to reduce significant declines in leaf water potential (Brodribb, 2017). *Symphonia* species might therefore respond to dry conditions by closing their stomata to cope with the water shortage. The effect of REW on LT and WMA of *Symphonia* species is larger and more significant for *S. globulifera* than for *S. sp. 1*. *Symphonia globulifera* preferentially grows in valley bottoms (Schmitt *et al*. 2021) that experience seasonal flooding, which may explain the increased response of *S. globulifera* to seasonality. This kind of stomatal behaviour has often been found for other tree species within the Amazon forests (Fisher *et al*. 2006; Stahl *et al*. 2013). Moreover, Baraloto *et al*. (2007) revealed a decrease in stomatal conductance under drought conditions for individuals of *Symphonia* species grown in greenhouse conditions, suggesting active stomatal control of water loss in *Symphonia* species. Recent studies also revealed drought avoidance in *Symphonia* species, with decreased sap flow rates in the dry season associated with very negative midday leaf water potentials (Ziegler *et al*. 2019; Ziegler 2021). Stomatal closure is known to increase leaf water content (Schulze *et al*. 1972; Maroco *et al*. 1997), which may contribute to the leaf thickening that we observed in the dry season. Furthermore, other studies have shown an increase in the thickness of palisade and spongy parenchyma of leaves experiencing low water deficits in drought-resistant species (Nautiyal *et al*. 1994; Guerfel *et al*. 2009; Ennajeh *et al*. 2010). In addition, the lack of a significant interaction between seasonality and tree size suggests an increased effect of seasonality on larger, more water-consuming trees, which should be explored in future studies.

Relative extractable water (REW) explains leaf thickening better than direct precipitation measurements (Fig. 1). REW has been shown to capture soil water dynamics in response to precipitation (Wagner *et al*. 2011). Thus, our results show that leaf thickening is mediated mainly by soil water processes rather than by a direct response to atmospheric conditions. This is because precipitation is a discrete measure of water availability, whereas REW integrates water supply and loss, through evaporation and drainage over time.

Implications for trait-based studies

Our results illustrate that accounting for seasonality improves our understanding of the variation in leaf traits in seasonally variable ecosystems, such as tropical forests. Our findings thus have strong implications for sampling design in studies measuring leaf functional traits. We encourage future studies dealing with community-wide measurements of functional traits to

14388677, 2022, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/plb.13395 by Cochrane France, Wiley Online Library on [22/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

sample within the same season to reduce potential trait variability induced by seasonal environmental variations. *A priori*, we expect seasonality to affect leaf functional traits less than other strong determinants, such as species identity ($\Delta\alpha_S > \beta_{REW,S}$). The observed effects of topography, which is related to nutrient availability (Schmitt *et al.* 2021), on leaf thickness (−0.585 and 0.07 in Schmitt *et al.* 2020) were similar or smaller than those of seasonality (−0.524 and −0.477 in this study when normalizing LT). Moreover, our study stresses the importance of measuring leaf traits with fully rehydrated leaves, following the recommendations of Pérez-Harguindeguy *et al.* (2013) in seasonally variable ecosystems. Experimental rehydration protocols have been recently established and show that, on average, detached leaves can effectively rehydrate to nearly saturated water content within ca. 8 h (John *et al.* 2018; Trueba *et al.* 2019). The application of such rehydration protocols before measurements might help to standardize leaf thickness estimations on turgid leaves closer to their saturated water content, ultimately leading to more reliable comparisons within and across studies.

The strength of the seasonal effect found here supports the need for further studies on the importance of environmental seasonality on leaf trait measurements. As stressed above, a decrease in soil water potential combined with an increase in local VPD during the dry season might drive stomatal closure to prevent desiccation. Gas exchange measurements across different seasons would allow us to confirm the hypothesis that, under dry conditions, stomatal closure is the mechanism leading to the increases in leaf thickness that we observed in *Symphonia*. Finally, to better assess seasonal variation in leaf traits, future studies should focus on repeated measurements on the same individuals or even the same leaves over time, season and years, and consider more species (Gotsh *et al.* 2010), while also controlling for tree ontogenic life stage, height and access to light.

ACKNOWLEDGEMENTS

We thank the University of Bordeaux for a PhD grant to Sylvain Schmitt. We are grateful to Pascal Petronelli and the CIRAD inventory team for their work on tree inventories and botanical identification, and to Fabien Wagner for producing the REW (relative extractable water) data. Special thanks to Saint-Omer Cazal, Anne Baranger, Josselin Cazal, Ilke Gelaldi and Fabien Lehuede for assistance during sampling in Paracou station. This study was partially funded by an Investissement d'Avenir grant of the ANR: CEBA (ANR-10-LABX-25-01).

AUTHOR CONTRIBUTIONS

SS, GD, BH and ED conceived the ideas; SS sampled individuals; SS and ED measured leaves; SS, GD, BH, ST and SC analysed outputs; SS and ST led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Functional traits data are available through the TRY initiative (Kattge *et al.* 2020) under the name ParacouITV (https://doi.org/10.17871/TRY.63). DBH and spatial positions of individuals were extracted from the Paracou Station database, for which access is modulated by the scientific director of the station (https://paracou.cirad.fr). Meteorological and relative extractable water (REW) data were extracted from the ECOFOG database and can be made available by contacting the authors.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Model S1. Stan code for the linear mixed model.
Figure S1. Correlations among leaf thickness descriptors.
Figure S2. Log-likelihood of tested models.
Figure S3. Posterior of interaction parameters for a model with interactions between REW and DBH.
Figure S4. Leaf water mass per area variation with relative extractable water.
Figure S5. Leaf thickness variation with relative extractable water for small (low DBH) and big (high DBH) individuals.

REFERENCES

Aguilos M., Stahl C., Burban B., Hérault B., Courtois E., Coste S. et al. (2018) Interannual and seasonal variations in ecosystem transpiration and water use efficiency in a tropical rainforest. *Forests*, **10**, 1999–4907.

Allié E., Pélissier R., Engel J., Petronelli P., Freycon V., Deblauwe V., Soucémarianadin L., Weigel J., Baraloto C. (2015) Pervasive local-scale tree-soil habitat association in a tropical forest community. *PLoS One*, **10**(11), e0141488. https://doi.org/10.1371/journal.pone.0141488

Aubry-Kientz M., Rossi V., Boreux J.-J., Hérault B. (2015) A joint individual-based model coupling growth and mortality reveals that tree vigor is a key component of tropical forest dynamics. *Ecology and Evolution*, **5**, 2457–2465.

Bachmann F. (1922) Studien über Dickenä nderungen von Laubblättern. *Jahrbuch F Wiss Bot*, **61**, 372–429.

Baraloto C., Morneau F., Bonal D., Blanc L., Ferry B. (2007) Seasonal water stress tolerance and habitat associations within four Neotropical tree genera. *Ecology*, **88**, 478–489.

Bonal D., Bosc A., Ponton S., Goret J.Y., Burban B.T., Gross P. et al. (2008) Impact of severe dry season on net ecosystem exchange in the Neotropical rainforest of French Guiana. *Global Change Biology*, **14**, 1917–1933.

Bonal D., Burban B., Stahl C., Wagner F., Hérault B. (2016) The response of tropical rainforests to drought – lessons from recent research and future prospects. *Annals of Forest Science*, **73**, 27–44.

Brodribb T.J. (2017) Progressing from 'functional' to mechanistic traits. *New Phytologist*, **215**, 9–11.

Bruelheide H., Dengler J., Purschke O., Lenoir J., Jiménez-Alfaro B., Hennekens S.M. et al. (2018) Global trait–environment relationships of plant communities. *Nature Ecology & Evolution*, **2**, 1906–1917.

Búrquez A. (1987) Leaf thickness and water deficit in plants: a tool for field studies. *Journal of Experimental Botany*, **38**, 109–114.

Carpenter B., Gelman A., Hoffman M.D., Lee D., Goodrich B., Betancourt M. et al. (2017) Sta: a probabilistic programming language. *Journal of Statistical Software*, **76**. www.jstatsoft.org/v76/i01/

Choat B., Brodribb T.J., Brodersen C.R., Duursma R.A., López R., Medlyn B.E. (2018) Triggers of tree mortality under drought. *Nature*, **558**, 531–539.

Dawkins H.C. (1958) The management of natural tropical high-forests with special reference to Uganda. *Imperial Forestry Institute Paper*, **34**, 1–155.

Ennajeh M., Vadel A.M., Cochard H., Khemira H. (2010) Comparative impacts of water stress on the leaf anatomy of a drought-resistant and a drought-sensitive olive cultivar. *Journal of Horticultural Science and Biotechnology*, **85**, 289–294.

Fisher R.A., Williams M., Do Vale R.L., Da Costa A.L., Meir P. (2006) Evidence from Amazonian forests is consistent with isohydric control of leaf water potential. *Plant, Cell and Environment*, **29**, 151–165.

Gotsch S.G., Powers J.S., Lerdau M.T. (2010) Leaf traits and water relations of 12 evergreen species in Costa

14388677, 2022, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/plb.13395 by Cochrane France, Wiley Online Library on [22/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Rican wet and dry forests: patterns of intra-specific variation across forests and seasons. *Plant Ecology*, **211**, 133–146.

Gourlet-Fleury S., Guehl J.-M., Laroussine O. (2004) *Ecology and management of a neotropical rainforest: lessons drawn from Paracou, a long-term experimental research site in French Guiana Ecology*. Elsevier, Paris, France. http://agritrop.cirad.fr/522004/

Grossiord C., Buckley T.N., Cernusak L.A., Novick K.A., Poulter B., Siegwolf R.T.W. et al. (2020) Plant responses to rising vapor pressure deficit. *New Phytologist*, **226**, 1550–1566.

Guerfel M., Baccouri O., Boujnah D., Chaïbi W., Zarrouk M. (2009) Impacts of water stress on gas exchange, water relations, chlorophyll content and leaf structure in the two main Tunisian olive (*Olea europaea* L.) cultivars. *Scientia Horticulturae*, **119**, 257–263.

Hulshof C.M., Swenson N.G. (2010) Variation in leaf functional trait values within and across individuals and species: an example from a Costa Rican dry forest. *Functional Ecology*, **24**, 217–223.

John G.P., Henry C., Sack L. (2018) Leaf rehydration capacity: associations with other indices of drought tolerance and environment. *Plant Cell and Environment*, **41**, 2638–2653.

Kattge J., Bönisch G., Díaz S., Lavorel S., Prentice I.C., Leadley P. et al. (2020) TRY plant trait database – enhanced coverage and open access. *Global Change Biology*, **26**, 119–188.

Maroco J.P., Pereira J.S., Chaves M.M. (1997) Stomatal responses to leaf-to-air vapour pressure deficit in Sahelian species. *Australian Journal of Plant Physiology*, **24**, 381–387.

Meidner H. (1952) An instrument for the continuous determination of leaf thickness changes in the field. *Journal of Experimental Botany*, **3**, 319–325.

Molino J.-F., Sabatier D. (2001) tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis. *Science*, **294**, 1702–1704.

Nautiyal S., Badola H.K., Pal M., Negi D.S. (1994) Plant responses to water stress: changes in growth, dry matter production, stomatal frequency and leaf anatomy. *Biologia Plantarum*, **36**, 91–97.

O'Brien S.T., Hubbell S.P., Spiro P., Condit R., Foster R.B. (1995) Diameter, height, crown, and age relationships in eight neotropical tree species. *Ecology*, **76**, 1926–1939. https://doi.org/10.2307/1940724

Oldham A.R., Sillett S.C., Tomescu A.M.F., Koch G.W. (2010) The hydrostatic gradient, not light availability, drives height-related variation in *Sequoia sempervirens* (Cupressaceae) leaf anatomy. *American Journal of Botany*, **97**, 1087–1097.

Osnas J.L.D., Katabuchi M., Kitajima K., Wright S.J., Reich P.B., Van Bael S.A. et al. (2018) Divergent drivers of leaf trait variation within species, among species, and among functional groups. *Proceedings of the National Academy of Sciences USA*, **115**, 5480–5485.

Pérez-Harguindeguy N., Diaz S., Garnier E., Lavorel S., Poorter H., Jaureguiberry P. et al. (2013) New Handbook for standardized measurement of plant functional traits worldwide. *Australian Journal of Botany*, **61**, 167–234.

R Core Team (2020) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Schmitt S. (2020) Génomique écologique de l'exploitation de niche et de la performance individuelle chez les arbres forestiers tropicaux. PhD thesis, University of Bordeaux, France. Available from: https://phdthesissylvainschmitt.netlify.app/

Schmitt S., Hérault B., Ducouret É., Baranger A., Tysklind N., Heuertz M. et al. (2020) Topography consistently drives intra- and inter-specific leaf trait variation within tree species complexes in a Neotropical forest. *Oikos*, **129**, 1521–1530. https://doi.org/10.1111/oik.07488

Schmitt S., Tysklind N., Hérault B., Heuertz M. (2021) Topography drives microgeographic adaptations of closely related species in two tropical tree species complexes. *Molecular Ecology*, **30**, 5080–5093. https://doi.org/10.1111/mec.16116.

Schneider C.A., Rasband W.S., Eliceiri K.W. (2012) NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, **9**, 671–675.

Schulze E.D., Lange O.L., Buschbom U., Kappen L., Evenari M. (1972) Stomatal responses to changes in humidity in plants growing in the desert. *Planta*, **108**, 259–270.

Seelig H.D., Hoehn A., Stodieck L.S., Klaus D.M., Adams W.W., Emery W.J. (2008) The assessment of leaf water content using leaf reflectance ratios in the visible, near-, and short-wave-infrared. *International Journal of Remote Sensing*, **29**, 3701–3713.

Stahl C., Burban B., Wagner F., Goret J.Y., Bompy F., Bonal D. (2013) Influence of seasonal variations in soil water availability on gas exchange of tropical canopy trees. *Biotropica*, **45**, 155–164.

Stan Development Team (2018) Rstan: the R interface to Stan. http://mc-stan.org/

Trueba S., Pan R., Scoffoni C., John G.P., Davis S.D., Sack L. (2019) Thresholds for leaf damage due to dehydration: declines of hydraulic function, stomatal conductance and cellular integrity precede those for photochemistry. *New Phytologist*, **223**, 134–149. https://doi.org/10.1111/nph.15779

Tucker C.J. (1980) Remote sensing of leaf water content in the near infrared. *Remote Sensing of Environment*, **10**, 23–32.

Van Langenhove L., Verryckt L.T., Stahl C., Courtois E.A., Urbina I., Grau O., Asensio D., Peguero G., Margalef O., Freycon V., Peñuelas J., Janssens I.A. (2021) Soil nutrient variation along a shallow catena in Paracou, French Guiana. *Soil Research*, **59**, 130–145.

Violle C., Navas M.-L., Vile D., Kazakou E., Fortunel C., Hummel I., Garnier E. (2007) Let the concept of trait be functional! *Oikos*, **116**(5), 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Wagner F., Hérault B., Stahl C., Bonal D., Rossi V. (2011) Modeling water availability for trees in tropical forests. *Agricultural and Forest Meteorology*, **151**, 1202–1213.

Wright I.J., Reich P.B., Westoby M., Ackerly D.D., Baruch Z., Bongers F. et al. (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.

Zhang L., Bi H., Cheng P., Davis C.J. (2004) Modeling spatial variation in tree diameter–height relationships. *Forest Ecology and Management*, **189**, 317–329.

Ziegler C. (2021) Diversité des mécanismes de résistance à la sécheresse des arbres en forêt tropicale humide. PhD thesis, Université de Lorraine, France.

Ziegler C., Coste S., Stahl C., Delzon S., Levionnois S., Cazal J. et al. (2019) Large hydraulic safety margins protect Neotropical canopy rainforest tree species against hydraulic failure during drought. *Annals of Forest Science*, **76**, 15.

14388677, 2022, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/plb.13395 by Cochrane France, Wiley Online Library on [22/12/2022]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License