Testing a Novel Method to Approximate Wood Specific Gravity of Trees

Michael C. Wiemann and G. Bruce Williamson

Abstract: Wood specific gravity (SG) has long been used by foresters as an index for wood properties. More recently, SG has been widely used by ecologists as a plant functional trait and as a key variable in estimates of biomass. However, sampling wood to determine SG can be problematic; at present, the most common method is sampling with an increment borer to extract a bark-to-pith core—a difficult task requiring considerable physical effort and sometimes repeated borings to hit the pith, with potential to damage the trunk of small trees. Here, we test a novel sampling method that reduces the effort to obtain an adequate increment core and results in less wood extracted from the tree. The Wiemann approximation predicts the point along a radius at which the wood SG equals the disk cross-sectional SG. When SG changes linearly across the radius, the point of approximation is at two-thirds of the radial distance. As a test, we compare SG at various points along the radius with the true SG of the disk. At all points except the point of approximation (i.e., at two-thirds of the radial distance), wood SG differed significantly from the true cross-sectional mean SG, whereas at two-thirds of the radial distance, the wood SG did not differ significantly from the tree mean SG for a group of 128 tropical trees and 25 temperate trees that had been sampled bark to pith. Overall, the method shows promise in that wood SG of a tree may be estimated accurately and without bias by boring the tree only to the point of approximation, that is, one-sixth of the trunk diameter. However, boring to one-sixth of the diameter provides an unbiased estimate of SG only if radial variation in SG is a linear function of radial distance. A limitation of the method is that an initial subsample of trees must be bored to determine the pattern of radial variation in a species before the approximation can be applied to other individuals. FOR. SCI. 58(6):577–591.

Keywords: increment borers, tree cores, Wiemann approximation, wood specific gravity

WOOD SPECIFIC GRAVITY (SG) is the single most important predictor of wood physical and mechanical properties (Panshin and de Zeeuw 1980). It measures the allocation of secondary xylem to structure, i.e., the amount of dry biomass per unit volume of wood. In addition, SG appears to be a determinant of a tree's ability to survive (Schniewind 1962, Putz et al. 1983, Borchert 1994, Wright et al. 2007, Poorter et al. 2008). Among plant functional traits, SG is the strongest indicator of a species position along the growth rate-mortality rate tradeoff (Wright et al. 2010). For ecosystem analyses, wood SG is a crucial variable in estimation of biomass and carbon stocks (Brown and Lugo 1992, Fearnside 1997, Chave et al. 2005, 2009, Nogueira et al. 2005, 2007, 2008a, 2008b, Malhi et al. 2006, Keeling and Phillips 2007, Baker et al. 2009).

In a standing tree, SG is usually determined from wood samples taken from the lower portion of the bole, typically by use of an increment borer or increment hammer. Increment hammers sample only the outermost 2–3 cm of a bole, whereas increment borers can sample radial cores, limited only by the length of the borer and one's ability to extract an adequate core. Borer diameters range from 4 to 12 mm, with the larger diameters giving the best samples when larger quantities of wood are required, as in SG measurements (Jozsa 1988, Grissino-Mayer 2003, Williamson and Wiemann 2010a). Larger diameter borers require disproportionately greater expenditures of energy to extract cores, so limiting the depth of penetration to only that required to obtain an adequate sample is desirable. However, SG estimates from the outermost wood may be unrepresentative of the entire trunk cross-section. Even complete pith-to-bark cores may result in biased estimates because SG can vary with radial distance, and the cross-sectional area of radial increments increases with radial distance from the pith (Williamson and Wiemann 2010a). This bias is especially problematic when radial variation in SG is large, as is the case for many tropical trees (Whitmore 1973, Wiemann and Williamson 1988, 1989a, 1989b, Rueda and Williamson 1992, Butterfield et al. 1993, Castro et al. 1993, Nock et al. 2009, Williamson and Wiemann 2010b). Therefore, SG determination from a pith-to-bark core requires an area-weighted mean to estimate disk SG (Williamson and Wiemann 2010a).

Manuscript received May 7, 2010; accepted July 11, 2011; published online February 16, 2012; http://dx.doi.org/10.5849/forsci.10-049.

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Acknowledgments: Sayra Navas, Toni Soto, and Jacqueline Henrot helped in extracting and measuring the cores. Luis Poveda and Nelson Zamora identified the tropical species. Vanessa Boukili, Jessica Deichmann, and Lindsay Wieland gave critical reviews that improved the manuscript. Financial support was provided by the Organization for Tropical Studies, the Michaux Fund of the American Philosophical Society, and the US National Science Foundation (DEB-0639114). This is publication number 578 in the Technical Series of the Biological Dynamics of Forest Fragments Project BDFFP-INPA-STRI. We gratefully acknowledge the cooperation of the Organization for Tropical Studies.

This article uses metric units; the applicable conversion factors are: millimeters (mm): 1 mm = 0.039 in.; centimeters (cm): 1 cm = 0.39 in.; meters (m): 1 m = 3.3 ft.

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Williamson and Wiemann (2010a) suggested a novel approach, based on stem geometry, which theoretically provides an alternative to the difficult tasks of extracting complete bark-to-pith cores, determining the SG of consecutive segments of cores, and calculating the area-weighted means. The proposed method is to sample only the wood that approximates the SG of a whole disk. If a function describing the radial variation in SG is known, then it can be used to determine the point along the radius at which the SG equals the area-weighted SG; in theory, the tree need only be bored to that point, termed the Wiemann approximation, to estimate cross-sectional SG (Williamson and Wiemann 2010a). For radial changes that are linear, the point of approximation falls at two-thirds of the wood radius; i.e., the wood SG at two-thirds of the distance from pith to bark, in theory, should equal the SG of the whole disk (Williamson and Wiemann 2010a).

Here, we present an initial test of this method using 153 trees from 70 species. There are two basic questions. First, does wood at two-thirds of the distance from the pith approximate the average area-weighted SG of the core? In application of the method, the point one-sixth of the diameter inward from the bark/xylem interface would be used to correspond to two-thirds of the distance from the pith outward. However, if a tree is eccentric, then a point that is one-sixth of the diameter inward from the bark might not coincide with two-thirds of the distance from the pith. Therein lies the second question: How well does the SG of wood at one-sixth of the diameter inward approximate the average area-weighted SG of the core for individual trees known to have eccentric pith?

Materials and Methods

Cores were collected from trees in temperate forests in New York and Mississippi and in tropical forests characterized as wet, dry, and montane in Costa Rica (modified from Hartshorn 1983). Names, abbreviations, geographic coordinates, and elevations of the sites are given in Table 1. The dbh of each tree was measured at 1.3-m height with a diameter tape. Bark-to-pith or bark-to-bark (through the pith) wood samples were obtained with a 12-mm increment borer in most cases, although 13 of the trees were felled and 1- to 2-cm-wide bark-to-bark strips were cut from disks. However, we will refer to all of the samples as "cores" in this article. Only those trees whose cores contained pith or almost reached the pith (within 1 cm, as determined by the convergence of the wood rays) and were at least 6 cm long from pith to bark were included in further analysis. Cores that did not reach within 1 cm of the pith were discarded, and the trees were re-bored. Tree cores from complete bark-to-bark sampling were divided at the pith, with bark and pith discarded, so both sides could be compared.

The trees selected were freestanding and reasonably straight. Cores were usually taken at breast height or higher (above buttresses) if necessary. After the bark and the pith were removed, the remainder of each fresh core was cut into 1-cm pieces from the innermost piece outward, although wood grain sometimes shifted the cutting blade, resulting in pieces slightly longer or shorter than 1.0 cm. Green volume of each piece was measured accurately by water displacement, as described in Wiemann and Williamson (1988, 1989a, 1989b). The pieces were then dried at 103 °C to constant weight (24–48 hours) and weighed on a top-loading balance. Basic SG of each piece was calculated as oven-dry weight/green volume/density of water. For the cores that did not quite reach the pith, the missing innermost 1-cm piece was assigned the same SG as its adjacent 1-cm piece.

The trees were partitioned into data sets for separate analyses based on whether we had one or both radial samples. Data from trees with only one core per tree were used to compare seven different estimates of SG as described below.

1. Arithmetic mean of all pieces (SG_M).
2. Weighted mean of all pieces (SG_W). This mean weights the SG of each piece by its relative contribution to the overall area calculated as ($SG_W = (SG_1 + 3SG_2 + 5SG_3 + \cdots + (2n - 1)SG_n)/n^2$).
3. Arithmetic mean of the innermost three pieces (SG_I).

Table 1. Collection sites, separated by forest type.

Locality	Site abbreviation	North latitude	West longitude	Elevation (m)
Temperate forests (Temp)				
Adirondacks, Harrietstown, NY	ADK	44°18′	74°11′	550
Homochitto National Forest, Mississippi	H	31°22′	91°08′	60
Tropical wet forests (TrWet)				
Bribri, Limón, Costa Rica	B	9°38′	82°50′	190
Cahuita, Limón, Costa Rica	C	9°44′	82°51′	50
Chilamate, Heredia, Costa Rica	CH	10°27′	84°05′	80
Guatuso, Cartago, Costa Rica	G	9°50′	83°57′	1400
Pueblo Nuevo, Heredia, Costa Rica	PN	10°29′	84°07′	80
Sarapiquí, Heredia, Costa Rica	S	10°27′	84°00′	30–140
Santa Elena, Puntarenas, Costa Rica	SE	10°19′	84°15′	1300
La Selva Succession Plots, Heredia, Costa Rica	SP	10°26′	83°59′	50
Tropical dry forests (TrDry)				
Palo Verde, Guanacaste, Costa Rica	PV	10°21′	85°21′	70
Montane/Premontane rain forests (Mont)				
Montane Forest, Cartago, Costa Rica	MF	9°35′	83°50′	2,200–3,000
Ojo de Agua, Cartago, Costa Rica	OA	9°37′	83°48′	2,500–2,900

The forest types correspond roughly to the Holdridge Life Zones (Hartshorn 1983).

4. Arithmetic mean of three pieces located at one-third of the distance from the pith to the bark ($SG_{1/3}$).
5. Arithmetic mean of the three pieces located midway between the pith and the bark ($SG_{1/2}$).
6. Arithmetic mean of the three pieces located at two-thirds of the distance from the pith to the bark ($SG_{2/3}$).
7. Arithmetic mean of the outermost three pieces (SG_O).

Trees sampled completely through provided two cores, which were used to compare their same 1–7 SG estimates above, as well as to compare the two within-tree estimates. In addition, these complete samples allowed comparisons based on the diameter inside the bark (dib), which was the sum of the two radii. The radii were often of unequal lengths, indicating some eccentricity, although the full extent of stem eccentricity remains unknown because we did not necessarily bore along the axis of maximum eccentricity. However, trees that appeared slightly elliptical rather than round were bored along the major axis, as practice has shown that the pith will lie on the major axis, but not the minor axis. The paired samples were analyzed as two data sets: short radii and long radii. Using the dib information, we defined an eighth SG estimate ($SG_{1/6dib}$) as the SG value at one-sixth of the dib measured inward from the outside edge of the core; in a symmetrical stem this point corresponds to the point two-thirds along a radius from the pith. In practice, $SG_{1/6dib}$ would be used to estimate $SG_{2/3}$ when trees are not bored all the way to the pith. Of course, $SG_{1/6dib}$ would exactly equal $SG_{2/3}$ if the trunk were perfectly round with no eccentricity. This eighth estimate of SG is given as follows:

8. Arithmetic mean of the three pieces located at one-sixth of the dib ($SG_{1/6dib}$), where dib is determined from the two summed radii.

Note that for all estimates of SG at points along the radius (estimates 3–8 above) we used the three pieces nearest to the point because single pieces sometimes give erratic values, especially in tropical pioneer species that annually grow several cm in diameter (Wiemann and Williamson 1988). Assuming SG_W as the "true" SG, we computed both the means of the residuals ($SG_X - SG_W$), where SG_X is an SG estimate other than SG_W, and the means of the absolute values (AVs) of the residuals. The mean of the residuals provides a measure of bias, and the mean of the AV of the residuals provides a measure of accuracy to the weighted means. All SG_X estimates were compared with SG_W values with paired *t*-tests performed in Microsoft Office Excel 2007.

Results

Summary information (species, tree number, collection site, forest type, dbh, number of 1-cm pieces from pith to bark, SG estimates 1–8, and the intercepts, slopes, and coefficients of determination of the regressions of SG on distance from pith) is given in the Appendix for 102 tropical trees (47 species) and 16 temperate trees (12 species) sampled only on one side and for the long and short cores of the 26 tropical trees (14 species) and 9 temperate trees (9 species) sampled from bark to bark through the pith. Two of the temperate trees showed no eccentricity, so their radii were arbitrarily designated as long or short.

Of the SG estimates based on only one bark-to-pith sample, paired *t*-tests showed significant differences ($P < 0.01$, $df = 117$) between SG_W and five SG estimates (SG_M, SG_I, $SG_{1/3}$, $SG_{1/2}$, and SG_O). Only one estimate, $SG_{2/3}$, was not significantly different from SG_W ($P = 0.28$). The quality of each SG estimate can be assessed visually by how accurately it follows the diagonal line for the estimate plotted against the true SG_W for these 118 trees (59 species) (Figure 1).

The residuals from each of the estimates are plotted in Figure 2 for trees cored pith to bark (one side) and the long cores and short cores for trees cored bark to bark. The means and SDs of the residuals and the means of the AVs of the residuals for each of the groups are given in Table 2. For all 153 trees considered together, the residual differences from the true SG_W and their absolute values were smallest for $SG_{2/3}$. For the pith-to-bark group, $SG_{2/3}$ has the lowest mean of the residuals (0.002) and the lowest mean AV of the residuals (0.016) (Table 2).

$SG_{1/6dib}$ also gave excellent estimates of SG_W. For the trees sampled across their entire diameters, the means of the residuals (-0.001 and -0.005 for the long and short cores, respectively) were smaller than those of any estimator except $SG_{2/3}$ (Table 2). The mean AVs of the residuals for $SG_{1/6dib}$ were also small (0.018 and 0.017 for the long and short cores, respectively), although they were slightly larger than those of $SG_{2/3}$ (Table 2). $SG_{1/6dib}$ was not significantly different from SG_W for either the short cores ($SG_{1/6dib} = 0.360$ and $SG_W = 0.365$; $P = 0.22$) or the long cores ($SG_{1/6dib} = 0.360$ and $SG_W = 0.361$; $P = 0.77$). $SG_{1/6dib}$ was different from $SG_{2/3}$ for the short cores ($SG_{2/3} = 0.372$; $P < 0.01$) but not for the long cores ($SG_{2/3} = 0.360$; $P = 0.97$). The mean of the residuals between $SG_{2/3}$ and $SG_{1/6dib}$ was -0.003 ± 0.0202, and the mean AV of the residuals was only 0.013 (compare with values in Table 2).

For the SG estimates from trees sampled bark to bark, paired *t*-tests showed no significant differences between the long and short radii estimates either for SG_M or $SG_{1/6dib}$ or at proportional points (0, 1/3, 1/2, 2/3, and 1) along the radii except for the inner wood, whose mean $SG_I = 0.300$ on the short radius differed from mean $SG_I = 0.291$ on the long radius ($P = 0.02$, $df = 34$).

SG_I underestimated SG_W in all but 19 of the 118 one-side trees (Figures 1 and 2). The negative residuals (Figure 2) reflect the fact that inner wood is usually the lowest SG wood in a tree, either because it is juvenile wood or because of the large shifts toward high SG wood typical with age (Wiemann and Williamson 1989a, Parolin 2002). In the 118 pith-to-bark cores, SG_O exceeded SG_I by more than 50% in 51 trees and by more than 100% in 15 trees. Low SG wood was found nearest the pith in trees from tropical dry (e.g.,

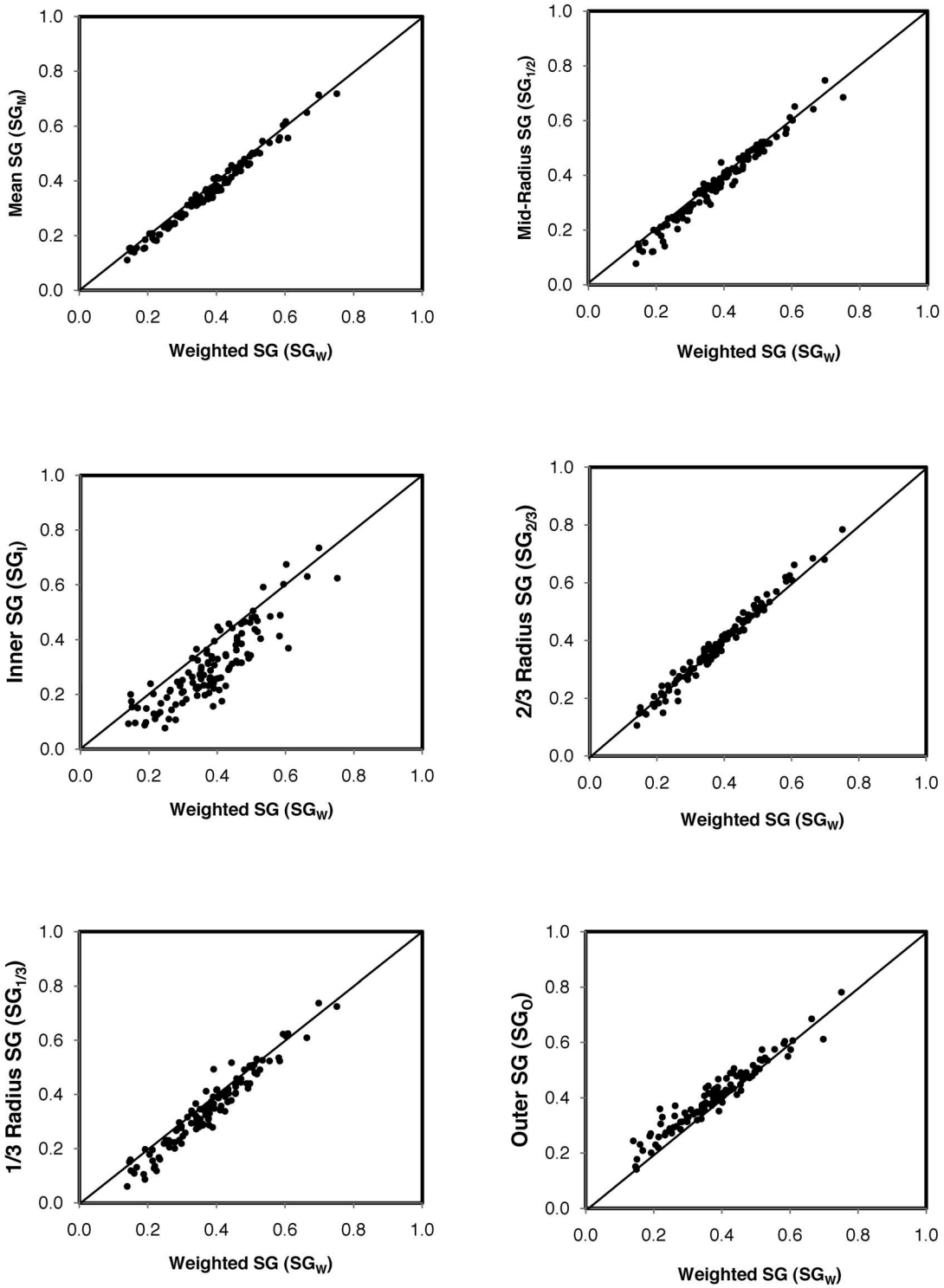

Figure 1. Plots of SG estimates (SG_X) as a function of the "true" (weighted) SG_W for the trees sampled from bark to pith. The diagonal lines represent $SG_X = SG_W$.

Bursera simaruba), tropical wet (e.g., *Ochroma pyramidale* and *Trema micrantha*), and temperate (e.g., *Sassafras albidum*) forests (Figure 3a–d).

The unweighted mean SG of all segments (SG_M) also underestimated SG_W, in general, because the low SG segments near the pith had the same weighting as the high SG segments near the bark even though they represented less wood. One would expect a large bias in trees with a high radial shift in SG when segments are weighted equally, so it is somewhat surprising that the SG_M did not deviate further from SG_W (Figure 1, top left, and Figure 2, top row), especially when so many trees showed large pith-to-bark SG changes. Nonetheless, the residuals and their absolute values for SG_M were still larger than those for $SG_{2/3}$ and $SG_{1/6dib}$ (Table 2).

Still, for some species with pronounced pith-to-bark SG

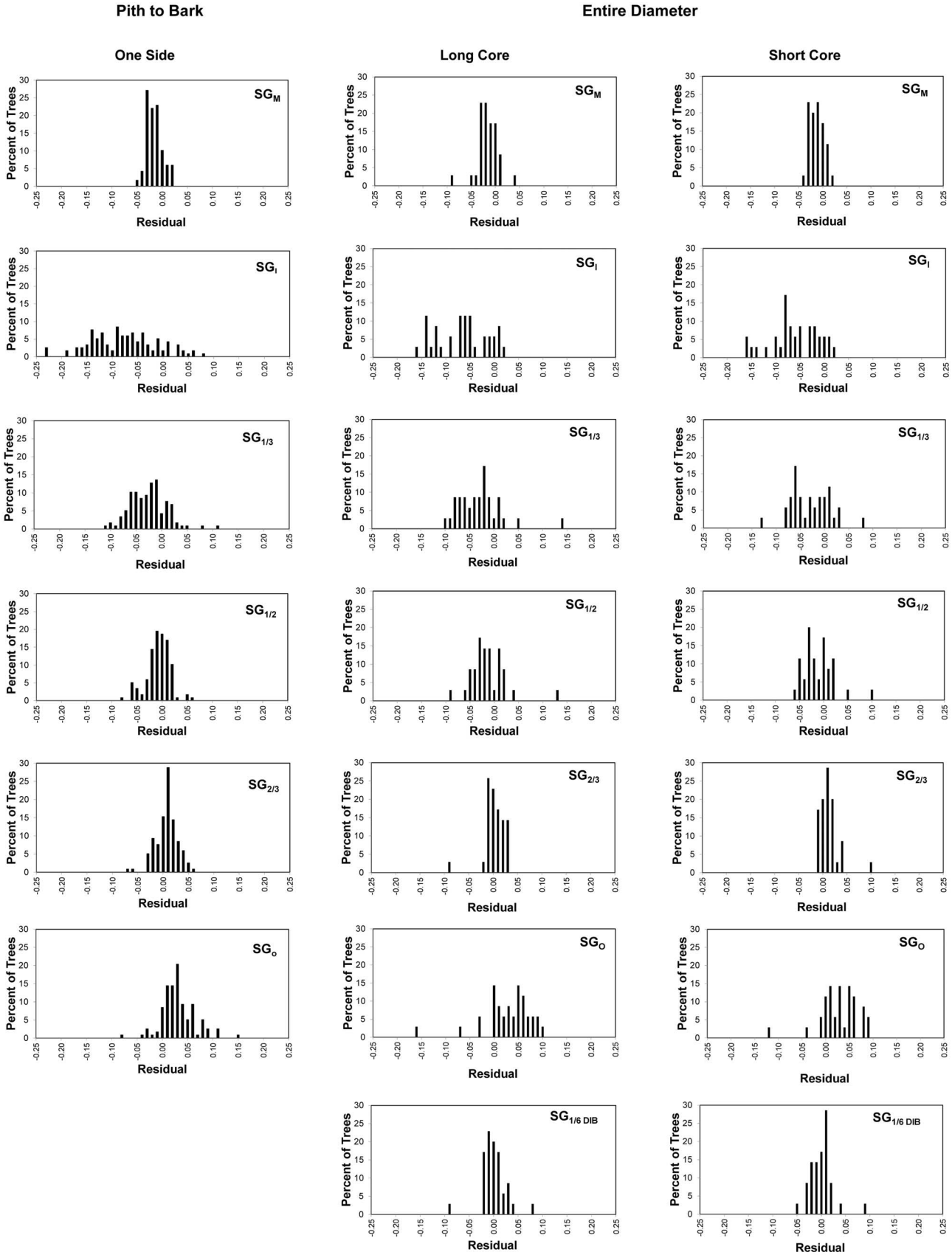

Figure 2. Residuals between the specific gravity estimates (SG_X) and SG_W for the three data sets (pith-to-bark, one side; entire diameter, long core; entire diameter, short core).

trends, such as *Bursera simaruba*, *Heliocarpus appendiculatus*, and *Ochroma pyramidale* (Table 3), the residuals varied predictably. They were large and negative when the estimation method was biased by inner wood and large and positive when biased by outer wood. With only a few exceptions, their SG estimates generally increased from

Table 2. Residuals between estimators and SG_W are summarized as means of the residuals, SDs of the residuals, and means of the AVs of the residuals for each of the three data sets (pith-to-bark one core only; entire diameter, long core; entire diameter, short core).

	No. trees	$SG_M - SG_W$	$SG_I - SG_W$	$SG_{1/3} - SG_W$	$SG_{1/2} - SG_W$	$SG_{2/3} - SG_W$	$SG_O - SG_W$	$SG_{1/6dib} - SG_W$
Means of residuals[a]								
Pith to bark	118	**−0.020**	**−0.081**	**−0.031**	**−0.012**	0.002	**0.026**	
Entire diameter								
Long core	35	**−0.021**	**−0.070**	**−0.036**	**−0.018**	−0.001	**0.024**	−0.001
Short core	35	**−0.018**	**−0.065**	**−0.034**	**−0.016**	0.006	**0.024**	−0.005
SDs of residuals								
Pith to bark	118	0.0154	0.0651	0.0359	0.0241	0.0210	0.0326	
Entire diameter								
Long core	35	0.0210	0.0519	0.0444	0.0366	0.0213	0.0497	0.0258
Short core	35	0.0149	0.0500	0.0418	0.0310	0.0206	0.0410	0.0232
Means of AVs of the residuals								
Pith to bark	118	0.022	0.088	0.039	0.020	0.016	0.032	
Entire diameter	35							
Long core		0.024	0.072	0.047	0.030	0.015	0.042	0.018
Short core		0.020	0.067	0.044	0.028	0.013	0.036	0.017

[a] Means of residuals significantly different from zero ($P < 0.05$) are in boldface.

SG_I through $SG_{1/3}$, SG_M, $SG_{1/2}$, $SG_{1/6dib}$, $SG_{2/3}$, and SG_O, with $SG_{2/3}$ having the smallest residuals (Table 3) and the smallest AVs of the residuals.

The five trees with the largest AVs of the residuals for the two-thirds approximation also had poor linear regressions of SG on radial distance as indicated by their coefficients of determination (r^2) (Appendix). Figure 3 shows that these trees, *Astronium graveolens* #56 (Figure 3g), *Trema micrantha* #141 (Figure 3c), *Apeiba aspera* #90 (Figure 3h), *Apeiba aspera* #89 (Figure 3i), and *Nectandra cufodontisii* #286 (Figure 3j), did not conform to the assumption of a linear relationship between SG and radial distance.

Discussion

Overall, how well did the $SG_{2/3}$ approximation perform in estimating disk wood specific gravity? Of the 188 pith-to-bark samples examined (118 from one side and 70 from two sides), 136 (72%) were within 0.02 SG unit of the true weighted SG and 183 (97%) were within 0.05 SG unit, as measured by the two-thirds radius method. The five samples with deviations of more than 0.05 SG unit all violated the assumption of linear radial changes in SG.

In general, the reliability of the $SG_{2/3}$ approximation is a result of the predictability in species' SG values. In angiosperms, studies of radial variation in SG usually show consistent patterns among individuals of a species (Panshin and de Zeeuw 1980, Wiemann and Williamson 1988, 1989a, 1989b, Parolin 2002, Nock et al. 2009). Individuals aberrant to a species' radial pattern are found occasionally, just as individuals aberrant to a species' mean SG are encountered. Both traits, mean SG and radial shift in SG, are species-specific, with considerably more variation among species than within a species.

The researcher in the field, confronted with trees to sample, faces two questions before the Wiemann approximation can be applied. First, is the form of the SG-radial distance relationship linear? Second, is the trunk eccentric?

Linear Radial Changes in SG

Application of the $SG_{2/3}$ approximation assumes that the SG change across the radius is linear. Here, the linear radial change requirement is satisfied by a significant (increasing or decreasing) slope by linear regression or a constant SG across the radius with a slope of zero. With no radial shift in SG, any point sample is an unbiased estimate of the trunk SG, so the two-thirds approximation would function. For example, the temperate *Magnolia grandiflora* (Figure 3e) and the tropical *Pseudobombax septenatum* (Figure 3f) and *Ficus insipida* (Appendix) had no changes in SG from pith to bark, except for random variation, and their residuals showed no significant differences between SG estimators and weighted SG (Table 3); their residuals reflected only random variation rather than trends.

With linear radial increases in SG, conspecifics often exhibit different slopes because SG appears to be determined by age not by size of the tree (Castro et al. 1993, Nock et al. 2009, Williamson and Wiemann 2010b, 2011). Therefore, trees of different sizes, but the same age, exhibit linear increases with different regression coefficients. In this regard, the Wiemann approximation accommodates natural variation as long as all radial increases are linear. However, if individual trees vary in the degree of linearity versus nonlinearity of radial increases, then the approximation is inapplicable.

The most common SG patterns in tropical trees are linear radial increases or constant SG across the radius (Wiemann and Williamson 1989a, 1989b, Rueda and Williamson 1992, Butterfield et al. 1993, Parolin 2002, Nock et al. 2009). In prior studies, radial variation was usually tested

Table 3. Coefficients of determination and significance values from regressions of SG on distance from pith (and residuals between their SG estimators and SG_W), for three species with no significant radial trends in SG, and three species with strong radial trends.

			Residuals						
	r^2	P	$SG_M - SG_W$	$SG_I - SG_W$	$SG_{1/3} - SG_W$	$SG_{1/2} - SG_W$	$SG_{2/3} - SG_W$	$SG_O - SG_W$	$SG_{1/6dib} - SG_W$
Magnolia grandiflora #2	0.14	0.10	−0.003	0.001	−0.006	−0.013	0.010	0.002	
Ficus insipida #116	0.04	0.26	−0.004	−0.036	0.000	0.016	−0.038	0.025	
Pseudobombax septenatum #58	0.02	0.40	0.003	0.034	−0.026	−0.014	−0.022	0.026	
Bursera simaruba #70									
Long core	0.93	<0.01	−0.034	−0.146	−0.048	−0.020	−0.006	0.046	0.004
Short core	0.98	<0.01	−0.038	−0.126	−0.068	−0.031	−0.010	0.052	−0.031
Heliocarpus appendiculatus #102									
Long core	0.98	<0.01	−0.051	−0.170	−0.087	−0.050	0.005	0.087	0.005
Short core	0.88	<0.01	−0.043	−0.168	−0.037	−0.068	0.000	0.075	−0.027
Ochroma pyramidale #115									
Long core	0.98	<0.01	−0.039	−0.140	−0.071	−0.013	−0.017	0.061	−0.022
Short core	0.82	<0.01	−0.017	−0.072	−0.085	−0.040	0.026	0.085	−0.027

for linearity by least-squares regression. In cases in which the SG-radius relationship has been determined for a series of conspecifics, the most significant linear increases are evident in medium and large diameter individuals. Radial changes in SG of small diameter trees are less predictable.

If linearity is not known and cannot be presumed and its assumption would result in an unacceptable error, the radial pattern from a small number of complete bark-to-pith samples can be examined initially to ascertain the degree of linearity in the SG-radius relationship. In general, a minimum of five individual trees should be bored to the pith, the cores extracted and cut into short segments, and the SG of segments determined to test the degree of linearity (Wiemann and Williamson 1988, Williamson and Wiemann 2011). If a point of approximation can be determined reliably, then additional trees need only be bored to that point. Therefore, the utility of the approximation is greatest when the SG values of a large number of individuals of a species need to be determined or when linearity can be assumed or is known. If the SG values are to be used in biomass studies that include many species, the accuracy of the method will depend on the degree of $SG_{2/3}$ overestimates versus underestimates across species and their sizes and abundance.

Nonlinear Radial Changes in SG

Nonlinear radial changes may characterize some species or occasionally an aberrant tree of a species that otherwise exhibits linear increases. $SG_{2/3}$ overestimated SG_W in *Astronium graveolens* and *Bombacopsis quinatum* but underestimated it in *Simarouba glauca*, all three dry forest species with nonlinear radial changes. The pith-to-bark SG trend for *Astronium graveolens* #56 was parabolic on both sides of the pith (Figure 3g), suggesting that this species would require a nonlinear SG-radial distance function to determine a point of approximation. $SG_{2/3}$ overestimated SG_W in one tree of *Apeiba aspera* (#85, 27-cm radius) but underestimated it in two others (#89, 24-cm radius and #90, 22-cm radius) (Appendix). The wood of *Apeiba* is characterized by wide, irregularly spaced bands of parenchyma, which affect the SG of the wood. When the low-density parenchyma is abundant, as it was in the segments from two-thirds of the radius in the shorter cores, $SG_{2/3}$ underestimates SG_W; when the parenchyma is absent, as it was in the longer core, $SG_{2/3}$ overestimates SG_W. One of our two *Nectandra cufodontisii* (#286) illustrated a stepwise trend in pith-to-bark SG (Figure 3j). Further sampling would be needed to determine whether these species are characterized by nonlinear radial variation.

Trema micrantha is a species characterized by a linear radial increase in SG, but we cored one aberrant individual. Six of the seven individuals sampled showed linear increases (Appendix), but the long core of *Trema* #141 showed a distinctly nonlinear radial increase (Figure 3c).

Eccentricity

Determining the degree of eccentricity may be equally important because application of the approximation assumes that a tree is symmetrical and not eccentric. Our results with cores extracted from opposite sides of the same tree showed that estimating true SG_W using $SG_{1/6dib}$ resulted in only slightly larger residuals and AVs of residuals than did using $SG_{2/3}$. Residual differences between SG_W and $SG_{1/6dib}$ across the 70 pith-to-bark cores from the 35 trees sampled bark to bark were within 0.02 SG unit for 44 (63%) of the cores and within 0.05 SG unit for 64 (91%) of the cores. The mean AV of the residuals between SG_W and $SG_{1/6dib}$ was 0.018 for the long cores and 0.017 for the short cores; only the $SG_{2/3}$ estimator gave smaller means (0.015, long cores; 0.013, short cores). SG_M had a relatively small mean AV of the residuals on the short cores (0.020) but a larger mean on the long cores (0.024) (Table 2).

Differences between $SG_{1/6dib}$ and $SG_{2/3}$ can result from eccentricity in the trunk such that pith-to-bark cores are not of equal length. The dib can be estimated by measuring the dbh and subtracting twice the value of the bark thickness. The one-sixth dib point is one-sixth of the dib measured from the outermost xylem inward toward the pith. When radii are different, the one-sixth dib will penetrate past one-third of the radius on the short core but not reach

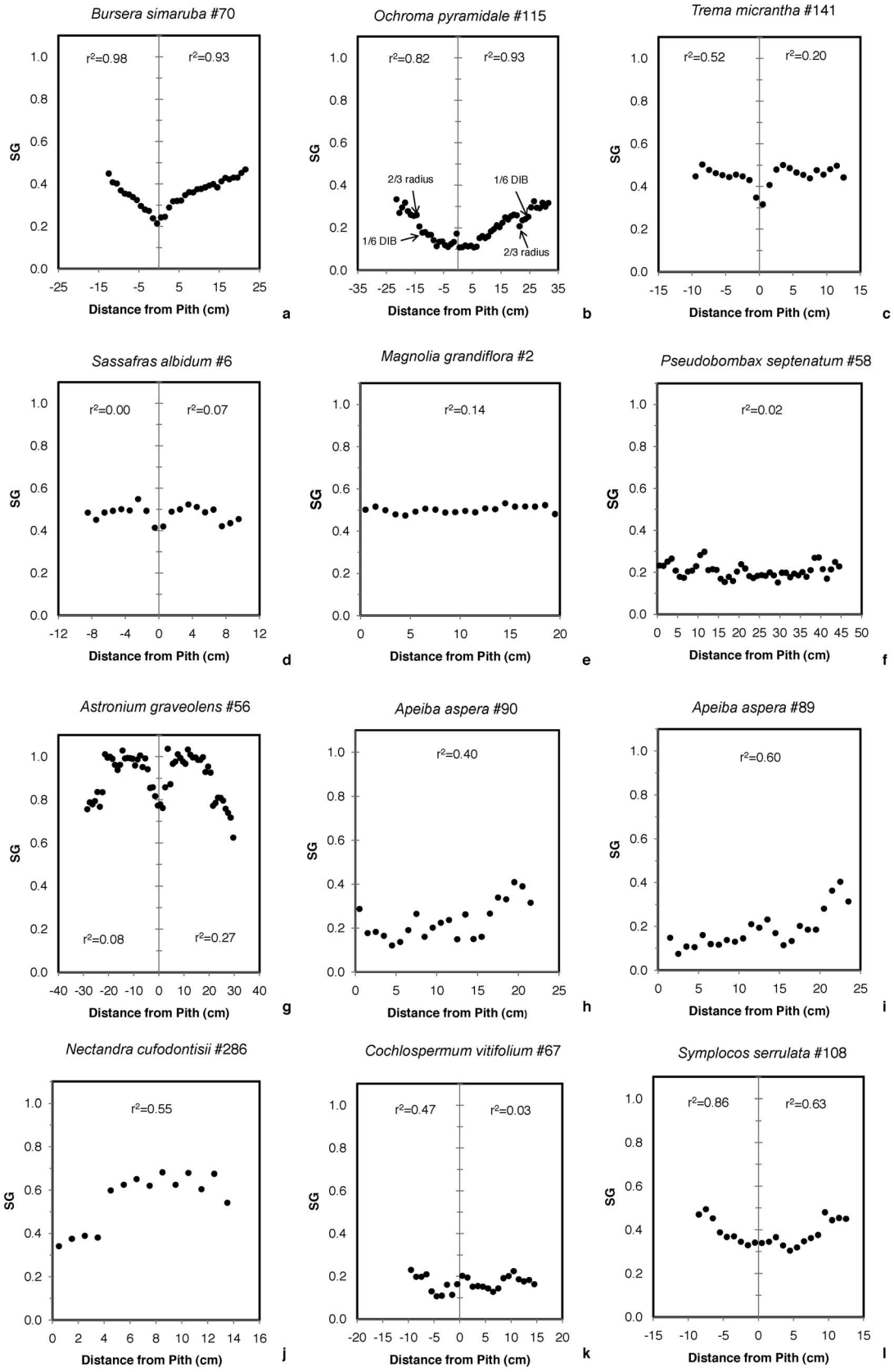

Figure 3. SG as a function of distance from pith for seven trees sampled across the entire diameter (a, b, c, d, g, k, and l) and five trees sampled bark to pith (e, f, h, i, and j).

one-third of the radius on the long core (Figure 3b). Therefore, when SG increases with distance from the pith, $SG_{1/6dib}$ from the short core will underestimate SG_W and $SG_{1/6dib}$ from the long core will overestimate SG_W. The differences will be minor as seen in our data, unless the eccentricity is large.

When compared with the AV of the residuals of $SG_{2/3}$, those of $SG_{1/6dib}$ were significantly larger (by at least 0.03 SG unit) for *Astronium graveolens* #56, long core (0.052 SG unit) (Figure 3g); *Bursera simaruba* #77, short core (0.032 SG unit); *Cochlospermum vitifolium* #67, short core (0.030 SG unit) (Figure 3k); *Ochroma pyramidale* #115, short core (0.054 SG unit) (Figure 3b); and *Symplocos serrulata* #108, short core (0.070 SG unit) (Figure 3l). Of these five trees, *Ochroma pyramidale* #115 (Figure 3b) and *Bursera simaruba* #77 exhibited regressions with high r^2 values but substantial eccentricity, with cores of 22 and 32 cm for *Ochroma pyramidale* #115 and 9 and 12 cm for *Bursera simaruba* #77. *Astronium graveolens* #56 was not eccentric but had SG-radius regressions with low r^2 values and nonlinear SG-distance variation (Figure 3g). Finally, *Cochlospermum vitifolium* #67 had both eccentricity and low r^2 (Figure 3k).

One remedy for the problem of notable eccentricity is to bore a tree to one-sixth of its dib from opposite sides and average the two samples, as the mean exhibits an improvement over either the long core or the short core estimate. In addition, taking two short core samples is considerably easier than completing a bark-to-pith core, especially in large trees or in species with very dense wood.

Other Estimators of SG_W

The worst estimator of SG_W was SG_I. On the one hand, this estimator is of little practical importance because the inner wood is the most inaccessible to sample in large trees. However, the inner wood is the wood first produced, so it is the wood of small trees. It should not be assumed to be representative of larger individuals. For species with radial increases in SG, SG_I will underestimate SG_W. If researchers use compiled SG data in their studies, large errors may result if the data are not representative. The extent to which smaller trees have been sampled to represent all individuals of a species is unknown, but one example illustrates the potential error. The online database initiated by Chave et al. (2006) (www.esapubs.org/archive/appl/A016/075/list-references.txt and www.esapubs.org/archive/appl/A016/075/wood-density-file.txt) lists 10 SG values for *Ochroma pyramidale*, ranging only from 0.11 to 0.22. However, wood SG of this species is known to increase sharply from approximately 0.04 for inner wood to 0.40 for outer wood of large individuals (Whitmore 1973). Therefore, the online database seems to reflect sampling of smaller dbh individuals.

Use of SG_O for estimating SG_W of a species can also produce errors. In the example above, the outermost wood of large individuals of *Ochroma pyramidale* would overestimate SG_W of individuals in an early successional stand. Outer wood may be sampled by default with increment hammers and short increment borers.

Even though it is not weighted to represent wood volume, SG_M gave surprisingly good estimates of SG_W. Its accuracy was better than that of all other estimators except $SG_{2/3}$ and $SG_{1/6dib}$, but it had a negative bias (Table 2; Figure 2). The bias can be attributed to the inclusion of a large number of species with radial increases in SG, but its better than expected accuracy is probably due to the inclusion of species whose SG did not change with radius (Figure 3e) or had irregular changes (Figure 3g). Overall, the adequacy of SG_M implies that prior studies based on cores, without weighting by area of each radial piece, may have provided relatively unbiased estimates of SG_W. $SG_{1/3}$ and $SG_{1/2}$ were, not surprisingly, intermediate between SG_I and $SG_{2/3}$. $SG_{1/3}$ and $SG_{1/2}$ are of little importance unless a researcher makes the erroneous assumption that small stem SG represents large stem SG ($SG_{1/3}$) or that wood midway between the pith and the bark is representative of the whole stem ($SG_{1/2}$).

Branch wood has also been used to estimate SG_W (Swenson and Enquist 2008), but even if branch wood approximates trunk sapwood SG, it may not be representative of trunk heartwood (Okai et al. 2004). In addition, for species with radial increases in SG, initial branch wood SG may be similar to that of the outer or the inner trunk wood xylem, depending on the age and height at which the branch is initiated (Rueda and Williamson 1992). Moreover, a recent, large survey of Amazonian trees revealed that branch wood xylem was surprisingly plastic despite having a genetic component (Patiño et al. 2009).

Limitations of the Current Study

Larger sample sizes per species are needed to further test the Wiemann approximation. We used the largest data sets available to us, in which SG was measured in 1-cm sections from bark to pith. Our data set for testing the approximation was moderately large because we had sampled trees previously to determine radial shifts in SG in prior studies, but the number of individuals was small for many species. These prior studies focused largely on successional species of lowland rainforests of Costa Rica, although we obtained and included parallel data for later successional species (Wiemann and Williamson 1988, 1989a, 1989b) as well as species of temperate, tropical dry, and tropical montane forests for comparisons. However, our data do not approximate a random or representative sample of tree species from any given community or biome. Obviously, information on radial patterns in SG from other species and the applicability of the approximation to them are needed to further test this methodology to estimate wood SG.

Conclusions

Wood SG values of tree cross-sections were estimated from cores for a sample of 102 tropical trees (47 species) and 16 temperate trees (12 species) sampled only on one side and for 26 tropical trees (14 species) and 9 temperate trees (9 species) sampled bark to bark through the pith. For linear (or no) changes in SG across the radius, the point of approximation, equal to the weighted mean wood SG, was found at two-thirds of the distance from pith to the bark. For trees with linear radial increases, SG at this two-thirds

distance was not significantly different from the weighted mean SG of a complete pith-to-bark core, but other points along the radius were different from the weighted mean. For this approximation to be useful in the field, the point would be estimated as one-sixth dib, measured as one-sixth of the distance from the inside of the bark toward the pith. For trees that are not eccentric, the location of one-sixth of the dib inward and two-thirds of the radius outward coincide. As trees become more eccentric, the two points diverge and SG estimates will diverge, although in the data set here, such divergences were minor and infrequent. Therefore, the Wiemann approximation shows promise. However, its usefulness in estimating the wood SG of a species is conditional on knowledge of the pattern of radial change in SG and the degree of eccentricity in the species (Williamson and Wiemann 2011).

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Appendix

Table A1. Summary of Collection Data, SG Estimates, and Regressions of SG on Distance from Pith for 153 Temperate and Tropical Trees.

Species	Tree no.	Collection site	Forest type	dbh (cm)	No. 1-cm pieces	Specific gravity								Regressions of SG on distance from pith		
						SG_M	SG_W	SG_I	$SG_{1/3}$	$SG_{1/2}$	$SG_{2/3}$	SG_O	$SG_{1/6dib}$	Intercept	Slope	r^{2a}
One radius																
Albizia caribaea	66	PV	TrDry	89	30	0.340	0.353	0.300	0.287	0.356	0.387	0.377		0.299	0.00272	**0.31**
Albizia guachapele	62	PV	TrDry	30	15	0.649	0.663	0.631	0.609	0.642	0.684	0.686		0.605	0.00585	**0.39**
Alnus acuminata	281	MF	Mont	48	23	0.441	0.455	0.380	0.440	0.453	0.462	0.448		0.399	0.00360	**0.64**
Alnus acuminata	282	MF	Mont	41	22	0.376	0.411	0.261	0.342	0.418	0.423	0.428		0.272	0.00945	**0.79**
Alnus acuminata	284	MF	Mont	37	12	0.355	0.380	0.287	0.353	0.368	0.387	0.404		0.281	0.01248	**0.92**
Apeiba aspera	85	S	TrWet	32	27	0.142	0.151	0.154	0.119	0.128	0.167	0.177		0.117	0.00189	**0.23**
Apeiba aspera	89	S	TrWet	44	24	0.184	0.218	0.110	0.128	0.212	0.150	0.360		0.063	0.00968	**0.60**
Apeiba aspera	90	S	TrWet	34	22	0.233	0.263	0.216	0.205	0.203	0.191	0.371		0.143	0.00819	**0.40**
Aralia spinosa	9	H	Temp	23	10	0.349	0.339	0.365	0.366	0.349	0.339	0.324		0.379	−0.00608	**0.66**
Astronium graveolens	47	PV	TrDry	40	18	0.718	0.751	0.624	0.724	0.685	0.784	0.781		0.619	0.01103	**0.78**
Bombacopsis quinatum	46	PV	TrDry	77	23	0.394	0.432	0.290	0.372	0.378	0.448	0.489		0.278	0.01005	**0.94**
Bombacopsis quinatum	73	PV	TrDry	53	18	0.360	0.373	0.312	0.359	0.366	0.378	0.380		0.322	0.00424	**0.49**
Brunellia costaricensis	103	OA	Mont	40	24	0.271	0.291	0.235	0.297	0.236	0.264	0.345		0.208	0.00520	**0.54**
Brunellia costaricensis	278	MF	Mont	47	28	0.309	0.328	0.243	0.331	0.334	0.336	0.347		0.252	0.00410	**0.55**
Brunellia costaricensis	283	MF	Mont	35	15	0.283	0.298	0.252	0.283	0.269	0.289	0.331		0.239	0.00589	**0.62**
Brunellia costaricensis	285	MF	Mont	47	18	0.348	0.380	0.261	0.331	0.350	0.384	0.432		0.252	0.01064	**0.91**
Brunellia costaricensis	295	MF	Mont	45	21	0.307	0.327	0.263	0.294	0.301	0.334	0.349		0.248	0.00567	**0.76**
Buddleia cordata	292	MF	Mont	58	26	0.549	0.582	0.413	0.535	0.552	0.619	0.596		0.432	0.00832	**0.70**
Bursera simaruba	298	C	TrWet	51	29	0.394	0.425	0.230	0.410	0.425	0.432	0.427		0.301	0.00642	**0.62**
Bursera simaruba	301	C	TrWet	73	29	0.366	0.413	0.175	0.357	0.405	0.426	0.470		0.223	0.00983	**0.85**
Bursera simaruba	302	C	TrWet	67	26	0.402	0.435	0.297	0.404	0.414	0.410	0.506		0.304	0.00759	**0.86**
Castilla elastica	27	S	TrWet	59	20	0.328	0.364	0.197	0.342	0.346	0.350	0.415		0.221	0.01067	**0.82**
Castilla elastica	32	S	TrWet	51	21	0.343	0.378	0.256	0.287	0.373	0.385	0.423		0.239	0.00993	**0.81**
Castilla elastica	81	S	TrWet	66	29	0.338	0.388	0.156	0.362	0.387	0.370	0.438		0.187	0.01037	**0.76**
Cecropia insignis	148	PN	TrWet	37	22	0.333	0.376	0.205	0.308	0.341	0.352	0.427		0.205	0.01164	**0.87**
Cecropia peltata	74	PV	TrDry	42	27	0.364	0.390	0.222	0.391	0.384	0.387	0.390		0.285	0.00584	**0.46**
Cecropia polyphlebia	307	MF	Mont	34	16	0.203	0.232	0.134	0.167	0.218	0.244	0.265		0.114	0.01110	**0.83**
Cedrela odorata	40	S	TrWet	78	23	0.341	0.389	0.241	0.279	0.357	0.397	0.467		0.196	0.01260	**0.91**
Cedrela odorata	sn3	PV	TrDry	77	33	0.377	0.402	0.258	0.391	0.409	0.421	0.417		0.300	0.00463	**0.67**
Ceiba pentandra	72	PV	TrDry	62	22	0.265	0.298	0.168	0.219	0.279	0.325	0.313		0.166	0.00900	**0.82**
Ceiba pentandra	147	PN	TrWet	123	64	0.242	0.278	0.107	0.201	0.244	0.301	0.286		0.126	0.00351	**0.84**
Ceiba pentandra	149	PN	TrWet	53	18	0.434	0.460	0.316	0.455	0.460	0.469	0.468		0.355	0.00873	**0.60**
Cespedesia macrophylla	119	S	TrWet	40	16	0.558	0.584	0.489	0.524	0.569	0.605	0.604		0.478	0.00995	**0.85**
Cochlospermum vitifolium	76	PV	TrDry	32	16	0.208	0.213	0.201	0.196	0.212	0.217	0.219		0.192	0.00200	**0.25**
Cochlospermum vitifolium	A	PV	TrDry	41	24	0.154	0.149	0.174	0.159	0.141	0.149	0.141		0.172	−0.00144	**0.42**
Cochlospermum vitifolium	B	PV	TrDry	31	16	0.185	0.192	0.148	0.198	0.200	0.171	0.201		0.162	0.00277	**0.26**
Cordia alliodora	101	S	TrWet	36	17	0.330	0.360	0.271	0.286	0.293	0.334	0.443		0.214	0.01288	**0.81**
Cordia alliodora	122	S	TrWet	45	18	0.269	0.291	0.231	0.232	0.269	0.280	0.346		0.202	0.00747	**0.77**
Cornus disciflora	291	MF	Mont	32	12	0.539	0.555	0.484	0.524	0.540	0.570	0.575		0.468	0.01081	**0.83**
Croton killipianus	151	PN	TrWet	48	24	0.374	0.385	0.331	0.373	0.360	0.386	0.404		0.340	0.00279	**0.58**
Croton killipianus	152	PN	TrWet	34	17	0.331	0.327	0.333	0.340	0.344	0.325	0.319		0.343	−0.00137	**0.24**
Dendropanax gonatopodus	277	MF	Mont	58	25	0.367	0.384	0.339	0.356	0.362	0.376	0.398		0.318	0.00396	**0.63**
Didymopanax pittieri	274	MF	Mont	53	18	0.363	0.369	0.362	0.324	0.368	0.376	0.379		0.347	0.00178	0.15
Didymopanax pittieri	276	MF	Mont	29	14	0.437	0.434	0.458	0.420	0.426	0.436	0.433		0.449	−0.00155	0.10
Erythrina poeppigiana	100	S	TrWet	73	31	0.319	0.349	0.273	0.280	0.305	0.317	0.407		0.231	0.00571	**0.78**
Ficus insipida	116	S	TrWet	98	36	0.312	0.316	0.280	0.316	0.332	0.278	0.341		0.300	0.00067	0.04
Fraxinus americana	124	H	Temp	58	30	0.616	0.602	0.674	0.615	0.601	0.608	0.574		0.666	−0.00309	**0.48**
Goethalsia meiantha	114	S	TrWet	53	19	0.325	0.353	0.256	0.309	0.305	0.322	0.436		0.242	0.00877	**0.70**
Hampea appendiculata	94	S	TrWet	36	12	0.273	0.297	0.206	0.277	0.289	0.295	0.318		0.201	0.01196	**0.85**
Hampea appendiculata	134	SE	TrWet	44	23	0.342	0.377	0.235	0.311	0.370	0.375	0.423		0.236	0.00922	**0.91**
Hampea appendiculata	135	SE	TrWet	48	23	0.309	0.341	0.196	0.318	0.350	0.351	0.367		0.213	0.00833	**0.78**
Hampea appendiculata	136	SE	TrWet	36	16	0.310	0.341	0.227	0.273	0.343	0.362	0.374		0.216	0.01172	**0.87**
Hedyosmum mexicanum	308	MF	Mont	23	10	0.383	0.400	0.329	0.417	0.404	0.403	0.402		0.331	0.01045	0.28
Hedyosmum mexicanum	309	MF	Mont	24	9	0.365	0.392	0.307	0.367	0.371	0.398	0.417		0.283	0.01810	**0.78**
Heliocarpus appendiculatus	123	S	TrWet	50	27	0.225	0.258	0.110	0.222	0.242	0.264	0.293		0.126	0.00734	**0.90**
Heliocarpus appendiculatus	138	SE	TrWet	49	39	0.110	0.140	0.093	0.061	0.078	0.105	0.244		0.021	0.00459	**0.66**
Heliocarpus appendiculatus	139	SE	TrWet	56	32	0.231	0.247	0.077	0.219	0.247	0.288	0.289		0.133	0.00632	**0.68**

Table A1. (continued)

Species	Tree no.	Collection site	Forest type	dbh (cm)	No. 1-cm pieces	Specific gravity								Regressions of SG on distance from pith		
						SG_M	SG_W	SG_I	$SG_{1/3}$	$SG_{1/2}$	$SG_{2/3}$	SG_O	$SG_{1/6dib}$	Intercept	Slope	r^{2a}
Heliocarpus appendiculatus	140	SE	TrWet	37	20	0.181	0.225	0.128	0.118	0.141	0.190	0.330		0.048	0.01324	**0.72**
Heliocarpus appendiculatus	205	SP	TrWet	32	14	0.152	0.188	0.088	0.105	0.121	0.179	0.261		0.046	0.01525	**0.76**
Heliocarpus appendiculatus	96	S	TrWet	47	27	0.139	0.160	0.095	0.109	0.121	0.150	0.231		0.067	0.00497	**0.82**
Hura crepitans	52	PV	TrDry	41	16	0.313	0.340	0.220	0.294	0.369	0.370	0.346		0.229	0.01045	**0.65**
Hura crepitans	79	PV	TrDry	56	25	0.317	0.347	0.226	0.286	0.349	0.367	0.377		0.227	0.00722	**0.84**
Hura crepitans	304	B	TrWet	65	34	0.340	0.352	0.291	0.346	0.363	0.343	0.382		0.296	0.00240	**0.50**
Hura crepitans	305	B	TrWet	30	14	0.368	0.370	0.350	0.412	0.383	0.347	0.372		0.365	0.00052	0.01
Hura crepitans	306	B	TrWet	31	15	0.408	0.392	0.395	0.494	0.447	0.364	0.352		0.456	−0.00644	0.20
Ilex opaca	8	H	Temp	31	13	0.544	0.534	0.592	0.526	0.517	0.533	0.535		0.575	−0.00477	0.28
Lippia torresii	287	MF	Mont	37	14	0.342	0.375	0.231	0.351	0.369	0.387	0.398		0.242	0.01422	**0.80**
Lippia torresii	288	MF	Mont	36	14	0.407	0.425	0.340	0.391	0.423	0.435	0.447		0.332	0.00941	**0.81**
Lippia torresii	289	MF	Mont	35	18	0.273	0.283	0.246	0.266	0.274	0.274	0.313		0.242	0.00340	**0.43**
Lippia torresii	297	MF	Mont	53	23	0.463	0.498	0.342	0.440	0.478	0.543	0.491		0.357	0.00916	**0.74**
Liquidambar styraciflua	15	H	Temp	36	18	0.480	0.481	0.465	0.492	0.492	0.486	0.472		0.475	0.00053	0.04
Liriodendron tulipifera	18	H	Temp	61	30	0.413	0.443	0.311	0.378	0.417	0.473	0.479		0.323	0.00602	**0.81**
Liriodendron tulipifera	24	H	Temp	55	27	0.431	0.456	0.361	0.406	0.435	0.468	0.482		0.356	0.00553	**0.88**
Liriodendron tulipifera	125	H	Temp	65	33	0.464	0.489	0.346	0.440	0.497	0.521	0.479		0.381	0.00477	**0.60**
Liriodendron tulipifera	129	H	Temp	67	29	0.456	0.471	0.385	0.445	0.466	0.480	0.488		0.411	0.00309	**0.60**
Liriodendron tulipifera	130	H	Temp	66	27	0.448	0.458	0.398	0.441	0.465	0.435	0.480		0.413	0.00245	**0.43**
Magnolia acuminata	5	H	Temp	42	19	0.499	0.510	0.438	0.509	0.521	0.529	0.504		0.467	0.00337	**0.28**
Magnolia grandiflora	2	H	Temp	40	20	0.501	0.505	0.505	0.499	0.492	0.514	0.507		0.491	0.00100	0.14
Magnolia macrophylla	128	H	Temp	27	11	0.489	0.497	0.462	0.505	0.512	0.490	0.495		0.466	0.00412	0.33
Morus rubra	19	H	Temp	29	13	0.361	0.394	0.256	0.348	0.390	0.414	0.415		0.260	0.01552	**0.77**
Nectandra cufodontisii	105	MF	Mont	29	15	0.446	0.458	0.408	0.459	0.462	0.437	0.488		0.408	0.00508	**0.37**
Nectandra cufodontisii	286	MF	Mont	34	14	0.556	0.608	0.368	0.624	0.651	0.662	0.607		0.399	0.02240	**0.55**
Nectandra reticulata	30	S	TrWet	52	12	0.393	0.425	0.346	0.338	0.365	0.425	0.489		0.295	0.01619	**0.78**
Ochroma pyramidale	91	S	TrWet	47	28	0.155	0.167	0.150	0.131	0.153	0.144	0.209		0.118	0.00261	**0.46**
Ochroma pyramidale	97	S	TrWet	65	26	0.183	0.220	0.121	0.136	0.157	0.210	0.305		0.070	0.00867	**0.80**
Ochroma pyramidale	144	CH	TrWet	83	37	0.203	0.235	0.167	0.161	0.242	0.226	0.274		0.107	0.00520	**0.75**
Ochroma pyramidale	161	PN	TrWet	49	27	0.190	0.214	0.129	0.155	0.179	0.243	0.258		0.119	0.00530	**0.68**
Ochroma pyramidale	164	PN	TrWet	54	30	0.155	0.191	0.097	0.087	0.122	0.206	0.271		0.045	0.00728	**0.75**
Pentaclethra macroloba	83	S	TrWet	40	19	0.502	0.517	0.429	0.531	0.522	0.518	0.535		0.456	0.00488	**0.40**
Pentaclethra macroloba	86	S	TrWet	48	20	0.461	0.471	0.423	0.457	0.486	0.472	0.491		0.432	0.00293	**0.35**
Phoebe hammeliana	296	MF	Mont	56	22	0.457	0.492	0.332	0.423	0.467	0.509	0.517		0.353	0.00949	**0.82**
Pourouma aspera	150	PN	TrWet	66	30	0.332	0.342	0.324	0.309	0.329	0.330	0.370		0.300	0.00211	**0.27**
Prunus serotina	14	H	Temp	53	27	0.603	0.594	0.602	0.623	0.612	0.624	0.550		0.632	−0.00213	**0.29**
Pseudobombax septenatum	58	PV	TrDry	101	45	0.207	0.205	0.238	0.178	0.191	0.183	0.230		0.215	−0.00034	0.02
Pseudobombax septenatum	59	PV	TrDry	82	37	0.153	0.146	0.200	0.151	0.150	0.147	0.151		0.172	−0.00103	**0.25**
Pseudobombax septenatum	63	PV	TrDry	113	49	0.248	0.261	0.211	0.231	0.236	0.222	0.334		0.209	0.00159	**0.28**
Pseudobombax septenatum	75	PV	TrDry	48	17	0.313	0.338	0.223	0.325	0.349	0.342	0.350		0.240	0.00862	**0.72**
Quercus copeyensis	104	MF	Mont	120	29	0.714	0.698	0.735	0.737	0.747	0.680	0.612		0.762	−0.00331	**0.43**
Sapium thelocarpum	78	PV	TrDry	48	23	0.500	0.527	0.403	0.492	0.516	0.559	0.545		0.421	0.00692	**0.79**
Sassafras albidum	20	H	Temp	30	13	0.413	0.401	0.446	0.418	0.411	0.406	0.383		0.448	−0.00532	**0.34**
Spondias mombin	38	S	TrWet	55	15	0.355	0.373	0.317	0.345	0.354	0.361	0.410		0.299	0.00741	**0.83**
Spondias mombin	61	PV	TrDry	36	15	0.436	0.471	0.316	0.449	0.461	0.489	0.487		0.330	0.01411	**0.68**
Spondias mombin	71	PV	TrDry	50	20	0.322	0.361	0.233	0.291	0.357	0.368	0.415		0.205	0.01173	**0.88**
Sterculia apetala	50	PV	TrDry	49	28	0.365	0.406	0.215	0.387	0.393	0.418	0.409		0.241	0.00882	**0.62**
Sterculia apetala	54	PV	TrDry	68	24	0.456	0.444	0.442	0.518	0.461	0.431	0.412		0.500	−0.00355	**0.35**
Sterculia apetala	65	PV	TrDry	67	22	0.435	0.456	0.322	0.429	0.472	0.496	0.426		0.371	0.00583	**0.40**
Symplocos austin-smithii	272	MF	Mont	32	18	0.409	0.408	0.434	0.397	0.395	0.405	0.416		0.410	−0.00018	0.00
Trema micrantha	98	S	TrWet	43	24	0.238	0.266	0.143	0.225	0.259	0.276	0.297		0.153	0.00707	**0.90**
Trema micrantha	174	SP	TrWet	27	16	0.277	0.309	0.182	0.258	0.294	0.303	0.357		0.179	0.01218	**0.92**
Trema micrantha	207	SP	TrWet	29	15	0.237	0.253	0.189	0.232	0.238	0.250	0.272		0.192	0.00610	**0.60**
Trema micrantha	215	SP	TrWet	30	14	0.245	0.278	0.162	0.224	0.265	0.299	0.312		0.147	0.01404	**0.89**
Trema micrantha	216	SP	TrWet	34	20	0.276	0.301	0.210	0.246	0.281	0.303	0.330		0.200	0.00756	**0.90**
Virola koschnyi	84	S	TrWet	86	28	0.428	0.455	0.321	0.403	0.423	0.467	0.491		0.348	0.00575	**0.84**
Vochysia hondurensis	80	S	TrWet	56	28	0.325	0.349	0.271	0.282	0.320	0.367	0.358		0.244	0.00540	**0.71**
Weinmannia fagaroides	279	MF	Mont	46	20	0.502	0.512	0.482	0.480	0.501	0.521	0.538		0.464	0.00357	**0.35**
Weinmannia fagaroides	280	MF	Mont	48	21	0.506	0.518	0.468	0.475	0.487	0.505	0.574		0.470	0.00342	**0.24**
Zanthoxylum clava-herculis	25	H	Temp	28	12	0.465	0.470	0.458	0.457	0.458	0.469	0.482		0.450	0.00259	**0.68**
Zanthoxylum panamense	42	S	TrWet	30	14	0.496	0.501	0.480	0.507	0.479	0.503	0.504		0.482	0.00202	0.12

Table A1. (continued)

Species	Tree no.	Collection site	Forest type	dbh (cm)	No. 1-cm pieces	Specific gravity								Regressions of SG on distance from pith		
						SG_M	SG_W	SG_I	$SG_{1/3}$	$SG_{1/2}$	$SG_{2/3}$	SG_O	$SG_{1/6dib}$	Intercept	Slope	r^{2a}
Means, 118 trees						0.359	0.379	0.298	0.348	0.367	0.381	0.405				
SDs, 118 trees						0.124	0.121	0.134	0.135	0.129	0.130	0.110				
Two radii: long core																
Astronium graveolens	56	PV	TrDry	64	30	0.894	0.860	0.800	0.992	0.989	0.884	0.693	0.936	0.995	−0.00675	**0.27**
Bombacopsis quinatum	55	PV	TrDry	82	32	0.345	0.347	0.274	0.327	0.366	0.372	0.314	0.372	0.338	0.00043	0.01
Bursera simaruba	70	PV	TrDry	41	22	0.371	0.404	0.259	0.356	0.385	0.398	0.450	0.408	0.270	0.00918	**0.93**
Bursera simaruba	77	PV	TrDry	26	12	0.281	0.322	0.198	0.235	0.288	0.336	0.375	0.336	0.160	0.02030	**0.96**
Cecropia insignis	143	PN	TrWet	58	28	0.310	0.325	0.232	0.336	0.329	0.333	0.326	0.333	0.263	0.00333	**0.42**
Cochlospermum vitifolium	67	PV	TrDry	42	15	0.173	0.175	0.182	0.140	0.154	0.204	0.174	0.204	0.164	0.00110	0.03
Fraxinus americana	21	H	Temp	21	10	0.583	0.594	0.565	0.577	0.579	0.582	0.606	0.582	0.546	0.00721	**0.43**
Hampea appendiculata	92	S	TrWet	44	21	0.198	0.225	0.169	0.154	0.168	0.207	0.311	0.207	0.116	0.00778	**0.68**
Hampea appendiculata	113	S	TrWet	44	22	0.216	0.244	0.188	0.149	0.223	0.217	0.318	0.217	0.130	0.00777	**0.71**
Hampea appendiculata	121	S	TrWet	48	23	0.265	0.300	0.178	0.235	0.270	0.312	0.346	0.312	0.160	0.00916	**0.95**
Hampea appendiculata	131	SE	TrWet	50	26	0.246	0.277	0.185	0.174	0.276	0.303	0.325	0.303	0.154	0.00709	**0.73**
Hampea appendiculata	132	SE	TrWet	44	23	0.226	0.245	0.196	0.232	0.231	0.244	0.294	0.244	0.169	0.00496	**0.67**
Heliocarpus appendiculatus	95	S	TrWet	36	18	0.127	0.157	0.078	0.095	0.106	0.142	0.229	0.128	0.036	0.01012	**0.82**
Heliocarpus appendiculatus	102	G	TrWet	44	20	0.204	0.255	0.086	0.168	0.205	0.260	0.342	0.260	0.052	0.01526	**0.98**
Heliocarpus appendiculatus	117	S	TrWet	50	24	0.171	0.210	0.068	0.135	0.166	0.200	0.301	0.200	0.033	0.01108	**0.96**
Heliocarpus appendiculatus	137	SE	TrWet	49	21	0.142	0.165	0.099	0.135	0.106	0.176	0.216	0.148	0.070	0.00678	**0.74**
Licania arborea	57	PV	TrDry	58	25	0.592	0.612	0.535	0.570	0.579	0.599	0.644	0.607	0.533	0.00473	**0.77**
Liriodendron tulipifera	126	H	Temp	56	27	0.435	0.460	0.350	0.422	0.420	0.445	0.515	0.438	0.360	0.00557	**0.78**
Magnolia macrophylla	26	H	Temp	18	10	0.443	0.463	0.396	0.437	0.442	0.458	0.485	0.458	0.382	0.01215	**0.79**
Ochroma pyramidale	28	S	TrWet	38	20	0.138	0.162	0.112	0.106	0.127	0.151	0.227	0.151	0.067	0.00716	**0.73**
Ochroma pyramidale	44	S	TrWet	36	19	0.112	0.129	0.101	0.073	0.106	0.118	0.184	0.115	0.064	0.00511	**0.53**
Ochroma pyramidale	115	S	TrWet	66	32	0.211	0.250	0.110	0.179	0.237	0.233	0.311	0.228	0.093	0.00736	**0.93**
Ochroma pyramidale	146	PN	TrWet	48	23	0.263	0.296	0.148	0.247	0.312	0.315	0.304	0.315	0.163	0.00865	**0.77**
Oxydendrum arboreum	22	H	Temp	23	12	0.534	0.534	0.528	0.538	0.547	0.531	0.525	0.545	0.533	0.00012	0.00
Populus deltoides	16	H	Temp	25	11	0.379	0.385	0.375	0.357	0.368	0.380	0.411	0.359	0.380	0.00375	0.20
Populus tremuloides	sn1	ADK	Temp	22	9	0.360	0.355	0.368	0.357	0.360	0.354	0.352	0.355	0.375	−0.00335	0.26
Rhus copallina	7	H	Temp	18	7	0.413	0.440	0.360	0.415	0.440	0.456	0.451	0.456	0.331	0.02339	**0.69**
Rollinia microsepala	35	S	TrWet	32	16	0.281	0.298	0.236	0.270	0.264	0.322	0.295	0.322	0.230	0.00633	**0.43**
Salix nigra	17	H	Temp	24	11	0.371	0.370	0.373	0.363	0.374	0.380	0.368	0.376	0.376	−0.00072	0.03
Sassafras albidum	6	H	Temp	22	10	0.474	0.468	0.469	0.511	0.499	0.468	0.436	0.468	0.491	−0.00339	0.07
Simarouba glauca	69	PV	TrDry	28	15	0.445	0.447	0.437	0.452	0.450	0.441	0.451	0.441	0.440	0.00066	0.16
Symplocos serrulata	108	OA	Mont	26	13	0.378	0.404	0.350	0.317	0.343	0.406	0.449	0.406	0.301	0.01190	**0.63**
Trema micrantha	36	S	TrWet	22	11	0.287	0.323	0.200	0.284	0.289	0.330	0.359	0.330	0.180	0.01958	**0.90**
Trema micrantha	141	SE	TrWet	26	12	0.454	0.547	0.401	0.484	0.452	0.456	0.473	0.456	0.417	0.00567	0.20
Weinmannia pinnata	293	MF	Mont	40	17	0.574	0.584	0.571	0.555	0.564	0.571	0.611	0.571	0.545	0.00343	**0.36**
Means, 35 trees						0.340	0.361	0.291	0.325	0.343	0.360	0.385	0.360			
SDs, 35 trees						0.166	0.158	0.174	0.189	0.179	0.157	0.129	0.165			
Two radii: short core																
Astronium graveolens	56	PV	TrDry	64	29	0.915	0.901	0.816	0.981	0.994	0.995	0.774	0.984	0.960	−0.00305	0.08
Bombacopsis quinatum	55	PV	TrDry	82	26	0.339	0.333	0.300	0.361	0.374	0.337	0.285	0.328	0.356	−0.00133	0.06
Bursera simaruba	70	PV	TrDry	41	13	0.330	0.368	0.242	0.300	0.337	0.358	0.420	0.337	0.216	0.01752	**0.98**
Bursera simaruba	77	PV	TrDry	26	9	0.263	0.291	0.214	0.227	0.241	0.290	0.334	0.258	0.177	0.01915	**0.76**
Cecropia insignis	143	PN	TrWet	58	25	0.322	0.343	0.242	0.304	0.339	0.363	0.344	0.343	0.261	0.00495	**0.73**
Cochlospermum vitifolium	67	PV	TrDry	42	10	0.161	0.178	0.145	0.125	0.148	0.178	0.208	0.148	0.110	0.01030	**0.47**
Fraxinus americana	21	H	Temp	21	8	0.569	0.571	0.569	0.568	0.566	0.564	0.570	0.566	0.561	0.00187	0.04
Hampea appendiculata	92	S	TrWet	44	18	0.221	0.241	0.204	0.186	0.213	0.235	0.298	0.232	0.162	0.00662	**0.61**
Hampea appendiculata	113	S	TrWet	44	21	0.248	0.282	0.182	0.211	0.247	0.299	0.353	0.285	0.146	0.00970	**0.82**
Hampea appendiculata	121	S	TrWet	48	20	0.207	0.242	0.153	0.159	0.202	0.229	0.320	0.220	0.104	0.01032	**0.84**
Hampea appendiculata	131	SE	TrWet	50	21	0.296	0.335	0.181	0.268	0.347	0.366	0.342	0.373	0.177	0.01132	**0.72**
Hampea appendiculata	132	SE	TrWet	44	19	0.217	0.226	0.213	0.196	0.191	0.211	0.274	0.209	0.190	0.00281	0.20
Heliocarpus appendiculatus	95	S	TrWet	36	17	0.142	0.173	0.086	0.094	0.116	0.173	0.231	0.150	0.050	0.01085	**0.82**
Heliocarpus appendiculatus	102	G	TrWet	44	18	0.221	0.264	0.096	0.227	0.196	0.264	0.339	0.237	0.091	0.01444	**0.88**
Heliocarpus appendiculatus	117	S	TrWet	50	20	0.200	0.235	0.069	0.104	0.196	0.248	0.320	0.235	−0.017	0.01889	**0.97**
Heliocarpus appendiculatus	137	SE	TrWet	49	19	0.199	0.217	0.167	0.162	0.198	0.230	0.243	0.224	0.145	0.00570	**0.79**
Licania arborea	57	PV	TrDry	58	17	0.570	0.589	0.526	0.560	0.569	0.570	0.630	0.575	0.513	0.00669	**0.82**
Liriodendron tulipifera	126	H	Temp	56	26	0.434	0.451	0.369	0.424	0.419	0.462	0.468	0.452	0.382	0.00398	**0.69**
Magnolia macrophylla	26	H	Temp	18	8	0.432	0.439	0.416	0.447	0.443	0.441	0.439	0.443	0.411	0.00533	0.26

Table A1. (continued)

Species	Tree no.	Collection site	Forest type	dbh (cm)	No. 1-cm pieces	Specific gravity								Regressions of SG on distance from pith		
						SG_M	SG_W	SG_I	$SG_{1/3}$	$SG_{1/2}$	$SG_{2/3}$	SG_O	$SG_{1/6dib}$	Intercept	Slope	r^{2a}
Ochroma pyramidale	28	S	TrWet	38	15	0.157	0.183	0.105	0.113	0.153	0.216	0.210	0.191	0.080	0.01033	**0.73**
Ochroma pyramidale	44	S	TrWet	36	12	0.211	0.237	0.148	0.190	0.226	0.241	0.271	0.226	0.130	0.01348	**0.95**
Ochroma pyramidale	115	S	TrWet	66	22	0.198	0.215	0.143	0.129	0.174	0.241	0.300	0.187	0.086	0.01017	**0.82**
Ochroma pyramidale	146	PN	TrWet	48	21	0.272	0.302	0.156	0.288	0.293	0.296	0.345	0.284	0.182	0.00858	**0.75**
Oxydendrum arboreum	22	H	Temp	23	10	0.542	0.538	0.546	0.552	0.551	0.548	0.526	0.551	0.556	−0.00264	0.24
Populus deltoides	16	H	Temp	25	10	0.423	0.444	0.375	0.429	0.409	0.428	0.468	0.428	0.362	0.01233	**0.54**
Populus tremuloides	sn1	ADK	Temp	22	8	0.386	0.379	0.395	0.384	0.385	0.380	0.376	0.385	0.407	−0.00542	0.28
Rhus copallina	7	H	Temp	18	7	0.434	0.455	0.396	0.445	0.452	0.463	0.461	0.463	0.370	0.01821	0.56
Rollinia microsepala	35	S	TrWet	32	15	0.273	0.291	0.263	0.231	0.233	0.277	0.348	0.269	0.221	0.00694	**0.44**
Salix nigra	17	H	Temp	24	11	0.360	0.358	0.364	0.361	0.369	0.364	0.351	0.368	0.371	−0.00176	0.18
Sassafras albidum	6	H	Temp	22	9	0.485	0.486	0.485	0.515	0.496	0.476	0.473	0.493	0.483	0.00050	0.00
Simarouba glauca	69	PV	TrDry	28	10	0.415	0.420	0.394	0.427	0.425	0.416	0.421	0.425	0.398	0.00336	0.30
Symplocos serrulata	108	OA	Mont	26	9	0.395	0.426	0.338	0.361	0.375	0.445	0.472	0.375	0.302	0.02072	**0.86**
Trema micrantha	36	S	TrWet	22	9	0.275	0.309	0.202	0.241	0.286	0.342	0.337	0.321	0.172	0.02297	**0.87**
Trema micrantha	141	SE	TrWet	26	10	0.447	0.462	0.408	0.449	0.453	0.464	0.476	0.453	0.399	0.00959	**0.52**
Weinmannia pinnata	293	MF	Mont	40	11	0.597	0.602	0.589	0.592	0.597	0.604	0.609	0.597	0.583	0.00264	0.29
Means, 35 trees						0.347	0.365	0.300	0.332	0.349	0.372	0.390	0.360			
SDs, 35 trees						0.162	0.153	0.173	0.186	0.175	0.161	0.127	0.166			

For definition of collection site and forest type, see Table 1. For definitions of SG measurements, see text.
[a] Coefficients of determination significant at the 0.05 level are in boldface.