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Biomass Determination Using Wood Specific Gravity from Increment Cores

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Abstract

Wood specific gravity (SG) is one of the most important variables used to determine biomass. Measurement of SG is problematic because it requires tedious, and often difficult, sampling of wood from standing trees. Sampling is complicated because the SG usually varies nonrandomly within trees, resulting in systematic errors. Off-center pith and hollow or decayed stems pose further problems in biomass estimation. When the pattern of variation within a tree is known, as it often is for a given species, the sampling procedure can be greatly simplified by sampling wood that approximates a mean value for the tree. Even when a pattern is not known, a representative approximation can produce reasonable estimates of SG. If whole above-ground woody biomass is required, corrections may be necessary to account for differences with height or in branches.

Keywords: biomass, increment borer, radial variation, specific gravity, tree cores

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Cover photo, by GBW, is of a large balsa tree (*Ochroma pyramidale*) on the Osa Peninsula, Costa Rica, with increment borer and extracted core.

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Introduction

Traditionally an index of wood properties, wood specific gravity (SG) of standing trees has become a fundamental component of biomass determinations in ecosystem studies and a cornerstone of functional trait analysis in community ecology (Fearnside 1997; Chave et al. 2009; Baraloto et al. 2010; Zanne et al. 2010; Wright et al. 2010). Many ecological studies use a single SG estimate for an individual tree or a given species. An extensive database compiled by Zanne et al. (2009) has gone a long way to fulfill the need for wood SG data. However, the Zanne database, like many others, is a metafile compiled from many contributors whose methodologies for SG determinations are likely to differ (Williamson and Wiemann 2010a) and whose trees may not be representative of the local flora. Furthermore, compiled databases lack SG values for hundreds of species, especially those from the tropics.

Field determinations of SG are the logical alternative to previously published values from other sites. On-site measurements provide true values, eliminating potential biases from geographic variation and nonrandom samples in databases. However, determining SG in the field is time consuming and difficult because wood samples must be obtained by felling trees or extracting cores. Historically, felling trees was widely employed by foresters, but in the mid-1800s Max Pressler invented the increment borer (Pressler 1866). Today, extracting cores is generally preferable to felling trees as conservation and ongoing research demand a nondestructive sampling methodology.

The best estimates of tree SG are derived from cores that extend from bark to pith because they reveal the full extent of radial variation. Sampling a tree's outer few centimeters of wood with an increment borer or an increment hammer is relatively simple. However, such a small sample is useful only if it is representative of wood across the tree bole. For some species this may be the case, but for many others SG varies dramatically across the radius (Whitmore 1973; Wiemann and Williamson 1988, 1989a, 2012; Williamson et al. 2012). Radial variation in SG is sufficiently extensive that it merits consideration in the prediction of physical or mechanical properties as well as in the estimation of biomass. Following is a summary of reported trends in radial variation in wood SG:

I. SG increases from pith to bark.

   A. Panshin and de Zeeuw (1980) for 26 gymnosperms, 12 diffuse-porous temperate angiosperms, three ring-porous temperate angiosperms, and 15 tropical angiosperms.

   B. Extreme linear increases in many tropical pioneers (Fimbel and Sjaastad 1994; Wiemann and Williamson 1988, 1989a, 2012).

   C. Extreme nonlinear (convex up) increases in the tropical pioneer *Schizolobium parahyba* (Vell.) S.F. Blake (Williamson et al. 2012).

II. SG decreases from pith, then increases to bark.

   A. Panshin and de Zeeuw (1980) for14 gymnosperms and one diffuse-porous temperate angiosperm.

   B. Schüller et al. (2013) reported only two such species (both late successional) in their study of 338 Mexican rainforest trees representing 45 species.

III. SG decreases from pith to bark.

   Panshin and de Zeeuw (1980) for seven gymnosperms, nine diffuse-porous temperate angiosperms, five ring-porous temperate angiosperms, and one tropical angiosperm.

IV. SG increases from pith, then decreases to bark.

   Tropical angiosperm *Astronium graveolens* Jacq. (Wiemann and Williamson 2012). This pattern may result from the combined effects of juvenile wood and the bulking of heartwood by extraneous materials.

V. SG is constant from pith to bark.

   Temperate angiosperms *Magnolia grandiflora* L. (Wiemann and Williamson 2012) and *Alnus rubra* Bong. (Harrington and DeBell 1980; Gartner et al. 1997) and seven tropical angiosperms (Wiemann and Williamson 1989b, 2012).

VI. SG is erratic.

   In tropical *Apeiba aspera* Aubl. due to irregularly spaced wide parenchyma bands (Wiemann and Williamson 2012).

The prevalence of within-tree variability requires that estimation of SG be more carefully considered. Ideally, each species could be characterized, not simply by an SG value, but by a function between SG and radial distance. However, radial increases in SG appear to be determined by age, not tree diameter (de Castro et al. 1993; Nock et al. 2009; Williamson and Wiemann 2010b, 2011; Williamson et al. 2012). Consequently, determining radial variation may require boring many individuals from bark to pith.

Unfortunately, boring trees from bark to pith is often difficult and replete with problems, as previously encountered by dendrochronologists and foresters (Grissino-Mayer 2003; Jozsa 1988; Maeglin 1979; Phipps 1985):

1. Trees are too large for the borer to reach the pith (Figs. 1, 2).
2. Trees have hollow or rotten centers (Fig. 3).
3. Borers miss the pith, passing to the side of it.
4. Borers are difficult to insert in trees with dense wood.
5. Borers are difficult to extract, for multiple reasons.

Given the problems of bark-to-pith boring, we developed an alternative technique for estimating tree SG even when radial variation is substantial (Williamson and Wiemann 2010a). The method has been tested and found to perform well for the majority of trees studied (Wiemann and Williamson 2012).

Approximation Method

Our method presumes that a sample of wood can be extracted at a point in the tree cross section that is representative of all the wood in that cross section. For the majority of trees that we tested (Wiemann and Williamson 2012), this sample is located at 2/3 the distance from the pith to the bark, so that its extraction requires that a tree be bored only to 1/3 of its radius inside of the bark. This method has the additional advantage that it avoids the problems enumerated above because only a short outer section of the tree is bored. For example, in very large trees, such as the canopy emergent *Ceiba pentandra* (L.) Gaertn., shown in Figure 1, boring to the pith is problematic, but boring to 1/3 the radius is relatively easy. Because the location of the pith is usually unknown, especially in a large tree, we tested the accuracy of cores taken from 1/6 the diameter inside of the bark (1/6 DIB); in a symmetrical tree, this point coincides with 1/3 of the radius inside the bark (Fig. 2). Errors may be introduced to the extent that a tree cross section is not symmetrical or its pattern of SG with distance from the pith is not linear.

The method we recommend to determine the mean SG of a tree, at the height at which it is bored, is as follows:

1. Determine if the species has a straight line trend in SG from pith to bark. This can be increasing, decreasing, or flat, and can be ascertained by reference to species descriptions or by complete bark to pith sampling of a few individuals.

Figure 1. Extraction of a core using a large-diameter (12-mm) extra long increment borer. The auger measures 81 cm from handle to the tip, and the diameter of this *Ceiba pentandra* from Costa Rica, measured above the buttresses with a diameter tape, was 146 cm. The auger was inserted until the handle was stopped by the buttresses, producing a core that we estimated was about 2 cm short of reaching the pith.

2. Measure the diameter outside the bark (DOB) in the boring direction with tree calipers.
3. Measure the bark thickness using a bark gauge or an increment borer.
4. Calculate the diameter inside the bark (DIB) by subtracting twice the bark thickness from the DOB.
5. Determine the point on the radius at which measured SG is equal to mean SG for the whole diameter.
6. For symmetrical trees in which the SG is a straight-line function of distance from pith, this value is 1/6 DIB. This is the depth to which the tree must be bored to determine its mean SG at that height.
7. For trees in which SG is not a straight-line function of distance from pith, the value must be determined, either from prior knowledge of the radial trend or by completely boring a number of representative individuals to determine the trend.
8. Bore the tree about 2 cm beyond the calculated depth to extract a segment whose SG is representative of the SG of the cross section as a whole. The depth to which the increment borer should be inserted into the tree will depend on the distance to 1/6 DIB and the length of the representative sample to be extracted. Shorter samples will more accurately represent the distance from the bark, but longer samples will give smaller weight and volume measurement errors. We recommend a segment length of 3 cm centered over the point of 1/6 DIB. The depth to which the borer should be inserted can be marked on the increment borer shaft with a marking crayon or with a small piece of tape or modeling clay.

Figure 2. *Bombacopsis quinata* (Jacq.) Dugand log from Panama showing diameter (180 cm), distance from bark to pith (105 cm), 1/3 of the "radius" (35 cm) and 1/6 of the DIB (30 cm). Because the growth of this tree was slightly eccentric, the distance from bark to pith in the direction indicated is somewhat greater than half the diameter, and 1/3 of this "radius" does not equal 1/6 of the DIB. Although the oversized (81-cm) increment borer of Figure 1 would not be able reach the pith of this stem, even a standard (45-cm) auger could be used to bore to 1/6 of the DIB. The smaller log to the right is a 140-cm-diameter *Anacardium excelsum* (Bertero and Balb. ex Kunth) Skeels; it also has a slightly off-center pith.

9. Remove the wood core and the borer immediately; borers left in the tree are much more difficult to remove due to "springback" of the compressed wood surrounding the shaft. Measure and mark the distance along the core from the bark to the indicated midpoint of the representative sample; in the case of trees that have a linear pith to bark SG trend and no eccentricity, the midpoint will be 1/6 DIB.
10. Cut the 3-cm segment from the core so that 1/6 DIB is centered in the segment, leaving 1.5 cm on each side of the mark.
11. Label the segment with a pencil or indelible ink, and store it so that it will not lose moisture below its fiber saturation point. Storage in sealed tubes, in water, or in cellophane film will prevent shrinkage due to drying, such that green volume can be measured at a later time by water immersion.
12. In the lab, green volume can be determined by water immersion on a precision balance. If the sample is a perfect cylinder, volume can be calculated from the diameter and length of the segment. Low-density woods can be cut cleanly using a razor blade, but harder species slice irregularly, yielding less accurate volume estimates by calculations. Cores can also be air dried if an air-dry volume is required. Finally, they must be ovendried at 101–105 °C to determine ovendry weight for SG calculation.
13. If there is reason to believe that the pith is not in the center of a tree, it might be advisable to take a second core on the opposite side. Indicators of off-center pith are leaning stems or stems growing on slopes, although this is by no means foolproof. For angiosperms, the shorter pith-to-bark radius will usually be on the underside of leaning stems; the reverse is true for gymnosperms. Cores taken parallel to hill slope, or perpendicular to the direction of tree lean, are more likely to have equal length radii and representative wood; the problem then becomes where to aim the increment borer in order to aim directly at the pith. Also, special care must be taken to preserve the integrity of these cores because they sometimes fragment more easily than usual. If the tree has branches fairly close to the point of insertion of the increment borer, aiming the borer in the same direction as a branch will also aim it at the pith.

If the assumption of a linear trend from pith to bark is violated, the method may still give adequate estimates for some purposes. Sajdak (1968) presented SG versus distance from pith data for *Acer saccharum* Marsh. His species average values for 61 trees from Michigan showed a parabolic relationship, with the highest value, 0.60, adjacent to both the pith and the bark (at 23 cm from pith), and the lowest value, 0.58, at 10–15 cm from the pith. Even though the trend for these trees was not linear, the maximum difference between the highest and lowest average SG values was only 3% because the radial variation was low, so any core segment would give an adequate value. Sajdak also presented data for four individual trees, and the most extreme of them showed only a 7% difference between the highest and lowest SG values. Our study of bark-to-bark samples from 35 trees (23 species) included seven species that did not have linear pith-to-bark trends; of these, the SG of a segment taken at 1/6 DIB was within 10% of the weighted SG in all seven (Wiemann and Williamson 2012).

The more serious problem of possible off-center pith in a pioneer that shows a steep radial trend in SG can be handled by taking two cores extracted from opposite sides of the tree. For example, 1/6 DIB segments from an eccentric stem of *Heliocarpus appendiculatus* Turcz. from Costa Rica gave a 36% SG underestimate on the short (11-cm) radius and a 14% SG overestimate on the long (18-cm) radius (M.C. Wiemann and G.B. Williamson, unpublished data). Averaging the SG values reduced the error to 11%. Boring both sides to 1/6 DIB still entails less work than boring to the pith, which can be difficult in such an eccentric tree.

Variation with Height

These procedures give SG estimates that are valid only at the sampling height. If estimates are required at heights that cannot be sampled easily (such as near ground level or high on the bole), knowledge of the SG trends with height are required. For whole-stem woody biomass estimates, the relationships of stem diameter and SG with height must be known. Figure 3 shows the changes in shape and diameter, from ground level to the point of stem bifurcation, in a

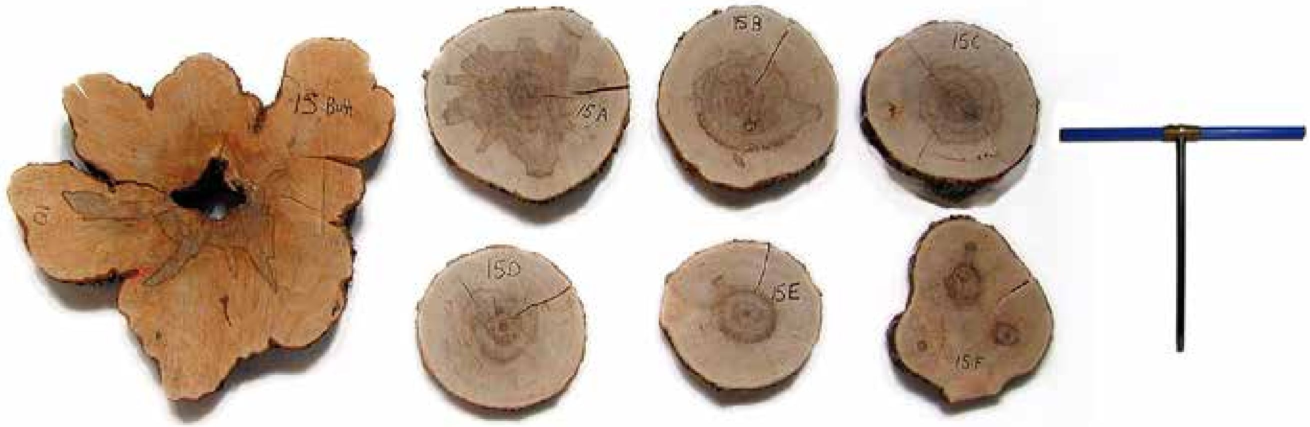

Figure 3. Cross sections from a 46-cm-DBH *Acer saccharum* from Wisconsin, showing change in shape, size, and stem integrity with height. Heights above ground are 15 Butt, <10cm; 15A, 3 m; 15B, 7 m; 15C, 10 m; 15D, 13 m; 15E, 16 m; 15F, 20 m. DIBs are Butt, 56 cm; A, 40 cm; B, 38 cm; C, 35 cm; D, 32 cm; E, 31 cm; F, 30 cm. The 12-mm-diameter increment borer has a 45-cm shaft. Although it is long enough to bore to the center of the tree, the hollow stem might make its extraction difficult. Boring to 1/6 DIB would be a solution to this sampling problem.

46-cm DBH *Acer saccharum* from Wisconsin. Note the hollow, fluted butt disk, the off-center pith in disk 15B, and the triple pith in disk 15F. Diameter with height can be inferred if the pattern of stem taper is known, or stem diameters at any height can be measured from the ground using a dendrometer (Wenger 1984). In either case, SG variation with height must be measured or estimated.

Although SG also varies from the base to the top of a tree, Zobel and van Buijtenen (1989) asserted that whole tree SG could be reliably estimated from breast-height SG for both gymnosperms and angiosperms. However, their notes on SG variation with height in some 40 species are heavily biased toward temperate trees, so studies on individual species might be necessary to make whole tree estimates for tropical species.

In temperate gymnosperms, SG as a function of height within a tree exhibits many species-specific patterns, such as decreasing linearly or curvilinearly, increasing, decreasing followed by an increase, or remaining relatively constant (Panshin and de Zeeuw 1980; Wahlgren and Fassnacht 1959; Wahlgren et al. 1966). Okkonen et al. (1972) related these trends to percentage of latewood. Some authors developed models to calculate SG from relative height, for example, Pong et al. (1986) for *Pseudotsuga menziesii* (Mirb.) Franco and *Tsuga heterophylla* (Raf.) Sarg., Antony et al. (2010) for *Pinus taeda* L., and Markstrom and Yerkes (1972) for *Pinus ponderosa* Laws.

Angiosperms show no consistent pattern. The most common trend in temperate angiosperms is an increase in SG with height, but other patterns have been reported (Taylor 1968, 1969a,b, 1971, 1979; Taylor and Wooten 1973; Wooten 1968; Wooten and Taylor 1968). Manwiller (1979) found that for small stems (<17 cm DBH) of 22 species of the southeastern United States, SG tended to remain constant or to decrease with height, but with substantial variation depending on species. Data on trends of SG with height are very limited for subtropical and tropical species. Taylor (1973) reported an increase in SG with height in *Eucalyptus grandis* Hill ex Maiden planted in South Africa, and Skolmen (1972) found the same trend in *Eucalyptus robusta* Sm. planted in Hawaii. Whitmore (1973) and Rueda and Williamson (1992) found a decrease in SG with height in Costa Rican *Ochroma pyramidale* (Cav. ex Lam.) Urb., Velásquez et al. (2009) found a decrease with height in Venezuelan *Erisma uncinatum* Warm., and M.C. Wiemann and G.B. Williamson (unpublished data for one tree of each species) found lower SG with height in the pioneer species *Ochroma pyramidale* and *Trema micrantha* (L.) Blume, higher SG with height in the pioneer species *Cecropia peltata* L. and *Cecropia obtusifolia* Bertol., and higher SG with height in the nonpioneer species *Rollinia microsepala* Standl. Bhat et al. (1990) found that the SG of stems and branches increased with height in five species, decreased in two, and was irregular in four others. More data are clearly needed to define prevalent patterns.

Branchwood versus Trunkwood

Fegel (1941) reported that branchwood SGs of four ring-porous angiosperms, eight diffuse-porous angiosperms, and eight gymnosperms of New York State were 10%, 6%, and 34% higher, respectively, than trunk wood SGs. Sarmiento (2011), averaging SG values from 1909 individual trees representing 565 French Guiana species, found that outermost trunk wood SG (0.201–0.960) was 9% greater than the branchwood SG (0.237–0.949) among all trees, with the greatest differences in species with high SG values. Because inner wood typically has lower SG than outer wood, this difference might diminish or disappear if the whole trunk cross section were considered. Swenson and Enquist (2008) compared stem and branchwood from 33 trees and 14 shrubs representing 27 species from Puerto Rico. Their samples included the outer wood from the tree stems, complete wood cross sections from 1- to 2-cm-diameter tree branches, complete wood cross sections from 1- to 2-cm-diameter shrub stems, and complete wood cross sections from 0.4- to 0.6-cm-diameter shrub branches. They found that stemwood had higher SG than branchwood in the same plant. By contrast, Okai et al. (2003) found that branchwood SG was 12% and 6% greater than stemwood SG in two Ghanaian species, but their sampling included inner, middle, and outer wood from large trees (2.5 m DBH) and large branches (≥10 cm) and included both sapwood and heartwood. Of 11 species grown in India, Bhat et al. (1990) found branchwood had the same SG as stemwood in all but two species.

Concluding Remarks

Estimating woody biomass in standing trees depends on the accurate measurement of SG. As SG is known to vary across the tree diameter, estimating whole tree biomass requires determination of tree mean SG. Where complete tree harvest is impractical or impossible, a method to estimate whole tree SG is proposed here. When the pattern of radial variation is known, a point along the radius has wood that is representative of the whole cross section. For trees with linear or no changes in SG across the radius, that point is 1/6 of the tree diameter inside the bark. With few exceptions, sampling to a depth of 1/6 of the DIB gives a good estimate of the SG of a cross section. Depending on how much of the tree is under consideration, corrections may be required for variation of SG with height and in branchwood.

Literature Cited

Antony, F.; Schimleck, L.R.; Daniels, R.F.; Clark III, A.; Hall, D.B. 2010. Modeling the longitudinal variation in wood specific gravity of planted loblolly pine (*Pinus taeda*) in the United States. Canadian Journal of Forest Research. 40: 2439–2451.

Baraloto, C.; Paine, C.E.T.; Patiño, S.; Bonal, D.; Hérault, B.; Chave, J. 2010. Functional trait variation and sampling strategies in species-rich plant communities. Functional Ecology. 24: 208–216.

Bhat, K.M.; Bhat, K.V.; Dhamodaran, T.K. 1990. Wood specific gravity in stem and branches of eleven timbers from Kerala. Indian Forester. 116: 541–546.

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

de Castro, F. D.; Williamson, G.B.; Moraes de Jesus, R. 1993. Radial variation in the wood specific gravity of *Joannesia princeps*: the role of age and diameter. Biotropica. 25: 176–182.

Fearnside, P.M. 1997. Wood density for estimating forest biomass in Brazilian Amazonia. Forest Ecology and Management. 90: 59–87.

Fegel, A.C. 1941. Comparative anatomy and varying physical properties of trunk, branch, and root wood in certain Northeastern trees. Bulletin of the New York State College of Forestry, Technical Publication No. 55. 20 p.

Fimbel, R.A.; Sjaastad, E.O. 1994. Wood specific gravity variability in *Ceiba pentandra*. Wood and Fiber Science. 26: 91–96.

Gartner, B.L.; Lei, H.; Milota, M.R. 1997. Variation in the anatomy and specific gravity of wood within and between trees of red alder (*Alnus rubra* Bong.). Wood and Fiber Science. 29: 10–20.

Grissino-Mayer, H.D. 2003. A manual and tutorial for the proper use of an increment borer. Tree-Ring Research. 59: 63–79.

Harrington, C.A.; DeBell, D.S. 1980. Variation in specific gravity of red alder (*Alnus rubra* Bong.). Canadian Journal of Forest Research. 10: 293–299.

Jozsa, L. 1988. Increment core sampling techniques for high quality cores. Special publication No. SP-30, Forintek Canada Corporation. 26 p.

Maeglin, R.R. 1979. Increment cores: How to collect, handle, and use them. General Technical Report FPL–GTR–25. Madison, WI: U.S. Department of Agriculture, Forest Service, Forest Products Laboratory. 18 p.

Manwiller, F.G. 1979. Wood and bark specific gravity of small diameter pine site hardwoods in the South. Wood Science. 11: 234–240.

Markstrom, D.C.; Yerkes, V.P. 1972. Specific gravity variation with height in Black Hills ponderosa pine. Research Note RM 213. 4 p.

Nock, C.A.; Geihofer, D.; Grabner, M.; Baker, P.J.; Bunyavejchewin, S.; Hietz, P. 2009. Wood density and its radial variation in six canopy tree species differing in shade-tolerance in western Thailand. Annals of Botany. 104: 297–306.

Okai, R.; Frimpong Mensah, K.; Yeboah, D. 2003. Characterization of moisture content and specific gravity of branchwood and stemwood of *Aningeria robusta* and *Terminalia ivorensis*. Holz als Roh- und Werkstoff. 61: 155–158.

Okkonen, E.A.; Wahlgren, H.E.; Maeglin, R.R. 1972. Relationships of specific gravity to tree height in commercially important species. Forest Products Journal. 22: 37–42.

Panshin, A.J.; de Zeeuw, C. 1980. Textbook of wood technology, 4th edition. New York: McGraw Hill Book Co. 722 p.

Phipps, R.L. 1985. Collecting, preparing, crossdating, and measuring tree increment cores. U.S. Geological Survey Water-Resources Investigations Report 85-4148. 48 p.

Pong, W.Y.; Waddell, D.R.; Lambert, M.B. 1986. Wood density-moisture profiles in old-growth douglas-fir and western hemlock. Res. Pap. PNW 347, Portland, OR. 30 p.

Pressler, M.R. 1866. Der forstliche Zuwachsbohrer neuester Construction und dessen praktische Bedeutung und Anwendung für die forstliche Forschungs-, Taxations-, Pflege- und Nutzungs-Technik. Tharander Jahrbuch. 17, III: 137–209.

Rueda, R.; Williamson, G.B. 1992. Radial and vertical wood specific gravity in *Ochroma pyramidale* (Cav. ex Lam.) Urb. (Bombacaceae). Biotropica. 24: 512–518.

Sajdak, R.L. 1968. Variation in bark characters and wood specific gravity of sugar maple. Pages 10–14 *in*: U.S. Forest Service Research Paper NC-23, Proceedings of the eighth Lake States Forest Tree Improvement Conference, September 12–13, 1967.

Sarmiento, C.; Patiño, S.; Paine, C.E.T.; Beauchêne, J.; Thibaut, A.; Baraloto, C. 2011. Within individual variation of trunk and branch xylem density in tropical trees. American Journal of Botany. 98: 140–149.

Schüller E.; Martínez Ramos, M.; Hietz, P. 2013. Radial gradients in wood specific gravity, water and gas content in trees of a Mexican tropical rain forest. Biotropica (on-line version, with supporting information at http://onlinelibrary.wiley.com/doi/10.1111/btp.12016/full).

Skolmen, R.G. 1972. Specific gravity variation in robusta eucalyptus grown in Hawaii. USDA Forest Service Research Paper PSW 78. 7 p.

Swenson, N.G.; Enquist, B.J. 2008. The relationship between stem and branch wood specific gravity and the ability of each measure to predict leaf area. American Journal of Botany. 95: 516–519.

Taylor, F.W. 1968. Specific gravity differences within and among yellow poplar trees. Forest Products Journal. 18: 75–81.

Taylor, F.W. 1969a. Variation of wood properties in sycamore. Research Report No. 7. Forest Products Utilization Laboratory, Mississippi State University, State College. 18 p.

Taylor, F.W. 1969b. Variation of wood properties in pecan. Research Report No. 8. Forest Products Utilization Laboratory, Mississippi State University, State College. 17 p.

Taylor, F.W. 1971. Variation of wood properties in sugarberry. Research Report No. 11. Forest Products Utilization Laboratory, Mississippi State University, State College. 17 p.

Taylor, F.W. 1973. Variations in the anatomical properties of South African grown *Eucalyptus grandis*. Appita. 27: 171–178.

Taylor, F.W. 1979. Property variation within stems of selected hardwoods growing in the Mid-South. Wood Science. 11: 193–199.

Taylor, F.W.; Wooten, T.E. 1973. Wood property variation of Mississippi Delta hardwoods. Wood and Fiber. 5: 2–13.

Velásquez, J.; Toro, M.E.; Gómez, L.; Terzo, F.M.; Márquez, A. 2009. Patrón de variación axial y radial del peso específico en la madera de *Erisma uncinatum* Warm. Interciencia. 34: 873–879.

Wahlgren, H.E.; Fassnacht, D.L. 1959. Estimating tree specific gravity from a single increment core. Rept. No. 2146, Forest Products Laboratory, Madison, WI.

Wahlgren, H.E.; Hart, A.C.; Maeglin, R.R. 1966. Estimating tree specific gravity of Maine conifers. Research Paper FPL–RP–61. Madison WI: U.S. Department of Agriculture, Forest Service, Forest Products Laboratory. 22 p.

Wenger, K.F. 1984. Forestry Handbook, 2nd edition. New York: John Wiley and Sons, Inc. 1,335 p.

Whitmore, J.L. 1973. Wood density variation in Costa Rican balsa. Wood Science. 5: 223–229.

Wiemann, M.C.; Williamson, G.B. 1988. Extreme radial changes in wood specific gravity in some tropical pioneers. Wood and Fiber Science. 20: 344–349.

Wiemann, M.C.; Williamson, G.B. 1989a. Radial gradients in the specific gravity of wood in some tropical and temperate trees. Forest Science. 35: 197–210.

Wiemann, M.C.; Williamson, G.B. 1989b. Wood specific gravity gradients in tropical dry and montane rain forest trees. American Journal of Botany. 76: 924–928.

Wiemann, M.C.; Williamson, G.B. 2012. Testing a novel method to approximate wood specific gravity of trees. Forest Science. 58: 577–591.

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

Williamson, G.B.; Wiemann, M.C. 2010b. Age dependent radial increases in wood specific gravity of tropical pioneers in Costa Rica. Biotropica. 42: 590–597.

Williamson, G.B.; Wiemann, M.C. 2011. Age versus size determination of radial variation in wood specific gravity: lessons from eccentrics. Trees. 25: 585–591.

Williamson, G.B.; Wiemann, M.C.; Geaghan, J.P. 2012. Radial wood allocation in *Schizolobium parahyba*. American Journal of Botany. 99: 1010–1019.

Wooten, T.E. 1968. Variation of wood properties in willow oak. Research Report No. 5. Forest Products Utilization Laboratory, Mississippi State University, State College. 12 p.

Wooten, T.E.; Taylor, F.W. 1968. The anatomical and chemical properties of black willow. Research Report No. 3. Forest Products Utilization Laboratory, Mississippi State University, State College. 24 p.

Wright, S.J.; Kitajima, K.; Kraft, N.J.B.; Reich, P.B.; Wright, I.J.; Bunker, D.E.; Condit, R.; Dalling, J.W.; Davies, S.J.; Díaz, S.; Engelbrecht, B.M.J.; Harms, K.E.; Hubbell, S.P.; Marks, C.O.; Ruiz Jaen, M.C.; Salvador, C.M.; Zanne, A.E. 2010. Functional traits and the growth mortality tradeoff in tropical trees. Ecology. 91: 3664–3674.

Zanne, A.E.; López-González, G.; Coomes, D.A.; Ilic, J.; Jansen, S.; Lewis, S.L.; Miller, R.B.; Swenson, N.G.; Wiemann, M.C.; Chave, J. 2009. Data from: Towards a worldwide wood economics spectrum. Dryad Digital Repository. doi:10.5061/dryad.234. http://datadryad.org/handle/10255/dryad.234?show=full

Zanne, A.E.; Westoby, M.; Falster, D.S.; Ackerly, D.D.; Loarie, S.R.; Arnold, S.E.J.; Coomes, D.A. 2010. Angiosperm wood structure: Global patterns in vessel anatomy and their relation to wood density and potential conductivity. American Journal of Botany. 97: 207–215.

Zobel, B.J.; van Buijtenen, J.P. 1989. Wood Variation: Its Causes and Control. Springer Verlag, Berlin. 363 p.