Received: 30 January 2020 | Revised: 3 November 2020 | Accepted: 6 November 2020

DOI: 10.1111/geb.13231

RESEARCH PAPER

Global Ecology and Biogeography A Journal of Macroecology WILEY

Pantropical variability in tree crown allometry

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Funding information
Wallonie-Bruxelles International (WBI), Grant/Award Number: SOR/2018/366139 and SOR/2019/423370; NERC, Grant/Award Number: NE/N011570/1

Editor: Andrew Kerkhoff

Abstract

Aim: Tree crowns determine light interception, carbon and water exchange. Thus, understanding the factors causing tree crown allometry to vary at the tree and stand level matters greatly for the development of future vegetation modelling and for the calibration of remote sensing products. Nevertheless, we know little about large-scale variation and determinants in tropical tree crown allometry. In this study, we explored the continental variation in scaling exponents of site-specific crown allometry and assessed their relationships with environmental and stand-level variables in the tropics.

Location: Global tropics.
Time period: Early 21st century.
Major taxa studied: Woody plants.
Methods: Using a dataset of 87,737 trees distributed among 245 forest and savanna sites across the tropics, we fitted site-specific allometric relationships between crown dimensions (crown depth, diameter and volume) and stem diameter using power-law models. Stand-level and environmental drivers of crown allometric relationships were assessed at pantropical and continental scales.
Results: The scaling exponents of allometric relationships between stem diameter and crown dimensions were higher in savannas than in forests. We identified that continental crown models were better than pantropical crown models and that continental differences in crown allometric relationships were driven by both stand-level (wood density) and environmental (precipitation, cation exchange capacity and soil texture) variables for both tropical biomes. For a given diameter, forest trees from Asia and savanna trees from Australia had smaller crown dimensions than trees in Africa and America, with crown volumes for some Asian forest trees being smaller than those of trees in African forests.
Main conclusions: Our results provide new insight into geographical variability, with large continental differences in tropical tree crown allometry that were driven by stand-level and environmental variables. They have implications for the assessment of ecosystem function and for the monitoring of woody biomass by remote sensing techniques in the global tropics.

KEYWORDS
crown allometry, environment, forest, precipitation, savanna, soil, stand-level variable, tropical biomes

1 | INTRODUCTION

Tree crowns form the interface between the terrestrial biosphere and the atmosphere and determine light interception and gas exchange of carbon and water through photosynthesis and evapotranspiration (Santiago et al., 2004; Strigul et al., 2008). As a result, tree crowns not only influence the growth, mortality and fecundity of individual trees (Pacala et al., 1996), but they also shape the local light environment, microclimate and biogeochemical fluxes of ecosystems (Montgomery & Chazdon, 2001). Characterizing tree crowns is of increasing importance for remote sensing methods, a crucial suite of tools to improve the monitoring of terrestrial ecosystems (Jucker et al., 2017). Nowhere is this more urgent than in tropical forests and savannas, which store 40–50% of the global vegetation carbon (Pan et al., 2011). For instance, taking into account crown dimensions in tropical forests can substantially improve estimation of tree biomass at the tree scale (Goodman et al., 2014; Ploton et al., 2016) and explain plot-scale spatial variation in biomass and carbon stocks (Loubota Panzou et al., 2018; Meyer et al., 2018). However, ground measurements of tree crowns are challenging and time consuming; therefore, they are available for only few sites and trees within inventory plots.

Tree crown allometry, which describes scaling relationships between the crown dimensions (crown area, crown depth and crown volume) and more easily measurable variables, such as stem diameter, is widely used in plant ecology to quantify ecosystem functions. For a wide range of plants, the power-law model has been used to describe plant allometry between two tree dimensions (Niklas, 1994), and there has been much debate about the meaning of the power-law scaling exponents for tropical trees (Sileshi, 2014). For example, the scaling exponent from tree height–stem diameter and crown dimensions–stem diameter allometric relationships reveals mechanical constraints that prevent trees from buckling under their own weight (Greenhill, 1881; McMahon, 1971) and/or hydraulic constraints (Ryan et al., 2006). In the tropics, scaling exponents from crown allometric relationships have been shown to vary between forests and savannas, with savanna tree crowns tending to be larger for a given stem diameter than those of forest trees at the

species scale (Archibald & Bond, 2003) and the site scale (Shenkin et al., 2020). However, the scaling exponents of crown allometric relationships do not change when comparing three neighbouring forest typologies (mixed forests, edge forests and regrowth forests) that have different light availability (Sellan et al., 2017).

Previous studies showed variation in crown allometry among tropical sites or regions (Blanchard et al., 2016; Loubota Panzou et al., 2018; Moncrieff et al., 2014; Shenkin et al., 2020). At a large scale, environmental variables are important in explaining differences in crown allometry among sites or regions in tropical biomes. For a given stem diameter, longer dry seasons appear to induce narrower crowns in the forest biome (Barbier et al., 2010) and in the savanna biome (Moncrieff et al., 2014). Likewise, mean annual temperatures were negatively related to crown diameters of trees at 20 cm stem diameter in savannas (Moncrieff et al., 2014) but no consistent pattern in species crown diameters was reported in Mediterranean forests for a range of mean annual temperatures varying from *c*. 6 to 17°C (Lines et al., 2012) at a given stem diameter. Soil physical and/or chemical properties might also affect variation in crown dimensions. For example, high rainfall regimens combined with poor drainage have been found to favour small crown dimensions in certain regions of the Amazon Basin (Barbier et al., 2010). Likewise, trees in sites with high sand content tended to have small crown diameters at 20 cm stem diameter in African and Australian savannas (Moncrieff et al., 2014).

Interspecific relationships with wood density in crown allometric relationships can also reflect environmental filtering, because species with high wood density are more likely to be found in highly shaded environments (Wright et al., 2010) and on soils with lower fertility (Muller-Landau, 2004; Quesada et al., 2012). At a given tree height, species with high wood density show wider and deeper crowns than species with low wood density (Forrester et al., 2017; Iida et al., 2012). However, increased competition between individual trees has a negative influence on crown width (Forrester et al., 2017; Lines et al., 2012) and a positive influence on crown depth (Forrester et al., 2017). All else being equal, narrower crowns in savannas have been associated with higher tree densities (Moncrieff et al., 2014).

In the tropics, there have been only three studies in the whole tropics to assess tree crown allometric relationships and their drivers at a large scale (Blanchard et al., 2016; Moncrieff et al., 2014; Shenkin et al., 2020), and none has yet evaluated such relationships at the pantropical scale. Nevertheless, understanding the exact nature of crown allometry and the factors causing tree crown allometry to vary at the tree or stand level matters greatly for the development of future vegetation modelling and for the calibration of remote sensing products.

The aim of this study was to identify the determinants of crown allometry in tropical biomes by fitting site-specific crown allometric relationships between crown dimensions and stem diameter using power-law models and assessing their statistical associations with stand-level and environmental variables and their fit to theoretical predictions. We addressed two research questions. First, do scaling exponents derived from crown allometric relationships differ among tropical forests and savannas? We expect that scaling exponents from crown allometric relationships are smaller for trees in forest than in savanna at continental scale. Second, how do stand-level and environmental variables influence crown allometric relationships at pantropical and continental scales? We expect that there are continental differences in crown allometry after accounting for stand-level and environmental variables, as reported by Feldpausch et al. (2011) and Banin et al. (2012) for tree height allometries. We tested these hypotheses by assembling the largest pantropical dataset compiled to date of ground-acquired, geographically dispersed information on tree crown dimensions (crown depth, diameter and volume) from 205 forest and 40 savanna sites, totalling 87,737 trees in Africa, America, Asia and Australia (Figure 1).

2 | MATERIALS AND METHODS

2.1 | Data collection

We assembled information on tree crown dimensions available from published and unpublished sources for the two major tropical biomes: forest and savanna (for data sources, see the Appendix Table A1). We considered the limit between open-canopy (savanna) and closed-canopy (forest) systems as 50% of tree cover (Torello-Raventos et al., 2013; Veenendaal et al., 2015). For this pantropical analysis, we included sites that were unlogged areas and where ≥30 trees over a large range of stem diameter had crown dimensions measured for each site. A total of 245 sites, including 205 forest sites and 40 savanna sites, were compiled across the tropics (within 23° north and south of the Equator) from Africa, America, Asia and Australia (Figure 1). Within each site, most trees were identified to species, but unidentified trees were also kept in the database.

For each tree, we considered three crown dimensions, namely crown depth (C_{dep}, in metres), crown diameter (C_{dia}, in metres) and crown volume (C_{vol}, in cubic metres), which were associated with stem diameter (D, in centimetres) measured at breast height (1.3 m) for regular stems or above the top of the buttresses for irregular stems. The C_{dep} was defined as the depth of the crown, calculated as the difference between total tree height (H, in metres) and the bole height, defined as the height from the ground to the first living branch or to the lowest foliage (H_f, in metres). Heights were measured for most trees using a trigonometric approach with either a manual clinometer or an electronic hypsometer. The C_{dia} was the crown width or diameter for regular crowns, most often obtained from ground measurements of several crown radii (corresponding to the cardinal and inter-cardinal directions) that were averaged and multiplied by two. In a few sites, values of C_{dia} were derived from manually delimited crowns on high-resolution aerial photographs. The C_{vol} was calculated from crown depth and crown diameter, assuming an ellipsoid shape. For most crown data, the crown measurement protocols were standardized (Loubota Panzou & Feldpausch, 2020) with quality-controlled tropical crown data uploaded to ForestPlots.net (Lopez-Gonzalez et al., 2009, 2011), which includes major tropical plot networks, such

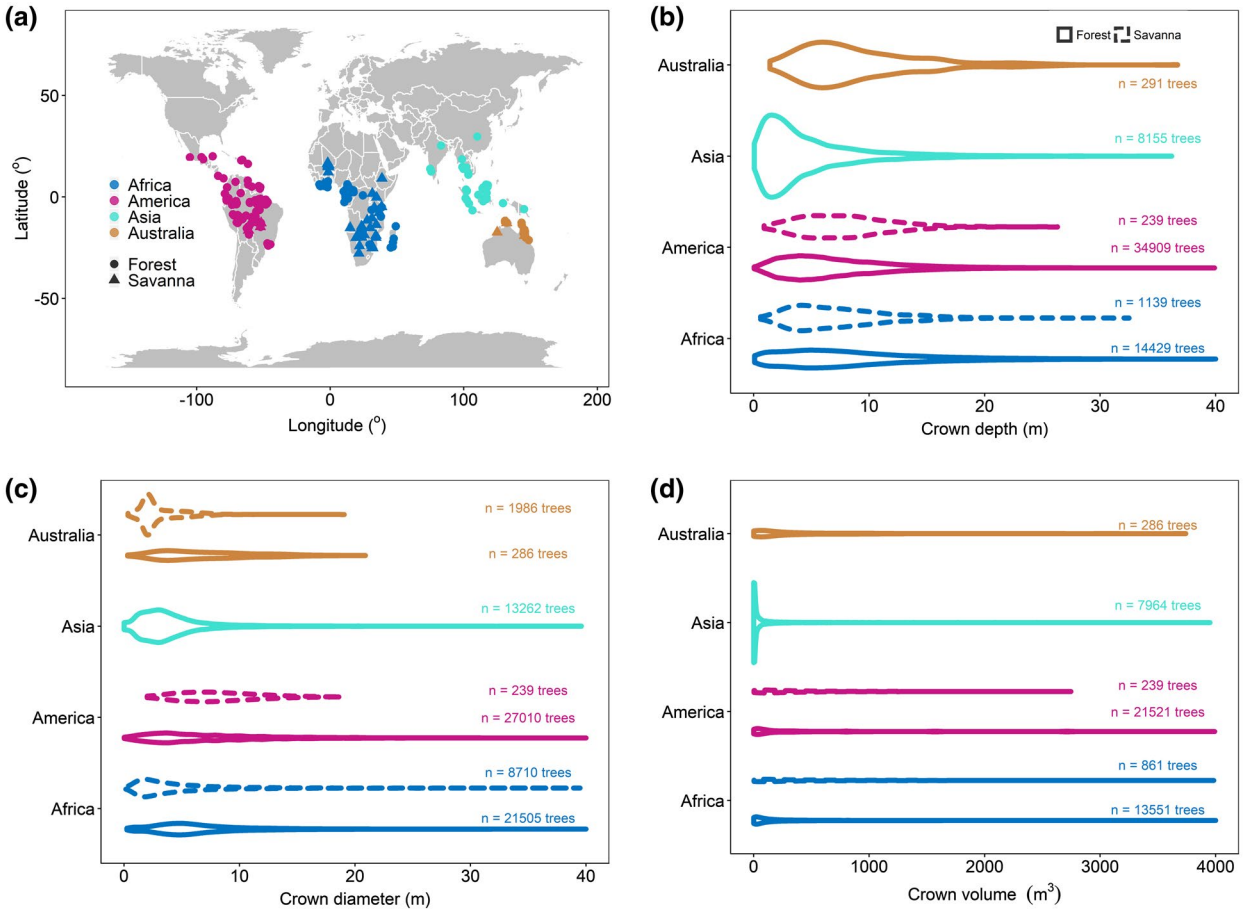

FIGURE 1 (a) Overview of the pantropical tree crown dataset for the four continents (Africa, America, Asia and Australia) including 87,737 trees from 205 forest and 40 savanna sites on a global map, with one point corresponding to a study site. (b–d) Number of samples (*n*) and the violin plots of the distribution of crown depth (b), crown diameter (c) and crown volume (d) [Colour figure can be viewed at wileyonlinelibrary.com]

as RAINFOR in Amazonia (Malhi et al., 2002; Quesada et al., 2012), AfriTRON in Africa (Lewis et al., 2009), T-FORCES in South-East Asia (Qie et al., 2017) and TROBIT at the global interface of savanna and forest (Lloyd et al., 2015). The criteria for including individual crown measurements were as follows: (a) tree stems were not broken; and (b) height measurements for determining crown depth were measured using clinometers, laser rangefinders, laser hypsometers or directly by climbing. After screening for quality control, our dataset consisted of 87,737 trees, including 59,162 trees for C_{dep}, 72,998 trees for C_{dia} and 44,422 trees for C_{vol} (Figure 1) over a large range of *D*, 0.22–293 cm in forests and 1–200 cm in savannas.

2.2 | Stand-level and environmental variables

For each site, the stand-level variables included stand structural variables, such as maximum height (H_{max}, in metres) and wood density (ρ, in grams per cubic centimetre), also known as wood specific gravity (Supporting Information Table S1). These two stand-level variables depend on the subset of trees/species selected for allometry measurements and reflect the successional stage of the studied sites, where young regenerating stands in the wet tropics will have low H_{max} and ρ relative to old-growth stands. The H_{max} was calculated for each site as the 95th percentile total height of the sampled trees. The ρ was estimated using species names that allow assignment of ρ corresponding to the species or genus average from the global wood density database (Chave et al., 2009; Zanne et al., 2009). Site-level ρ means were weighted by the number of stems of each taxon.

Using the geographical coordinates of each site, interpolated values of 16 environmental variables, including 11 climatic and five soil variables, were obtained from online global databases. Mean annual precipitation (*A*, in millimetres), the precipitation coefficient of variation (*S*), mean annual temperature (*T*, in degrees Celsius), mean annual solar radiation (*Q*, in watts per square metre), mean annual wind speed (*U*, in metres per second), mean water vapour pressure (*V*) and elevation (A_l, in metres) were obtained from WorldClim global coverage at *c*. 1 km^2 spatial resolution based on meteorological station data from 1970–2000 (Fick & Hijmans, 2017). The aridity index (A_r) and potential evapotranspiration (*P*) were extracted at *c*. 1 km^2 spatial resolution from the Consortium of Spatial Information (CGIAR-CSI) website (www.cgiar-csi.org) for data from 1970–2000 (Trabucco & Zomer, 2019).

The climate water deficit (*C*) and environmental stress factor (*E*) were obtained from the global gridded layer at 2.5 arc s resolution (http://chave.ups-tlse.fr/pantropical_allometry.htm). Two soil chemical properties [pH in water (*pH*) and cation exchange capacity (*CEC*)] and three soil physical properties [sand content (50–2,000 μm), silt content (2–50 μm) and clay content (0–2 μm) mass fraction] were extracted from the SOILGRIDS project (https://soilgrids.org/, licensed by ISRIC, World Soil Information), downloaded at 250 m resolution. We generated predictions at seven standard depths for all numerical soil properties: 0, 5, 15, 30, 60, 100 and 200 cm. Averages over (standard) depth intervals, 0–30 cm, were derived by taking a weighted average of the predictions within the depth interval using the method developed by Hengl et al. (2017).

To avoid collinearity and reduce the number of environmental variables to test in our models, we retained only weakly correlated variables ($|r| < .6$) for modelling purposes. For the analyses, we retained four climate variables (*A*, *S*, *Q* and *U*), four soil variables (*CEC*, *pH*, *clay* and *silt*) and the two stand-level variables (H_{max} and ρ). The median and range of key site-level environmental and stand variables by continent are shown in the Supporting Information (Table S1).

2.3 | Data analysis

As a preliminary analysis, we ignored site-level differences and aggregated data for all sites within each continent according to three stem diameter (*D*) classes: the lower stratum with small trees ($D \leq 20$ cm), the middle stratum with large trees, most of which reach the canopy (20 cm $< D \leq 40$ cm), and the upper stratum corresponding to the largest trees, which are either in the canopy or emergent, with $D > 40$ cm. This distribution of three stem diameter classes has been used to take into account the variability in crown dimensions that can exist between different strata of the ecosystem, as shown by several studies on forest structure in the tropics (Bastin et al., 2018; Slik et al., 2013). Given the non-normality and skewed distributions of the data, we used the nonparametric Kruskal–Wallis rank sum test to evaluate differences in crown dimensions by continent according to stem diameter classes. For the nonparametric Kruskal–Wallis test (Hollander & Wolfe, 1973), the null hypothesis was "no difference between medians for each variable". When the null hypothesis was rejected, we conducted post hoc Kruskal–Wallis multiple comparisons between medians (Siegel & Castellan, 1988).

Crown allometric relationships were fitted between crown dimensions and stem diameter using power model ($Y \sim \beta D^{\alpha} + e_i$) which is linearized via the $\log_{10}$-transformation:

$$\log(y_i) = \beta + \alpha \times \log(D_i) + e_i \quad (1)$$

where α and β are the scaling exponent (slope) and intercept, respectively, *e* is the error term, *D* is stem diameter, and *y* represents crown depth, crown diameter or crown volume of tree *i*.

To investigate variation in the scaling exponent among crown dimensions–stem diameter allometric relationships, we first estimated the model coefficients (intercept and slope) from crown allometric relationships for each site and the means across sites for each continent. Next, we used Student's unpaired *t* tests to compare the means of scaling exponents for crown allometric relationships at the continental level between the forest and savanna.

To examine how crown–stem diameter allometric relationships at the tree level were influenced by stand-level (H_{max} and ρ) and environmental variables (*A*, *S*, *Q*, *U*, *CEC*, *pH*, *clay* and *silt*), log–log regressions were used. In these regressions, $\log_{10}$-transformed crown dimensions (depth, diameter and volume) were the response variable and $\log_{10}$-transformed stem diameter was an independent variable. These regressions were performed as mixed-effects linear models, where site (nested in geographical location) was incorporated as a random effect factor. The incorporation of appropriate random effects ensured that the model parameters were accurate and appropriate to generalize the conclusions (Bolker et al., 2009). Four alternative log–log mixed-effect regressions were tested: (1) a null crown dimensions–stem diameter allometric model without stand-level or environmental predictors; (2) a crown dimensions–stem diameter allometric model with stand-level variables; (3) a crown dimensions–stem diameter allometric model with environmental variables; and (4) a crown dimensions–stem diameter allometric model including stand-level and environmental variables. Stand-level and environmental attributes were incorporated as fixed-effect factors affecting the intercept and the slope (interaction between each stand-level and environmental variable with stem diameter) in models 2, 3 and 4 as appropriate. These four alternative models were performed at the pantropical and the continental scales, with the continent as a fixed-effect factor affecting the intercept and the slope between crown dimensions and stem diameter. A total of eight alternative log–log mixed-effect regressions were tested for each response variable at both pantropical and continental scales. These eight crown dimensions–stem diameter allometric models were fitted for forest and savanna biomes separately, with model selection based on the lowest Akaike information criterion (AIC) and Bayesian information criterion (BIC) values (Burnham & Anderson, 2002). A pseudo-*R*-squared (R^2) for log–log mixed regressions was used to assess the quality of model fit. We report both the marginal R^2 (R^2_m), which includes the variance of fixed factors, and the conditional R^2 (R^2_c), which includes the variance of both the fixed and random factors and is, as a result, always higher (Nakagawa & Schielzeth, 2013).

All statistical analyses were computed using the open-source R environment (R Core Team, 2018), using the following packages: "lme4" for linear mixed regression (Bates et al., 2015); "MuMIn" for calculating pseudo-*R*-squared (R^2) values for linear mixed regression (Barton, 2019); PGIRMESS package for post hoc test (Giraudoux, 2013); and "ggplot2" for graphical outputs (Wickham, 2016). The conditions of normality and homoscedasticity of residuals were checked graphically and with Shapiro–Wilk and Breusch–Pagan tests, respectively. When these conditions were invalidated, a nonparametric test (Kruskal–Wallis rank sum test) was used to test the differences in crown dimensions. We chose nonparametric tests because most of the variables had skewed

distributions that would have required data transformations to meet the assumptions of parametric tests.

3 | RESULTS

3.1 | Overview of the pantropical crown dimensions

Intercontinental differences in crown dimensions were visible through all three stem diameter classes (Figure 2). Following the stem diameter classes, the rank order of crown size for each continent was from largest to smallest for forest trees. The patterns were less clear for savanna trees. The differences of tree crowns between Africa and America were substantial but differed by biome. African trees had larger median crown dimensions for forests, and American trees had the larger median crown dimensions for savannas. Interestingly, the differences between Africa and Australia in all crown dimensions could be observed solely in the smallest stem diameter class for forest trees, and for crown diameter in the highest stem diameter class for the savanna trees.

3.2 | Scaling exponent of crown allometry

Our pantropical analysis provided strong support for the hypothesis that the scaling of crown dimensions–stem diameter allometric relationships differed between trees in savanna compared with trees in forest at the continental scale (Figure 3). For all trees together in each biome, the mean scaling exponent of crown allometric relationships tended to be significantly higher in savanna than in forest (Table 1).

3.3 | Continental–stand–environment model

Crown dimensions–stem diameter allometric relationships including a continent effect had a slightly better fit to the data, based on

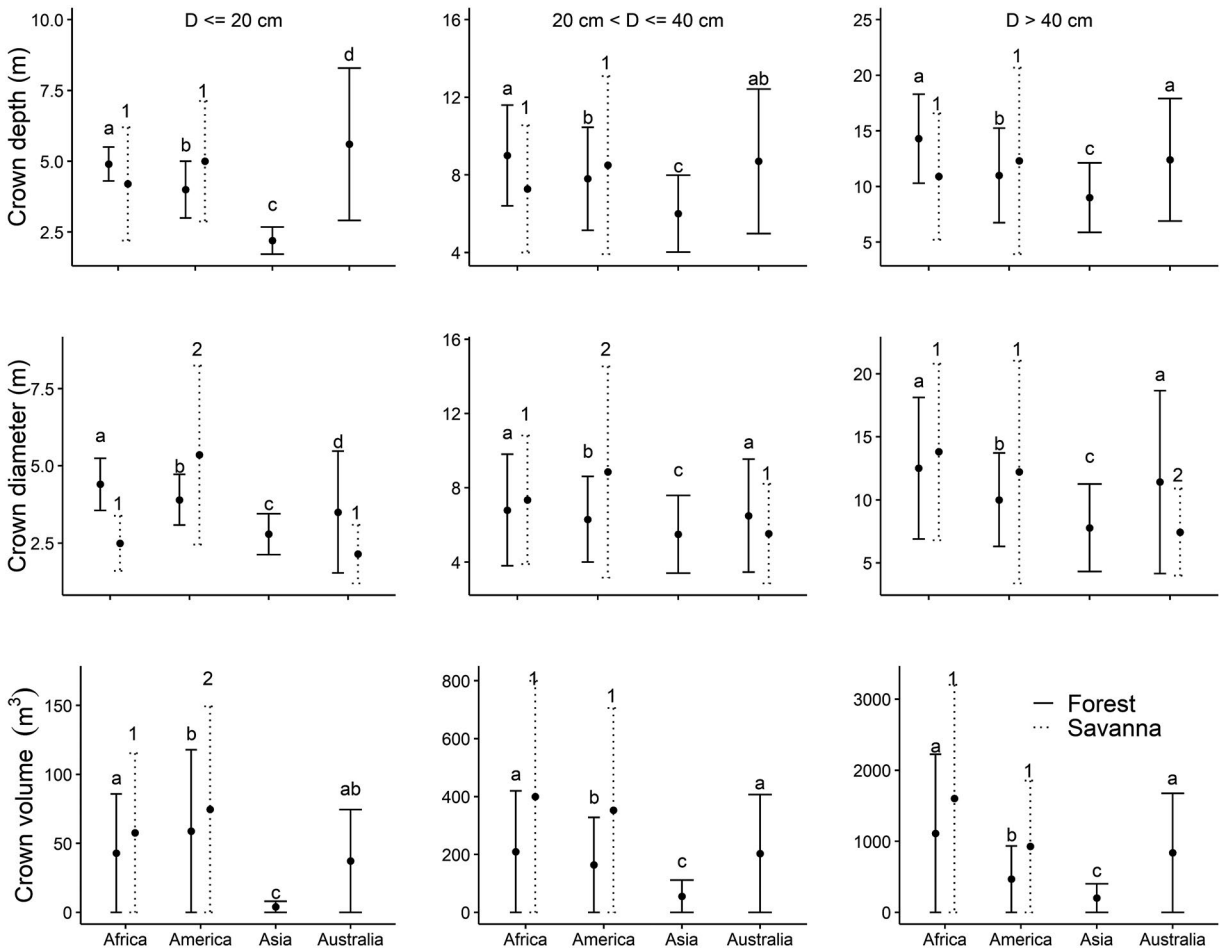

FIGURE 2 Distribution of crown depth, crown diameter and crown volume according to three stem diameter (*D*) classes: the lower stratum with small trees ($D \leq 20$ cm), the middle stratum with large trees, most of which reach the canopy ($20 \text{ cm} < D \leq 40$ cm), and the upper stratum corresponding to the largest trees, which were either in the canopy or emergent, with $D > 40$ cm. Lines with median (filled circle) indicate upper and lower .05 quantiles for crown depth and crown diameter or .5 quantiles for crown volume. Different letters and numbers within each panel indicate significant differences ($p < .05$ with Kruskal–Wallis test) among continents for the forest and savanna biome, respectively

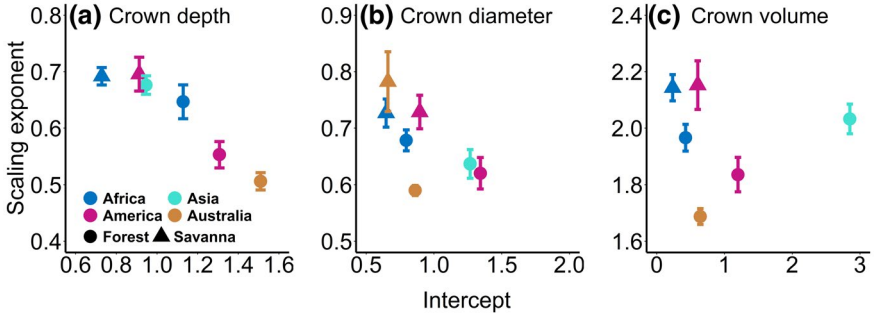

FIGURE 3 Crown allometric relationships between stem diameter and: (a) crown depth; (b) crown diameter; and (c) crown volume, for each continent in the forest and savanna. Mean values of the model coefficients with 95% confidence intervals of the scaling exponent [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Mean and 95% confidence interval [lower–upper] of scaling exponent with Student's unpaired *t* test (*p*-value) for the significant differences between forest and savanna for crown depth–stem diameter (C_{dep}–*D* allometry), crown diameter–stem diameter (C_{dia}–*D* allometry) and crown volume–stem diameter (C_{vol}–*D* allometry) allometries

	C_{dep}–*D* allometry	C_{dia}–*D* allometry	C_{vol}–*D* allometry
Forest	0.60 [0.47–0.72]	0.63 [0.57–0.69]	1.88 [1.64–2.12]
Savanna	0.69 [0.67–0.72]	0.75 [0.67–0.82]	2.15 [2.10–2.21]
p-value	.015	.003	.036

AIC and BIC values, than the general pantropical models for four alternative log–log mixed regressions in both biomes (Table 2). At the continental scale, the goodness-of-fit (R^2_m and R^2_c) of both biomes was high for four alternative log–log mixed regressions, with an average of R^2_m = .52 (range = .45–.59) and R^2_c = .61 (range = .56–.65) for crown depth–stem diameter allometric relationships, R^2_m = .55 (range = .38–.72) and R^2_c = .80 (range = .62–.99) for crown diameter–stem diameter allometric relationships, and R^2_m = .55 (range = .31–.77) and R^2_c = .77 (range = .73–.80) for crown volume–stem diameter allometric relationships (Table 2). Among the four alternative log–log mixed regressions, we identified that continental models including both stand-level and environmental variables were the best models (Table 2), indicating that continental crown allometric relationships were influenced by both stand-level and environmental variables rather than by only one set of variables in both biomes.

The precipitation influenced the slope and the intercept of crown allometric relationships in both biomes (Supporting Information Table S2). A higher scaling exponent from crown allometric relationships was related negatively to precipitation. The wind speed and solar radiation were also significant in crown allometric relationships in the forest biome. For the same stem diameter, trees with deeper and wider crowns were associated with higher wind speed and lower solar radiation in the forest biome. In addition, the soil chemical properties (*CEC*) and soil texture (*silt* and *clay*) showed contrasting influence on the slopes and intercepts of crown allometric relationships in both biomes (Supporting Information Table S2). For a given stem diameter, high *CEC* was associated with deeper and narrower crowns than low *CEC*. Crown depth was associated positively with *clay* and negatively with *silt* content, whereas the crown diameter and crown volume were associated negatively with *clay* and *silt* contents for the same stem diameter. Finally, the wood density was the main stand-level variable that influenced the crown depth–stem diameter allometry positively and the crown volume–stem diameter allometry negatively (Supporting Information Table S2).

When the same best crown dimensions–stem diameter allometric model, which includes environmental variables and stand-level variables, was applied to all continents (Table 3), trees from Asian forest and from Australian savanna had lower crown dimensions than trees in Africa and America (Figure 4). The one exception was that crown diameters for Australian savanna trees were similarly small to the crown diameters of Asian forest trees. This indicates that Asian forest trees and Australian savanna trees had different crown allometric relationships compared with all the other regions, even taking into account the environmental and stand variables used in this study.

4 | DISCUSSION

In this study, we found that stand-level (wood density) and environmental (precipitation, *CEC* and soil texture) variables explained the variation of crown dimensions–stem diameter allometric relationships within both tropical biomes. Crown allometric relationships differed between trees in savanna compared with trees in forest. Scaling exponents for savanna trees tended to be much higher compared with that of forest trees. The comparison of models among continents highlighted that forest trees from Asia and savanna trees from Australia have smaller crown dimensions than trees in Africa and America. Our results provide new important insights into the geographical variability of tropical tree crown allometry, which will improve the assessment of woody biomass by remote sensing techniques in the tropics.

4.1 | Contrasting crown allometry between forest and savanna trees

The hypothesis of contrasting crown dimensions–stem diameter allometric relationships between the two major tropical biomes has been confirmed by this study, in agreement with the results of

TABLE 2 Summary of statistical tests using mixed-effects models to determine the effects of structural and environmental (climate and soil) variables for crown depth–stem diameter (C_{dep}–D allometry), crown diameter–stem diameter (C_{dia}–D allometry) and crown volume–stem diameter (C_{vol}–D allometry) allometries in the forest and savanna biomes

	C_{dep}–D allometry				C_{dia}–D allometry				C_{vol}–D allometry			
	AIC	BIC	R^2_m	R^2_c	AIC	BIC	R^2_m	R^2_c	AIC	BIC	R^2_m	R^2_c
Forest												
Pantropical model												
Simple	90,067	90,103	.48	.56	90,112	90,148	.43	.68	141,963	141,997	.37	.78
Stand-level only	73,786	73,857	.51	.57	70,583	70,652	.41	.61	114,225	114,292	.34	.72
Environment only	66,862	67,036	.45	.57	82,202	82,382	.32	.99	127,575	127,575	.31	.78
Stand + environment	51,930	52,134	.55	.62	63,003	63,210	.31	.99	102,587	102,587	.30	.73
Continental model												
Simple	89,748	89,838	.49	.56	89,730	89,820	.42	.68	141,653	141,739	.40	.78
Stand-level only	73,701	73,824	.51	.57	70,263	70,385	.42	.62	114,016	114,135	.36	.73
Environment only	66,684	66,910	.45	.57	82,159	82,392	.38	.99	127,388	127,610	.34	.78
Stand + environment	**51,768**	**52,023**	**.55**	**.62**	**62,882**	**63,140**	**.40**	**.99**	**102,394**	**102,644**	**.31**	**.74**
Savanna												
Pantropical model												
Simple	1,225	1,246	.52	.64	10,093	10,122	.64	.74	2,488	2,508	.73	.77
Stand-level only	1,245	1,277	.52	.64	10,000	10,044	.68	.75	2,492	2,522	.74	.78
Environment only	**1,083**	**1,114**	**.53**	**.66**	6,512	6,554	.67	.77	2,143	2,172	.73	.78
Stand + environment	1,103	1,144	.53	.66	6,335	6,391	.71	.79	2,148	2,187	.76	.79
Continental model												
Simple	1,234	1,265	.52	.64	9,359	9,418	.69	.76	2,490	2,520	.72	.77
Stand-level only	1,253	1,295	.52	.64	9,372	9,445	.72	.77	2,494	2,534	.74	.78
Environment only	1,089	1,130	.52	.65	6,242	6,312	.66	.79	2,135	2,174	.77	.80
Stand + environment	1,101	1,152	.59	.62	**6,251**	**6,335**	**.70**	**.80**	**2,132**	**2,180**	**.77**	**.80**

Note: Significant relationships are shown in bold. Common indices [Akaike information criterion (AIC) and Bayesian information criterion (BIC) values] with marginal R^2 (R^2_m) and conditional R^2 (R^2_c) for four alternative log–log mixed regressions: a null model without fixed effects (simple); a model with stand-level variables (stand); a model with environmental variables (environment); and a model including stand-level and environmental variables (all), at pantropical and continental scales.

Shenkin et al. (2020). Our results indicated that the scaling exponent derived from crown allometric relationships tended to be much higher in savanna than in forest (Figure 3). Small-sized trees in savanna had smaller crowns, but large-sized trees had larger crowns than in forest. The allocation to vertical and lateral crown growth increases at larger stem diameters in savannas, but is less marked for large individuals in forests (Muller-Landau et al., 2006). The differences in scaling exponent between forest (closed canopy) trees and savanna (open canopy) trees are probably also related to light availability, which is central to metabolic scaling theory (MST) predictions (Muller-Landau et al., 2006). Crown scaling exponents from MST varied across environmental gradients and biogeographical regions (Shenkin et al., 2020). For all trees together, the scaling exponent of the open canopy tended to be close to the MST predictions. Savannas are open systems that do not form closed canopies (Ratnam et al., 2011); therefore, the consistency of savanna trees with MST predictions might be attributable to the development of the height and width of tree crowns being unconstrained by competition for light. In this way, trees could achieve the optimal relationship among crown dimensions and stem diameter predicted by the MST model. In contrast, previous studies showed the lack of correspondence of observed crown scaling allometry of the closed canopy to MST predictions (Blanchard et al., 2016; Muller-Landau et al., 2006).

Specific environmental conditions within each tropical biome could also explain the difference in scaling exponents between the savanna and the forest. The higher scaling exponent values in savanna trees might be related to two important factors: fire and herbivory. Savanna trees develop specific ecological strategies to reduce the risk of being killed by fire, a key element of mortality for savanna trees. Individuals with smaller stem diameter have a higher vulnerability to vascular cambium and xylem damage from fire (Lawes et al., 2011; Ryan & Williams, 2011). Likewise, browsing pressure by large mammals that roam in savanna areas should be important, and might alter crowns of small trees. For instance, wider canopies in savanna might protect inner canopy leaves from herbivory by non-arboreal mammals (Archibald & Bond, 2003). In this study, we found smaller scaling exponent values for crown allometric relationships for forest trees. The scaling relationships between crown dimensions and stem

TABLE 3 The fitted model has be written in terms of its fixed effects only, including (H_{max} = maximum height; ρ = wood density,) and environmental (*A* = precipitation; *CEC* = cation exchange capacity; *pH*, *silt* and *clay* content; *Q* = solar radiation; *S* = precipitation seasonality; *U* = wind speed) variables for crown depth–stem diameter (C_{dep}–*D* allometry), crown diameter–stem diameter (C_{dia}–*D* allometry) and crown volume–stem diameter (C_{vol}–*D* allometry) allometries in the forest and savanna biomes

	C_{dep}–*D* allometry	C_{dia}–*D* allometry	C_{vol}–*D* allometry
Forest biome			
Pantropical	$\log(C_{dep}) = 0.052 + 0.648 \times \log(D) + 0.141 \times H_{max} + 0.339 \times 0.085 \times \rho \times \log(D) + 0.049 \times U \times \log(D) + 0.190 \times 0.057 \times S \times \log(D) + 0.234 \times A - 0.066 \times A \times \log(D) - 0.153 \times CEC + 0.047 \times CEC \times \log(D) + 0.294 \times pH - 0.135 \times pH \times \log(D) - 0.106 \times silt + 0.022 \times silt \times \log(D) - 0.101 \times clay - 0.032 \times clay \times \log(D)$	$\log(C_{dia}) = 0.526 + 0.718 \times \log(D) - 0.060 \times H_{max} \times \log(D) + 0.053 \times \rho \times \log(D) - 13.160 \times U + 0.033 \times U \times \log(D) - 3.671 \times Q + 0.042 \times Q \times \log(D) - 7.052 \times S + 0.104 \times S \times \log(D) + 0.297 \times A - 0.104 \times A \times \log(D) + 0.091 \times CEC - 0.028 \times CEC \times \log(D) + 0.282 \times pH - 0.064 \times pH \times \log(D) + 0.227 \times silt - 0.062 \times silt \times \log(D) - 0.423 \times clay + 0.102 \times clay \times \log(D)$	$\log(C_{vol}) = 0.815 + 1.561 \times \log(D) - 0.152 \times H_{max} \times \log(D) - 0.615 \times \rho + 0.131 \times \rho \times \log(D) - 0.425 \times S + 0.160 \times S \times \log(D) + 1.108 \times A - 0.349 \times A \times \log(D) + 0.579 \times CEC - 0.152 \times CEC \times \log(D) - 2.811 \times pH + 0.783 \times pH \times \log(D) + 0.221 \times silt - 0.075 \times silt \times \log(D) - 1.937 \times clay + 0.413 \times clay \times \log(D)$
Continental	$\log(C_{dep}) = \beta_c + \alpha_c \times \log(D) + 0.029 \times H_{max} \times \log(D) + 0.331 \times \rho - 0.083 \times \rho \times \log(D) - 0.171 \times U + 0.092 \times U \times \log(D) + 0.088 \times Q - 0.027 \times Q \times \log(D) - 0.070 \times S + 0.024 \times S \times \log(D) + 0.159 \times A - 0.040 \times A \times \log(D) - 0.162 \times CEC + 0.049 \times CEC \times \log(D) + 0.202 \times pH - 0.094 \times pH \times \log(D) - 0.076 \times silt + 0.012 \times silt \times \log(D) - 0.066 \times clay - 0.044 \times clay \times \log(D)$	$\log(C_{dia}) = \beta_c + \alpha_c \times \log(D) - 0.092 \times H_{max} \times \log(D) + 0.058 \times \rho \times \log(D) + 13.190 \times U + 0.033 \times U \times \log(D) - 3.719 \times Q + 0.057 \times Q \times \log(D) - 7.002 \times S + 0.092 \times S \times \log(D) + 0.256 \times A - 0.088 \times A \times \log(D) + 0.082 \times CEC - 0.025 \times CEC \times \log(D) + 0.270 \times pH - 0.069 \times pH \times \log(D) + 0.225 \times silt - 0.060 \times silt \times \log(D) - 0.449 \times clay + 0.115 \times clay \times \log(D)$	$\log(C_{vol}) = \beta_c + \alpha_c \times \log(D) - 0.146 \times H_{max} \times \log(D) - 0.611 \times \rho + 0.114 \times \rho \times \log(D) + 0.095 \times S \times \log(D) + 1.213 \times A - 0.386 \times A \times \log(D) + 0.468 \times CEC - 0.119 \times CEC \times \log(D) - 2.680 \times pH + 0.755 \times pH \times \log(D) + 0.303 \times silt - 0.096 \times silt \times \log(D) - 1.947 \times clay + 0.414 \times clay \times \log(D)$
Africa	$\beta_c = 0.187$ and $\alpha_c = 0.607$	$\beta_c = 6.150$ and $\alpha_c = 0.820$	$\beta_c = 0.648$ and $\alpha_c = 1.528$
America	$\beta_c = -0.186$ and $\alpha_c = 0.012$	$\beta_c = -4.830$ and $\alpha_c = -0.087$	$\beta_c = -0.063$ and $\alpha_c = 0.102$
Asia	$\beta_c = -0.727$ and $\alpha_c = 0.221$	$\beta_c = -3.148$ and $\alpha_c = -0.160$	$\beta_c = -0.179$ and $\alpha_c = -0.014$
Australia	$\beta_c = 0.838$ and $\alpha_c = -0.314$	$\beta_c = -21.820$ and $\alpha_c = -0.414$	$\beta_c = 1.666$ and $\alpha_c = -0.259$
Savanna biome			
Pantropical	$\log(C_{dep}) = -11.466 + 3.498 \times \log(D) + 1.668 \times H_{max} + 0.1700 \times \rho + 6.219 \times Q - 2.458 \times S - 7.578 \times CEC + 18.890 \times pH - 4.600 \times clay$	$\log(C_{dia}) = -0.134 + 0.529 \times \log(D) + 0.127 \times \rho - 0.022 \times \rho \times \log(D) - 0.075 \times U \times \log(D) - 0.111 \times Q \times \log(D) - 0.177 \times S + 0.134 \times S \times \log(D) + 0.352 \times A - 0.139 \times A \times \log(D) + 0.462 \times pH + 0.622 \times silt - 0.191 \times silt \times \log(D) - 0.383 \times clay + 0.166 \times clay \times \log(D)$	$\log(C_{vol}) = 4.016 + 1.455 \times \log(D) - 0.897 \times H_{max} \times \log(D)$
Continental	$\log(C_{dep}) = \beta_c + \alpha_c \times \log(D) + 1.376 \times H_{max} + 1.945 \times \rho + 6.859 \times Q - 5.149 \times CEC + 17.889 \times pH$	$\log(C_{dia}) = \beta_c + \alpha_c \times \log(D) + 0.107 \times \rho - 0.067 \times U \times \log(D) - 0.122 \times Q \times \log(D) - 0.163 \times S + 0.122 \times S \times \log(D) - 0.128 \times A \times \log(D) + 0.603 \times silt - 0.181 \times silt \times \log(D) - 0.404 \times clay + 0.153 \times clay \times \log(D)$	$\log(C_{vol}) = \beta_c + \alpha_c \times \log(D) - 0.861 \times H_{max} \times \log(D)$
Africa	$\beta_c = -10.156$ and $\alpha_c = 3.222$	$\beta_c = -0.240$ and $\alpha_c = 0.571$	$\beta_c = 4.684$ and $\alpha_c = 1.248$
America	$\beta_c = 2.565$ and $\alpha_c = -0.541$	$\beta_c = 0.442$ and $\alpha_c = -0.125$	$\beta_c = 2.497$ and $\alpha_c = -0.775$
Australia	Not assessed	$\beta_c = 0.150$ and $\alpha_c = -0.024$	Not assessed

diameter govern how forest trees utilize canopy space and compete for light (Farrior et al., 2016; Muller-Landau et al., 2006). Once trees are freed from competition for light in the understorey, the dramatic increase in light availability elicits a change in the pattern of resource allocation towards more investment in lateral crown expansion in the canopy and less investment in height growth (Alves & Santos, 2002; Barthélémy & Caraglio, 2007).

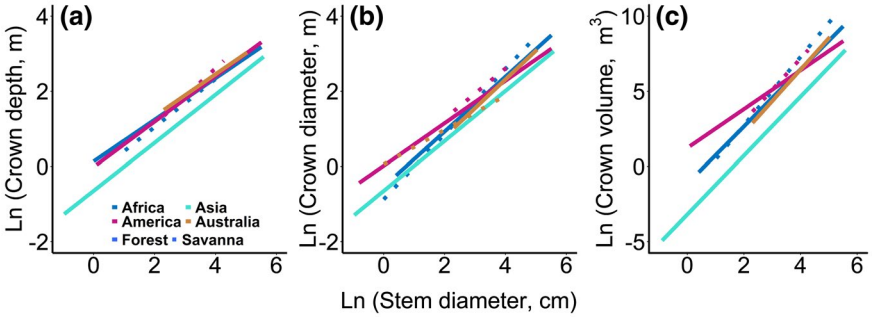

FIGURE 4 Between-continents differences using fixed-effects of mixed linear models with significant determinants (stand-level and environmental variables) from crown allometric relationships between ln(stem diameter) and: (a) ln(crown depth); (b) ln(crown diameter); and (c) ln(crown volume), in the forest (continuous lines) and savanna (dashed lines) [Colour figure can be viewed at wileyonlinelibrary.com]

4.2 | Determinants of the tropical crown allometry

Allometric relationships indicate how trees modify and react to their growing patterns and provide clues about the physiological, mechanical and environmental factors that constrain their development. Taking into account stand-level and environmental variables in crown dimensions–stem diameter allometry improved continental crown allometric models. The best continental–stand–environment models in tree crown allometries included climate (precipitation and wind speed), soil texture and stand-level variables.

Annual precipitation and precipitation seasonality significantly influenced crown dimensions–stem diameter allometric relationships across continents for the two tropical biomes. Crown dimensions at a given stem diameter were negatively related to precipitation for forest trees, indicating that water impacts tree allocation to crown development. At the lower end of the rainfall gradient, forest trees developed deeper and larger crowns compared with savanna trees. The positive correlation of crown dimensions with precipitation seasonality might indicate that lack of soil water availability for trees in both biomes, especially during the dry season, can promote crown lateral development. Likewise, wind speed had positive effects in crown allometric relationships for forest trees. In sites with high average wind speeds, trees developed deeper and wider crowns compared with forests having low average wind speeds. Tropical forest trees develop larger crowns at smaller stem sizes in response to wind dynamic loading. In contrast, tropical savanna regions have markedly higher average annual wind velocities (Supporting Information Table S1), with negative effects on crown allometric relationships (Supporting Information Table S2). These high average wind speeds are likely to perturb the display of individual leaves, branches and tree crowns, resulting in increased light availability. In addition, low solar radiation was associated with deeper and narrower crowns in the forest and wider crowns in the savanna (Supporting Information Table S2). This could be explained by there being less lateral light availability owing to neighbouring canopies in forest compared with the more widely spaced canopies in savanna (Forrester et al., 2018).

Soil variables were also environmental determinants of crown allometry and explained continental differences in crown allometric relationships in tropical forests. In general, crown width and volume, but not crown depth, were negatively related to silt and clay content for forest trees. Forest sites on clay-rich soils had shallower and narrower crowns than trees growing on sandy soils. This indicates that water availability is a key factor, with drier, well-drained, coarse-textured soils supporting higher crown dimensions, as shown in the Amazon (Barbier et al., 2010).

Lastly, wood density had a significant influence in the forest crown allometric models. Forest trees with low wood density were able to increase crown depth substantially with stem diameter in tall canopy forest trees. Tall, mature forests usually consist of species with high wood density, with branches that persist for a longer time in deeper crowns because the leaves can be stacked in more layers (Slik, 2005).

4.3 | Continental differences in tropical crown allometry

Crown dimensions–stem diameter allometric relationships differed substantially across continents for the two tropical biomes, but these differences were better explained by the differing stand-level and environmental variables found on each continent than by biogeography. This indicates that crown dimensions could be predicted with some certainty for tropical areas, even those with access limitations, based solely on environmental data that are available from global databases, rather than stand-level variables.

However, there were still some differences among continents that could not be accounted for by the model that included environment and structural variables. Comparing models in each continent, forest trees from Asia and savanna trees from Australia have smaller crown dimensions than trees in Africa and America. Differences in savanna allometry among continents might relate to the different evolutionary histories of African and Australian savannas, which share no woody species (Moncrieff et al., 2014). Likewise, evolutionary history that affects crown allometric relationships might also explain the differences between Asian versus African and American tropical forest allometries. Asian forest trees are dominated by the Dipterocarpaceae, which have higher height–stem diameter allometry and lower wood density (Banin et al., 2012; Feldpausch

et al., 2011) and tended to have significantly smaller crowns than trees in African and American forests. Moreover, for the tall, wind-dispersed trees that dominate Asian forests, a narrower crown would increase wind exposure of seeds within the crown, aiding transport from the mother tree. In contrast, animal or ballistic dispersal dominate African and American forests, and the broad, stretching crown and massive branches are well suited for dropping these heavy fruits from a great height and helping spread away from the tree (Malhi et al., 2018). The understorey of Asian forests is dominated by juveniles of canopy species with smaller crowns, whereas the understorey of American forests is reported to have a greater proportion of sub-canopy species with larger crowns (LaFrankie et al., 2006). In contrast, there is a unique phytogeographical affinity between African and American forests that is likely to be attributable to the dominance of a particular lineage, the Fabaceae, the most basal members of the legume family, and with similar dominances of the same or closely related genera (LaFrankie, 2005). This might explain the similarity in crown allometric relationships between Africa and America. These intercontinental differences in composition and traits of the different forest strata remain to be explored further.

4.4 | Conclusions

Based on a large dataset of tree crown dimensions available from published and unpublished sources of tropical plot data, this study advances the understanding of large-scale variation and determinants in tropical tree crown allometry. By analysing variation in crown dimensions–stem diameter allometric relationships across the global tropics and by accounting for their drivers, we found a general pattern for significantly smaller scaling exponents in crown allometric relationships in forests than in savannas. Our results highlight a significant role of environmental factors, including precipitation, wind speed and soil texture, in explaining intercontinental differences in the crown allometric relationships of tropical trees. These findings provide important insights, both for the development of future vegetation modelling (e.g., to understand competition for light and its impacts on tree and forest structure) and for the calibration of remote sensing products (e.g., estimating crown attributes and the biomass of trees observed from air or from space). This worldwide analysis of tropical tree crowns should therefore contribute to improving both the modelling and the assessment of tropical canopy and ecosystem function.

ACKNOWLEDGMENTS

This work is the product of a postdoctoral project (G.J.L.P.) funded by Wallonia-Brussels-International (WBI). We thank Dr Andrew Kerkhoff and two anonymous reviewers for their insightful comments on an earlier version of this manuscript. The major portion of the tree crown data was collected with the support of NERC, including Tropical Biomes in Transition (TROBIT; NE/D005590/1/), AMAZONICA (NE/F005806/1), and additional grants to the RAINFOR network from the Moore Foundation (#1656), support for the AfriTRON and T-Forces networks from the European Research Council (Advanced Grant 291585) and a University of Leeds NERC PhD studentship to L.B. T.R.F. and O.L.P. were also supported by NERC grant NE/N011570/1. T.J. was supported by a U.K. NERC Independent Research Fellowship (grant number: NE/S01537X/1). A part of these data was acquired by the Sustainable Landscapes Brazil project supported by the Brazilian Agricultural Research Corporation (EMBRAPA), the U.S. Forest Service, and USAID, and the U.S. Department of State. We are grateful to Aurora Levesley and ForestPlots.net for archiving the major portion of the tree crown data compiled under this study and connecting the lead authors to data owners (ForestPlots Project #44). We thank colleagues and additional research projects with their respective funding agencies that have shared crown data (including SEOSAW with NE/P008755/1; DynAfFor and P3FAC projects with grant numbers CZZ1636.01D and CZZ1636.02D; International Foundation for Science with grant number D/5822-1; National Natural Science Foundation of China with grant number 31700356; Gatsby Plants; CAPES and ABC-CNPq grant 004/96, Brazil; Manchester Metropolitan University). We are grateful to Professor Jon Lloyd for helpful comments on earlier versions of the manuscript and for coordinating the TROBIT data collection. We gratefully acknowledge Dr Sandra Patiño (deceased) for the crown depth data she collected in numerous long-term RAINFOR forest plots across Amazonia.

AUTHOR CONTRIBUTIONS

G.J.L.P., A.F. and T.R.F. designed the study, with the assistance of T.J. and J.J.L. G.J.L.P., T.J. and T.R.F. compiled the crown database, with all authors providing data. G.J.L.P., O.L.P. and T.R.F. archived the major portion of crown data in the ForestPlot database. G.J.L.P. completed environmental data, conducted the analyses, and wrote the manuscript with input from all authors, who provided substantial revisions improving the manuscript.

DATA AVAILABILITY STATEMENT

The crown data are available as a data package on ForestPlots.net: http://doi.org/10.5521/forestplots.net/2020_8 (Loubota Panzou et al., 2020).

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BIOSKETCH

The authors have broad research interests in theoretical and applied plant ecology in tropical biomes. This study was carried out as a collaborative effort in the ForestPlots network (https://www.forestplots.net/) and among people interested in understanding the determinants on tree crown allometry at the global scale. The results of this study are part of a post-doctoral research project of Grace Jopaul Loubota Panzou at the University of Exeter (UK) under the supervision of Adeline Fayolle and Ted R. Feldpausch.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Loubota Panzou GJ, Fayolle A, Jucker T, et al. Pantropical variability in tree crown allometry. *Global Ecol Biogeogr.* 2021;30:459–475. https://doi.org/10.1111/geb.13231

APPENDIX

DATA SOURCES

TABLE A1. List of data sources used in this study

Scale	Country	Tropical biome	Data source
Global	Multiple countries	Forest/savanna	Unpublished, ForestPlot.net
Global	Multiple countries	Forest/savanna	Jucker et al. (2017)
Global	Multiple countries	Forest	Ploton et al. (2016)
Africa	Angola	Savanna	Unpublished
Africa	Burkina Faso	Savanna	Unpublished
Africa	Cameroon	Forest	Unpublished
Africa	Cameroon	Forest/savanna	Mitchard et al. (2009)
Africa	Congo	Forest	Unpublished
Africa	Congo	Forest	(Loubota Panzou et al., 2018; Loubota Panzou, Ligot, et al., 2018)
Africa	DRC	Forest	Unpublished
Africa	DRC	Forest	Sellan et al. (2017)
Africa	Gabon	Forest	Unpublished
Africa	Mozambique	Savanna	Unpublished
Africa	Mozambique	Savanna	Ryan and Williams (2011)
Africa	South Africa	Savanna	Unpublished
Africa	Tanzania	Savanna	Unpublished
Africa	Two countries	Savanna	Kuyah et al. (2012); Kuyah et al. (2014)
America	BCI	Forest	Cano et al. (2019)
America	Brazil	Forest	https://www.paisagenslidar.cnptia.embrapa.br/webgis/
America	Brazil	Forest	Dias et al. (2017)
America	Mexico	Forest	Vovides et al. (2018)
Asia	China	Forest	Xu et al. (2019)
Asia	Indonesia	Forest	Falster et al. (2015)
Asia	Malaysia	Forest	Sellan (2019)
Asia	Malaysia	Forest	Iida et al. (2012)

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