



Modelling conductive sapwood area of *Gmelina arborea* trees grown in the tropical dry forest of Colombia

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Abstract

Quantifying tree water use is crucial for developing adaptive forest management strategies to address water scarcity. Transpiration, the major component of tree water consumption, is estimated using stem sap flow velocity and scaled to the conductive sapwood area (S_A). As a vital trait for understanding forest hydrology, S_A provides insights into hydraulic functionality and water use. This study examined the dimensions (depth and area) and some wood properties (density and moisture content) of the sapwood in *Gmelina arborea* trees from tropical dry forests. Non-destructive sampling was conducted on 133 trees across seven stands, aged 4 to 13 years, with site indices ranging from 17.3 to 27.3 m and stand density ranging from 355 to 1750 trees ha⁻¹. Measurements included diameter at breast height (DBH) and crown projection area (CPA). Sapwood cores were extracted from four cardinal directions to assess sapwood dimensions and wood properties. Tree- and stand-level variation were the primary sources of variation in sapwood dimensions and properties, while within-tree variation influenced sapwood depth and properties but was negligible for S_A . No significant effect of cardinal direction on sapwood dimensions or properties was observed, suggesting a uniform radial distribution. Strong correlations were found between S_A and DBH and CPA. Allometric models using DBH and CPA predicted S_A with high accuracy ($R^2 = 0.91$ and 0.63), improving further with site index inclusion ($R^2 = 0.93$ and 0.67). The developed S_A models are vital tools for enhancing adaptive forest management, optimizing resource use efficiency, and promoting sustainability in dry climates, providing valuable insights into tree water transport dynamics.

Keywords Water use · Adaptive forest management · Site index · Allometric models · Tree transpiration

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Introduction

Quantification of water used by forests is fundamental to understanding their role in the water balance and the functioning of ecosystems. In particular, this becomes critically relevant in dry forest ecosystems, where water is a limited resource, and in forest production systems that depend on the efficient management of this resource (Medrano et al. 2007; Bhattacharya 2019; Suárez et al. 2021). Knowing the water requirements of forests is essential not only to assess their resilience capacity in the face of extreme climatic events, such as prolonged droughts, but also to anticipate how they might respond to projected climate changes (IPCC 2014). Furthermore, this information is crucial for developing management and adaptation strategies that ensure the sustainability of forests and the ecosystem services they provide, such as the regulation of the water cycle and climate change mitigation (Hakamada et al. 2020).

The water used by a tree is typically determined by quantifying the water transpired by its leaves. Transpiration is influenced by environmental variables such as vapor pressure deficit, temperature, relative humidity, and soil water content (Chen et al. 2023a, b). It is also affected by species-specific factors, such as root depth, conductive sapwood area, and canopy structure (Ghimire et al. 2022; Hendler et al. 2024).

Among the methods available for quantifying transpiration, measuring sap flow rates has been found to be an efficient approach for assessing whole tree and forest transpiration (Burgess et al. 2001). The available sap flow methods are thermal and estimate sap flow by measuring sap flow velocity and scaling it by the area of conductive sapwood (Quiñonez-Piñón and Valeo 2019). Therefore, the conductive sapwood area (S_A) of the stem is an essential parameter for estimating the amount of water consumed and ultimately transpired by the leaves.

During the tree aging process, parenchyma cells die, and tracheids and vessels lose their ability to conduct water (Plomion et al. 2001). Conductive sapwood is the living portion of the stem and is crucial for the transport of both water and nutrients from the roots to the leaves (Güney 2018). Within the stem, the proportion of sapwood and heartwood varies between species and even between trees of the same species and with age (Yang and Hazenberg 1991; Kort 1993; Cherelli et al. 2018; Güney 2018; Hendler et al. 2024). S_A is also an indicator of tree health, since stressed trees usually have less sapwood (Kort 1993; Pappas et al. 2022; Hendler et al. 2024). S_A plays a critical role in tree water relations, as it determines the capacity for water transport and storage. In times of water scarcity, a larger S_A can improve access to water and buffer short-term deficits, thereby increasing the chances of survival and maintaining physiological activity (van der Sande et al. 2015). A larger S_A also enables higher potential rates of photosynthesis, supporting growth and productivity when water availability is not limiting (Zhu & Zhao 2023). However, a large S_A is often associated with lower wood density, which may reduce mechanical strength and wood quality. Conversely, a reduction in S_A during prolonged drought can be an adaptive strategy, lowering transpirational demand and allowing the tree to maintain a baseline level of physiological activity even at the cost of reduced growth (Sevanto et al. 2014; Ferriz et al. 2021; Valeriano et al. 2021). Thus, the optimal S_A size represents a trade-off between maximizing water transport capacity under favorable conditions and minimizing water loss under water-limited conditions. Previous studies have also shown that S_A in the stem is a

strong predictor of tree- and plot-level leaf area, leaf biomass, and leaf area index (Morataya et al. 1999; Jones et al. 2015).

Sapwood area measurement often involves destructive sampling of trees (Lubczynski et al. 2017). However, non-destructive sampling through wood coring has also proven to be highly accurate (Quiñonez-Piñón and Valeo 2017; Arisandi et al. 2023). Since S_A measurements are difficult, time-consuming, and therefore, expensive, the use of allometric models to predict S_A from easily measured tree-level variables is common (Schoppach et al. 2023). Moreover, with recent advances in spatial image acquisition and processing systems, allometric models that include crown variables are of great interest (Lubczynski et al. 2017).

Gmelina arborea Roxb. is an important tree species native in the humid to dry habitats of India, Bangladesh, Sri Lanka, Myanmar, Thailand, and part of the Asian continent, among others (Dvorak 2004; Hodge and Dvorak 2004). *G. arborea* is widely planted for its fast growth, high-quality wood, and adaptability to poor soils. It plays a key role in reforestation and carbon sequestration in degraded tropical dry forests. The species was introduced to Colombia in the 1980s and has since become one of the fastest-growing broadleaf species used in forest plantation systems, surpassed only by some species of the *Eucalyptus* genus in terms of growth (Osorio 2004; MADR 2023). The species grows in the tropical dry forest known as one of most restrictive ecosystems considering water availability. With the increasing frequency and intensity of drought events due to climate change, tropical dry forests are experiencing significant productivity losses and, in some cases, tree mortality (Arguedas et al. 2018). Therefore, studies on water use are important for adapting forest management of this species to the new scenarios imposed by water scarcity.

The primarily aim of the study was to develop allometric models to predict the conductive sapwood area of *G. arborea* trees grown in a water-limited environment to facilitate the quantification of transpiration at tree- and stand-level to contribute to hydrological balance studies. The specific objectives include (i) to evaluate the variation of dimensions (depth and area), and some wood properties (density and moisture content) of conductive sapwood of *G. arborea* trees, (ii) to analyze correlations between conductive sapwood dimensions and wood properties and tree- and stand-level variables, and (iii) to develop and select allometric models to predict S_A from tree- and stand-level variables.

Materials and methods

Study area

Study area is located in the inter-Andean valleys of the Magdalena River at Colombia, this area belongs to the tropical dry forest which is distributed between 0 and 1000 m above sea level and is characterized by an average annual temperature above 24 °C and average annual rainfall between 700 and 2000 mm per year, with two rainy periods, one that occurs in the months of March to May, and the strongest towards the months of September and November (Fig. 1).

Two study sites were selected. Site 1, located at north has soils derived from volcanic and fluviovolcanic deposits and have a sandy clay loam texture with a pH of 5.45. They contain low organic matter (0.85%), have a low-to-moderate cation exchange capacity (7.45 meq 100 g⁻¹), and moderate base saturation (~112%). Exchangeable calcium and magne-

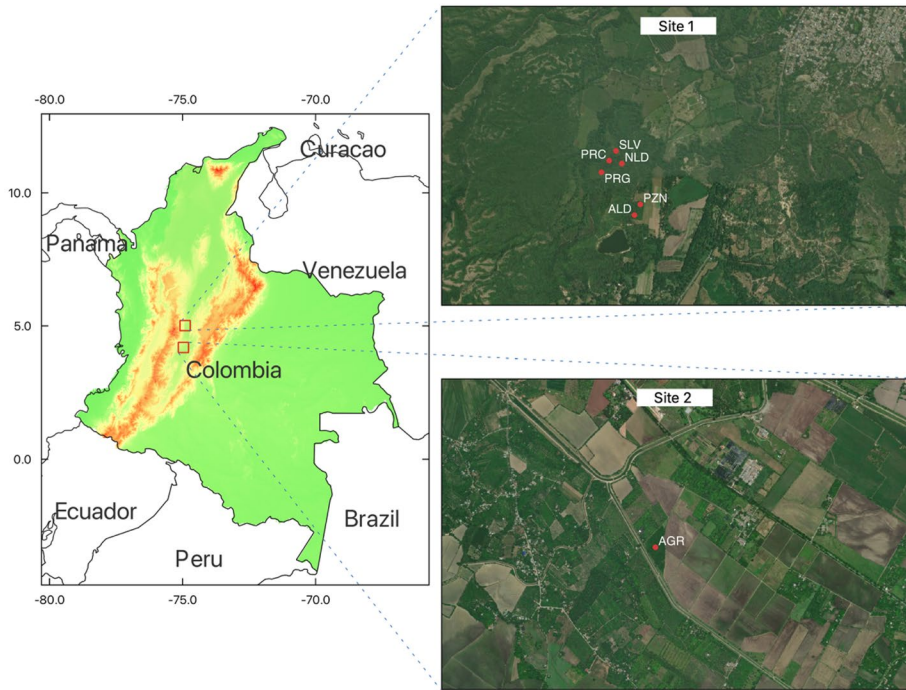


Fig. 1 Geographical location of the sampling area within the inter-Andean valleys

sium are adequate, but potassium levels are low. Soil fertility is further constrained by variable drainage and localized compaction. Annual rainfall at this site averages approximately 1,788 mm, distributed across 142 rainy days per year (López-Aguirre 2025).

Soils at Site 2 are formed from recent alluvial deposits in the Magdalena River Valley and have a sandy clay loam texture. They are moderately acidic (pH 5.3), contain very low organic matter (0.4%), have a moderate cation exchange capacity (11 meq 100 g⁻¹), and high base saturation (88%). Exchangeable calcium and magnesium are adequate, phosphorus is high, and potassium is at moderate levels. Annual precipitation at this site is lower, averaging about 1,475 mm per year, though distributed over fewer rainy days (~134 days) (López-Aguirre 2025).

A total of seven stands of *G. arborea* were sampled: six stands in Site 1 and one stand in Site 2. Stands ranged from young plantations to rotation-age plantations, with ages between 4 and 13 years. At each stand a 500 m² sample plot was measured to determine the main stand-level parameter, such as number of trees, and dominant height, site index was assessed based on dominant height at base age 10 using the model developed by López-Aguirre et al. (2011).

These stands were chosen to cover a variety of productivity levels, including both low and high productivity stands, with site indices ranging from 17 to 27 m and stand densities between 355 and 1750 trees ha⁻¹ (Table 1).

Compared to Site 1, *G. arborea* trees in Site 2 have a lower site index, likely due to the higher sand content reducing water-holding capacity and the warmer, drier microclimate

Table 1 Description of sampled stands and tree variables of selected *G. arborea* trees

Stand	<i>n</i>	Elevation (m)	Age (yr)	SI (m)	<i>N</i> (trees ha ⁻¹)	DBH (cm)	CPA (m ²)
SLV	20	276	4	24.4	1315	17.0±3.4	15.3±5.4
NLD	20	280	5	24.9	1750	17.4±4.2	20.7±11.1
PZN	20	275	10	22.9	907	19.2±5.4	24.0±10.8
PRC	20	277	10	27.0	733	22.3±7.3	19.1±6.3
PRG	13	280	10	27.3	900	25.8±7.3	27.1±7.0
AGR	20	374	12	17.3	825	30.1±13.1	40.5±31.1
ALD	20	277	13	20.7	355	19.4±7.3	24.3±17.5
All	133	291.3	9.1	23.5	969.3	21.4±8.6	24.3±17.1

For tree variables mean and standard deviation are provided

SI site index, *N* stand density, DBH diameter at 1.3 m, CPA crown projection area, and *n* sampled trees

associated with its slightly greater altitude. These factors together increase seasonal water stress and limit growth potential.

Tree selection and biometric measurements

Sampling was conducted between 2022 and 2023. Twenty trees were selected in each stand, except in the stand PRG, where 13 trees were sampled, resulting in a total of 133 trees measured. These trees were healthy trees, without forks, and without noticeable defects. Biometric measurements were taken for each tree, diameter at 1.3 m above the ground (DBH) was measured with a diametric tape, and crown radii (CR) in the north, south, east, and west directions were measured with a metric tape. The crown projection area (CPA) was

determined from the average crown radius ($CPA = \pi \bar{CR}^2$). Sampled trees ranged from 8 to 50.4 cm in DBH (mean of 21.4 cm), and from 1.0 to 106 m² in CPA (mean of 24.3 m²) (Table 1).

Sapwood and wood properties measurement

A 7–10 cm wood core was extracted in all four cardinal directions (north, south, east, and west) from each of the 133 sampled trees, using a 5.15 mm diameter Pressler borer. After the core extraction, the bark was separated and measured with a caliper. The transition between sapwood and heartwood was visually identified in each core based on color differentiation, and the sapwood portion of the core was cut for subsequent measurements. Immediately after separation, the depth of the conductive sapwood (*S_D*) was measured using a caliper.

The *S_A* was calculated as $S_A = \pi (\bar{R}^2 - \bar{r}^2)$, where $\bar{R}$ is the radius from the pith to the base of the bark and $\bar{r}$ is the radius of the heartwood (from the pith to the transition between sapwood and heartwood).

The fresh weight of the sapwood core was then determined using a precision scale with an accuracy of 0.001 g. The sapwood cores were labeled and immediately stored in test tubes filled with water to prevent breakage due to moisture loss. In the laboratory, the sapwood cores were oven-dried at 103 °C for 48 h until a constant weight was achieved. Subsequently, the sapwood cores were weighed again on a precision scale to obtain their oven-dry weight. Conductive sapwood basic density (WD) was determined as the ratio of oven-dry

weight and fresh volume. Fresh volume was obtained from the core dimensions (diameter and length). The moisture content of conductive sapwood (MC) was determined as the ratio of water content (fresh weight minus oven-dry weight) to oven-dry weight.

Statistical analysis and S_A modeling

All data analyses were conducted using R version 4.4.1 (R Core Team 2024). Basic descriptive statistics were computed for sapwood dimensions and wood properties. Variance component analysis was carried out using a mixed-effects linear model, fitted with the ‘lme4’ package in R, to partition the total variance into its main components: between-stand, between-tree within stands, and within-tree variation across cardinal directions. In the model, all components were treated as random effects, enabling a comprehensive assessment of each factor’s contribution to the overall variability in the analyzed traits.

To examine the effect of cardinal direction on the measured traits, we performed an analysis of variance based on a linear mixed-effects model that reflected the hierarchical structure of the data (trees nested within stands). Stand and tree were included as random effects to appropriately account for this structure.

Pearson’s correlation coefficients were calculated to quantify the associations between sapwood dimensions, wood properties, and tree- and stand-level variables. Finally, allometric models were developed to predict S_A using nonlinear regression. These models incorporated predictor variables that are easily measured in forest inventories, such as DBH and CPA. The latter variable can recently also be obtained through the analysis of spatial images.

The allometric S_A models were fitted using weighted nonlinear regression with the ‘gnls’ function, which is part of the ‘nlme’ package in R version 4.4.1 (R Core Team 2024). A power function (varPower) of an absolute variance covariate given by the fitted values with a fixed power around 0.5 was used as a weighting function (Pinheiro and Bates 2000). For each model, Monte Carlo cross-validation (MCCV) was conducted, which involved generating 100 random resampling without replacement. In each resampling, 80% (106 trees) of the data were used for training, while the remaining 20% (27 trees) were used for testing the model. The estimated parameters and their confidence intervals were determined using the percentiles of its distribution considering the median and the 2.5 and 97.5 percentiles. The average coefficient of determination (R^2) and average Akaike’s criterion (AIC) were used as goodness-of-fit measures (Despotovic et al. 2016; Aliffia and Karnaningroem 2019), while the criteria used for testing corresponded to the average mean absolute error. The following formulas were used:

$$R^2 = \frac{1}{R} \sum_{r=1}^R \left(1 - \frac{\sum_{i=1}^{n_{\text{train}}} (y_i - \hat{y}_i)^2}{\sum_{i=1}^{n_{\text{train}}} (y_i - \bar{y})^2} \right) \quad (1)$$

$$\text{AIC} = \frac{1}{R} \sum_{r=1}^R (2 \cdot k - 2 \cdot \ln(L)) \quad (2)$$

$$\text{MAE} = \frac{1}{R} \sum_{r=1}^R \left(\frac{1}{n_{\text{test}}} \sum_{i=1}^{n_{\text{test}}} |y_i - \hat{y}_i| \right) \quad (3)$$

where y_i and $\hat{y}_i$ are the observed and predicted values, respectively, and n_{train} and n_{test} are the sample sizes for training and testing ($n_{\text{train}} = 106$ and $n_{\text{test}} = 27$, respectively), k is the number of parameters of the model, $\ln(L)$ is the log-likelihood function for the model and R is the number of resamples used in MCCV.

Results

Sapwood dimensions and wood properties

For the 133 trees sampled, S_D ranged from 1.05 to 6.02 cm with a mean of 2.79 ± 0.80 cm, and S_A ranged from 19.10 to 624.58 cm² with a mean of 151.92 ± 104.65 cm². WD showed a minimum of 256.97 and a maximum of 685.69 kg m⁻³ with a mean of $445.88 \text{ kg m}^{-3} \pm 61.48 \text{ kg m}^{-3}$. Finally, MC ranged from 0.83 to 2.63 kg kg⁻¹ with a mean of $1.40 \text{ kg kg}^{-1} \pm 0.28 \text{ kg kg}^{-1}$ (Table 2). As shown in Table 2, S_D showed a lower variation with average CV of 28.77% compared to S_A with average CV of 68.89%. Wood properties showed lower variation than sapwood dimensions with average CV equal to 13.79% for WD and 19.80% for MC.

Sources of variation in sapwood and wood properties

Figure 2 displays the proportion of total variance attributed to between-stand, between-tree within-stand, and within-tree (cardinal direction) components for each trait. Variation in

Table 2 Basic statistics for conductive sapwood dimensions and wood properties of *G. arborea* trees

Variable	Cardinal direction	<i>n</i>	Mean	Minimum	Maximum	Standard deviation	CV (%)
S_D	North	133	2.88	1.05	5.60	0.77	26.82
	South	133	2.76	1.23	4.90	0.78	28.12
	East	133	2.78	1.28	6.02	0.84	30.17
	West	133	2.74	1.25	4.98	0.82	30.04
	All	532	2.79	1.05	6.02	0.80	28.77
S_A	North	133	154.26	19.10	580.29	100.18	64.94
	South	133	150.86	38.49	589.61	104.52	69.28
	East	133	152.60	38.49	595.05	109.79	71.95
	West	133	149.98	20.83	624.58	105.05	70.04
	All	532	151.92	19.10	624.58	104.65	68.89
WD	North	133	444.84	306.81	621.25	62.94	14.15
	South	133	447.75	330.74	613.64	57.06	12.74
	East	133	446.86	295.66	685.69	66.41	14.86
	West	133	444.05	256.97	586.91	59.76	13.46
	All	532	445.88	256.97	685.69	61.48	13.79
MC	North	133	1.41	0.83	2.54	0.31	21.99
	South	133	1.38	0.84	2.18	0.25	18.49
	East	133	1.41	0.85	2.63	0.27	19.53
	West	133	1.42	0.93	2.35	0.27	19.08
	All	532	1.40	0.83	2.63	0.28	19.80

S_D sapwood depth (cm), S_A sapwood area (cm²), WD wood density (kg m⁻³), MC moisture content (kg kg⁻¹) and CV coefficient of variation

Fig. 2 Variance components for sapwood depth (a), area (b), wood density (c) and moisture content (d) in *G. arborea* trees

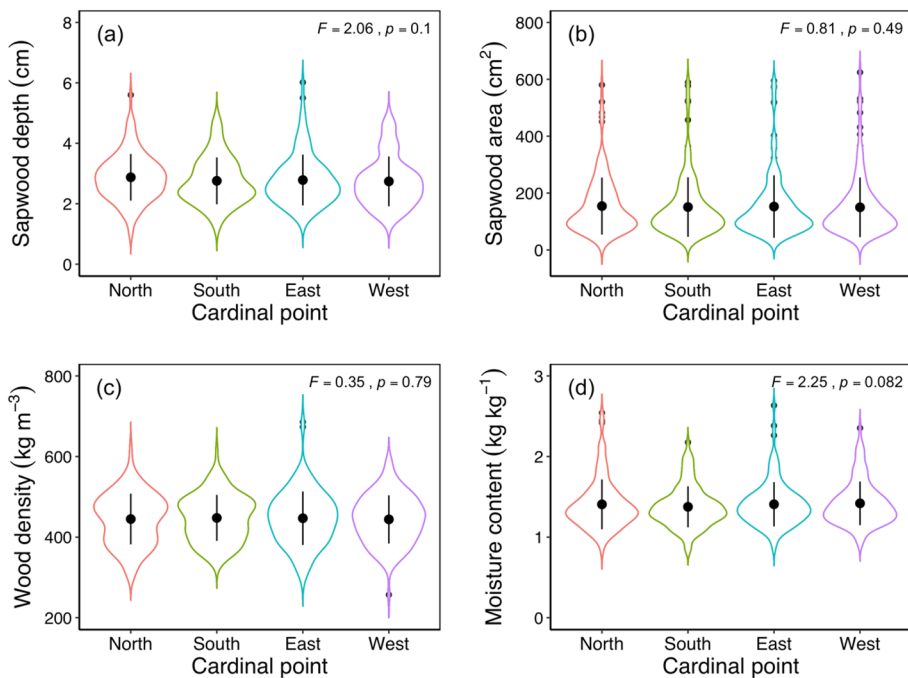
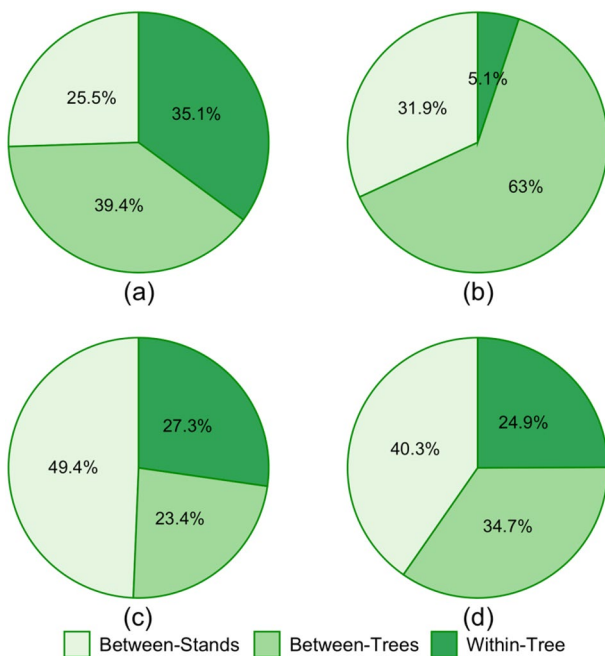


Fig. 3 Variation of sapwood depth (a), sapwood area (b), wood density (c) and moisture content (d) by cardinal direction of *G. arborea* trees together with F-values and significance levels

sapwood dimensions was primarily attributable to differences between trees within stands, representing 39.4% of the total variance in S_D and 63.0% in S_A . Between-stand variation also was an important source of variation in the data, accounting with 25.5% and 31.9% of the observed total variance in S_D and S_A , respectively. Interestingly, for S_D within-tree (cardinal direction) variation contributing 35.1% of total variance, but conversely, this component only contributed with 5.1% of total variance in S_A .

For sapwood properties, between-stand variation was the primary source of total variation, accounting for 49.4% and 40.3% of the variation in WD (Fig. 2c) and MC (Fig. 2d), respectively. Between-tree variation also contributed significantly, particularly for MC. Within-tree variation accounted for 27.3% and 24.9% of the total variation in WD and MC, respectively (Fig. 2).

No significant differences ($p > 0.05$) were observed in conductive sapwood dimensions or wood properties between cardinal directions in the evaluated *G. arborea* trees (Fig. 3). The distribution of S_D across the four cardinal points was highly similar among the sampled trees, with a slight skew observed in the north and east directions (Fig. 3a). Sapwood area exhibited a skewed distribution in all cardinal directions toward larger values, likely due to the overrepresentation of larger trees with greater S_A (Fig. 3b). WD and MC exhibited less variation compared to sapwood dimensions, and similar to S_D , both showed a slight skew in the north and east cardinal points (Fig. 3c and d).

Correlation among traits

Conductive sapwood dimensions exhibited weak to low correlations with sapwood properties. Specifically, S_D was not significantly correlated with either WD or MC ($p > 0.05$), while S_A showed a significant positive correlation with WD ($r = 0.30$, $p < 0.001$), but no correlation with MC ($p > 0.05$). Stronger correlations were observed between sapwood dimensions and tree-level variables such as DBH, and CPA (Table 3). For S_D , significant positive correlations were found with DBH ($r = 0.43$, $p < 0.001$), and CPA ($r = 0.42$, $p < 0.001$). S_A exhibited even stronger significant positive correlations with DBH ($r = 0.94$, $p < 0.001$), and CPA ($r = 0.80$, $p < 0.001$). DBH and CPA showed moderate positive correlations with WD ($r = 0.38$ and $r = 0.39$, $p < 0.001$) and weak negative correlations with MC ($r = -0.21$ and $r = -0.18$, $p < 0.05$), respectively. Additionally, CPA was strongly correlated with DBH ($r = 0.80$, $p < 0.001$).

Among the stand-level variables, SI showed negative correlation with S_D ($r = -0.35$, $p < 0.001$), S_A ($r = -0.32$, $p < 0.001$), and WD ($r = -0.41$, $p < 0.001$). Age was positively correlated with S_A ($r = 0.26$, $p < 0.01$) but not with S_D ($p > 0.05$), and was also positively correlated with WD ($r = 0.60$, $p < 0.001$) and negatively with MC ($r = -0.60$, $p < 0.001$). Stand density (N) was not correlated with sapwood dimension variables ($p > 0.05$) but showed significant negative correlations with WD ($r = -0.39$, $p < 0.001$) and a positive correlation with MC ($r = 0.50$, $p < 0.001$). Age was positively correlated with DBH and CPA ($r = 0.32$ and $r = 0.29$, $p < 0.001$), and while SI showed a negative correlation with DBH and CPA ($r = -0.23$ and $r = -0.34$, $p < 0.001$). N also exhibited a weak negative correlation with DBH ($r = -0.21$, $p < 0.05$).

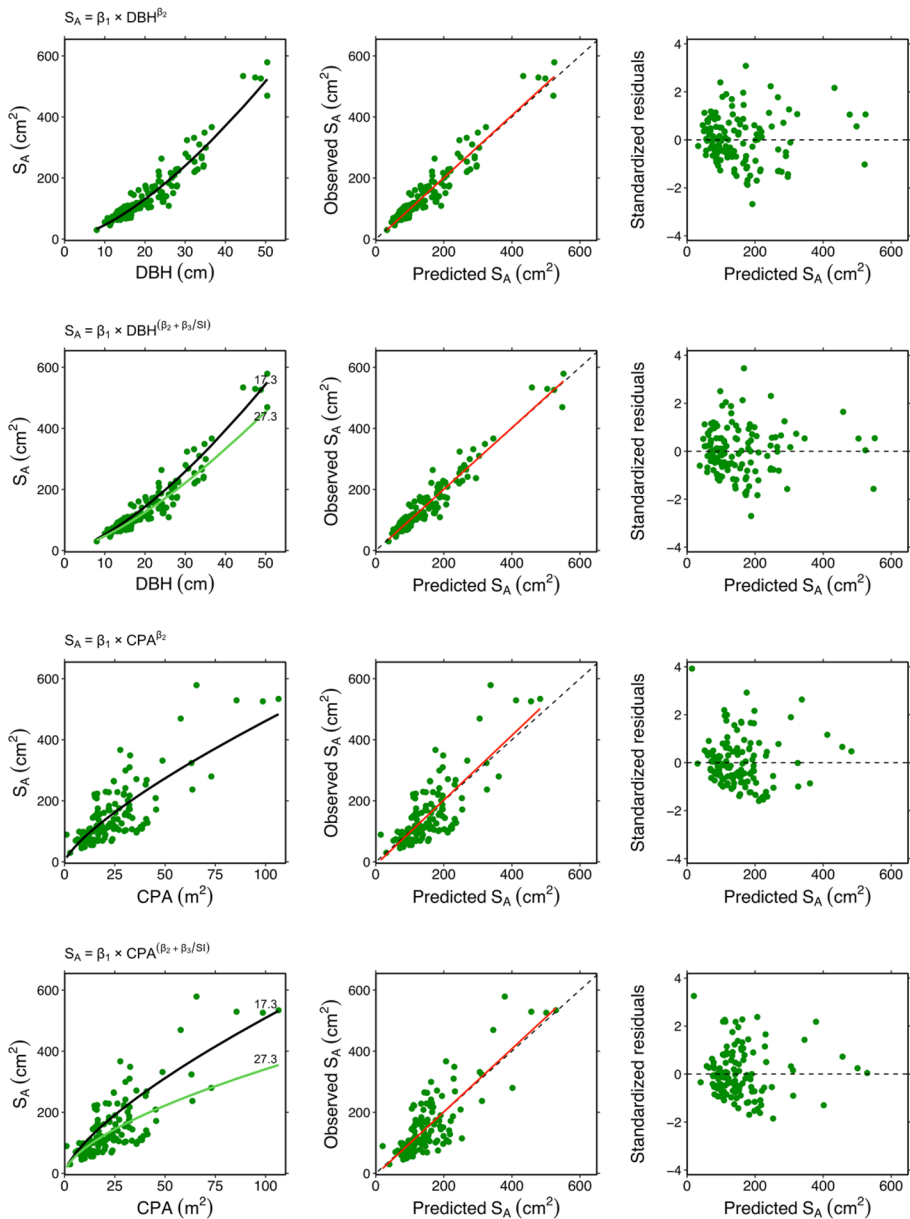


Fig. 4 Fitted prediction models for S_A of *G. arborea* trees. Fitted curves for each of four models and for models 2 and 4 the prediction curve for minimum and maximum observed SI (a), observed versus predicted values (b) and distribution of standardized residuals (c) are plotted

Table 3 Correlation matrix among conductive sapwood dimensions and wood properties and stand and tree-level variables for *G. arborea* trees

Variable	S _A	WD	MC	Age	SI	N	DBH	CPA
S _D	0.66***	0.00 ^{ns}	0.07 ^{ns}	0.03 ^{ns}	-0.35***	-0.04 ^{ns}	0.43***	0.42***
S _A		0.30***	-0.12 ^{ns}	0.26**	-0.32***	-0.16 ^{ns}	0.94***	0.80***
WD			-0.67***	0.60***	-0.41***	-0.39***	0.38***	0.39***
MC				-0.60***	0.11 ^{ns}	0.50***	-0.21*	-0.18*
Age					-0.49***	-0.90***	0.32***	0.29***
SI						0.33***	-0.23**	-0.34***
N							-0.21*	-0.15 ^{ns}
DBH								0.80***

***, significant at $p < 0.001$, **, significant at $p < 0.01$, *, significant at $p < 0.05$, ns, nonsignificant

Table 4 Fitted models, model parameters and confidence interval estimated and measures of fit and prediction for S_A prediction of *G. arborea* trees

Model number	Model	Parameter	Estimate	Confidence interval		R ²	AIC	MAE (cm ²)
				Lower	Upper			
1	S _A = $\beta_1 \beta_1$		1.4573	1.3199	1.6339	0.91	988.6	23.1
		DBH ^{β_2}	1.4991	1.4627	1.5320			
2	S _A = $\beta_1 \beta_1$		1.8262	1.6299	2.0115	0.93	981.4	21.2
		DBH ^{$\beta_2 + \beta_3$}	1.3327	1.2933	1.3736			
		SI ^{β_3}	2.1667	1.6244	2.6812			
3	S _A = $\beta_1 \beta_1$		14.17493	12.1510	17.5045	0.63	1163.1	47.5
		CPA ^{β_2}	0.75843	0.6878	0.8055			
4	S _A = $\beta_1 \beta_1$		19.4602	15.6933	23.7990	0.67	1154.8	46.2
		CPA ^{$\beta_2 + \beta_3$}	0.46833	0.3436	0.6011			
		SI ^{β_3}	4.16929	2.2615	5.7695			

Allometric models for S_A for *G. arborea*

Four models were fitted by nonlinear weighted regression and validated by MCCV to predict the average S_A per tree, calculated as the mean S_A across the four cardinal directions for each tree. All models follow the power law using DBH (models 1 and 2) and CPA (models 3 and 4) as the base variable. In models 2 and 4, SI was included as a covariate modifying the power of the model to account for between-stand variation (Table 4).

Model 1, which only includes DBH, presented R²=0.91, indicating that this variable explains 91% of the variability observed in S_A. Additionally, this model presented an AIC=988.6 and an MAE=23.1 cm². When SI was included in the model (model 2), this additional stand-level variable improved the predictive accuracy of the model, increasing the R² by 2% and reducing the AIC to 981.4 (1%) and the MAE to 21.3 cm² (8%). Model 3, which only included CPA, showed lower R² (0.63), AIC (1163.1) and MAE (47.5 cm²) compared to models 1 and 2. When SI was included in the model (model 4), all predictive accuracy improved by 6%, 0.7% and 2.7% in R², AIC and MAE, respectively (Table 4).

The performance of the four models evaluated in predicting S_A, demonstrating a consistent relationship between the variables analyzed is presented in Fig. 4. The predicted versus observed values and the standardized residuals do not show signs of autocorrelation or het-

eroscedasticity in any model variant. Additionally, Models 2 and 4 exhibit a fit curve for low and high SI, respectively, which align well with the observed data. Graphically, Models 1 and 2 show better consistency with the data compared to the other two models.

Discussion

This study assesses the dimensions and wood properties of sapwood of *G. arborea* trees cultivated in the dry forests of two sites located in the inter-Andean valleys of Colombia, South America. Conductive sapwood and its wood properties are crucial as they play a vital role in the transport of water within the tree (Looker et al. 2016). By instance, the S_A determines the capacity of a tree to absorb water from the soil and distribute it throughout its structure, directly influencing water balance, growth, and overall health (Lubczynski et al. 2017).

Sapwood dimensions and wood properties

In the sampled *G. arborea* trees, S_D averaged 2.79 ± 0.80 cm; however, in the 4-year-old stand, S_D was slightly higher, averaging 3.19 cm (range: 2.34–4.68 cm), although this value remained lower than that reported for 3-year-old clones in Costa Rica (Cruz-Vargas et al. 2023), where S_D ranged from 4.99 to 7.30 cm. Such differences likely reflect age, site conditions, climate, and management practices.

WD averaged 445.9 kg m^{-3} , consistent with previous studies in Colombia (López & Barrios 2023), Venezuela (Espinoza 2003), and Costa Rica (Moya & Filho 2009). MC averaged 1.40 kg kg^{-1} , comparable to values reported for *G. arborea* in Central America (Muñoz-Acosta and Moya 2008; Cruz-Vargas et al. 2023) and within the general range observed across tree species (Glass and Zelinka 2010). The alignment of WD with industry standards indicates suitability for furniture and light construction markets, while MC values support its use in drying and processing operations (Arevalo and Iondoño 2005; Muñoz and Moya 2008; Hernández-Álvarez et al. 2024).

When compared to other tropical dry forest species, *G. arborea* shows lower WD than many native hardwoods such as *Swietenia macrophylla* ($420\text{--}540 \text{ kg m}^{-3}$), *Tabebuia rosea* (540 kg m^{-3}), and *Dipteryx odorata* ($810\text{--}890 \text{ kg m}^{-3}$) as well as lower WD than some fast-growing exotics such as *Acacia mangium* (560 kg m^{-3}), *Eucalyptus pellita* (580 kg m^{-3}), *Eucalyptus grandis* (460 kg m^{-3}) and *Tectona grandis* (550 kg m^{-3}) (Brown 1997; Charria et al. 2014; Arango and Tamayo 2014; Barrios-Trilleras and López-Aguirre 2024).

The relatively low WD and S_D observed suggest a strategy favoring fast growth and efficient water transport, which is advantageous under variable tropical dry forest conditions but may limit long-term mechanical support and resistance to stress (Poorter et al. 2010; Olaniran et al. 2023; Mahendru 2024).

Sources of variation in sapwood and wood properties

Our analysis shows that between-tree variation is the predominant source of variance for S_D and S_A traits, suggesting that genetic variation and micro-site conditions within the stand account for an important amount of variability in S_D and S_A . Between-stand variation was also an important source of variation, suggesting that environmental or management fac-

tors at the stand level exert considerable influence on these traits. Similarly, in a previous study on *Quercus* trees, Schoppach et al. (2023) identified the site as the primary source of variation influencing the S_A -DBH relationship. However, the mentioned study evaluated the potential impact of topographic factors on this relationship, but none of the factors assessed were found to have a significant effect.

Interestingly, for S_D the within-tree variation account for a large amount of variation (35.1%), but this variance component was no relevant for S_A , accounting only for a 5.1% of total observed variation. The large within-tree variation in S_D highlights localized anatomical adaptations or growth anomalies, while the relatively small within-tree variation in S_A underscores its role as a global, functionally consistent attribute of the tree. This pattern aligns with the physiological need for maintaining a stable S_A for hydraulic functionality, even in the face of local structural or environmental heterogeneity (Meinzer et al. 2005; Magnani et al. 2002; Looker et al. 2016; Cruickshank et al. 2015). Research indicates that trees maintain a relatively stable S_A to balance water transport needs with leaf area and overall tree demand (Meinzer et al. 2005; Magnani et al. 2002). O'Grady et al. (2009) and Looker et al. (2016) found that S_A is a key functional trait optimized to match tree transpiration needs. Its stability across varying growth conditions highlights its critical role in the tree's water transport system. Cruickshank et al. (2015) noted that uniform sapwood dimensions are essential for maintaining hydraulic conductivity, regardless of directional or structural anomalies within the tree.

Analysis of variance across cardinal directions indicate homogeneity in sapwood dimensions and wood properties within the trees, as no significant differences were detected among wood samples taken from the four cardinal directions of each sampled tree. This finding has important implications for sampling protocols, suggesting that a single wood sample taken from any cardinal point around the tree can provide reliable information on sapwood dimensions and properties, thereby reducing both time and costs associated with the sampling process. Studies have shown that sapwood dimensions, such as sapwood depth and area, often exhibit uniformity around the circumference of the tree (Longuetaud et al. 2006). This uniformity is generally attributed to the consistent role of sapwood in water transport and nutrient storage across the tree stem, regardless of the direction from which the sample is taken (Cruickshank et al. 2015; Qiao et al. 2023). Additionally, the relatively low slopes in the sample stands (<2.7%) may contribute to the uniformity in sapwood formation, promoting homogeneity in sapwood properties across the trees (Schoppach et al. 2023). Although *G. arborea* is typically established on flat sites, other studies have reported plantations on slopes of up to 30% (Rojas Rodríguez et al. 2004). In plantations on steeper terrain, the formation of tension wood is expected; therefore, caution should be exercised when extrapolating the results presented here. Moreover, other studies have reported differences in S_D according of the cardinal point of sampling. For instance, Quiñonez-Piñón and Valeo (2017) found significant differences in S_D between the four cardinal directions around the trunk with statistical analyses showing that species such as *Pinus banksiana* has a well-defined preference to grow thicker in the North-East side.

For sapwood properties the main source of variation was the between-stand variation, indicating that stand-level variables such as age, density, and site quality play an important role for defining wood characteristics. The observed between-stand variation in sapwood properties of *G. arborea* can be largely explained by differences in site productivity (site index) and the associated density-dependent growth dynamics. As reported in previous stud-

ies, rapid growth on more productive sites tends to favor the formation of lighter, less dense wood (Moya and Tomazello 2007). For other species, previous studies have demonstrated that factors such as site quality, stand age, and stand density may influence these variations (Jaskierniak et al. 2015; Câmara et al. 2023). Additionally, differences in climate and soil quality can impact growth rates, the transition from sapwood to heartwood, and consequently, the wood properties of the trees (Moya 2004; Moya and Tomazello 2006; Barrios et al. 2021). Similar than previous research, between-tree variation contributed for a substantial portion of the total variation, mainly attributed to genetic variation and intra-species competition (Knapic et al. 2008; Barrios et al. 2017). Additionally, within-tree variation also accounted for considerable amount of the total variation. Within-tree variation of wood properties is largely influenced by the internal tree physiology and structural demands. WD often varies radially from pith to cambium due to changes in cambial age and growth rate (Zobel and Van Buijtenen 1989; Moya and Tomazello 2007; Barrios et al. 2017). Similarly, MC variation within a tree can result from differences in sap flow dynamics, storage of free and bound water, and specific adaptations to mechanical and environmental stressors (Muñoz-Acosta and Moya 2008).

Correlations among traits

Conductive sapwood dimensions exhibited weak to low correlations with sapwood properties. However, S_A was positively correlated with sapwood WD, indicating that trees with larger S_A also tended to have higher WD. This association is consistent with the view that increased S_A may be linked to greater structural support and water transport capacity (De Guzman et al. 2021). Consistent with previous research, our study reveals a strong correlation between DBH and sapwood dimensions, particularly S_A (Schoppach et al. 2023; Câmara et al. 2023; Longuetaud et al. 2006). These correlations likely reflect the increase in tree diameter as trees grow, with older and larger trees having wider rings formed within sapwood compared to younger and smaller trees. Similarly, the significant correlations observed between sapwood dimensions and CPA may reflect the higher water requirements of trees with larger crowns due to physiological processes such as photosynthesis and transpiration (Coyea and Margolis 1992; Morataya et al. 1999; Forrester et al. 2022). This statement is also supported by the strong correlation found between DBH and CPA. The relationship between DBH and CPA is well-established, with larger trees typically having broader crowns. This correlation suggests that trees with larger crowns have more leaf area, which enhances their capacity for photosynthesis, providing the energy necessary for wood growth, including stem thickening. Studies have shown that as trees grow in size, their crowns expand, supporting increased photosynthesis and wood production (Roy et al. 2005).

The positive correlation between S_A and age can be explained by the rapid initial growth of *G. arborea*, which likely results in the development of a larger S_A . Additionally, this species may take time to transition from active sapwood to heartwood. If this transition is slow, the S_A can remain relatively large as the tree ages. Previous studies conducted in another tree species have shown that stand age has a significant impact on sapwood dimensions and wood properties (Barrios et al. 2017). As trees mature, their growth patterns and wood properties change. With age, trees form heartwood, and the proportion of sapwood

to heartwood shifts. Younger trees may have a higher proportion of sapwood compared to older trees (Lehnebach et al. 2017).

The negative relationship between S_A and SI suggests that trees in less favorable sites may allocate more resources to formation of sapwood to compete for scarce resources. This phenomenon has been observed in various *Eucalyptus* species (Almeida et al. 2020; Câmara et al. 2023; Schoppach et al. 2023). Furthermore, this relationship may also be associated with the negative correlation observed between SI and both DBH and CPA, as well as the positive correlation between SI and stand density. Barrios et al. (2021) reported density-dependence in *G. arborea*, where stands with a lower SI typically have reduced stand density, resulting in trees with larger DBH. In contrast, stands with a higher SI often exhibit greater stand density, producing taller trees with smaller DBH. Moreover, while stand density was not significantly correlated to sapwood dimensions, it did have a notable impact on wood properties. Specifically, increases in stand density were associated with reductions in WD and increases in MC, further highlighting the complex interplay between stand characteristics, tree dimensions, and wood properties.

Allometric models of sapwood area

The allometric models evaluated for *G. arborea*, using DBH and CPA as independent variables, achieved R^2 of 0.91 and 0.63, respectively, demonstrating their ability to capture the key allometric relationships between the structural size of the tree and its S_A . This relationship is crucial for understanding transpiration and water flow through the xylem (Zhao et al. 2023). The effectiveness of these models is supported by various studies, which have shown that using DBH and CPA as indicators of leaf area index allows for accurate estimation of the conductive sapwood area conducting sap flow at different scales (Lubczynski et al. 2017; Güney 2018; Aparecido et al. 2018; Forrester et al. 2022; Yaemphum et al. 2022).

Including DBH as a predictor variable in the S_A models for *G. arborea* has significantly improved prediction accuracy, both in fit statistics and validation metrics, compared to models based on crown area. This suggests a strong relationship between DBH and the growth characteristics of *G. arborea* in the inter-Andean valleys of Colombia. This association can be attributed to the deciduous nature of the species, which is linked to more efficient water transport and a larger conductive area. Additionally, crown area may not fully reflect the physiological state and growth of the tree due to factors such as phenology and leaf fall. In dry environments, lower relationships between leaf area index and sapwood area per unit of transpired leaf area are expected (Togashi et al. 2015).

The inclusion of SI as a stand-level variable in the model significantly improve S_A predictions. This addition is important because it allows for the consideration of site effects in the estimates, thereby broadening the applicability of the developed models to a wider range of environmental conditions. In other species, it has been shown that the relationship between S_A and DBH and CPA can be modified by site and stand parameters such as altitude, density, and age (Hernández-Santana et al. 2015; Mitra et al. 2020).

The practical implications of our findings are significant for the forest management of *G. arborea*. The strong correlation observed between DBH and S_A indicates that DBH can serve as a reliable proxy for estimating tree transpiration rates and overall water balance within forest plantations. Nonetheless, accurate application of this relationship requires prior calibration of sap flow rates in trees of comparable size and growing under similar

environmental conditions to those in which S_A was measured. Without such calibration, the risk of substantial estimation errors remains high. This is particularly relevant under increasing drought frequency, where reliable water-use estimates can guide thinning and stand density regulation to reduce competition and improve resilience (Schoppach et al. 2023).

Furthermore, the development of allometric models incorporating CPA can improve the accuracy of S_A predictions across diverse environmental conditions and extensive geographic regions (Lubczynski et al. 2017). By integrating satellite and unmanned aerial vehicles imagery into these models, it becomes possible to obtain detailed and large-scale assessments of CPA, thereby facilitating more precise and comprehensive predictions of S_A and transpiration (Kubo et al. 2007; Panagiotidis et al. 2017), enabling precision silviculture that tailors management intensity to site-specific conditions. These tools can inform decisions on species-site matching, irrigation planning, and restoration design, ultimately supporting the establishment of more resilient plantations and restoration projects with optimized growth, water balance, and wood quality.

Conclusions

This study evaluates the dimensions and wood properties of *G. arborea* sapwood grown in the tropical dry forests of the inter-Andean valleys of Colombia. The study highlighted that sapwood dimensions (depth and area) of *G. arborea* exhibited substantial between-tree and between-stand variation. This variability reflects the influence of genetic diversity, environmental factors, and stand management practices on tree water transport capacity. The study revealed no significant differences in sapwood dimensions and wood properties (e.g., density and moisture content) across cardinal directions. This uniformity simplifies sampling protocols, as wood samples from any cardinal point provide representative data, thus reducing sampling effort and costs. This finding aligns with the functional necessity of uniform sapwood characteristics to maintain efficient water transport within the tree. The observed strong correlation between S_A and DBH underscores DBH as a reliable predictor of S_A , which is critical for assessing tree water balance and transpiration at both tree and stand levels. The developed allometric models, particularly those incorporating DBH as a predictor variable, showed high accuracy. These models effectively quantify conductive sapwood area, providing a valuable tool for estimating transpiration and hydrological dynamics in water-limited environments. Incorporating SI further improved model performance, emphasizing the significance of site-level factors in predicting S_A to improve the generalizability of S_A predictions across varying site qualities.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

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References

- Aliffia A, Karnaningroem N (2019) Simulation of pollution load capacity using QUAL2Kw model in Kali Surabaya river (Cangkir-Sepanjang segment). IOP Conf Ser: Earth Environ Sci 259:012019. <https://doi.org/10.1088/1755-1315/259/1/012019>
- Almeida MNFD, Vidaurre GB, Pezzopane JEM et al (2020) Heartwood variation of *Eucalyptus urophylla* is influenced by Climatic conditions. Ecol Manag 458:117743. <https://doi.org/10.1016/j.foreco.2019.117743>
- Aparecido LM, Higuchi N, Santos J, Kunert N (2018) Relevance of wood anatomy and size of Amazonian trees in the determination and allometry of sapwood area. Acta Amazon 49:1–10. <https://doi.org/10.1590/1809-4392201800961>
- Arango B, Tamayo L (2014) Wood density in *Eucalyptus* clones by X-rays densitometry. RevFacIngUnivAntioquia 87–99. <https://doi.org/10.17533/udea.redin.18116>
- Arevalo R, Iondoño A (2005) Manual Para La identificación de Maderas Que se comercializan En El departamento Del Tolima. Universidad del Tolima, Ibagué
- Arguedas M, Rodriguez-Solis M, Moya R, Berrocal A (2018) *Gmelina Arborea* death disease in fast-growth plantations: effects of soil and Climatic conditions on severity and incidence and its implications for wood quality. Syst 27:e003. <https://doi.org/10.5424/fs/2018271-12236>
- Arisandi R, Nugroho Marsoem S, Pramana Gentur Sutapa J, Lukmandaru G (2023) The methods for measuring the area of Heartwood and sapwood. Rev Agric Sci 11:76–92. https://doi.org/10.7831/ras.11.0_76
- Barrios A, López AM, Báez CA (2021) Modelamiento de la productividad de *Gmelina arborea* Roxb. con base en variables biofísicas y de rodal. Colomb For 24:71–87. <https://doi.org/10.14483/2256201X.15345>
- Barrios A, Trincado G, Watt M (2017) Wood properties of juvenile and mature wood of *Pinus radiata* D. Don trees growing on contrasting sites in Chile. Sci 63:184–191. <https://doi.org/10.5849/forsci.2016-060>
- Barrios-Trilleras A, López-Aguirre AM (2024) Aboveground biomass models for *Acacia mangium* willd. Growing at the Eastern plains of Colombia. Floresta Ambient 31:e20230021. <https://doi.org/10.1590/2179-8087-floram-2023-2021>
- Bhattacharya A (2019) Changing climate and resource use efficiency in plants. Elsevier
- Brown S (1997) Estimating biomass and biomass change of tropical forests: A primer. FAO Forestry Paper 134
- Burgess SSO, Adams MA, Turner NC et al (2001) An improved heat pulse method to measure low and reverse rates of Sap flow in Woody plants. Tree Physiol 21:589–598. <https://doi.org/10.1093/treephys/21.9.589>
- Charria DLG, Rodríguez VN, Oviedo MBS, Gonçalves NMB (2014) Estimación indirecta de densidad Por El Uso de Pilodyn En *Eucalyptus pellita* F. Muell. Colomb for 17:181. <https://doi.org/10.14483/udistrital.jour.colomb.for.2014.2.a04>
- Chen S, Chen Z, Feng Z et al (2023a) Species difference of transpiration in three urban coniferous forests in a semiarid region of China. J Hydrol 617:129098. <https://doi.org/10.1016/j.jhydrol.2023.129098>
- Chen S, Wei W, Tong B, Chen L (2023b) Effects of soil moisture and vapor pressure deficit on canopy transpiration for two coniferous forests in the loess plateau of China. Agric Meteorol 339:109581. <https://doi.org/10.1016/j.agrformet.2023.109581>

- Cherelli SG, Sartori MMP, Próspero AG, Ballarin AW (2018) Heartwood and sapwood in *Eucalyptus* trees: non-conventional approach to wood quality. *Acad Bras Ciênc* 90:425–438. <https://doi.org/10.1590/0001-3765201820160195>
- Câmara AP, Vidaurre GB, De Oliveira JCL et al (2023) Rainfall exclusion changes the sapwood of *Eucalyptus* wood in humid and dry sites. *Eur J Res* 142:627–640. <https://doi.org/10.1007/s10342-023-01546-z>
- Coyea MR, Margolis HA (1992) Factors affecting the relationship between sapwood area and leaf area of Balsam Fir. *Can J Res* 22:1684–1693. <https://doi.org/10.1139/x92-222>
- Cruikshank MG, Cameron IR, Groot A et al (2015) Models of the vertical distribution of sapwood area for lodgepole pine and Western Hemlock in Western Canada. *Sci* 61:973–987. <https://doi.org/10.5849/forsci.14-206>
- Cruz-Vargas MA, Gaitán-Álvarez J, Ávila-Arias C et al (2023) Características Genéticas de Las propiedades de La Madera de 14 clones de *Gmelina Arborea* roxb. En El Pacífico Sur de Costa Rica. <https://doi.org/10.5154/r.rchscfa.2022.12.083>. Rev Cha Se Cie For y del Amb 29:
- De Guzman ME, Acosta-Rangel A, Winter K et al (2021) Hydraulic traits of Neotropical canopy liana and tree species across a broad range of wood density: implications for predicting drought mortality with models. *Tree Physiol* 41:24–34. <https://doi.org/10.1093/treephys/tpaa106>
- de Kort I (1993) Relationships between sapwood amount, latewood percentage, moisture content and crown vitality of Douglas fir, *Pseudotsuga menziesii*. *IAWA J* 14:413–427. <https://doi.org/10.1163/22941932-90000596>
- Despotovic M, Nedic V, Despotovic D, Cvetanovic S (2016) Evaluation of empirical models for predicting monthly mean horizontal diffuse solar radiation. *Renew Sust Energ Rev* 56:246–260. <https://doi.org/10.1016/j.rser.2015.11.058>
- Dvorak WS (2004) World view of *Gmelina arborea*: opportunities and challenges. *New for* 28:111–126. <https://doi.org/10.1023/B:NEFO.0000040940.32574.22>
- Espinoza JA (2003) Genetic variation in wood density of *Gmelina arborea* planted on different sites in western Venezuela. M.Sc. Thesis, North Carolina State University
- Forrester DI, Limousin J-M, Pfautsch S (2022) The relationship between tree size and tree water-use: is competition for water size-symmetric or size-asymmetric? *Tree Physiol* 42:1916–1927. <https://doi.org/10.1093/treephys/tpac018>
- Férriz M, Martín-Benito D, Cañellas I, Gea-Izquierdo G (2021) Sensitivity to water stress drives differential decline and mortality dynamics of three co-occurring conifers with different drought tolerance. *Ecol Manag* 486:118964. <https://doi.org/10.1016/j.foreco.2021.118964>
- Ghimire CP, (Ilja), Van Meerveld HJ, Zwartendijk BW et al (eds) (2022) Vapour pressure deficit and solar radiation are the major drivers of transpiration in montane tropical secondary forests in eastern Madagascar. *Agric For Meteorol* 326:109159. <https://doi.org/10.1016/j.agrformet.2022.109159>
- Glass S, Zelinka S (2010) Moisture relations and physical properties of wood. In: *Wood handbook: wood as an engineering material*: Chap. 4. Centennial ed, Madison, WI : U.S., p 4.1–4.19
- Güney A (2018) Sapwood area related to tree size, tree age, and leaf area index in *Cedrus libani*. *Bilge Int J Sci Technol Res* 2:83–91. <https://doi.org/10.30516/bilgesci.389609>
- Hakamada RE, Hubbard RM, Moreira GG et al (2020) Influence of stand density on growth and water use efficiency in *Eucalyptus* clones. *Ecol Manag* 466:118125. <https://doi.org/10.1016/j.foreco.2020.118125>
- Hendler R, Herkenrath T, Shikangalah R et al (2024) Allometric relationships between sapwood area and shrub dimensions for six common Southern African savanna Bush encroacher species: universal or species-specific? *Ecophysiol* 17:e2609. <https://doi.org/10.1002/eco.2609>
- Hernández-Álvarez E, Ruiz-Blandon BA, Gómez-Cárdenas M, Quiñonez-Barraza G (2024) Análisis tecnológico En *Gmelina Arborea* roxb. Proveniente de Rodales juveniles Puros y Mezclados En México. *Colomb for* 27:e21313. <https://doi.org/10.14483/2256201X.21313>
- Hernández-Santana V, Hernandez-Hernandez A, Asbjornsen H, Vadeboncoeur M (2015) Scaling from single-point Sap velocity measurements to stand transpiration in a multi-species deciduous forest: uncertainty sources, stand structure effect and future scenarios impacts. *Can J Res* 45:1489–1497. <https://doi.org/10.1139/cjfr-2015-0009>
- Hodge GR, Dvorak WS (2004) The CAMCORE international provenance/progeny trials of *Gmelina arborea*: genetic parameters and potential gain. *New for* 28:147–166. <https://doi.org/10.1023/B:NEFO.0000040942.34566.a7>
- IPCC (2014) In: Pachauri RK, Meyer LA (eds) Climate change 2014: synthesis report. Contribution of working groups I, II and III to the fifth assessment report. intergovernmental panel on climate change [Core Writing Team. Geneva, Switzerland
- Jaskierniak D, Benyon R, Kuczera G, Robinson A (2015) A new method for measuring stand sapwood area in forests. *Ecophysiol* 8:504–517. <https://doi.org/10.1002/eco.1520>
- Jones D, O'Hara K, Battles J, Gersonde R (2015) Leaf area prediction using three alternative sampling methods for seven Sierra Nevada conifer species. *Forests* 6:2631–2654. <https://doi.org/10.3390/f6082631>

- Knapic S, Louzada JL, Leal S, Pereira H (2008) Within-tree and between-tree variation of wood density components in Cork oak trees in two sites in Portugal. *Forestry* 81:465–473. <https://doi.org/10.1093/forestry/cpn012>
- Kubo M, Nishikawa S, Yamamoto E, Muramoto K (2007) Identification of individual tree crowns from satellite image and image-to-map rectification. In: 2007 IEEE International Geoscience and Remote Sensing Symposium. IEEE, Barcelona, Spain, pp 1905–1908
- Lehnebach R, Morel H, Bossu J et al (2017) Heartwood/sapwood profile and the tradeoff between trunk and crown increment in a natural forest: the case study of a tropical tree (*Dicorynia Guianensis* Amsh. Fabaceae) *Trees* 31:199–214. <https://doi.org/10.1007/s00468-016-1473-7>
- Longuetaud F, Leban J-M, MOTHE F, Mäkelä A (2006) *Picea abies* sapwood width: variations within and between trees. *Scand J Res* 21:41–53. <https://doi.org/10.1080/02827580500518632>
- Looker N, Martin J, Jencso K, Hu J (2016) Contribution of Sapwood traits to uncertainty in conifer Sap flow as estimated with the heat-ratio method. *Agric Meteorol* 223:60–71. <https://doi.org/10.1016/j.agrformet.2016.03.014>
- López Aguirre AM (2025) Estrategias de adaptación del manejo forestal orientadas a la mejora de la productividad y la eficiencia en el uso del agua de *Gmelina arborea* creciendo en condiciones de clima cambiante en el bosque seco tropical de Colombia. Tesis Doctoral, Universidad del Tolima
- López Aguirre AM, Barrios Trilleras, Trincado G, Nieto V (2011) Monitoreo y Modelamiento Del Crecimiento Para El Manejo de Plantaciones forestales comerciales. Corporación Nacional de Investigación y Fomento Forestal – CONIF, Bogotá
- López AM, Barrios A (2023) Variación genética de los rasgos de crecimiento y las características de la madera en razas locales de *Gmelina arborea* Roxb. en el alto Magdalena, Colombia. *Rev Acad Colomb Cienc Ex Fis Nat* 47:641–653. <https://doi.org/10.18257/raccefyn.1878>
- Lubczynski MW, Chavarro-Rincon DC, Rossiter DG (2017) Conductive sapwood area prediction from stem and canopy areas—allometric equations of Kalahari trees. *Botsw Ecohydrol* 10:e1856. <https://doi.org/10.1002/eco.1856>
- Magnani F, Grace J, Borghetti M (2002) Adjustment of tree structure in response to the environment under hydraulic constraints. *Funct Ecol* 16:385–393. <https://doi.org/10.1046/j.1365-2435.2002.00630.x>
- Mahendru N (2024) Ecological, medicinal, and economic importance of *Gmelina Arborea* Roxb. a native tree of India, Zenodo
- Medrano H, Bota J, Flexas J et al (2007) Eficiencia En El Uso Del Agua Por Las Plantas. *Investig Geogr* 63. <https://doi.org/10.14198/INGEO2007.43.04>
- Meinzer FC, Bond BJ, Warren JM, Woodruff DR (2005) Does water transport scale universally with tree size? *Funct Ecol* 19:558–565. <https://doi.org/10.1111/j.1365-2435.2005.01017.x>
- Ministerio de Agricultura y Desarrollo Rural (MADR) (2023) Boletín estadístico forestal Marzo 2023. MADR, Bogotá
- Mitra B, Papuga SA, Alexander MR et al (2020) Allometric relationships between primary size measures and sapwood area for six common tree species in snow-dependent ecosystems in the Southwest united States. *J Res* 31:2171–2180. <https://doi.org/10.1007/s11676-019-01048-y>
- Morataya R, Galloway G, Berninger F, Kanninen M (1999) Foliage biomass - sapwood (area And volume) relationships of *Tectona grandis* L.F. And *Gmelina Arborea* roxb.: silvicultural implications. *For Ecol Manag* 113:231–239. [https://doi.org/10.1016/S0378-1127\(98\)00429-0](https://doi.org/10.1016/S0378-1127(98)00429-0)
- Moya R (2004) Effect of management treatment and growing regions on wood properties of *Gmelina Arborea* in Costa Rica. *New for* 28:325–330. <https://doi.org/10.1023/B:NEFO.0000040965.76119.bc>
- Moya R, Tomazello M (2006) Variation in the wood anatomical structure of *Gmelina Arborea* (Verbenaceae) trees at different ecological conditions in Costa Rica. *Rev Biol Trop*. <https://doi.org/10.15517/rbt.v56i2.5617>
- Moya R, Tomazello M (2007) Wood density and fiber dimensions of *Gmelina Arborea* in fast growth trees in Costa rica: relation to the growth rate. *Syst* 16:267–276. <https://doi.org/10.5424/srf/2007163-01015>
- Moya R, Tomazello M (2009) Wood density variation and tree ring demarcation in *Gmelina Arborea* trees using X-ray densitometry. *Cerne* 15:92–100
- Muñoz-Acosta F, Moya R (2008) Moisture content variability in kiln-dried *Gmelina Arborea* wood: effect of radial position and anatomical features. *J Wood Sci* 54:318–322. <https://doi.org/10.1007/s10086-008-0954-8>
- Muñoz F, Moya R (2008) Moisture content variability in kiln-dried *Gmelina Arborea* wood: effect of radial position and anatomical features. *J Wood Sci* 54:318–322. <https://doi.org/10.1007/s10086-008-0954-8>
- O’Grady AP, Cook PG, Eamus D et al (2009) Convergence of tree water use within an arid-zone woodland. *Oecologia* 160:643–655. <https://doi.org/10.1007/s00442-009-1332-y>
- Olaniran SO, Iyiola E, Oyekola AA (2023) Investigation of wood properties and resistance of 25-year-old *Gmelina Arborea* wood selected from crown region to termite attack. *Maderas-Cienc Tecnol* 26. <https://doi.org/10.22320/s0718221x/2024.16>

- Osorio L (2004) Provenance results of *Gmelina Arborea* in Southwest Colombia at three years of age. *New* for 28:179–185. <https://doi.org/10.1023/B:NEFO.0000040944.23096.08>
- Panagiotidis D, Abdollahnejad A, Surový P, Chiteculo V (2017) Determining tree height and crown diameter from high-resolution UAV imagery. *Int J Remote Sens* 38:2392–2410. <https://doi.org/10.1080/01431161.2016.1264028>
- Pappas C, Bélanger N, Bastien-Beaudet G et al (2022) Xylem porosity, sapwood characteristics, and uncertainties in temperate and boreal forest water use. *Agric Meteorol* 323:109092. <https://doi.org/10.1016/j.agrformet.2022.109092>
- Pinheiro JC, Bates DM (2000) Mixed-effects models in S and S-PLUS. Springer-, New York
- Plomion C, Leprovost G, Stokes A (2001) Wood formation in trees. *Plant Physiol* 127:1513–1523. <https://doi.org/10.1104/pp.010816>
- Poorter L, McDonald I, Alarcón A et al (2010) The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. *New Phytol* 185:481–492. <https://doi.org/10.1111/j.1469-8137.2009.03092.x>
- Qiao Y, Yang S-I, Hao Y et al (2023) Quantifying the profiles of heartwood, sapwood, and bark using a seemingly unrelated mixed-effect model for *Larix olgensis* in Northeast China. *Forests* 14:1216. <https://doi.org/10.3390/f14061216>
- Quiñonez-Piñón M, Valeo C (2017) Allometry of sapwood depth in five boreal trees. *Forests* 8:457. <https://doi.org/10.3390/f8110457>
- Quiñonez-Piñón M, Valeo C (2019) Scaling approach for estimating stand sapwood area from leaf area index in five boreal species. *Forests* 10:829. <https://doi.org/10.3390/f10100829>
- R Core Team (2024) R: A Language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Rojas Rodríguez F, Dagoberto A, Aguilar R et al (2004) Manual Para productores de melina *Gmelina Arborea* En Costa Rica. Fondo Nacional de Financiamiento Forestal, San José, Costa Rica
- Roy B, Hart L, Weih R, Smith K (2005) Crown radius and diameter at breast height relationships for six Bottomland hardwood species. *J Ark Acad Sci* 59
- Schoppach R, Chun KP, Klaus J (2023) Allometric relations between DBH and sapwood area for predicting stand transpiration: lessons learned from the *Quercus* genus. *Eur J Res* 142:797–809. <https://doi.org/10.1007/s10342-023-01558-9>
- Sevanto S, McDowell NG, Dickman LT et al (2014) How do trees die? A test of the hydraulic failure and carbon starvation hypotheses. *Plant Cell Environ* 37:153–161. <https://doi.org/10.1111/pce.12141>
- Suárez JC, Casanoves F, Bieng MAN et al (2021) Prediction model for Sap flow in Cacao trees under different radiation intensities in the Western Colombian Amazon. *Sci Rep* 11:10512. <https://doi.org/10.1038/s41598-021-89876-z>
- Togashi HF, Prentice IC, Evans BJ et al (2015) Morphological and moisture availability controls of the leaf area-to-sapwood area ratio: analysis of measurements on Australian trees. *Ecol Evol* 5:1263–1270. <https://doi.org/10.1002/ece3.1344>
- Valeriano C, Gazol A, Colangelo M et al (2021) Modeling climate impacts on tree growth to assess tree vulnerability to drought during forest dieback. *Front Plant Sci* 12:672855. <https://doi.org/10.3389/fpls.2021.672855>
- van der Sande MT, Zuidema PA, Sterck F (2015) Explaining biomass growth of tropical canopy trees: the importance of sapwood. *Oecologia* 177:1145–1155. <https://doi.org/10.1007/s00442-015-3220-y>
- Yaemphum S, Unawong W, Tor-ngern P (2022) Sapwood area~dbh allometries for 14 common tree species in a successional tropical forest in Thailand. *Int J Res* 95:562–571. <https://doi.org/10.1093/forestry/cpab054>
- Yang K, Hazenberg G (1991) Sapwood and Heartwood width relationship to tree age in *Pinus Banksiana*. *Can J Res* 21:521–525
- Zhao X, Li X, Hu W et al (2023) Long-term variation of the Sap flow to tree diameter relation in a temperate Poplar forest. *J Hydrol* 618:129189. <https://doi.org/10.1016/j.jhydrol.2023.129189>
- Zhu LW, Zhao P (2023) Climate-driven sapwood-specific hydraulic conductivity and the Huber value but not leaf-specific hydraulic conductivity on a global scale. *Sci Total Environ* 857:159334. <https://doi.org/10.1016/j.scitotenv.2022.159334>
- Zobel BJ, Van Buijtenen JP (1989) Wood variation. Springer Berlin Heidelberg, Berlin, Heidelberg