

## ORIGINAL ARTICLE

# Relevance of wood anatomy and size of Amazonian trees in the determination and allometry of sapwood area

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## ABSTRACT

Hydrological processes in forest stands are mainly influenced by tree species composition and morpho-physiological characteristics. Few studies on anatomical patterns that govern plant hydraulics were conducted in tropical forest ecosystems. Thus, we used dye immersion to analyze sapwood area patterns of 34 trees belonging to 26 species from a *terra firme* forest in the central Brazilian Amazon. The sapwood area was related with wood anatomy and tree size parameters (diameter-at-breast-height - DBH, total height and estimated whole-tree volume). Exponential allometric equations were used to model sapwood area using the biometrical variables measured. Sapwood area traits (cross-section non-uniformity and heartwood visibility) varied significantly among and within species even though all were classified as diffuse porous. DBH was strongly and non-linearly correlated with sapwood area ( $R^2 = 0.46$ ,  $P < 0.001$ ), while no correlation was observed with vessel-lumen diameter ( $P = 0.94$ ) and frequency ( $P = 0.58$ ). Sapwood area and shape were also affected by the occurrence of vessel obstruction (i.e., tyloses), hollow stems and diseases. Our results suggest that sapwood area patterns and correlated variables are driven by intrinsic species characteristics, microclimate and ecological succession within the stand. We believe that individual tree sapwood characteristics have strong implications over water use, hydrological stand upsaling and biomass quantification. These characteristics should be taken into account (e.g., through a multi-point sampling approach) when estimating forest stand transpiration in a highly biodiverse ecosystem.

**KEYWORDS:** ecohydrology; active xylem; tyloses; vessels; Brazilian Amazon

## Relevância da anatomia da madeira e dimensões de árvores amazônicas na determinação e alometria do alburno

### RESUMO

Processos hidrológicos de povoamentos florestais são predominantemente influenciados pela composição de espécies arbóreas e suas características morfo-fisiológicas. No entanto, existem poucos estudos sobre os padrões anatômicos que determinam o sistema hidráulico de plantas em ecossistemas tropicais. Por isso, nosso objetivo foi o de analisar os padrões da área do xilema ativo em 34 árvores de 26 espécies de uma floresta de terra firme na Amazônia central por meio de imersão em solução de corante. A área do xilema ativo foi relacionada a características autoecológicas das espécies, anatomia da madeira e parâmetros de crescimento (diâmetro à altura do peito - DAP, altura total e volume total). Equações alométricas exponenciais foram utilizadas para ajustar a área do xilema às variáveis medidas. Características do alburno (área transversal não-uniforme e visibilidade do cerne) variaram significativamente entre e dentro de espécies, apesar de que todas as espécies apresentaram vasos difusos. DAP foi fortemente e não-linearmente correlacionado à área do alburno ( $R^2 = 0,46$ ;  $P < 0,001$ ), enquanto diâmetro ( $P = 0,94$ ) e frequência ( $P = 0.58$ ) de vasos não apresentaram nenhum grau de relacionamento. O tamanho e forma do alburno foram afetados pela ocorrência de obstrução de poros (tilose) e troncos ocos. Estes padrões sugerem que a área do xilema é influenciada por características intrínsecas de cada espécie, microclima e estágio sucessional dentro do povoamento. Nossos resultados implicam que características individuais de árvores podem fortemente influenciar o transporte de água e, consequentemente, os processos hidrológicos e a quantificação de biomassa do povoamento. Essas características deveriam ser consideradas (por exemplo, por meio da coleta de amostras da área do xilema ativo ao longo da área transversal) ao estimar-se a transpiração de uma floresta altamente biodiversa.

**PALAVRAS-CHAVE:** ecohidrologia; xilema ativo; tilose; vasos; Amazônia brasileira**CITE AS:** Aparecido, L.M.T.; Santos, J. dos; Higuchi, N.; Kunert, N. 2018. Relevance of wood anatomy and size of Amazonian trees in the determination and allometry of sapwood area. *Acta Amazonica* 49: 1-10.

## INTRODUCTION

The Amazonian forest harbors the most biodiverse plant communities of the world (ter Steege *et al.* 2013) and maintains a significant role in global water recycling and carbon storage within its mostly old, pristine forests (Shuttleworth 1988; Fauset *et al.* 2015). These older stands have developed very complex vertical canopy structures composed of large trees with vast canopies that shade less robust midstory strata and an even sparser understory canopy (Amaral *et al.* 2000). These multi-layered, heterogeneous stands influence the microclimatic conditions within the canopy, which will directly affect the development of plant individuals (Kammesheidt 2000; Dietz *et al.* 2007). The increase in light intensity, lower relative humidity and higher vapor pressure deficit resulting from natural and anthropogenic forest gaps can be detrimental for late successional trees and favor the expansion of early successional species (Kammesheidt 2000). Not only will species differ, but reminiscent trees are required to develop certain physiological strategies to cope with these changes, such as increasing sapwood area to avoid cavitation-embolism (Brodersen and McElrone 2013).

Sapwood area plays an important role when estimating whole-tree and stand transpiration (Cermak and Nadezhdina 1998). The use of sapwood area as an upscaling parameter has been widely studied and applied in the field of ecohydrology, specifically when coupled with sap flux measurements (Meinzer *et al.* 2004; Horna *et al.* 2011; Aparecido *et al.* 2016; Kunert *et al.* 2017; Moore *et al.* 2017). However, sapwood area determination is difficult when using destructive methods, such as dye-immersed or thermo-imaged fallen tree samples (Granier *et al.* 1994), or non-destructive methods, such as dyed increment cores (Gebauer *et al.* 2008) or electromagnetic imaging equipment (Bieker and Rust 2010). The major issue underlying non-destructive methods is the clarity of sapwood delimitation (e.g., heartwood color distinction; Granier *et al.* 1994; Giothioni and Dougal 2002) and its uniformity throughout the cross-section, especially when few measurement points are taken and extrapolated to all other directions (Gebauer *et al.* 2008).

With secondary growth, trees naturally tend to a gradual deactivation of old xylem tissues, although at different rates and magnitude (Stewart 1966), due to regulatory processes that maintain the sapwood area at an optimum metabolic level (i.e., water use and growth; Bamber 1975). However, xylem deactivation can be accelerated through vessel embolism-cavitation, when trees are fully exposed to high amounts of radiation, vapor pressure and/or soil moisture deficit (Machado and Tyree 1994; Schultz and Matthews 1997). There are very few studies that describe in detail the external and internal wood characteristics of tropical tree species and the different growth rates that might affect sapwood area formation and over or underestimation of its allometric

modelling (Enquist 2002; Čermák *et al.* 2004). Thus, to avoid errors that might lead to over or underestimation of evapotranspiration and carbon storage, it is important to assess the drivers that might influence the development of sapwood in tropical trees (e.g., wood anatomy and ecological traits), and which variables are the most reliable for the indirect estimation of sapwood area. Hence, we determined the sapwood area of 34 trees (26 species) from an old-growth *terra firme* forest in the central Brazilian Amazon. Our objective was to determine whether wood anatomical variables (vessel-lumen diameter, frequency and vessel element length) and tree size variables (diameter at breast height, total height and volume) are directly related to xylem development. We used macroscopic and microscopic wood descriptions and allometric equation modelling for a heterogeneous group of Amazonian tree species. We hypothesized that sapwood area allometry is not universal (Meinzer *et al.* 2001) and will vary as a function of ecological successional stage, independently of size and species.

## MATERIAL AND METHODS

### Study site and tree sampling

The study was conducted in an old growth, lowland forest located approximately 60 km northeast of the city of Manaus, Amazonas state, Brazil, in the Experimental Station for Tropical Silviculture ZF-2 (02°37'31.8"S; 60°08'24.7"W) of the Instituto Nacional de Pesquisas da Amazônia (INPA). The non-inundating, flat terrain is covered with a mature and species-rich evergreen *terra firme* forest. The climate is characterized as hot and humid with an average annual temperature of 25.8°C, relative air humidity between 84 and 90% throughout the year, and 2547 mm of annual rainfall (Kunert *et al.* 2017).

Thirty-four sample trees were selected at random between December 2012 and May 2013 close to a vicinal road and up to 100 m inside the forest. The tree selection was based on logistics and tree size criteria (ability to transport and handle log samples). The trees belonged to 26 species (Supplementary Material, Table S1), identified by means of their wood anatomy characteristics and, whenever necessary, botanical samples (Aparecido *et al.* 2015). None of the trees had buttressed stems reaching above a meter from the ground. Log sections of 0.40 m in length were extracted at breast height (1.30 m) for sapwood area determination and wood samples for macro and microscopic analyses. Total height (including the crown) was measured in the field after the tree was felled. After logs were extracted, the diameter at breast height (DBH) was obtained by averaging two measurements from the tree's cross-section (widest and narrowest diameters, as done when using tree calipers). Volume was estimated using an equation developed for the same area [Volume (m<sup>3</sup>) = a·DBH<sup>b</sup>·H<sup>c</sup>; where, a = 3.29; b = 2.16; c = 4.20] (Fernandes *et al.* 1983). We chose an equation that uses total height and DBH as

independent variables to evaluate to which extent sapwood area may be influenced by variables that have different degrees of dependence to stand density and quality (Machado and Figueiredo Filho 2006).

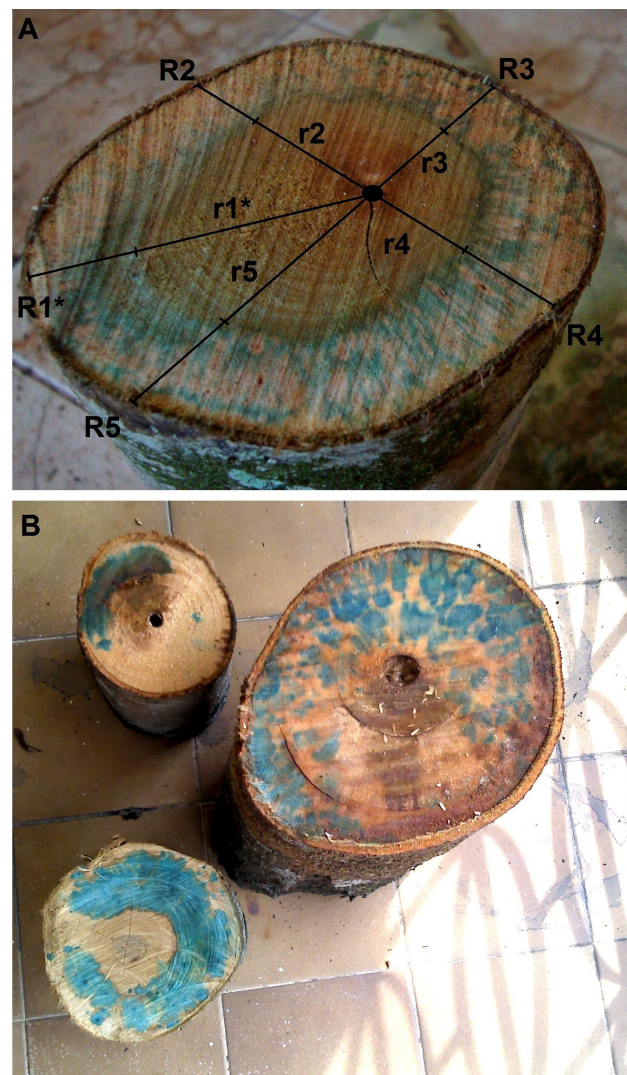
### Sapwood area determination

Sapwood area was determined through immersion of the harvested tree logs (Chavarro-Rincon 2009) in an aqueous dye solution (0.1% indigo carmine) (Andrade *et al.* 1998; Meinzer *et al.* 2001) immediately after harvest. Logs were left immersed for up to four hours until blue staining was fully apparent on the top cross-section surface, indicating the active conductive area. Most of the sections showed signs of staining within a couple of hours after immersion. Samples that did not show clear sapwood staining after that time were excluded from the dataset. Sapwood area ( $A_s$ ) was measured using five radii marked along the cross-section starting from the pith (Nutto *et al.* 2012). The first radius was the longest (i.e., the reference radius –  $R_n^*$  of Figure 1a). Each radius had two measurements: total radius [distance from the pith to the bark base ( $R$ )] and heartwood (or inactive area) radius [distance from the pith to the base of the dye-stained area ( $r$ )] (Figure 1a). The difference between  $R$  and  $r$  resulted in the sapwood depth (Supplementary Material, Table S1). Through each radius we estimated total cross-section area and heartwood cross-section area and subtracted these variables to achieve total sapwood area of each tree [ $A_s = \pi(\bar{R}^2 - \bar{r}^2)$ ] (Aparecido *et al.* 2015). Measuring five different radii guaranteed that variations within an irregularly shaped cross-section and non-continuous conductive sapwood area were properly accounted for (Figure 1b). To test this hypothesis, we also estimated sapwood area using only two radii measurements (longest and shortest) and compared them with the estimates obtained through the 5-radii method (Supplementary Material, Table S2).

### Wood anatomy characterization

The tree samples were characterized through macroscopic (wood characteristics for species identification) and microscopic wood description techniques (histological slides and maceration for vessel diameter and frequency measurements). The macroscopic description followed the technical standards recommended by the Pan-American Technical Standards Commission (COPANT 1974). Dry wood samples were taken from each tree section and were later shaped into 1.5 × 2.0 × 3.0 cm blocks. Wood structures and characteristics such as heartwood color, smell, texture, type of bark, and parenchyma description were used to determine and validate tree species identification. Characteristics observed during harvesting (e.g., exudates, smell, disease, hollow stem) were also considered for tree identification and as complementary wood characteristics.

Histological microscope slides were prepared for the measurement of tangential vessel dimensions, specifically for



**Figure 1.** Indigo carmine stained sapwood area of a few log sections. A. *Protium heptaphyllum* sapwood area demarcation and illustration of the 5-radii ( $R_n$ ) measurements in a non-uniform cross-section.  $R_n^*$  indicates the larger, reference radius and  $r_n$  the inner radii (equivalent to heartwood area). B. *Eschweilera wachenheimii* (bottom log section) and *Cecropia sciadophylla* (two log sections on top). This figure is in color in the electronic version.

lumen-diameter ( $\mu\text{m}$ ) and frequency (vessels per  $\text{mm}^2$ ), and to record tylose occurrence. Slides were mounted with 18  $\mu\text{m}$  thick wood sections (American Optical 860 microtome, AO Scientific Division, Buffalo, NY) previously dehydrated in an ethyl series (50, 70, and 100%; Johansen 1940) and stained with safranin-fucsin for tissue observations. Vessel diameter and frequency were measured using an Olympus Tokyo projector at 100× resolution (TandD VR-71, T&D Corporation, Shimadachi Matsumoto City, Japan) by randomly choosing 25 vessels per tree sample for each measurement type (Carlquist 1988).



Vessel element length ( $\mu\text{m}$ ) required a chemical maceration process to dissociate the vessel elements from fiber and parenchyma (Johansen 1940; Franklin 1945). Small wood slivers were submerged and stored in sealed beakers for 48 hours in a maceration solution consisting of 1:4:5 of hydrogen peroxide, distilled water and acetic acid. After washing with distilled water, the samples were loosened and dissociated, and then submerged in safranin-fuchsin dye. The vessel elements were then set on microscope slides and 25 vessel elements were randomly measured using a ruler and the same Olympus Tokyo projector at 100 $\times$  resolution. All wood anatomy variables were quantified and categorized according to COPANT (1974) technical standard classifications for wood structure characteristics. This classification allowed a broader view of the wood property diversity of the sampled trees (Supplementary Material, Figure S1). Wood samples were registered and stored in the xyarium of INPA.

### Data analyses

The correlations of tree size and wood anatomy variables with sapwood area were analyzed using Pearson's correlation coefficient ( $r$ ) and linear and exponential regressions to determine variable relationship and line-curve trend and to develop a practical allometric equation to estimate sapwood area in a non-destructive manner for this region and forest type (Supplementary Material, Table S2). The primary models used were an exponential power model ( $Y = aX^b$ ) and an exponential decay model ( $Y = ae^{(-bX)}$ ), where  $Y$  is sapwood area,  $a$  is the normalization constant,  $X$  is one of the biometrical or wood anatomy variables and  $b$  is an allometric scale exponent) (Wullscheleger *et al.* 2001; Meinzer *et al.* 2005; Gebauer *et al.* 2008). Model selection was based on the coefficient of determination ( $R^2$ ),  $F$ -values and  $P$ -values ( $\alpha = 0.05$ , 0.01 and 0.001) obtained from each model fit. Statistical analyses were performed with R version 2.6.2 (R Development Core Team 2008) and SYSTAT 12 (SYSTAT Software, Inc.; Richmond, CA).

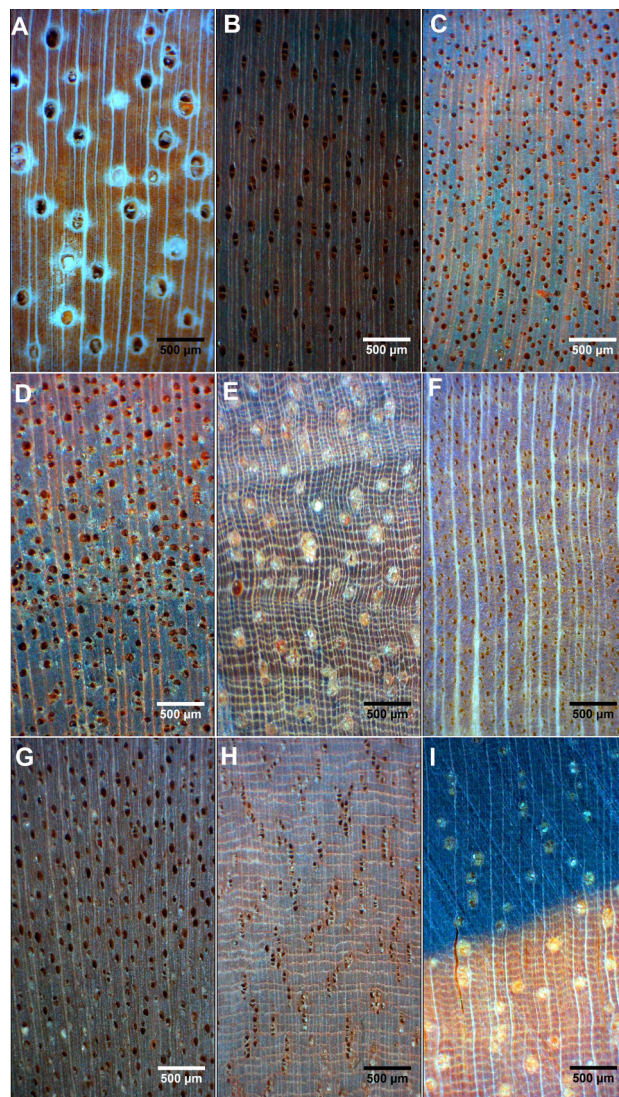
## RESULTS

### Sapwood area description

Sapwood area varied between 32 and 951  $\text{cm}^2$ , and the ratio between sapwood area and cross-section varied between 10% and 100% (Supplementary Material, Table S1; Figure S1). Sapwood area depth varied substantially between the measured radii along the cross-section of most trees. Longest and shortest radii differed in up to 37% in some trees. Consequently, the diameter estimated by five radii resulted in only nine trees with  $\pm 1\%$  difference from the diameters estimated by two radii measurements (Supplementary Material, Table S2). The most extreme differences between 5-radii and 2-radii estimates were 88% (12% underestimated) and 108% (8% overestimated), with an average of  $99 \pm 12\%$  ( $D_{R-Avg\%}$  in Supplementary Material, Table S1). When considering only one of the radii to estimate DBH, our estimate differences ranged from 67%

and 147% ( $D_{R\%}$  in Supplementary Material, Table S2). Consequently, cross-sections with highly variable radii lengths resulted in drastically different sapwood area estimates when considering randomly only one radius. For example, sapwood area was 49% smaller when using the shortest radius of *Vantanea micrantha* (Figure 1b; Supplementary Material, Table S2), with an overall average of  $34 \pm 11\%$  smaller than the reference radius.

Wood anatomy analyses showed interspecific differences in the presence of visible heartwood in the sapwood area (65% with complete or partial visibility), exudates (26% had some type of exudate), tyloses (50% had partial or complete apparent vessel obstruction; Figure 2), hollow stem or disease (38%), and/or sapwood area that did not reach the heartwood



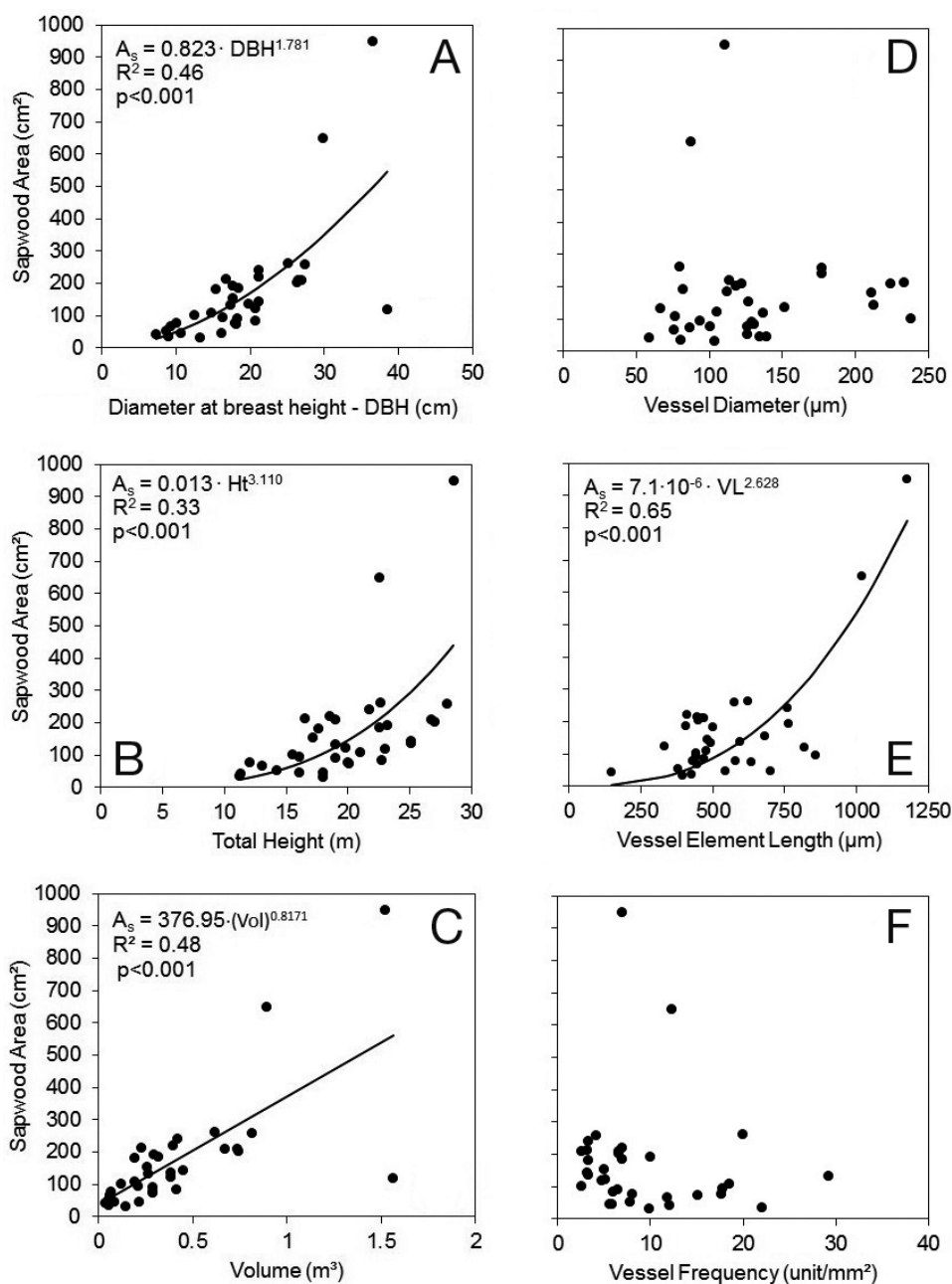
**Figure 2.** Macroscopic view of diffuse vessels in 10 $\times$  resolution from nine tree species. A. *Cecropia sciadophylla*; B. *Virola calophylla*; C. *Protium heptaphyllum*; D. *Ocotea neesiana*; E. *Eschweilera wachenheimii*; F. *Gustavia speciosa*; G. *Gyrsonima crispera*; H. *Pouteria caimito*; I. *Micrandropsis scleroxylon*. Panels A, E and I show vessels obstructed by tyloses. This figure is in color in the electronic version.

(47%) (Supplementary Material, Table S3). The only characters common to all species were diffuse porosity, which is a common feature of Amazonian tree species (Ferreira *et al.* 2004; Marques 2008; Moutinho 2008), and the predominant occurrence of solitary vessels (68% of samples), followed by groupings of vessel multiples of 2 (20%) (Supplementary Material, Figure S1).

### Allometric relationships

DBH had a positive and strong relationship with sapwood area ( $R^2 = 0.46$ ,  $r = 0.68$ ;  $P < 0.001$ ). DBH varied widely

when above 30 cm, which led to a weaker fit (Figure 3a; Supplementary Material, Table S4). Outliers were included while performing the regression analyses to maintain a representative sample, since ~90% of trees in the study area are in DBH classes < 30 cm (Higuchi *et al.* 2012). Additionally, excluding outliers did not result in a significantly better model fit for any of the variables analyzed in this study. Total height had a slightly weaker fit when compared to DBH, due to greater variability among trees (Figure 3a-b;  $R^2 = 0.33$ ;  $r = 0.54$ ;  $P < 0.001$ ). The relationship of tree volume with



**Figure 3.** Non-linear relationships between sapwood area and tree size and wood anatomy variables. Only significant ( $P < 0.05$ ) curves represented. A. Diameter at breast height (DBH, cm); B. Total height (Ht, m); C. Volume estimated from DBH and Ht (Vol, m<sup>3</sup>); D. Vessel diameter (μm); E. Vessel element length (μm); F. Vessel frequency (vessels per mm<sup>2</sup>).

sapwood area was only slightly stronger than using only DBH as a predictive variable ( $R^2 = 0.48$ ,  $r = 0.70$ ;  $P < 0.001$ ).

Vessel-lumen diameter did not vary widely among the sampled tree species. Although average vessel diameter of all trees ranged between 59 and 238  $\mu\text{m}$ , 51% of the trees had diameters of 100 - 200  $\mu\text{m}$  (Figure 3d; Supplementary Material, Figure S1), with an average of  $127.6 \pm 49.2 \mu\text{m}$  (see Supplementary Material, Table S1 for individual tree averages). Vessel-lumen diameter had the worst fit among the variables tested and, thus, had no influence on sapwood area variation ( $R^2 = 0.001$ ;  $r = 0.03$ ). Similarly to diameter, vessel frequency also varied little among trees. A third (34%) of the trees had few vessels per  $\text{mm}^2$  (Figure 3f; Supplementary Material, Figure S1b), and there was no correlation between vessel frequency and sapwood area ( $R^2 = 0.01$ ;  $r = -0.10$ ). Within-tree average vessel frequency varied between 2.5 and 29.2 vessels per  $\text{mm}^2$ , with an overall average of  $9.1 \pm 6.5$  vessels per  $\text{mm}^2$  (see Supplementary Material, Table S1 for individual tree averages). Contrary to all other variables, vessel frequency decreased with sapwood area increase (Figure 3f; Supplementary Material, Table S1). Average vessel element length varied between 148 and 1177  $\mu\text{m}$ , with an average of  $555 \pm 202 \mu\text{m}$ . Most vessel element lengths (54%) were shorter than 300  $\mu\text{m}$  (Supplementary Material, Figure S1). Unexpectedly, vessel element length had the strongest relationship with sapwood area ( $R^2 = 0.65$ ,  $r = 0.69$ ;  $P < 0.001$ ) (Figure 3e; Supplementary Material, Table S1).

## DISCUSSION

### Tree size

Our results showed that vessel element length was the strongest predictor of sapwood area among the tested variables, followed by volume and DBH. Of the three variables, DBH is the easiest to measure, and, hence, more practical to estimate sapwood area. Even though DBH was not as strongly correlated to sapwood area as expected, other studies have considered DBH as the best variable for sapwood area estimation (Gebauer *et al.* 2008; Moore *et al.* 2010; Horna *et al.* 2011). The assumption of a strong relationship between DBH and sapwood area is based on the hypothesis that water consumption increases with tree size (Meinzer *et al.* 2005). To allocate the necessary amount of carbon for biomass production (e.g., increase in trunk, branch and leaf biomass), trees need to maximize their water absorption through the increase of their sapwood area (Gebauer *et al.* 2008).

The weaker than expected model fit of the relationship between sapwood area and DBH may have been due to a wide range of intrinsic differences within each tree. For example, species belonging to different successional stages transpire at different rates and, consequently, alter the size of their sapwood area according to their water use (Horna *et al.* 2011; Kunert *et al.* 2017). Other studies in tropical regions

found that heliophylle (or pioneer) trees (i.e., plants with rapid growth under high light intensities) transpire more than co-existing late successional trees, specially closer to the forest edge (Horna *et al.* 2011; Kunert *et al.* 2015; Kunert *et al.* 2017). To compensate water loss, pioneer species may require a larger sapwood area in order to transport larger volumes of water. For instance, one of our sampled species, *Cecropia sciadophylla*, is a common pioneer tree in Amazonian forests, and its sapwood area occupied  $> 80\%$  of the cross-section in all three sampled specimens. In contrast, in *Ocotea neesiana*, a late successional tree (Paula *et al.* 2004), sapwood area occupied only 30% of the cross-section, which suggests that inherent successional stage might be one of the factors that influence the size of the active xylem area and, possibly, other physiological adaptations, such as leaf shedding.

The weaker relationship between total height and sapwood area, when compared to DBH, may be attributed to vertical tree growth dynamics not being related to horizontal tree growth (in diameter), or to the ability of generating new vessels in its cross-section (Brodersen and McElrone 2013). Although a weaker predictor than DBH, total height was significantly correlated with sapwood area, which suggests that sapwood growth may be related to tree height to some extent, i.e., enabling vertical growth expansion and maintenance (Kostner *et al.* 2002; Gebauer *et al.* 2008). Even though an increase in photosynthetic activity due to greater solar exposure may lead to tree growth (Andrade *et al.* 1998), it does not necessarily mean that total height will increase in the same manner as sapwood area. Thus, if tall trees are not assimilating the amount of carbon required to maintain their size/biomass, they may reduce sapwood area to avoid water loss. Tall, younger trees are likely to have more exposure to solar radiation, which will increase their water use. In this way, the combination of short and tall young trees in a forest stand will result in a high variability of sapwood area and, consequently, in a weaker model fit. Taller, more exposed, trees also have a greater disadvantage during the dry season, when high vapor pressure deficits ( $\text{VPD} > 1 \text{ kPa}$ ) may result in significant loss of hydraulic conductivity due to cavitation and embolism (Tyree and Sperry 1989; Gebauer *et al.* 2008). Therefore, some trees can maintain a smaller sapwood area to avoid embolism and cavitation (Cochard and Tyree 1990; Christman *et al.* 2012), specially those with medium to large-sized vessels (Tyree *et al.* 1994).

### Sapwood area

The sapwood areas determined in this study (32 - 951  $\text{cm}^2$ ) were similar in range to those observed in other Neotropical lowland and montane forests, with extremes ranging between 20 and 4000  $\text{cm}^2$  (Granier *et al.* 1996; Anhof *et al.* 1999; Motzer *et al.* 2005; Parolin *et al.* 2008; Aparecido *et al.* 2016; Kunert *et al.* 2017; Moore *et al.* 2017). The significant heterogeneity in sapwood area patterns in our samples suggests



that certain stem anatomical traits may affect the results of allometric modeling and determination of sapwood area. For example, the fact that in 47% of our sampled trees the active xylem did not reach the inferred and visible heartwood area suggests that sapwood area can be overestimated by some methodologies, such as the determination of sapwood area solely on heartwood coloration (Granier *et al.* 1996; Gartner 2002; Giothiomi and Dougal 2002). Heartwood coloration may therefore not be suitable as a sapwood estimation method for most Amazonian species. Additionally, most of the trees sampled did not have a uniformly, round-shaped stem, which would also over or underestimate sapwood area based on a single core extraction.

Another possible source of sapwood area (and transpiration) overestimation was the unexpected presence of hollow stems and tyloses, which are rarely acknowledged in other ecohydrological studies (James *et al.* 2003). Hollow stems were found in 20% of our trees, but can affect 50-75% of trees and account for up to 83% of the stem's cross section in other tropical sites (Bakshi 1960; Heineman *et al.* 2015). Other studies in the Brazilian Amazon found hollow stems in 30-40% of sampled trees (Apolinario and Martius 2004; Eleuterio 2011). Hollow stem incidence is higher in larger trees (DBH > 50 cm) (Heineman *et al.* 2015), which may explain why hollow trees were relatively less frequent in our sample than in the aforementioned studies. Hollow stems can lead to 7% less biomass in a forest stand, affecting carbon stock quantification (Heineman *et al.* 2015). Hence, without proper sapwood determination methods, there is increased uncertainty as to what degree factors such as heart rot or termite and ant colonies have affected the heartwood. Since hollow trunks are not exclusive to a certain tree species or age, and are typically associated with tree size, habitat and soil conditions (Heineman *et al.* 2015), it is only possible to non-destructively predict whether a certain tree cross-section is whole by employing specialized equipment, such as laser scanners, x-rays or electromagnetic resonance (Nikolova *et al.* 2009; Bieker and Rust 2010). However, these methods are expensive, laborious and practically inviable to use in the tropics (due to humidity, and the number and size of samples needed). Increment borers may provide a less laborious and little-invasive alternative to assess trunk hollowness, yet, as previously mentioned, non-uniformity of tree stems may lead to errors if only one core is extracted.

Tyloses have been reported to occur in some specific tree families, such as Lecythidaceae (Moutinho 2008) and Salicaceae (Mota *et al.* 2017). Considering that half the trees from this study presented some type of vessel obstruction, we can assume that tyloses are a major contributor to sapwood area deactivation or partial obstruction of water and nutrient pathways in the active xylem of Amazonian trees (Bamber 1975; Kitin *et al.* 2010). These deactivated portions may not be homogeneous and can occur in any portion of the stem, as

is the case of heartwood wounds that develop after cambium injuries (Bamber 1975). This can result in significant errors in hydrological measurements, such as sap flux, when probes are inserted in partially deactivated sapwood (Clearwater *et al.* 1999; McDowell *et al.* 2002; Gebauer *et al.* 2008).

### Wood anatomy

Our results indicated clearly that the anatomical characters analyzed were not responsible for sapwood area growth or deactivation. Unlike sapwood area, the number and tangential dimensions of vessels are not altered due to seasonal variations or ecological traits (Sterck *et al.* 2008). These variables can be altered only through certain genetic mutations or as an adaptation to local microclimates at different altitudes and/or latitudes (Fisher *et al.* 2007). Since our samples were collected in a small area on a flat terrain, the occurrence of genetic or geographical variation is unlikely. Likewise, Noshiro and Baas (2000) concluded that insufficient distance between forest stands explained the lack of significant variation in vessel diameter and frequency in relation to DBH and sapwood area between stands.

The surprisingly strong relationship observed between vessel element length and sapwood area may be attributed to the local microclimate (Baas 1982). Through paleoecology, Baas (1982) associated smaller vessel element length to accentuated seasonality of the local climate (e.g., elevated precipitation rates or rigorous drought periods). Considering that the Amazon region does not have a strong dry season, and temperatures and precipitation are predominantly constant over the years, we can assume that interspecific variation in vessel element lengths is due to different water use strategies and the effect of microclimatic variation within a forest stand, such as the occurrence of forest gaps (Kunert *et al.* 2015), which may also directly affect sapwood area size (Copenhagen and Tinker 2014). Although being an evolutionary insightful parameter, vessel element length is extremely difficult to measure, for it requires tree harvesting and laborious and expensive laboratory analyses, which makes it unpractical as a variable to estimate sapwood area.

### CONCLUSIONS

Our study sheds light on the importance of considering wood anatomy traits and tree size variations when estimating sapwood area in a heterogeneous tropical forest stand. The frequent occurrence of tyloses and hollow stems can potentially affect the accuracy of allometric modeling and the estimation of ecohydrological parameters. Neglect in accounting for hollow stems may lead to significant overestimation of aboveground tree biomass in the Amazon, while not accounting for the occurrence of tyloses (specially in Lecythidaceae) may lead to overestimation of stand transpiration. Even though xylem vessels are important components of sapwood area, the variables that mainly affected this parameter were related to

tree size, ecological succession and location inside the stand (canopy exposure). Our results suggest that sapwood area allometry may not be constant in Amazonian forests, but vary with tree diameter, species autoecology and stand dynamics. Future studies aiming at sapwood area estimation in the Amazon should take into account these aspects when sampling highly heterogeneous stands. Our findings also can improve sapwood area determination through non-destructive multi-point sampling, especially when dealing with non-uniform tree stems. Differential adaptability to microclimates will affect water use rates of trees, and consequently their sapwood area size. Our study provides useful insights for future studies on Amazonian tree water use and carbon stock estimation.

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**SUPPLEMENTARY MATERIAL** (only available in the electronic version)

APARECIDO *et al.* Relevance of wood anatomy and size of Amazonian trees in the determination and allometry of sapwood area

**Table S1.** Size and characteristics of wood anatomy of all sampled trees. Values are the mean  $\pm$  standard deviation, when more than one measurement was taken.

Family/species	Height (m)	DBH <sup>1</sup> (cm)	Sapwood depth <sup>2</sup> (cm)	Sapwood area (cm <sup>2</sup> )	Basal area (cm <sup>2</sup> )	Sapwood-to-basal area ratio (%)	Avg vessel diameter ( $\mu$ m)	Avg vessel frequency (vessels/mm <sup>2</sup> )	Avg vessel element length ( $\mu$ m)
ANNONACEAE									
<i>Bocageopsis multiflora</i> (Mart.) R. E. Fries	26.7	26.8 $\pm$ 1.1	2.8 $\pm$ 0.2	209.9	545.7	38.5	122.0 $\pm$ 32.9	6.6 $\pm$ 2.4	463.0 $\pm$ 107.0
<i>Duguetia flagellaris</i> Huber	13.0	9.4 $\pm$ 0.2	4.6 $\pm$ 0.5	66.5	66.5	100.0	75.2 $\pm$ 24.0	11.8 $\pm$ 3.1	448.4 $\pm$ 35.1
BIGNONIACEAE									
<i>Jacaranda copaia</i> (Aubl.) D. Don	25.1	20.4 $\pm$ 0.2	2.5 $\pm$ 0.3	137.1	305.4	44.9	151.6 $\pm$ 43.6	3.3 $\pm$ 1.3	595.9 $\pm$ 382.4
BORAGINACEAE									
<i>Cordia silvestris</i> Fresen. <sup>3</sup>	19.8	20.6 $\pm$ 4.3	2.1 $\pm$ 0.8	124.1	333.3	37.2	105.2 $\pm$ 40.1	5.1 $\pm$ 3.0	331.6 $\pm$ 74.8
BURSERACEAE									
<i>Protium heptaphyllum</i> (Aubl.) March.	11.2	8.8 $\pm$ 0.8	1.6 $\pm$ 0.4	36.8	63.6	57.9	80.4 $\pm$ 27.2	22.0 $\pm$ 4.1	428.8 $\pm$ 109.2
EUPHORBIACEAE									
<i>Mabea caudata</i> Pax & K. Hoffm.	16.0	11.5 $\pm$ 1.2	1.7 $\pm$ 0.4	47.5	89.6	53.0	134.4 $\pm$ 28.4	5.6 $\pm$ 2.2	701.5 $\pm$ 206.3
<i>Mabea caudata</i> Pax & K. Hoffm.	17.2	17.5 $\pm$ 0.7	3.4 $\pm$ 0.8	152.8	244.4	62.5	126.8 $\pm$ 38.2	4.9 $\pm$ 1.6	681.2 $\pm$ 163.6
<i>Micrandropsis scleroxylon</i> W. Rodr.	28.0	28.1 $\pm$ 3.4	3.5 $\pm$ 0.7	259.4	586.2	44.2	176.4 $\pm$ 51.2	5.1 $\pm$ 2.1	575.8 $\pm$ 200.5
FABACEAE - CAESALPINOIDEAE									
<i>Sclerolobium chrysophyllum</i> Poepp.	25.1	20.9 $\pm$ 0.2	2.4 $\pm$ 0.4	143.2	350.3	40.9	212.4 $\pm$ 29.8	3.1 $\pm$ 1.5	482.1 $\pm$ 99.6
<i>Tachigali paniculata</i> Aubl.	14.2	8.4 $\pm$ 0.5	3.1 $\pm$ 0.4	53.9	58.1	92.7	125.6 $\pm$ 38.4	7.8 $\pm$ 3.4	381.7 $\pm$ 97.0
HUMIRIACEAE									
<i>Vantanea micrantha</i> Ducke	21.7	20.5 $\pm$ 0.5	4.7 $\pm$ 2.7	241.9	349.0	69.3	176.4 $\pm$ 37.3	3.3 $\pm$ 1.2	759.0 $\pm$ 143.7
<i>Vantanea micrantha</i> Ducke	23.0	40.6 $\pm$ 2.3	1.0 $\pm$ 0.3	117.6	1160.5	10.1	136.4 $\pm$ 21.0	4.7 $\pm$ 1.4	818.0 $\pm$ 176.2
LAURACEAE									
<i>Ocotea neesiana</i> (Miq.) Kosterm.	20.0	18.8 $\pm$ 0.4	1.5 $\pm$ 0.1	76.6	253.3	30.3	100.0 $\pm$ 30.0	17.6 $\pm$ 4.5	578.4 $\pm$ 161.3
LECYTHIDACEAE									
<i>Eschweilera fracta</i> R. Knuth	18.5	21.9 $\pm$ 0.9	4.2 $\pm$ 0.5	222.2	351.7	63.2	113.2 $\pm$ 34.2	6.9 $\pm$ 2.4	410.8 $\pm$ 119.1
<i>Eschweilera odora</i> (Poepp. ex O. Berg)	22.7	20.7 $\pm$ 1.2	2.6 $\pm$ 0.4	83.8	334.9	25.0	130.4 $\pm$ 42.1	5.9 $\pm$ 3.2	470.8 $\pm$ 131.5
<i>Eschweilera wachenheimii</i> Sandwith	12.0	10.5 $\pm$ 0.7	4.5 $\pm$ 0.4	78.4	79.2	99.0	126.0 $\pm$ 46.2	8.0 $\pm$ 2.9	432.7 $\pm$ 142.2
<i>Eschweilera wachenheimii</i> Sandwith	22.5	18.1 $\pm$ 0.2	4.2 $\pm$ 0.7	186.7	265.9	70.2	112.0 $\pm$ 31.4	6.9 $\pm$ 2.6	406.0 $\pm$ 86.3
<i>Eschweilera wachenheimii</i> Sandwith	19.0	20.8 $\pm$ 1.1	1.8 $\pm$ 1.8	91.6	259.0	35.4	129.2 $\pm$ 48.6	6.4 $\pm$ 2.4	443.1 $\pm$ 119.6
<i>Eschweilera wachenheimii</i> Sandwith	18.0	16.0 $\pm$ 0.0	0.9 $\pm$ 0.2	44.6	202.1	22.1	139.2 $\pm$ 33.3	5.8 $\pm$ 2.2	543.6 $\pm$ 105.9
<i>Eschweilera wachenheimii</i> Sandwith	18.0	12.9 $\pm$ 0.5	0.8 $\pm$ 0.1	31.8	136.0	23.4	103.2 $\pm$ 28.1	9.8 $\pm$ 4.1	395.2 $\pm$ 80.4
<i>Gustavia speciosa</i> (Kunth) DC.	19.0	17.9 $\pm$ 0.5	3.0 $\pm$ 0.4	133.9	236.7	56.6	66.0 $\pm$ 17.3	29.2 $\pm$ 4.6	495.2 $\pm$ 77.9
MALPIGHIACEAE									
<i>Byrsonima crispera</i> A. Juss	16.0	15.9 $\pm$ 2.3	2.2 $\pm$ 0.6	95.8	208.2	46.0	93.6 $\pm$ 19.6	17.7 $\pm$ 4.6	857.2 $\pm$ 164.9
MORACEAE									
<i>Brosimum utile</i> (Kunth) Pittier	27.0	26.7 $\pm$ 1.9	2.7 $\pm$ 0.8	203.0	544.1	37.3	118.0 $\pm$ 28.7	6.5 $\pm$ 2.4	452.5 $\pm$ 85.8



**Table S1.** Continued.

Family/species	Height (m)	DBH <sup>1</sup> (cm)	Sapwood depth <sup>2</sup> (cm)	Sapwood area (cm <sup>2</sup> )	Basal area (cm <sup>2</sup> )	Sapwood-to-basal area ratio (%)	Avg vessel diameter (µm)	Avg vessel frequency (vessels/mm <sup>2</sup> )	Avg vessel element length (µm)
MYRISTICACEAE									
<i>Iryanthera ulei</i> Warb	23.2	19.4 ± 0.5	4.7 ± 1.4	192.7	245.5	78.5	82.0 ± 22.4	10.0 ± 2.6	765.6 ± 142.2
<i>Virola calophylla</i> (Spruce) Warb.	22.5	30.1 ± 1.3	11.0 ± 1.0	648.8	695.6	93.3	87.2 ± 28.5	12.3 ± 4.6	1020.7 ± 198.6
<i>Virola surinamensis</i> (Rol. Ex. Rottb.) Warb	28.5	36.4 ± 1.3	12.9 ± 0.6	950.7	1040.6	91.4	110.4 ± 28.9	6.9 ± 2.6	1176.6 ± 220.8
MYRTACEAE									
<i>Caliptanthes spruceana</i> Berg.	21.0	13.9 ± 1.1	2.9 ± 0.4	108.6	171.1	63.5	76.4 ± 19.3	18.5 ± 5.6	479.8 ± 132.8
NYCTAGINACEAE									
<i>Neea madeirana</i> Standl.	11.3	7.2 ± 0.3	3.6 ± 0.5	41.6	41.6	100.0	58.8 ± 19.2	12.0 ± 3.8	147.7 ± 37.8
SAPOTACEAE									
<i>Chrysophyllum ucuquirana-branca</i> (Aubrev & Pellegr) T. D. Penn.	20.1	18.3 ± 1.1	1.4 ± 0.7	72.2	255.6	28.3	86.0 ± 19.2	15.1 ± 4.3	636.9 ± 173.0
<i>Pouteria caimito</i> Radlk.	22.6	26.0 ± 1.4	4.0 ± 0.8	262.8	494.0	53.2	79.6 ± 14.9	19.9 ± 4.7	622.8 ± 156.4
URTICACEAE									
<i>Cecropia sciadophylla</i> Mart.	15.5	12.2 ± 0.3	3.7 ± 0.8	101.7	122.3	83.2	238.0 ± 44.2	2.5 ± 0.8	441.5 ± 85.8
<i>Cecropia sciadophylla</i> Mart.	17.6	15.1 ± 1.8	6.9 ± 1.4	182.4	184.3	99.0	210.4 ± 37.8	3.2 ± 1.3	500.4 ± 118.1
<i>Cecropia sciadophylla</i> Mart.	16.5	17.3 ± 1.5	7.4 ± 1.4	214.9	217.5	98.8	232.8 ± 53.5	3.1 ± 1.0	448.0 ± 79.6
<i>Pourouma guianensis</i> Aubl.	19.0	27.3 ± 1.1	2.8 ± 0.5	210.8	569.2	37.0	224.0 ± 29.6	2.6 ± 1.2	485.5 ± 111.6
Overall average	19.6	19.2	3.5	171.4	325.3	58.4	127.6	9.1	554.8
Overall standard deviation	4.7	8.4	2.6	177.6	258.5	27.0	49.2	6.5	201.9
Overall minimum	11.2	7.2	0.8	31.8	41.6	10.1	58.8	2.5	147.7
Overall maximum	28.5	40.6	13.0	950.7	1160.5	100.0	238	29.2	1176.6

<sup>1</sup>Diameter-at-breast-height obtained from the measures of the smallest and largest diameter; <sup>2</sup>Based on measurement of five radii; <sup>3</sup>DBH was obtained through radii measurements of a fragmented stem section.

**Table S2.** Sapwood data of 34 trees belonging to 26 species sampled in a *terra firme* forest in the central Brazilian Amazon. Sapwood area depth was estimated from each of five radii measured (A<sub>r</sub>n). Sapwood area was estimated considering all five radii estimates (A<sub>s</sub>). DBH = diameter-at-breast-height (in cm) (average of two measures); D<sub>r</sub> = average diameter estimated for each of the five radii (in cm); D<sub>r</sub>\_Avg = average diameter considering all five radii estimates (in cm); D<sub>r</sub>% = percentage difference between DBH and each D<sub>r</sub>; D<sub>r</sub>\_Avg% = total average difference between DBH and each D<sub>r</sub>. Overall average, standard deviation, minimum and maximum values of the measurements are also presented at the end of the table. Note: \*Diameter was obtained through radii measurements of a fragmented stem section. N/A represents "non available" data.

Species	A <sub>r</sub> 1	A <sub>r</sub> 2	A <sub>r</sub> 3	A <sub>r</sub> 4	A <sub>r</sub> 5	A <sub>s</sub>	DBH	D <sub>1</sub>	D <sub>2</sub>	D <sub>3</sub>	D <sub>4</sub>	D <sub>5</sub>	D <sub>r</sub> _Avg	D <sub>1</sub> %	D <sub>2</sub> %	D <sub>3</sub> %	D <sub>4</sub> %	D <sub>5</sub> %	D <sub>r</sub> _Avg%
<i>Bocageopsis multiflora</i>	2.5	2.7	3.0	3.0	3.0	<b>2.8 ± 0.2</b>	<b>26.8 ± 1.1</b>	27.4	25.6	26.8	25.0	27.0	<b>26.4 ± 1.0</b>	102	96	100	93	101	<b>99 ± 4</b>
<i>Brosimum utile</i>	3.3	2.2	3.8	2.5	1.9	<b>2.7 ± 0.8</b>	<b>26.7 ± 1.9</b>	29.0	26.0	27.6	21.6	27.4	<b>26.3 ± 2.8</b>	109	98	104	81	103	<b>99 ± 11</b>
<i>Byrsonima crista</i>	2.3	2.7	2.7	1.6	1.5	<b>2.2 ± 0.6</b>	<b>15.9 ± 2.3</b>	18.4	17.6	15.4	16.0	14.0	<b>16.3 ± 1.8</b>	116	111	97	101	88	<b>102 ± 11</b>
<i>Caliptanthes spruceana</i>	3.6	3.0	2.7	2.9	2.4	<b>2.9 ± 0.4</b>	<b>13.9 ± 1.1</b>	18.0	16.6	11.4	11.4	16.4	<b>14.8 ± 3.1</b>	129	119	82	82	118	<b>106 ± 22</b>
<i>Cecropia sciadophylla</i>	4.7	4.0	3.1	2.7	3.9	<b>3.7 ± 0.8</b>	<b>12.2 ± 0.3</b>	14.0	14.0	11.6	10.2	12.6	<b>12.5 ± 1.6</b>	115	115	95	84	103	<b>102 ± 13</b>
<i>Cecropia sciadophylla</i>	8.7	7.3	4.7	6.7	7.0	<b>6.9 ± 1.4</b>	<b>15.1 ± 1.8</b>	18.6	15.8	11.8	15.0	15.4	<b>15.3 ± 2.4</b>	123	105	78	99	102	<b>101 ± 16</b>
<i>Cecropia sciadophylla</i>	9.5	7.0	5.9	6.5	8.2	<b>7.4 ± 1.4</b>	<b>17.3 ± 1.5</b>	21.0	16.0	13.2	15.0	18.0	<b>16.6 ± 3.0</b>	122	93	77	87	104	<b>96 ± 17</b>
<i>Chrysophyllum ucuquirana-branca</i>	2.0	1.5	0.6	0.8	2.0	<b>1.4 ± 0.7</b>	<b>18.3 ± 1.1</b>	19.4	19.0	17.2	17.6	17.0	<b>18.0 ± 1.1</b>	106	104	94	96	93	<b>99 ± 6</b>

**Table S2.** Continued.

Species	A <sub>R1</sub>	A <sub>R2</sub>	A <sub>R3</sub>	A <sub>R4</sub>	A <sub>R5</sub>	A <sub>s</sub>	DBH	D <sub>1</sub>	D <sub>2</sub>	D <sub>3</sub>	D <sub>4</sub>	D <sub>5</sub>	D <sub>R_Avg</sub>	D <sub>1%</sub>	D <sub>2%</sub>	D <sub>3%</sub>	D <sub>4%</sub>	D <sub>5%</sub>	D <sub>R_Avg%</sub>
<i>Cordia silvestris</i>	3.5	2.0	2.0	1.7	1.5	<b>2.1 ± 0.8</b>	<b>20.6 ± 4.3</b>	26.0	24.0	17.0	16.0	20.0	<b>20.6 ± 4.3</b>	N/A	N/A	N/A	N/A	N/A	<b>N/A</b>
<i>Duguetia flagellaris</i>	5.1	4.7	4.0	4.2	5.0	<b>4.6 ± 0.5</b>	<b>9.4 ± 0.2</b>	10.2	9.4	8.0	8.4	10.0	<b>9.2 ± 1.0</b>	109	101	86	90	107	<b>98 ± 10</b>
<i>Eschweilera fracta</i>	4.4	4.4	4.3	3.3	4.4	<b>4.2 ± 0.5</b>	<b>21.9 ± 0.9</b>	23.2	22.8	19.8	18.0	22.0	<b>21.2 ± 2.2</b>	106	104	91	82	101	<b>97 ± 10</b>
<i>Eschweilera odora</i>	2.8	2.6	3.1	2.6	2.0	<b>2.6 ± 0.4</b>	<b>20.7 ± 1.2</b>	22.7	22.0	23.8	21.0	22.3	<b>22.3 ± 1.0</b>	110	107	115	107	102	<b>108 ± 5</b>
<i>Eschweilera wachenheimii</i>	4.9	4.8	4.6	4.3	4.0	<b>4.5 ± 0.4</b>	<b>10.5 ± 0.7</b>	10.4	10.6	10.2	9.8	9.2	<b>10.0 ± 1.0</b>	99	101	97	93	88	<b>96 ± 5</b>
<i>Eschweilera wachenheimii</i>	4.4	4.7	4.8	3.7	3.3	<b>4.2 ± 0.7</b>	<b>18.1 ± 0.2</b>	19.4	18.6	17.0	18.6	18.4	<b>18.4 ± 0.9</b>	107	103	94	103	102	<b>102 ± 5</b>
<i>Eschweilera wachenheimii</i>	3.5	2.7	3.1	0.5	0.1	<b>1.8 ± 1.8</b>	<b>20.8 ± 1.1</b>	22.0	18.0	18.8	17.0	16.0	<b>18.4 ± 2.3</b>	106	87	91	82	77	<b>88 ± 11</b>
<i>Eschweilera wachenheimii</i>	0.8	1.3	0.9	1.0	0.7	<b>0.9 ± 0.2</b>	<b>16.0 ± 0.0</b>	18.0	17.6	14.2	14.0	16.4	<b>16.0 ± 1.9</b>	113	110	89	88	103	<b>100 ± 12</b>
<i>Eschweilera wachenheimii</i>	0.8	0.8	0.8	0.8	0.9	<b>0.8 ± 0.1</b>	<b>12.9 ± 0.5</b>	13.6	13.0	13.0	12.6	13.6	<b>13.2 ± 0.4</b>	106	101	101	98	106	<b>102 ± 4</b>
<i>Gustavia speciosa</i>	3.3	2.8	3.4	3.0	2.3	<b>3.0 ± 0.4</b>	<b>17.9 ± 0.5</b>	19.4	19.0	16.8	15.0	16.6	<b>17.4 ± 1.8</b>	109	106	94	84	93	<b>97 ± 10</b>
<i>Iryanthera ulei</i>	7.1	3.9	3.7	5.1	3.9	<b>4.7 ± 1.4</b>	<b>19.4 ± 0.5</b>	25.6	16.8	13.0	19.6	13.4	<b>17.7 ± 5.2</b>	132	87	67	101	69	<b>91 ± 27</b>
<i>Jacaranda copaia</i>	3.0	2.5	2.6	2.5	2.1	<b>2.5 ± 0.3</b>	<b>20.4 ± 0.2</b>	20.8	20.6	20.6	18.4	18.2	<b>19.7 ± 1.3</b>	102	101	101	90	89	<b>97 ± 7</b>
<i>Mabea caudata</i>	2.2	1.6	1.9	1.2	1.5	<b>1.7 ± 0.4</b>	<b>11.5 ± 1.2</b>	12.0	10.0	10.4	11.0	10.0	<b>10.7 ± 0.8</b>	108	90	93	99	90	<b>96 ± 8</b>
<i>Mabea caudata</i>	4.0	2.3	2.8	4.0	4.0	<b>3.4 ± 0.8</b>	<b>17.5 ± 0.7</b>	23.0	17.0	13.6	15.6	19.0	<b>17.6 ± 3.6</b>	131	97	78	89	109	<b>101 ± 20</b>
<i>Micrandropsis scleroxylon</i>	4.5	3.8	3.0	3.0	3.0	<b>3.5 ± 0.7</b>	<b>28.1 ± 3.4</b>	31.0	24.0	27.0	26.6	28.0	<b>27.3 ± 2.5</b>	110	85	96	95	100	<b>97 ± 9</b>
<i>Neea madeirana</i>	4.2	4.1	3.4	3.3	3.2	<b>3.6 ± 0.5</b>	<b>7.2 ± 0.3</b>	8.4	8.2	6.8	6.6	6.4	<b>7.3 ± 0.9</b>	117	114	94	92	89	<b>101 ± 13</b>
<i>Ocotea neesiana</i>	1.6	1.5	1.4	1.4	1.5	<b>1.5 ± 0.1</b>	<b>18.8 ± 0.4</b>	19.0	19.0	16.8	17.0	18.0	<b>18.0 ± 1.1</b>	101	101	90	91	96	<b>96 ± 5</b>
<i>Pourouma guianensis</i>	2.5	2.8	2.1	3.5	3.0	<b>2.8 ± 0.5</b>	<b>27.3 ± 1.1</b>	30.4	25.0	25.8	25.4	28.0	<b>26.9 ± 2.3</b>	112	92	95	93	103	<b>99 ± 8</b>
<i>Pouteria caimito</i>	4.9	2.9	3.6	4.3	4.1	<b>4.0 ± 0.7</b>	<b>26.0 ± 1.4</b>	32.0	27.0	24.6	18.4	23.4	<b>25.1 ± 5.0</b>	123	104	95	71	90	<b>96 ± 19</b>
<i>Protium heptaphyllum</i>	2.0	1.9	1.4	1.7	0.9	<b>1.6 ± 0.4</b>	<b>8.8 ± 0.8</b>	10.6	9.6	7.0	8.2	9.6	<b>9.0 ± 1.4</b>	121	110	80	94	110	<b>103 ± 16</b>
<i>Sclerobium chrysophyllum</i>	2.4	3.0	2.6	2.4	1.8	<b>2.4 ± 0.4</b>	<b>20.9 ± 0.2</b>	25.4	21.0	18.0	19.2	22.0	<b>21.1 ± 2.9</b>	122	101	86	92	106	<b>101 ± 14</b>
<i>Tachigali paniculata</i>	3.8	3.2	2.8	3.0	2.9	<b>3.1 ± 0.4</b>	<b>8.4 ± 0.5</b>	9.6	8.8	8.6	8.6	7.4	<b>8.6 ± 0.8</b>	115	105	103	103	89	<b>103 ± 9</b>
<i>Vantanea micrantha</i>	1.0	1.0	0.5	1.3	1.2	<b>1.0 ± 0.3</b>	<b>40.6 ± 2.3</b>	49.0	40.2	36.4	31.6	35.0	<b>38.4 ± 6.7</b>	121	99	90	78	86	<b>95 ± 16</b>
<i>Vantanea micrantha</i>	9.0	3.2	2.1	3.7	5.5	<b>4.7 ± 2.7</b>	<b>20.5 ± 0.5</b>	29.0	19.0	15.0	20.4	22.0	<b>21.1 ± 5.1</b>	142	93	73	100	108	<b>103 ± 25</b>
<i>Virola calophylla</i>	12.5	9.7	10.8	10.8	11.3	<b>11.0 ± 1.0</b>	<b>30.1 ± 1.3</b>	33.0	30.0	28.0	27.2	30.6	<b>29.8 ± 2.3</b>	110	100	93	90	102	<b>99 ± 8</b>
<i>Virola surinamensis</i>	13.0	12.1	13.0	13.7	13.2	<b>12.9 ± 0.6</b>	<b>36.4 ± 1.3</b>	38.0	35.0	36.0	36.4	36.0	<b>36.3 ± 1.1</b>	104	96	99	100	99	<b>100 ± 3</b>
Average	4.0	3.3	3.1	3.1	3.2	<b>3.5 ± 0.7</b>	<b>19.2 ± 0.9</b>	21.5	18.7	16.9	16.7	18.2	<b>19.0 ± 2.2</b>	114	100	91	92	97	<b>99 ± 9</b>
Standard Deviation	2.6	1.9	1.9	2.1	2.5	<b>2.6</b>	<b>8.4</b>	8.5	6.8	7.0	6.0	6.9	<b>7.4</b>	10	9	10	8	10	<b>4 ± 1</b>
Minimum	0.8	0.8	0.5	0.5	0.1	<b>0.8</b>	<b>7.2</b>	8.4	8.2	6.8	6.6	6.4	<b>7.3</b>	99	79	67	71	69	<b>88 ± 13</b>
Maximum	12.5	9.7	10.8	10.8	11.3	<b>13</b>	<b>40.6</b>	49.0	40.2	36.4	31.6	35.0	<b>38.4</b>	142	119	115	107	118	<b>108 ± 13</b>

**Table S3.** Descriptors of the physical characteristics observed on each sampled tree log cross-section surface (n = 34). For heartwood visibility: V = completely visible, P = partially visible.

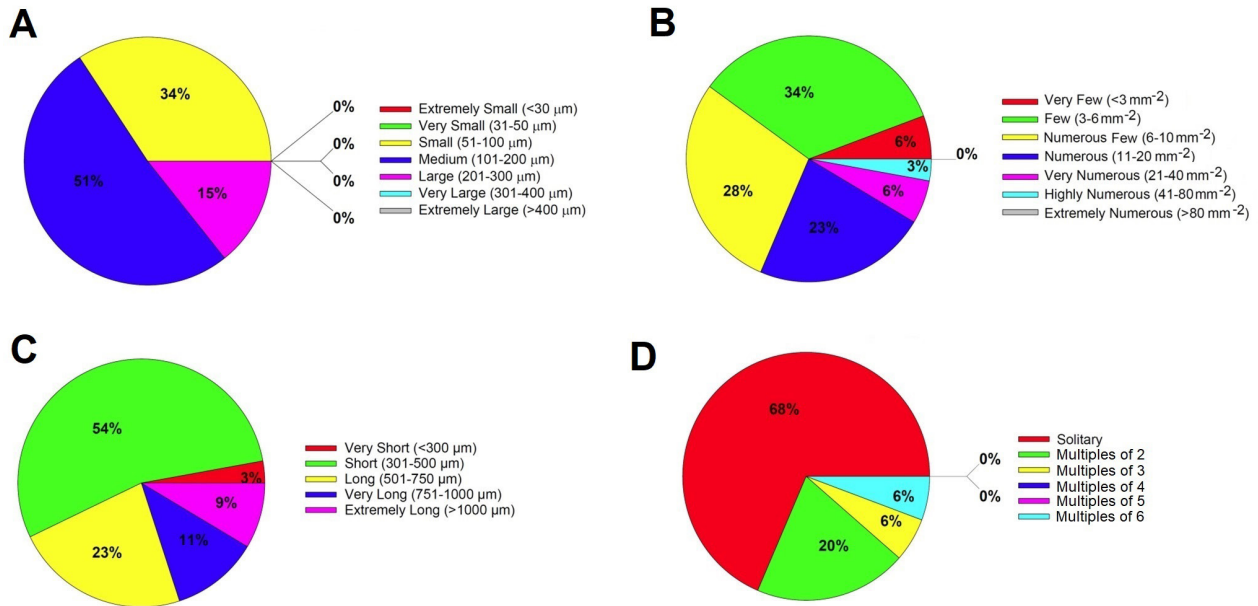
Species	Vessel type	Heartwood visibility	Exudate	Tylose	Hollow stem	Sapwood reaches heartwood
<i>Bocageopsis multiflora</i> (Mart.) R. E. Fries	Diffuse	V	Sap	-	-	X
<i>Brosimum utile</i> (Kunth) Pittier	Diffuse	V	Resin	-	-	-
<i>Byrsonima crisa</i> A. Juss	Diffuse	<b>P</b>	-	-	X	-
<i>Caliptanthes spruceana</i> Berg.	Diffuse	-	-	X	-	-
<i>Cecropia sciadophylla</i> Mart.	Diffuse	-	-	-	-	X
<i>Cecropia sciadophylla</i> Mart.	Diffuse	-	-	-	X	X
<i>Cecropia sciadophylla</i> Mart.	Diffuse	-	-	-	X	X
<i>Chrysophyllum ucuquirana-branca</i> (Aubrev & Pellegr) T. D. Penn.	Diffuse	V	Latex	-	-	-
<i>Cordia silvestris</i> Fresen.	Diffuse	<b>P</b>	-	X	-	-
<i>Duguetia flagellaris</i> Huber	Diffuse	V	-	-	-	X
<i>Eschweilera fracta</i> R. Knuth	Diffuse	V	-	X	X <sup>1</sup>	-
<i>Eschweilera odora</i> (Poepp. ex O. Berg)	Diffuse	V	-	X	X	-
<i>Eschweilera wachenheimii</i> Sandwith	Diffuse	V	-	X	X	X
<i>Eschweilera wachenheimii</i> Sandwith	Diffuse	V	Resin	X	X	X
<i>Eschweilera wachenheimii</i> Sandwith	Diffuse	V	-	X	X	-
<i>Eschweilera wachenheimii</i> Sandwith	Diffuse	V	-	-	X	-
<i>Eschweilera wachenheimii</i> Sandwith	Diffuse	V	-	X	-	-
<i>Gustavia speciosa</i> (Kunth) DC.	Diffuse	<b>P</b>	-	-	-	-
<i>Iryanthera ulei</i> Warb	Diffuse	-	Resin	X	-	X
<i>Jacaranda copaia</i> (Aubl.) D. Don	Diffuse	V	-	X	-	X
<i>Mabea caudata</i> Pax & K. Hoffm.	Diffuse	-	-	X	-	-
<i>Mabea caudata</i> Pax & K. Hoffm.	Diffuse	V	-	X	-	-
<i>Micrandropsis scleroxylon</i> W. Rodr.	Diffuse	V	Latex	X	-	-
<i>Neea madeirana</i> Standl.	Diffuse	-	-	-	-	-
<i>Ocotea neesiana</i> (Miq.) Kosterm.	Diffuse	V	-	-	X	X
<i>Pourouma guianensis</i> Aubl.	Diffuse	<b>P</b>	Latex	-	-	X
<i>Pouteria caimito</i> Radlk.	Diffuse	-	-	X	-	-
<i>Protium heptaphyllum</i> (Aubl.) March.	Diffuse	<b>P</b>	-	-	-	X
<i>Sclerolobium chrysophyllum</i> Poepp.	Diffuse	V	Latex	-	-	X
<i>Tachigali paniculata</i> Aubl.	Diffuse	-	-	-	X	X
<i>Vantanea micrantha</i> Ducke	Diffuse	V	-	X	X	X
<i>Vantanea micrantha</i> Ducke	Diffuse	<b>P</b>	-	X	-	-
<i>Virola calophylla</i> (Spruce) Warb.	Diffuse	-	-	-	-	X
Total trait occurrences (n)	34	22	9	17	13	18
% occurrences	100	65	26	50	38	53

<sup>1</sup>Diseased.

**Table S4.** Descriptive statistical parameters of exponential power model fits using sapwood area and tree size [diameter-at-breast-height (DBH), total height (Ht)], volume (estimated using DBH and Ht), and anatomical variables (vessel diameter, element length and frequency). Significance is set at 5%. \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ ; ns = non-significant.  $a$  and  $b$  = model coefficients ( $Y = aX^b$ );  $R^2$  = coefficient of determination;  $r$  = Pearson correlation coefficient; † = fitted with an exponential decay model ( $Y = a \cdot e^{-bx}$ ). Note: only the best allometric model fits are shown.

Variables	a	b	$R^2$	r	F
DBH	0.823	1.781	0.46***	0.68	27.32
Total height	0.013	3.110	0.33***	0.58	16.08
Volume (DBH, Ht)	376.95	0.817	0.48***	0.70	29.96
DBC	0.188	2.307	0.71***	0.84	39.52
Vessel diameter	11.848	0.499	0.001 <sup>ns</sup>	0.03	0.02
Vessel element length	0.000007	2.628	0.65***	0.80	58.63
Vessel frequency <sup>†</sup>	197.96	0.016	0.01 <sup>ns</sup>	-0.10	0.32





**Figure S1.** Microscopic wood properties classified according to their vessel dimensions as proposed by Copant (1974) and the percentage of trees included in each category. A. Vessel-lumen diameter (µm); B. vessel frequency (vessels per mm<sup>2</sup>); C. vessel element length (µm); D. vessel groupings (solitary or multiples). This figure is in color in the electronic version.