American Journal of Botany

RESEARCH ARTICLE

New formula and conversion factor to compute basic wood density of tree species using a global wood technology database

Ghislain Vieilledent[1,2,3,7], Fabian Jörg Fischer[4], Jérôme Chave[4], Daniel Guibal[5,6], Patrick Langbour[5,6], and Jean Gérard[5,6]

Manuscript received 2 March 2018; revision accepted 4 July 2018.

[1] CIRAD, UPR Forêts et Sociétés, F-34398 Montpellier, France

[2] Forêts et Sociétés, Univ Montpellier, CIRAD, Montpellier, France

[3] Joint Research Centre of the European Commission, Bio-economy unit, I-21027 Ispra, Italy

[4] UMR 5174 Laboratoire Evolution et Diversité Biologique, Université Paul Sabatier, CNRS, IRD, Toulouse, France

[5] CIRAD, UPR BioWooEB, F-34398 Montpellier, France

[6] BioWooEB, Univ Montpellier, CIRAD, Montpellier, France

[7] Author for correspondence (e-mail: ghislain.vieilledent@cirad.fr)

Citation: Vieilledent, G., F. J. Fischer, J. Chave, D. Guibal, P. Langbour, and J. Gérard. 2018. New formula and conversion factor to compute basic wood density of tree species using a global wood technology database. *American Journal of Botany* 105(10): 1–9.

doi:10.1002/ajb2.1175

PREMISE OF THE STUDY: Basic wood density is an important ecological trait for woody plants. It is used to characterize species performance and fitness in community ecology and to compute tree and forest biomass in carbon cycle studies. While wood density has been historically measured at 12% moisture, it is convenient for ecological purposes to convert this measure to basic wood density, i.e., the ratio of dry mass over green volume. Basic wood density can then be used to compute tree dry biomass from living tree volume.

METHODS: Here, we derive a new exact formula to compute the basic wood density D_b from the density at moisture content w denoted D_w, the fiber saturation point S, and the volumetric shrinkage coefficient R. We estimated a new conversion factor using a global wood technology database where values to use this formula are available for 4022 trees collected in 64 countries (mostly tropical) and representing 872 species.

KEY RESULTS: We show that previous conversion factors used to convert densities at 12% moisture into basic wood densities are inconsistent. Based on theory and data, we found that basic wood density could be inferred from the density at 12% moisture using the following formula: $D_b = 0.828D_{12}$. This value of 0.828 provides basic wood density estimates 4–5% smaller than values inferred from previous conversion factors.

CONCLUSIONS: This new conversion factor should be used to derive basic wood densities in global wood density databases. Its use would prevent overestimating global forest carbon stocks and allow predicting better tree species community dynamics from wood density.

KEY WORDS basic wood density; biomass; carbon stock; fiber saturation point; forest dynamics; functional trait; tree species; tropical forest; wood specific gravity.

Wood density of woody plants is a key functional trait (Violle et al., 2007; Chave et al., 2009) and helps us understand the functioning of forest ecosystems in terms of carbon sequestration (Chave et al., 2005; Vieilledent et al., 2012) and community dynamics (Westoby and Wright, 2006; Díaz et al., 2016; Kunstler et al., 2016). In carbon cycle research, tree wood density is used to compute forest carbon stock and assess the role of forests in mitigating climate change (Pan et al., 2011; Vieilledent et al., 2016) or evaluate the impact of deforestation on climate (Achard et al., 2014). In community ecology, wood density is a proxy for species performance (Lachenbruch and McCulloh, 2014), reflecting a trade-off between growth potential and mortality risk from biomechanical or hydraulic failure (Díaz et al., 2016). Fast-growing, short-lived species tend to have a lower wood density, while slow-growing, long-lived species tend to have a higher wood density (Chave et al., 2009; Greenwood et al., 2017). In wood technology, most physical and mechanical properties of wood (e.g., strength, stiffness, porosity, heat transmission, yield of pulp per unit volume) are closely related to wood density (Sallenave, 1955; Thibaut et al., 2001; Shmulsky and Jones, 2011). This explains why wood density has been commonly measured in forestry institutes, where wood was principally studied for construction or paper making.

Wood density was originally measured at ambient air moisture after air drying (Glass and Zelinka, 2010), but is now measured at a fixed moisture content, such as 15% or the international standard of 12% (Sallenave, 1955). In temperate countries, construction wood is at equilibrium with ambient air at an average moisture close to 12%. Wood density at 12% moisture is the ratio between the mass and volume of a wood sample at 12% moisture and is expressed in g/cm^3. In the past, this measure was also commonly reported in the British literature in pounds per cubic foot (1 g/cm^3 = 62.427 lb/ft^3) (Sallenave, 1971; Reyes et al., 1992). In carbon cycle research and ecology, the most useful metric is the basic wood density, the ratio between oven-dry mass (at 0% moisture) and green volume (water-saturated wood volume) in g/cm^3. This trait is sometimes referred to as wood specific gravity (abbreviated WSG). Both terms describe the same quantity, but wood specific gravity is usually the ratio between the mass of a given volume of wood and the mass of the same volume of water and is therefore unitless (Williamson and Wiemann, 2010). Here, we use the term basic wood density. Basic wood density can be directly used to compute tree dry biomass and carbon stock from a standing tree volume estimated using an allometric equation (Brown, 1997; Chave et al., 2005, 2014; Vieilledent et al., 2012). For example, Chave et al. (2014) have estimated the following pantropical tree biomass allometric equation: $\mathrm{AGB} = 0.0673(\rho D^2 H)^{0.976}$ with AGB the tree dry aboveground biomass (kg), D the tree diameter (cm) at 1.30 m, H the tree height (m), and ρ the basic wood density (g/cm^3). Tree dry biomass can then be converted to carbon stock using the Intergovernmental Panel on Climate Change (IPCC) default carbon fraction of 0.47 (McGroddy et al., 2004).

Different methods have been used to convert measures of wood density at 12% moisture (D_{12}), which are often available in forestry institute databases, into basic wood density (D_b). Based on basic wood density data and air-dry wood density data (supposedly close to 12% moisture) for 379 tropical species or genera (Chudnoff, 1984), Reyes et al. (1992) proposed a linear regression between D_b and D_{12}:

$$D_\mathrm{b} = 0.0134 + 0.800 D_{12}. \qquad \text{(Eq. 1)}$$

This relationship has been used to estimate the basic wood densities of 223 species in Reyes et al. (1992), successively reported by Brown (1997), IPCC (2006), and Zanne et al. (2009). Sallenave (1971) proposed another formula to compute basic wood density from the wood density at 12% moisture:

$$D_\mathrm{b} = \frac{D_{12} - 12d}{1 + (v/100)(S - 12)}, \qquad \text{(Eq. 2)}$$

where d is a density conversion factor per 1% change in moisture content designated “hygroscopicity” by Sallenave (1971), S is the fiber saturation point (moisture content S in % at which wood volume starts decreasing in the drying process), and v is the variation in volume on a dry basis per 1% change in moisture content (in %/%). The values of d, v, and S vary between species and individual trees. Sallenave (1955, 1964, 1971) published values of D_{12}, d, v, and S for 1893 trees sampled worldwide in tropical forests.

Using Sallenave’s data and formula, it is possible to compute $D_{\mathrm{b},i}$ for each wood sample i and estimate the conversion factor α_{12} between wood density at 12% moisture and basic wood density from the following statistical model: $D_{\mathrm{b},i} = \alpha_{12} D_{12,i} + \varepsilon_i$, assuming a normal error term $\varepsilon_i \sim \mathrm{Normal}(0, \sigma^2)$. Using the wood samples of the Sallenave data set, Chave et al. (2006) obtained a value of 0.872 for the conversion factor α_{12} between D_{12} and D_b. Several studies have since used Sallenave’s method to derive conversion factors for particular sets of species (Muller-Landau, 2004) or to convert wood density at a particular moisture content w into basic wood density (Swenson and Enquist, 2007; Chave et al., 2009; Bastin et al., 2015) by extending Sallenave’s original formula assuming that $D_\mathrm{b} = (D_\mathrm{w} - wd)/[1 + (v/100)(S - w)]$. The resulting conversion factors were close to 0.872. Notably, Chave et al. (2009) used a value of 0.861 (see Appendix S1 in Supplemental Data for the cited reference) to convert any wood density between 10–18% moisture content into basic wood density. The estimated basic wood densities were included in the Global Wood Density Database, a large global compilation of wood density data (Chave et al., 2009; Zanne et al., 2009). This database combines measured (40% of the data) and inferred (60% of the data) basic wood densities. It has been extensively used to compute forest biomass and carbon stock with the aim of studying the role of forest in the global carbon cycle (Saatchi et al., 2011; Baccini et al., 2012, 2017; Avitabile et al., 2016; Vieilledent et al., 2016) or addressing questions in functional ecology (Chave et al., 2009; Baraloto et al., 2010; Kunstler et al., 2016).

Simpson (1993) proposed a simplified formula to compute wood density at any moisture content from basic wood density. With this formula, the relationship only depends on the moisture content w: $D_\mathrm{w} = D_\mathrm{b}(1 + w/100)/(1 - 0.265 a D_\mathrm{b})$, with $a = 1 - w/30$. Simpson’s formula can be inverted to compute D_b from D_w:

$$D_\mathrm{b} = 1/[0.265a + (100 + w)/(100 D_\mathrm{w})]. \qquad \text{(Eq. 3)}$$

Two assumptions were made to derive this formula. (1) The fiber saturation point S can be approximated to 30% for all tree species. (2) The total volumetric shrinkage R_T (in %) from S to 0% moisture content is proportional to the basic wood density D_b and can be approximated by the following relationship (Stamm, 1964): $R_\mathrm{T}/100 = 0.265 D_\mathrm{b}$.

Because relationships proposed by Reyes et al. (1992), Sallenave (1971), and Simpson (1993) give significantly different estimates of the basic wood density for a same value of wood density at 12% moisture, it is important to further test their underlying theories.

In this study, we present a new and exact formula to convert wood density at any moisture content into basic wood density. The formula is derived from the definitions of the fiber saturation point and the volumetric shrinkage coefficient. We compare this new formula with formulas provided by Reyes, Sallenave, and Simpson and explain why they differ. We combine our theoretical formula with the latest version of a wood technology database compiled by CIRAD (French Agricultural Research Centre for International Development) to estimate a new conversion factor between density at 12% moisture and basic wood density. We finally discuss the consequences of this new conversion factor in carbon cycle research and ecology.

MATERIALS AND METHODS

The CIRAD wood technology database

A global database including 872 tree species—The CIRAD wood technology database includes data from 4022 individual trees. Tree species names (Latin binomial) were first spell-checked with the Global Names Resolver available in the taxize R package (Chamberlain and Szöcs, 2013) using The Encyclopedia of Life (https://eol.org), The International Plant Names Index (https://www.ipni.org), and Tropicos (http://www.tropicos.org) databases as references. Then, we searched for synonyms in the list of species names and corrected the species names when necessary using The Plant List version 1.1 (http://www.theplantlist.org) as reference. We used the Taxonstand R package (Cayuela et al., 2017) to do so. Taxonomic families were retrieved from updated species names using The Plant List. Trees belong to 1010 taxa from 484 genera and 94 taxonomic families. Most of the taxa (872) were identified to the species level, with varieties and subspecies combined. Of the 872 species names, 832 were "accepted" species names, and 40 were "unresolved", according to The Plant List. The rest of the taxa (138) were identified to the genus level. The data set includes 834 angiosperm species and 38 gymnosperm species. The data set includes trees from 64 countries, but the major part of the trees come from 13 tropical countries (countries with more than 20 tree species), mostly in South America, Africa, and in Oceanic islands (Table 1, Fig. 1). Sallenave was working for a tropical forestry institute that is now part of CIRAD; the database is thus the direct continuation and extension of Sallenave's (1955, 1964, 1971).

Measuring wood mass, moisture content, and volume—The volume V_w and mass m_w of a wood sample depend on its water content w. The moisture content of wood is a function of both relative humidity and temperature of ambient air (Hailwood and Horrobin, 1946; Glass and Zelinka, 2010). In the CIRAD database, wood volume and mass measurements were done in the same laboratory following the French standard AFNOR NF B51-005 (09/1985). Wood samples are cubes of about 20 mm side (±0.5 mm). To measure V_w and m_w, we placed wood samples in controlled and fixed atmospheric conditions to reach a water content w. Wood samples were supposed to be stabilized when their variation in mass (g) after 4 h was less than 0.5%.

Wood mass m_w (g) was measured with a 0.01 g precision balance. The exact moisture content w (in %) of a wood sample is defined as a percentage of the dry mass, $w = 100(m_w - m_0)\ m_0$, where m_0 is the mass of the wood sample at the anhydrous state and m_w being the mass of the wood at moisture content w.

TABLE 1. Countries with the highest number of tree species (>20) in the CIRAD wood density database. The data set includes values from 64 countries, but most measurements of wood physical and mechanical properties have been done in tropical countries in South America, Africa, and tropical Oceanic islands.

Country	*n* species
South America	
Brazil	108
French Guiana	168
Africa	
Burundi	29
Cameroon	83
Central African Republic	27
Côte d'Ivoire	117
Congo–Brazzaville	59
Gabon	105
Guinea	20
Asia	
Viet Nam	20
Oceanic Islands	
Guadeloupe	43
Madagascar	94
New Caledonia	87

Wood volume V_w (in cm^3) was measured with three different methods. For wood samples of irregular dimensions, we used a mercury volumenometer, or the water displacement method based on Archimede's principle (Williamson and Wiemann, 2010). The mercury volumenometer for volume measurement was progressively abandoned from the end of the 1990s due to mercury toxicity. For perfectly rectangular parallelepiped or cubic wood samples, a stereometric method was used to measure the wood cube size in the three dimensions using a digital caliper having a 0.02 mm precision. With one of these three methods, wood volume was measured with a precision <0.003 cm^3.

Measuring fiber saturation point, volumetric shrinkage coefficient, and wood density at 12% moisture

The fiber saturation point S (in %) is commonly defined as the water content above which the wood volume does not increase (Skaar, 1988). Water can exist in wood as liquid water ("free" water) or water vapor in cell lumens and cavities, and as water held chemically within cell walls ("bound" water). The fiber saturation point is the point in the wood drying process at which the only remaining water is that "bound" to the cell walls. Further drying of the wood results in the strengthening of the wood fibers and is usually accompanied by shrinkage (Skaar, 1988).

To estimate the fiber saturation point S, we first measured wood volume at the saturated state V_S using the water displacement method. To reach a state saturated in water, with $w > S$, wood samples were autoclaved, subjected to 1 h of vacuum (to accelerate water impregnation) and then soaked in water for 15 h at 5 bar pressure (500 kPa). Then, wood samples were stabilized at four decreasing moisture contents w until reaching the anhydrous state. First, wood samples were put in a stove at 30°C temperature and 85% humidity to reach a moisture content close to 18%. Second, wood samples were put in an air-conditioned room at 20°C and 65% humidity to reach a moisture content close to 12%. Third, they were put in a stove at 20°C and 50% humidity to reach a moisture content close to 9%. Fourth, they were put in a stove at 103°C to reach the anhydrous state. Wood mass m_w and wood volume V_w were measured at each of the four stabilized stages. The exact water content w at the three stabilized states previous to the anhydrous state was computed from the mass m_w and the anhydrous mass m_0. Three volumetric shrinkage values $\Delta V/V = 100(V_S - V_w)/V_S$ were computed between the saturated state and the three other stabilized states. The fiber saturation point S is defined as the intercept of the linear model $w = S + b \times \Delta V/V$ (Stamm, 1964). To minimize error in estimating S, only the relationships with a coefficient of determination $r^2 > 98\%$ were considered.

The volumetric shrinkage coefficient R (in %/%) is the variation in volume per 1% change in water content. The total volumetric shrinkage R_T of the wood samples from the saturated state to the anhydrous state (in %) was computed from V_S and V_0: $R_T = 100(V_S - V_0)/V_S$. Then, the volumetric shrinkage coefficient R (in %/%) was estimated from R_T and the fiber saturation point S: $R = R_T/S$. This definition of the volumetric shrinkage coefficient differs from the one used in Sallenave's work. Sallenave used the anhydrous volume V_0 as the reference volume, and v was defined as $v = B/S$ with $B = 100(V_S - V_0)/V_0$. Because this definition corresponded to wood swelling and not to wood shrinkage, it has been changed when compiling the new CIRAD wood technology database. Sallenave's B values were converted to R_T values with the

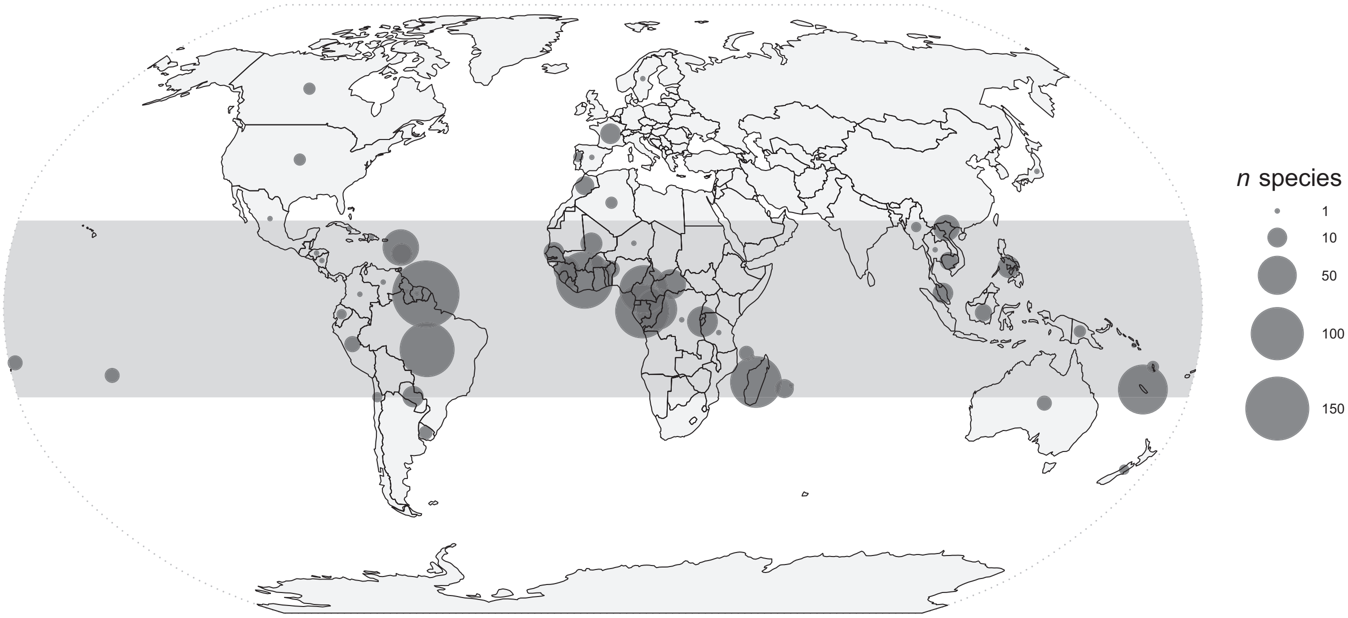

FIGURE 1. Global repartition of the data available in the CIRAD wood density database. Data repartition is provided as number of species per country. Most of the species in the database (830/872) are found in the tropics (marked by the gray band on the map).

following formula derived from the definitions of B and R_T: $R_T = 100[1 - 1/(B/100 + 1)]$.

Wood density at 12% moisture (D_{12} in g/cm^3) was obtained computing the ratio m_w/V_w with w close to 12% moisture (when wood samples were stabilized at 20°C temperature and 65% humidity). Because the moisture content w was not exactly 12%, densities were initially corrected using the “hygroscopicity” term d defined by Sallenave and the formula $D_{12} = D_w - (w - 12)d$ (Sallenave, 1971). This correction affected only the third decimal of the wood density value, so it was progressively abandoned. Given the precision of wood mass and volume measurements, uncertainty regarding wood densities at 12% moisture for individual samples was considered to be about 0.01 g/cm^3.

In the CIRAD database, average values for S, R, and D_{12} for each tree were historically recorded using >10 wood samples taken at various positions in the trunk. Of the 4022 trees present in the CIRAD database, 190 trees had only measurements for D_{12}, with no values for S and R. Definitions and units of wood physical and mechanical properties used in the present study are all summarized in Appendix S1 (see the Supplemental Data with this article).

Model relating D_w and D_b

Using D_w (wood density at moisture content w), R (newly defined volumetric shrinkage coefficient), and S (fiber saturation point), we derived a new relationship linking basic wood density D_b with D_w. We first considered the relationship between V_S and V_w. The volumetric shrinkage coefficient R (variation in volume per 1% change in water content) is defined as $R = (100\Delta V)/(V\Delta w)$. Let’s consider a wood sample saturated in water ($w = S$) that would be dried until reaching a water content w. The volume of the wood sample would decrease (wood shrinkage) and R can be written as:

$$R = [100(V_S - V_w)]/[V_S(S - w)]. \qquad \text{(Eq. 4)}$$

Using Eq. 4, we can express V_S as a function of V_w, R, S and w:

$$V_S = V_w/[1 - (R/100)(S - w)]. \qquad \text{(Eq. 5)}$$

We then considered the relationship between m_0 and m_w. Water content w is defined as $w = 100(m_w - m_0)/m_0$. Using this definition, we expressed m_0 as a function of m_w and w:

$$m_0 = m_w/(1 + w/100). \qquad \text{(Eq. 6)}$$

Following the definition of the basic wood density D_b ($D_b = m_0/V_S$) and replacing V_S and m_0 by their expressions in Eq. 5 and Eq. 6, respectively, we obtained $D_b = [m_w/(1 + w/100)]\{[1 - (R/100)(S - w)]/V_w\}$. Given that $D_w = m_w/V_w$, we found the following relationship between D_b and D_w:

$$D_b = \frac{1 - (R/100)(S - w)}{1 + w/100} D_w. \qquad \text{(Eq. 7)}$$

For each individual tree i, we used this new formula to compute the basic wood density $D_{b,i}$ from the values of $D_{12,i}$ (wood density at 12% moisture), R_i, and S_i reported for 3832 trees in the CIRAD wood technology database (190 trees had no values for R or S). We then estimated the parameters of a statistical linear regression model linking $D_{b,i}$ to $D_{12,i}$, where parameter α_{12} corresponds to the conversion factor between D_{12} and D_b (Eq. 8).

$$D_{b,i} = \alpha_{12} D_{12,i} + \varepsilon_i,\ \varepsilon_i \sim N(0, \sigma^2) \qquad \text{(Eq. 8)}$$

We extended this approach to compute an additional conversion factor α_{15} between D_{15}, the wood density at 15% moisture (which was the French standard before international conventions fixed the moisture content at 12%, see Sallenave, [1955]) and D_b. We inverted Eq. 7 to compute $D_{15,i}$ from previously computed $D_{b,i}$ values and estimated the slope of a linear regression model linking $D_{b,i}$ to $D_{15,i}$.

Comparison with the Global Wood Density Database

The Global Wood Density Database (GWDD, https://doi.org/10.5061/dryad.234) provides wood densities for 8412 species from around the world (Chave et al., 2009; Zanne et al., 2009). The GWDD and CIRAD wood density databases share common wood samples and measurements from Sallenave (1955, 1964, 1971). We quantified the amount of novel information in the CIRAD wood density database. We identified and computed (1) the number of species studied by Sallenave and present in the two databases, (2) the number of species common to the two databases but not studied by Sallenave (for which wood density values were independent), and (3) the number of species in the CIRAD database not present in the GWDD. For the species shared between databases, and with independent measurements, we compared the mean basic wood density values in the two databases. To quantify the differences between the two databases, we computed the Pearson correlation coefficient between the two values, a measure of the linear correlation (dependence), and the coefficient of variation (in %) between the two databases. The coefficient of variation is the ratio of the standard deviation of the differences between density values in the two databases divided by the mean basic wood density in the CIRAD database. It is a measure of the average difference between the wood density values in the two databases. Finally, we quantified the bias (in %) in the GWDD compared to the CIRAD database. This bias was defined as the mean difference between density values in the two databases divided by the mean basic wood density in the CIRAD database.

RESULTS

Relationship between D_b and D_w

The linear regression model linking D_b and D_{12} had a coefficient of determination $r^2 = 0.999$ and a residual standard error of 0.015 g/cm^3 (Fig. 2). We estimated a new conversion factor $\alpha_{12} = 0.828$ based on the slope estimate of the linear regression. Thus, the basic wood density can be estimated from wood density at 12% moisture from Eq. 9.

$$[D_b]_{est} = 0.828 D_{12}. \quad \text{(Eq. 9)}$$

With this new conversion factor, we were able to compute the basic wood density D_b from D_{12} for the 190 trees without values for R or S. At the species level, when accounting for all the trees in the database, D_b ranged from 0.191 to 1.105 g/cm^3 (Table 2).

We also observed that R, S, and D_{12} were not independent (Fig. 3). Thus, it is not possible to directly estimate the conversion factor from the means of R and S on the basis of the formula we derived to link basic wood density to wood density at moisture content w (Eq. 7). Instead, the conversion factor estimated with the linear regression model must be used.

The linear regression model linking D_b and D_{15} had a coefficient of determination $r^2 = 0.999$ and a residual standard error of 0.014 g/cm^3. We estimated a conversion factor $\alpha_{15} = 0.819$ between D_{15} and D_b.

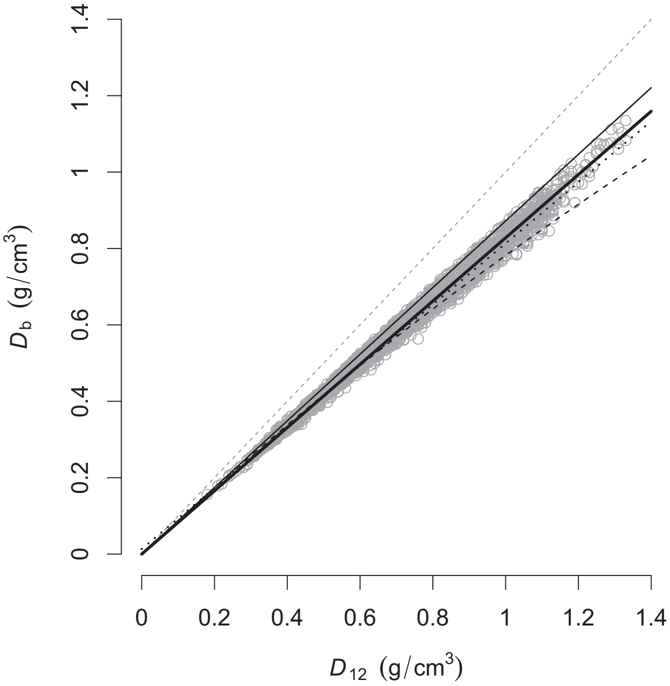

FIGURE 2. Relationship between basic wood density (D_b oven dry mass/green volume, in g/cm^3) and wood density at 12% moisture (D_{12}). Gray dots represent the 3832 trees from the CIRAD database for which D_{12}, R, and S have been measured and D_b computed with our new formula. The gray dashed line represents the identity line. Based on D_{12} and D_b values, we estimated the following relationship (plain large black line): $D_b = 0.828D_{12}$ ($n = 3832$, $r^2 = 0.999$). Using data and formula from Sallenave (1955, 1964, 1971), Chave et al. (2006) estimated a significantly different conversion factor of 0.872 (plain thin black line). We also plotted the relationships of Simpson (1993) (dashed black curve) and Reyes et al. (1992) (dotted black line).

TABLE 2. Descriptive statistics at the species level (872 species) for wood physical and mechanical properties in the CIRAD database. See Appendix S1 for variable definitions.

Variable	Min	Max	Mean	Median	SD	95% Quantiles
R (%/%)	0.190	0.810	0.461	0.456	0.098	0.292–0.660
S (%)	17	41	27.93	28.00	4.06	20.18–36.00
D_{12} (g/cm^3)	0.228	1.290	0.736	0.720	0.194	0.396–1.107
D_b (g/cm^3)	0.191	1.105	0.608	0.600	0.157	0.331–0.916

Comparison with the Global Wood Density Database

Of the 872 species in the CIRAD wood density database, we identified 260 species that were measured by Sallenave (1955, 1964, 1971) and for which one or more samples were already included in the GWDD. For these species, the CIRAD database provides additional information compared to the GWDD, with values for R, S, and D_{12}. We also identified 411 species common to the two databases but for which measurements of D_b were completely independant. For these species, the CIRAD wood density database also provides R, S, and D_{12} values. Finally, we identified 201 original species in the CIRAD database that were not present in the GWDD. Both R and S were highly variable among species (Table 2). In particular, S ranged

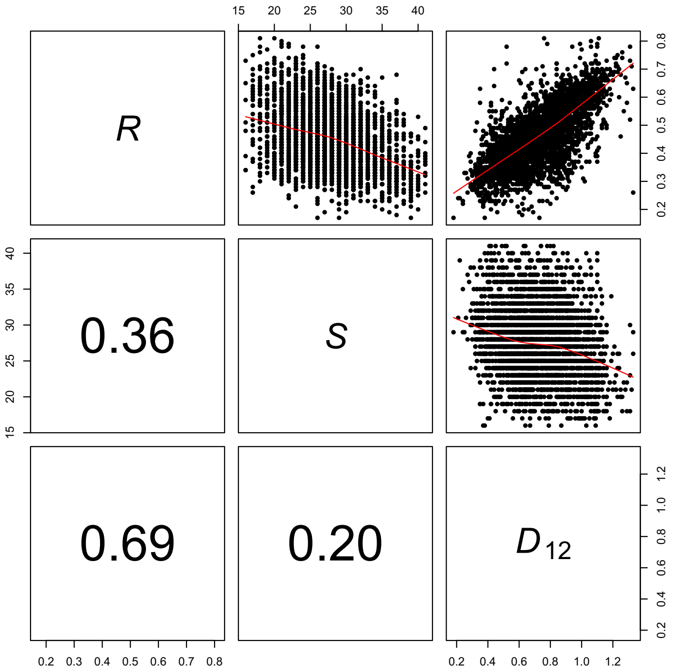

FIGURE 3. Correlation between variables describing wood properties. This figure shows the correlation between the volumetric shrinkage coefficient *R*, the fiber saturation point *S*, and the wood density at 12% moisture D_{12}. In the lower-left panels, numbers indicate the absolute value of Pearson's correlation coefficient for each pair of variables. In the upper-right panels, figures show the scatter plot for each pair of variables with a nonparametric smoother in red.

from 17 to 41% with a mean of 27.93% and a standard deviation of 4.06%.

Using the independent measurements for the 411 common species in the two databases, we estimated a Pearson correlation coefficient of 86% and a coefficient of variation of 13.69% (Fig. 4). We also observed that, on average, D_b values in the GWDD were 3.05% higher compared to D_b values in the CIRAD database.

DISCUSSION

Relationship between D_b and D_{12}

We found a new value of 0.828 for the conversion factor between the wood density at 12% moisture and the basic wood density. This value is 5% lower compared to the value of 0.872 used by Chave et al. (2006) and based on Sallenave's data and formula. To compare this value with the results obtained by Reyes et al. (1992), we derived the expectation $\mathbf{E}(D_b/D_{12})$ from Reyes' formula $D_b = 0.0134 + 0.800D_{12}$. We obtained $\mathbf{E}(D_b/D_{12}) = 0.0134 \times \mathbf{E}(1/D_{12}) + 0.800$, which led to an estimate of 0.821 for the conversion factor. This value is much closer to our value of 0.828 than the value of 0.872 (Chave et al., 2006).

Why was the conversion factor overestimated by Chave et al. (2006)? As calculations were based on the formula from Sallenave (1971), we decided to re-examine its derivation. When looking more closely at Sallenave's (1971, p. 11) own example, a discrepancy became apparent. For the African tree species *Khaya ivorensis* (with D_{12} = 0.57 g/cm³, d = 0.0030, S = 24%, v = 0.46 and measured D_b = 0.483 g/cm³), Sallenave's formula (Eq. 2) led to an estimate of 0.506 g/cm³ for the basic wood density. Our formula, on the other hand, gave an estimate of 0.484 g/cm³, which is much closer to the measured basic wood density value of 0.483 g/cm³. Given these findings, we suspected an error or approximation in Sallenave's formula.

Based on the definition of the basic wood density $D_b = m_0/V_S$ and the definition of the parameters used by Sallenave (1971), we demonstrate that Sallenave's formula is true only if $V_0 = V_{12}$ (Eq. 10 and demonstration in Appendix S2). This assumption, however, is too strong if we want to estimate an accurate conversion factor.

$$D_b = \frac{V_0(D_{12} - 12d)}{V_{12}[1 + (v/100)(S - 12)]} \qquad \text{(Eq. 10)}$$

We thus recommend the use of the new formula we derived in this study (Eq. 7) to compute individual basic wood density D_b from D_{12}, the wood density at 12% moisture, when *R* and *S* are available. This formula is more appropriate than Sallenave's. It not only avoids making the strong assumption that $V_0 = V_{12}$, but also needs only two variables to compute D_b compared to Sallenave's formula, which includes a third variable, "hygroscopicity" *d*. Moreover, the new formula, unlike Sallenave's, implies $D_0 = 0$ when $D_{12} = 0$, which is physically consistent. Finally, the new formula we derived in this

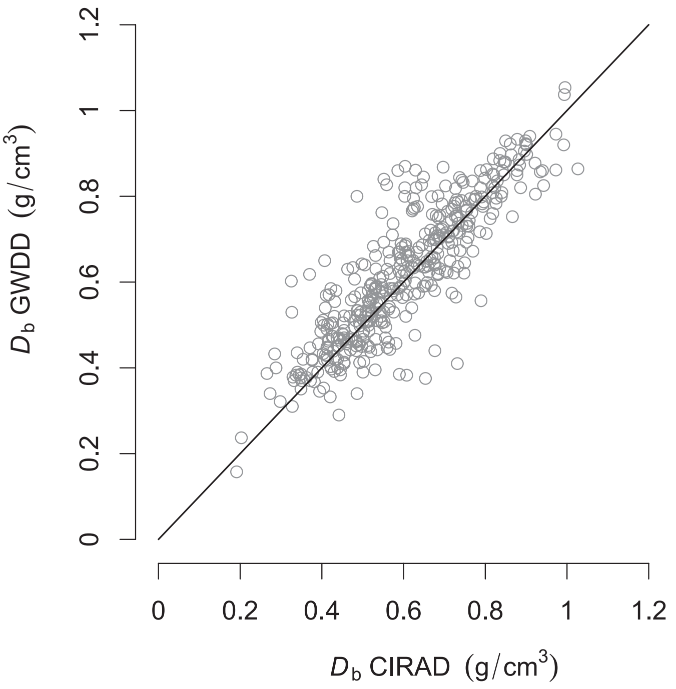

FIGURE 4. Relationship between basic wood density (D_b oven dry mass/green volume, in g/cm³) from the CIRAD and GWDD databases for 411 species. The black line represents the identity line. Gray dots represent species mean basic wood densities from the CIRAD and GWDD databases. These 411 species are common to the two databases, but wood samples and measurement protocols differ in each database. Comparing the two databases, we obtained a Pearson correlation coefficient of 86% and a coefficient of variation of 13.69%. We also observed that, on average, D_b values in the GWDD were higher by 3.05% than the D_b values in the CIRAD database.

study is more generic than the original formula of Reyes et al. (1992) and of Sallenave (1971). It can be used, with the data set on wood properties we provide as supplemental data, to derive conversion factors between D_b and density D_w at any water content w under the fiber saturation point S.

We also demonstrate that our formula is more appropriate than Simpson's (1993). Assumptions used to derive Simpson's formula are not supported by our data. In the CIRAD database, the fiber saturation point S is highly variable between species and cannot be assumed as constant at 30%. We also estimated a coefficient of 0.201 for the relationship between $R_T/100$ and D_b, a value different from the coefficient of 0.265 suggested by Stamm (1964). We estimated a mean error (coefficient of variation of the root-mean-square-error) of 26% for $R_T/100$ predictions, suggesting that $R_T/100$ cannot be precisely estimated from D_b using a simple correlation coefficient (see also Fig. 3). As a consequence, Simpson's formula leads to a large under-estimation of basic wood densities for $D_{12} > 0.7$ g/cm^3 (Fig. 2).

If only D_{12} and no other measurement is available, we recommend the use of the value 0.828 for the conversion factor to compute the basic wood density D_b. We also recommend this value of 0.828 over the value of 0.821 obtained with the relationship of Reyes et al. (1992). The conversion factor of 0.828 is based on a larger and more consistent database than the one used by Reyes et al., which combined density data at the species and genera level and included air-dry densities not stabilized at 12% (Chudnoff, 1984).

Additional value of the CIRAD wood density database

Using the new formula we obtained in this study (Eq. 7), the new estimated conversion factor 0.828, and the CIRAD database, we estimated the basic wood density of 4022 trees belonging to 872 species (1010 taxa), 484 genera, and 94 families; thus, we provide basic wood density for 201 more tree species than in the Global Wood Density Database (Zanne et al., 2009). Most of the 872 species come from 13 oceanic tropical islands or countries.

In the CIRAD wood density database, the fiber saturation point is provided for each tree. The fiber saturation point is an essential wood characteristic that can be used, in combination with the green volume, green mass and dry mass, to estimate the volume of water for each of the three bulk phases in a tree: (1) "free" liquid water in cell lumens and cavities, (2) water vapor in gas-filled voids, and (3) "bound" water held chemically within cell walls (sometimes also called "solid" water, see Berry and Roderick [2005]). The volume of bound water is an essential plant functional trait as it determines wood strength and constraints on plant architecture (Niklas, 1993), as is the volume of free liquid water, which is the ultimate source for biochemical activity in living plants (Berry and Roderick, 2005).

Wood characteristic values for trees in the CIRAD database are the average of >10 wood samples taken at various positions in the trunk. These values integrate the intra-individual variability (e.g., difference in wood density values for the same tree, which can vary with the position in the trunk [Bastin et al., 2015]). Providing wood characteristics for individual trees, the CIRAD database can be used to compute both intraspecific and interspecific trait variability. Intraspecific trait variability, due to genetic variability and phenotypic plasticity, participates in determining species fitness and community assemblages (Roughgarden, 1979; Albert et al., 2011; Courbaud et al., 2012). The CIRAD database could also help quantify phylogenetic conservatism and divergences of wood densities in tree species (Flores and Coomes, 2011).

Limits and ecological perspectives of the new conversion factor value

We found a new empirical value of 0.828 for the conversion factor. This value is obtained from a theoretical equation derived from the exact definitions of R, S and D_{12}. Some uncertainty, which comes from methodological limitations associated with the measurement of these variables, surrounds this value. In particular, the fiber saturation point S remains a theoretical concept. In practice, some free water is still present in wood cells when shrinkage (associated to the loss of bound water) starts during the drying process, and some low molecular weight organic compounds are lost during drying (Rosner et al., 2009). This introduces some uncertainty in the measurement of the water content at each stage of the drying process, and thus on the estimates of S and R. Also, from the field to the laboratory, wood samples might have experienced some drying during the transport and storage, which explains why wood samples had to be re-saturated. Wood that has been re-saturated can show different shrinkage behavior (Glass and Zelinka, 2010), which introduces some uncertainty regarding the measurement of S and R. Moreover, the conversion factor could theoretically vary between species or individuals having different wood anatomies. For example, the proportion of parenchyma (representing the bulk of living cells in wood) is typically higher in angiosperms, tropical, and low wood density species than in gymnosperms, temperate, and high wood density species, respectively (Morris et al., 2016). In our data set, we found statistically significant differences between these groups of trees for the value of the conversion factor (Appendix S3). But the magnitude of the differences between groups was of the same order (≤0.01) as the uncertainty for the wood density value at 12% moisture D_{12}. So we considered these differences not meaningful.

This new value of 0.828 for the conversion factor has significant implications for the study of the role of forests in the global carbon cycle. The error on the conversion factor between wood density at 12% moisture and basic wood density propagates to forest carbon stock. Combined with biomass allometric equations available in the literature (Chave et al., 2005, 2014; Vieilledent et al., 2012), these wood density values have been used to compute forest carbon maps globally (Saatchi et al., 2011; Baccini et al., 2012, 2017; Avitabile et al., 2016). About 60% of the basic wood densities in the Global Wood Density Database have been estimated with an overestimated conversion factor. On the basis of 411 tree species, we showed that the GWDD overestimates wood densities by +3.05% on average. It is hard to quantify precisely the consequences of this bias on forest carbon stock estimates as it depends on relative species abundance in the forest and relative tree size distribution between species. However, if dominant species (in terms of size and abundance) have an overestimated basic wood density, due to the use of an inaccurate conversion factor (compare 0.872 or 0.861 used by Chave et al. [2009, 2006] with 0.828 used in our study), it can potentially lead to an overestimation of 4–5% of the forest biomass and carbon stock. We are currently in the process of updating the GWDD, and the present study provides a firm basis for this revision.

This study will also provide a firmer basis for future ecological research on wood density as a functional trait. Indeed, wood density is often considered as a key tree functional trait determining species performance and fitness (Chave et al., 2009; Baraloto et al., 2010; Díaz et al., 2016; Kunstler et al., 2016; Greenwood et al., 2017). For example, recent global studies have demonstrated that values of wood density explained the competition outcome between pairs of tree species (Kunstler et al., 2016), and that drought-induced mortality was promoted by lower wood densities (Greenwood et al., 2017). Using a wood density database with unbiased values of basic wood densities would allow proper estimates of species' differences with regards to this trait and better predict the dynamics of a tree species community.

ACKNOWLEDGEMENTS

The authors thank G. Bruce Williamson and another anonymous reviewer for relevant remarks and constructive comments on a previous version of the manuscript. They warmly thank all researchers, technicians, and students who intensively and accurately measured wood properties of thousands of trees and hundreds of species from the tropical forests at the Centre Technique Forestier Tropical and CIRAD since the 1950s. They thank in particular Pierre Sallenave who contributed considerably to this research by describing protocols and compiling data on wood properties in his three volumes (Sallenave, 1955, 1964, 1971). G.V. was funded by CIRAD and through the European Commission ReCaREDD project at the Joint Research Centre. This work has benefitted from Investissement d'Avenir grants managed by Agence Nationale de la Recherche (CEBA: ANR-10-LABX-25-01; TULIP: ANR-10-LABX-0041).

AUTHOR CONTRIBUTIONS

G.V., F.F., J.C., and J.G. conceived the ideas and designed methodology; D.G., P.L., and J.G. collected the data; G.V. and F.F. analyzed the data; G.V. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data (including the CIRAD wood density database) and R script associated to the present study have been archived in the CIRAD Dataverse research data repository (https://doi.org/10.18167/dvn1/krvf0e) (Vieilledent et al., 2018).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

LITERATURE CITED

Achard, F., R. Beuchle, P. Mayaux, H. J. Stibig, C. Bodart, A. Brink, S. Carboni, et al. 2014. Determination of tropical deforestation rates and related carbon losses from 1990 to 2010. *Global Change Biology* 20: 2540–2554.

Albert, C. H., F. Grassein, F. M. Schurr, G. Vieilledent, and C. Violle. 2011. When and how should intraspecific variability be considered in trait-based plant ecology? *Perspectives in Plant Ecology, Evolution and Systematics* 13: 217–225.

Avitabile, V., M. Herold, G. Heuvelink, S. L. Lewis, O. L. Phillips, G. P. Asner, J. Armston, et al. 2016. An integrated pan-tropical biomass map using multiple reference datasets. *Global Change Biology* 22: 1406–1420.

Baccini, A., S. J. Goetz, W. S. Walker, N. T. Laporte, M. Sun, D. Sulla-Menashe, J. Hackler, et al. 2012. Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps. *Nature Climate Change* 2: 182–185.

Baccini, A., W. Walker, L. Carvalho, M. Farina, D. Sulla-Menashe, and R. A. Houghton. 2017. Tropical forests are a net carbon source based on aboveground measurements of gain and loss. *Science* 358: 230–234.

Baraloto, C., C. E. T. Paine, L. Poorter, J. Beauchene, D. Bonal, A. M. Domenach, B. Hérault, et al. 2010. Decoupled leaf and stem economics in rain forest trees. *Ecology Letters* 13: 1338–1347.

Bastin, J. F., A. Fayolle, Y. Tarelkin, J. Van den Bulcke, T. de Haulleville, F. Mortier, H. Beeckman, et al. 2015. Wood specific gravity variations and biomass of central African tree species: The simple choice of the outer wood. *PLoS ONE* 10: 1–16.

Berry, S. L., and M. L. Roderick. 2005. Plant–water relations and the fibre saturation point. *New Phytologist* 168: 25–37.

Brown, S. 1997. Estimating biomass and biomass change of tropical forests: a primer. Technical Report, FAO Forestry Paper 134. Food and Agriculture Organization, Rome, Italy.

Cayuela, L., A. Stein, and J. Oksanen. 2017. Taxonstand: Taxonomic standardization of plant species names. R package version 2.1. https://CRAN.R-project.org/package=Taxonstand.

Chamberlain, S. A., and E. Szöcs. (2013) taxize: taxonomic search and retrieval in R. *F1000Research* 2: 191.

Chave, J., C. Andalo, S. Brown, M. A. Cairns, J. Q. Chambers, D. Eamus, H. Folster, et al. 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* 145: 87–99.

Chave, J., H. C. Muller-Landau, T. R. Baker, T. A. Easdale, H. T. Steege, and C. O. Webb. 2006. Regional and phylogenetic variation of wood density across 2456 neotropical tree species. *Ecological Applications* 16: 2356–2367.

Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* 12: 351–366.

Chave, J., M. Réjou-Méchain, A. Búrquez, E. Chidumayo, M. S. Colgan, W. B. Delitti, A. Duque, et al. 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology* 20: 3177–3190.

Chudnoff, M. 1984. Tropical timbers of the world. Agriculture handbook 607. U.S. Department of Agriculture, Forest Service, Washington D.C., USA.

Courbaud, B., G. Vieilledent, and G. Kunstler. 2012. Intra-specific variability and the competition-colonisation trade-off: coexistence, abundance and stability patterns. *Theoretical Ecology* 5: 61–71.

Díaz, S., J. Kattge, J. H. C. Cornelissen, I. J. Wright, S. Lavorel, S. Dray, B. Reu, et al. 2016. The global spectrum of plant form and function. *Nature* 529: 167–171.

Flores, O., and D. A. Coomes. 2011. Estimating the wood density of species for carbon stock assessments. *Methods in Ecology and Evolution* 2: 214–220.

Glass, S. V., and S. L. Zelinka. 2010. Moisture relations and physical properties of wood. *In* Wood handbook: wood as an engineering material, 4-1–19. General Technical Report FPL-GTR-190. U.S. Dept. of Agriculture, Forest Service, Forest Products Laboratory, Madison, WI, USA.

Greenwood, S., P. Ruiz-Benito, J. Martínez-Vilalta, F. Lloret, T. Kitzberger, C. D. Allen, R. Fensham, et al. 2017. Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. *Ecology Letters* 20: 539–553.

Hailwood, A., and S. Horrobin. 1946. Absorption of water by polymers: analysis in terms of a simple model. *Transactions of the Faraday Society* 42: B084–B092.

IPCC [Intergovernmental Panel on Climate Change]. 2006. Guidelines for national greenhouse gas inventories – a primer. Prepared by the National Greenhouse Gas Inventories Programme, H. S. Eggleston, M. K. Srivastava, and K. Tanabe [eds.]. Intergovernmental Panel on Climate Change/Institute for Global Environmental Strategies [IPCC/IGES], Hayama, Japan.

Kunstler, G., D. Falster, D. A. Coomes, F. Hui, R. M. Kooyman, D. C. Laughlin, L. Poorter, et al. 2016. Plant functional traits have globally consistent effects on competition. *Nature* 529: 204–207.

Lachenbruch, B., and K. A. McCulloh. 2014. Traits, properties, and performance: how woody plants combine hydraulic and mechanical functions in a cell, tissue, or whole plant. *New Phytologist* 204: 747–764.

McGroddy, M. E., T. Daufresne, and L. O. Hedin. 2004. Scaling of C:N: P stoichiometry in forests worldwide: implications of terrestrial redfield-type ratios. *Ecology* 85: 2390–2401.

Morris, H., L. Plavcová, P. Cvecko, E. Fichtler, M. A. F. Gillingham, H. I. Martínez-Cabrera, D. J. McGlinn, et al. 2016. A global analysis of parenchyma tissue fractions in secondary xylem of seed plants. *New Phytologist* 209: 1553–1565.

Muller-Landau, H. C. 2004. Interspecific and inter-site variation in wood specific gravity of tropical trees. *Biotropica* 36: 20–32.

Niklas, K. J. 1993. Influence of tissue density-specific mechanical properties on the scaling of plant height. *Annals of Botany* 72: 173–179.

Pan, Y., R. A. Birdsey, J. Fang, R. Houghton, P. E. Kauppi, W. A. Kurz, O. L. Phillips, et al. 2011. A large and persistent carbon sink in the world's forests. *Science* 333: 988–993.

Reyes, G., S. Brown, J. Chapman, and A. E. Lugo. 1992. Wood densities of tropical tree species. General Technical Report SO-88. U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station, New Orleans, LA, USA.

Rosner, S., B. Karlsson, J. Konnerth, and C. Hansmann. 2009. Shrinkage processes in standard-size norway spruce wood specimens with different vulnerability to cavitation. *Tree Physiology* 29: 1419–1431.

Roughgarden, J. 1979. Theory of population genetics and evolutionary ecology: an introduction. Macmillan, NY, NY, USA.

Saatchi, S. S., N. L. Harris, S. Brown, M. Lefsky, E. T. A. Mitchard, W. Salas, B. R. Zutta, et al. 2011. Benchmark map of forest carbon stocks in tropical regions across three continents. *Proceedings of the National Academy of Sciences, USA* 108: 9899–9904.

Sallenave, P. 1955. Propriétés physiques et mécaniques des bois tropicaux de l'Union française. Centre technique forestier tropical, Nogent-sur-Marne, France. https://doi.org/10.18167/agritrop/00359.

Sallenave, P. 1964. Propriétés physiques et mécaniques des bois tropicaux. Premier supplément. Centre technique forestier tropical, Nogent-sur-Marne, France. https://doi.org/10.18167/agritrop/00357.

Sallenave, P. 1971. Propriétés physiques et mécaniques des bois tropicaux. Deuxième supplément. Centre technique forestier tropical, Nogent-sur-Marne, France. https://doi.org/10.18167/agritrop/00358.

Shmulsky, R., and P. Jones. 2011. Forest products and wood science. Wiley, Oxford, UK.

Simpson, W. T. 1993. Specific gravity, moisture content, and density relationship for wood. Technical report FPL, GTR-76. U.S. Department of Agriculture, Forest Service, Forest Products Laboratory, Madison, WI, USA. https://doi.org/10.2737/fpl-gtr-76.

Skaar, C. 1988. Wood-water relations. Springer-Verlag, Berlin, Germany.

Stamm, A. 1964. Wood and cellulose science. Ronald Press, NY, NY, USA.

Swenson, N. G., and B. J. Enquist. 2007. Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. *American Journal of Botany* 94: 451–459.

Thibaut, B., J. Gril, and M. Fournier. 2001. Mechanics of wood and trees: some new highlights for an old story. *Comptes Rendus de l'Académie des Sciences, IIB, Mechanics* 329: 701–716.

Vieilledent, G., R. Vaudry, S. F. D. Andriamanohisoa, O. S. Rakotonarivo, H. Z. Randrianasolo, H. N. Razafindrabe, C. B. Rakotoarivony, et al. 2012. A universal approach to estimate biomass and carbon stock in tropical forests using generic allometric models. *Ecological Applications* 22: 572–583.

Vieilledent, G., O. Gardi, C. Grinand, C. Burren, M. Andriamanjato, C. Camara, C. J. Gardner, et al. 2016. Bioclimatic envelope models predict a decrease in tropical forest carbon stocks with climate change in Madagascar. *Journal of Ecology* 104: 703–715.

Vieilledent, G., F. J. Fischer, J. Chave, D. Guibal, P. Langbour, and J. Gérard. 2018. Code and data for: New formula and conversion factor to compute basic wood density of tree species using a global wood technology database. CIRAD Dataverse, V2.0. https://doi.org/10.18167/dvn1/krvf0e.

Violle, C., M. L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007. Let the concept of trait be functional! *Oikos* 116: 882–892.

Westoby, M., and I. J. Wright. 2006. Land-plant ecology on the basis of functional traits. *Trends in Ecology & Evolution* 21: 261–268.

Williamson, G. B., and M. C. Wiemann. 2010. Measuring wood specific gravity … correctly. *American Journal of Botany* 97: 519–524.

Zanne, A., G. Lopez-Gonzalez, D. Coomes, J. Ilic, S. Jansen, S. Lewis, R. Miller, et al. 2009. Data from: Towards a worldwide wood economics spectrum. Dryad, https://doi.org/10.5061/dryad.234.