Trees (2011) 25:585–591
DOI 10.1007/s00468-010-0535-5

ORIGINAL PAPER

# Age versus size determination of radial variation in wood specific gravity: lessons from eccentrics

**G. Bruce Williamson · Michael C. Wiemann**

Received: 8 October 2010 / Revised: 10 December 2010 / Accepted: 15 December 2010 / Published online: 5 January 2011


**Abstract** Radial increases in wood specific gravity have been shown to characterize early successional trees from tropical forests. Here, we develop and apply a novel method to test whether radial increases are determined by tree age or tree size. The method compares the slopes of specific gravity changes across a short radius and a long radius of trees with eccentric trunks. If radial changes are determined by size, then the slope of the change should be the same on both radii. If radial changes are determined by age, then the slope should be greater on the short radius. For 30 trees from 12 species with eccentricity of at least 4%, the ratio of the slopes of the linear regressions of specific gravity on radial distance (short radius slope/long radius slope) was regressed on the ratio of radii lengths (long radius/short radius). The regression was highly significant, and the faster increase in specific gravity on the short radius was sufficient to compensate for the difference in radius lengths, so the specific gravity of wood along the short radius was equal to the specific gravity on the long radius at any given proportional distance on the radius. Therefore, trees that are producing xylem faster on one radius than another produce wood of comparable specific gravity on both radii at the same time, so radial increases in specific gravity are dependent on tree age, not tree size.

Communicated by R. Aloni.

G. B. Williamson (✉)
Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803, USA
e-mail: btwill@lsu.edu

M. C. Wiemann
Center for Wood Anatomy Research, USDA Forest Service, Forest Products Laboratory, One Gifford Pinchot Drive, Madison, WI 53726-2398, USA

**Keywords** Costa Rica · Tree eccentricity · Radial gradients · Tree age and size · Wood specific gravity

## Introduction

As wood specific gravity (SG) measures the allocation of dry biomass per unit volume of green wood, it is the single best predictor of wood functional properties, especially those related to structural support. SG has been linked to nearly all mechanical properties (impact strength, modulus of rupture, modulus of elasticity), physiological traits (shade tolerance, light compensation point, fluid conductivity), demographic characteristics (growth rate, survival rate), and reproductive variables (age of first reproduction, fecundity, seed and fruit size) (Malhi et al. 2006; Wright et al. 2006; Poorter et al. 2008; Baker et al. 2009; Chave et al. 2009). In addition, SG is the primary weighting variable in the estimation of biomass to assess global carbon stocks (Brown and Lugo 1992; Fearnside 1997; Baker et al. 2004; Chave et al. 2005; Nogueira et al. 2005; Keeling and Phillips 2007; Nogueira et al. 2007, 2008a, b; Baker et al. 2009).

SG is relatively constant across the radius for many angiosperms, but tropical wet forest trees sometimes exhibit large linear increases across the radius, resulting in cylinders of increasingly stronger wood as trees grow. Among tropical pioneers, radial increases in SG may reach 200–300% although only about 100 species have been investigated in detail (Whitmore 1973; Wiemann and Williamson 1988, 1989a; Rueda and Williamson 1992; Butterfield et al. 1993; Castro et al. 1993; Nock et al. 2009; Williamson and Wiemann 2010a, b). Radial changes within a trunk can drastically affect the determination of biomass in assessing carbon stocks although current

methodology employs a single wood density value per species, because very little is known about radial variation. Thus, unveiling the patterns of variation within tree boles should greatly improve estimates of global carbon (Keeling and Phillips 2007; Nogueira et al. 2005; 2008b).

The pattern of wood SG across the radius of a tree offers a record of the changes in the allocation of biomass during growth and development. This record can indicate whether radial increases in SG are determined by age or by size of a tree. Teasing apart these two alternatives requires radial measurements of SG on trees of known size and age. However, aging tropical trees is often impossible. One alternative is to measure SG of trees of different diameters that represent a cohort, even if the age is unknown. This is sometimes the case in experimental forestry plantations (Castro et al. 1993) and in natural, regenerating stands (Williamson and Wiemann 2010b). Studies of these cohorts, based on a handful of species (Castro et al. 1993; Williamson and Wiemann 2010b), together with one species where aging was possible (Nock et al. 2009), offer a preliminary conclusion to the age versus size question: even-aged trees increase SG radially mainly as a function of age, irrespective of size. However, these studies include only a few species and the SG–age relationships exhibit considerable unexplained variation. Sources of residual variation in even-aged stands could include the genetics of individual trees and their micro-environments during growth.

Here, we offer a novel method to test the age versus size dichotomy for radial variation in SG—namely, different sides of the same tree. Trees exhibit eccentricity to varying degrees. Wood at the ends of two radii along an axis are usually the same age, share the same genetic identity and experience similar micro-environments, although aspect, tension/compression stresses and illumination may differ. If SG is size-dependent, then the slope of the SG-radial distance regression on the long radius (Fig. 1, line A) would be the same as the slope on the short radius (Fig. 1, line B). If SG is age-dependent, then the slope on the long radius would be less than the slope on the short radius (Fig. 1, line C). Our working hypothesis, based on those prior studies mentioned above, is that age-dependent radial increases should result in slopes that are steeper on the short radius than on the long radius.

## Materials and methods

In our wood core datasets from prior studies comparing radial shifts among trees in Costa Rica and Mississippi (Wiemann and Williamson 1988, 1989a, b; Williamson and Wiemann 2010b), we found 55 trees that had been bored completely through, each yielding two cores, pith-to-bark, from the opposite sides of a tree. Surprisingly, 54 trees were eccentric by at least 1 cm. Each radius of a tree was then stringently tested for radial increases in SG through least-squares linear regression of SG on radial distance from the pith. Only trees that had both radii yielding significant linear increases in SG ($P < 0.01$) were included in the analysis dataset. These 30 trees from 12 species, most of them from lowland, tropical wet forests, showed highly significant increases in SG across their long and short radii (Table 1). They had diameters (inside the bark) of 14–60 cm and exhibited eccentricity of at least 4%. Sample size for each regression was the same as the length of core, as cores were cut into 1-cm pieces (Table 1).

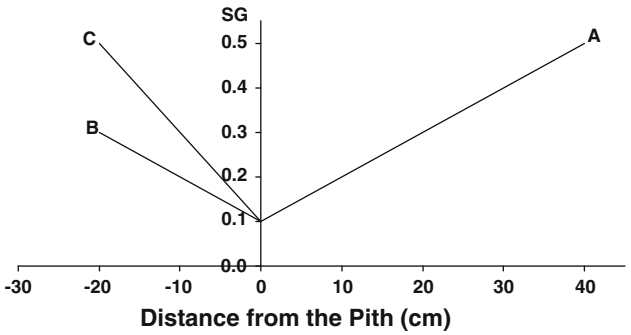


**Fig. 1** SG as a function of distance from the pith along the long radius *A* and along the short radius, either *B* (size-dependent) or *C* (age-dependent)

For each tree we created two variables relating the two radii on opposite sides of the pith: "ratio of radii" = the length of the long side divided by the length of the short side, and "ratio of slopes" = the slope of the SG-radial distance regression along the short radius divided by the slope of the regression along the long radius (Table 1). If SG is age-dependent, then the ratio of slopes should be the same as the ratio of radii (Fig. 1). Assuming that the radii are the independent variables, we then regressed the ratio of slopes on the ratio of radii. If radial increases in SG are controlled by age, the short radius slope would be greater than the long radius slope. If radial increases in SG are size-dependent, the short and long radius slopes would be the same and their ratio would be 1.0. As the degree of eccentricity decreases, the ratio of lengths will be closer to 1.0 and the ratio of slopes would be expected to be closer to 1.0 also, regardless of age-dependence or size-dependence.

Even if the slope along the short radius were larger than the long radius, a critical question is, whether the increased slope would compensate for the shorter radius. In other words, would the SG increase on the short radius keep pace with the SG increase on the long radius? The ages at given points along a radius were unknown, so we assumed that proportional distances along the radii were the same age;

**Table 1** Each line represents one tree bored bark-to-bark, yielding two cores, a short core and a long core, and cores were cut into 1-cm pieces whose SG values were regressed on their radial distances from the pith

| Species | Forest Type | Dbh (cm) | Regressions, short core | | | | | Regressions, long core | | | | | Slopes Short/long | Radii Long/short |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Length (cm) | Intercept | Slope | $P$ | $R^2$ | Length (cm) | Intercept | Slope | $P$ | $R^2$ | | |
| *Bursera simaruba* (L.) Sarg. | Trop. Dry | 41 | 13 | 0.22 | 0.0175 | 0.0001 | 0.98 | 22 | 0.27 | 0.0092 | 0.0001 | 0.93 | 1.91 | 1.69 |
| *Bursera simaruba* | Trop. Dry | 26 | 9 | 0.18 | 0.0192 | 0.002 | 0.76 | 12 | 0.16 | 0.0203 | 0.0001 | 0.96 | 0.95 | 1.33 |
| *Cecropia insignis* Liebm. | Trop. Wet | 58 | 25 | 0.26 | 0.0050 | 0.0001 | 0.73 | 28 | 0.26 | 0.0033 | 0.0002 | 0.42 | 1.49 | 1.12 |
| *Cecropia obtusifolia* Bertol. | Trop. Wet | 47 | 13 | 0.11 | 0.0261 | 0.0001 | 0.94 | 22 | 0.13 | 0.0121 | 0.0001 | 0.89 | 2.16 | 1.69 |
| *Cecropia peltata* L. | Trop. Dry | 29 | 8 | 0.21 | 0.0243 | 0.001 | 0.85 | 19 | 0.20 | 0.0083 | 0.0004 | 0.53 | 2.94 | 2.38 |
| *Cecropia peltata* | Trop. Dry | 28 | 10 | 0.18 | 0.0222 | 0.0006 | 0.79 | 12 | 0.21 | 0.0149 | 0.0001 | 0.84 | 1.49 | 1.20 |
| *Hampea appendiculata* (Donn. Sm.) Standl. | Trop. Wet | 37 | 16 | 0.12 | 0.0152 | 0.0001 | 0.99 | 17 | 0.09 | 0.0090 | 0.0001 | 0.78 | 1.69 | 1.06 |
| *Hampea appendiculata* | Trop. Wet | 44 | 18 | 0.16 | 0.0066 | 0.0001 | 0.61 | 21 | 0.12 | 0.0078 | 0.0001 | 0.68 | 0.85 | 1.17 |
| *Hampea appendiculata* | Trop. Wet | 35 | 14 | 0.15 | 0.0127 | 0.0001 | 0.94 | 17 | 0.10 | 0.0114 | 0.0001 | 0.81 | 1.11 | 1.21 |
| *Hampea appendiculata* | Trop. Wet | 35 | 15 | 0.18 | 0.0067 | 0.0002 | 0.68 | 17 | 0.12 | 0.0091 | 0.0001 | 0.71 | 0.74 | 1.13 |
| *Hampea appendiculata* | Trop. Wet | 44 | 21 | 0.15 | 0.0097 | 0.0001 | 0.82 | 22 | 0.13 | 0.0078 | 0.0001 | 0.71 | 1.25 | 1.05 |
| *Hampea appendiculata* | Trop. Wet | 38 | 16 | 0.13 | 0.0200 | 0.0001 | 0.94 | 19 | 0.13 | 0.0134 | 0.0001 | 0.86 | 1.49 | 1.19 |
| *Hampea appendiculata* | Trop. Wet | 48 | 20 | 0.10 | 0.0103 | 0.0001 | 0.84 | 23 | 0.16 | 0.0092 | 0.0001 | 0.95 | 1.12 | 1.15 |
| *Hampea appendiculata* | Montane | 50 | 21 | 0.18 | 0.0113 | 0.0001 | 0.72 | 26 | 0.15 | 0.0071 | 0.0001 | 0.74 | 1.59 | 1.24 |
| *Heliocarpus appendiculatus* Turcz. | Trop. Wet | 36 | 17 | 0.05 | 0.0108 | 0.0001 | 0.82 | 18 | 0.04 | 0.0101 | 0.0001 | 0.82 | 1.07 | 1.06 |
| *Heliocarpus appendiculatus* | Trop. Wet | 47 | 26 | 0.06 | 0.0055 | 0.0001 | 0.79 | 27 | 0.07 | 0.0048 | 0.0001 | 0.81 | 1.16 | 1.04 |
| *Heliocarpus appendiculatus* | Trop. Wet | 44 | 18 | 0.09 | 0.0144 | 0.0001 | 0.88 | 20 | 0.05 | 0.0153 | 0.0001 | 0.98 | 0.94 | 1.11 |
| *Heliocarpus appendiculatus* | Montane | 49 | 19 | 0.15 | 0.0057 | 0.0001 | 0.79 | 21 | 0.07 | 0.0068 | 0.0001 | 0.74 | 0.84 | 1.11 |
| *Heliocarpus appendiculatus* | Trop. Wet | 33 | 11 | 0.02 | 0.0259 | 0.0001 | 0.90 | 18 | 0.06 | 0.0088 | 0.0001 | 0.69 | 2.94 | 1.64 |
| *Licania arborea* Seem. | Trop. Dry | 58 | 17 | 0.51 | 0.0067 | 0.0001 | 0.82 | 25 | 0.53 | 0.0047 | 0.0001 | 0.77 | 1.41 | 1.47 |
| *Liriodendron tulipifera* L. | Temp. | 56 | 26 | 0.38 | 0.0040 | 0.0001 | 0.70 | 27 | 0.36 | 0.0056 | 0.0001 | 0.78 | 0.71 | 1.04 |
| *Ochroma pyramidale* (Cav. ex Lam.) Urb. | Trop. Wet | 38 | 15 | 0.08 | 0.0103 | 0.0001 | 0.73 | 20 | 0.07 | 0.0072 | 0.0001 | 0.73 | 1.44 | 1.33 |
| *Ochroma pyramidale* | Trop. Wet | 36 | 13 | 0.07 | 0.0099 | 0.0007 | 0.67 | 18 | 0.06 | 0.0060 | 0.0001 | 0.78 | 1.64 | 1.38 |
| *Ochroma pyramidale* | Trop. Wet | 36 | 12 | 0.01 | 0.0135 | 0.0001 | 0.95 | 19 | 0.06 | 0.0051 | 0.0004 | 0.53 | 2.64 | 1.58 |
| *Ochroma pyramidale* | Trop. Wet | 66 | 23 | 0.09 | 0.0102 | 0.0001 | 0.82 | 32 | 0.09 | 0.0074 | 0.0001 | 0.93 | 1.39 | 1.39 |
| *Ochroma pyramidale* | Trop. Wet | 48 | 21 | 0.18 | 0.0086 | 0.0001 | 0.75 | 23 | 0.16 | 0.0087 | 0.0001 | 0.77 | 0.99 | 1.10 |
| *Ochroma pyramidale* | Trop. Wet | 38 | 18 | 0.12 | 0.0087 | 0.0001 | 0.75 | 19 | 0.10 | 0.0075 | 0.0001 | 0.63 | 1.15 | 1.06 |
| *Rollinia microsepala Standl.* | Trop. Wet | 32 | 15 | 0.22 | 0.0069 | 0.007 | 0.44 | 16 | 0.23 | 0.0063 | 0.006 | 0.43 | 1.10 | 1.07 |
| *Symplocos serrulata Bonpl.* | Montane | 26 | 9 | 0.30 | 0.0207 | 0.0003 | 0.86 | 13 | 0.30 | 0.0119 | 0.001 | 0.63 | 1.74 | 1.44 |
| *Trema micrantha (L.) Blume* | Trop. Wet | 22 | 9 | 0.17 | 0.0230 | 0.0002 | 0.87 | 11 | 0.18 | 0.0196 | 0.001 | 0.90 | 1.17 | 1.22 |

Columns show species, forest type, dbh and then properties of the short and long cores, respectively: length ($N$ for the regression), parameters from regression of SG on radial distance for each side core (intercept, slope, significance, and coefficient of determination). The final two columns are the ratios of the short core slope to the long core slope and the long radius to the short radius

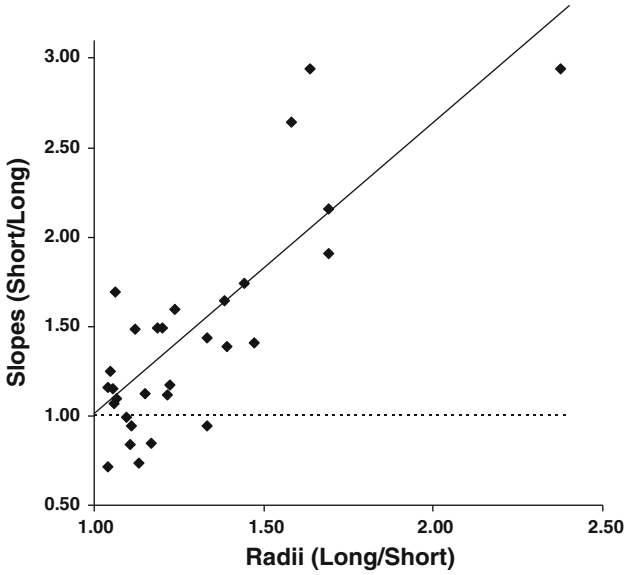


**Fig. 2** As eccentricity increases, the ratio of the slopes increases. *Solid line* is the linear regression of the ratio of slopes (short core to long core) of the SG-radial distance regressions as a function of the ratio of lengths (long core to short core). *Dotted line* at slopes = 1.0 represents points of no difference in the ratio of slopes

for example, at 1/3 the distance from the pith on both short and long radii the wood should be the same age and the same SG, if the radial increase in SG is age-dependent. To test if the slope increases compensate, we compared SG values at arbitrarily chosen, proportional distances along the two radii with paired *t* tests. Comparisons were made for SG of initial wood beside the pith ($SG_{0.0}$), wood at one-third of the radius ($SG_{1/3}$), wood at one-half of the radius ($SG_{1/2}$), wood at two-thirds of the radius ($SG_{2/3}$) and outer wood beside the phloem ($SG_{1.0}$). For comparison, we also asked if SG values changed from the adjacent proportional points (0–1/3, 1/3–1/2, 1/2–2/3, and 2/3–1) along each radius separately. The SG value assigned to each point on a radius was the mean of the three 1-cm pieces nearest to the point because single pieces sometimes give erratic values, apparently a sampling phenomenon (Wiemann and Williamson 1988).

## Results

The ratio of the slopes of SG on radial distance (short radius to long radius) were close to 1.0 when the ratio of the radial lengths was close to 1.0 (Fig. 2). Then, as the ratio of lengths increased, the ratio of slopes also increased, indicating that greater eccentricity was accompanied by greater differences in slopes of the SG-radial distance regressions (Fig. 2). The overall regression of the ratio of slopes ($Y$) on the ratio of radii ($X$) was statistically

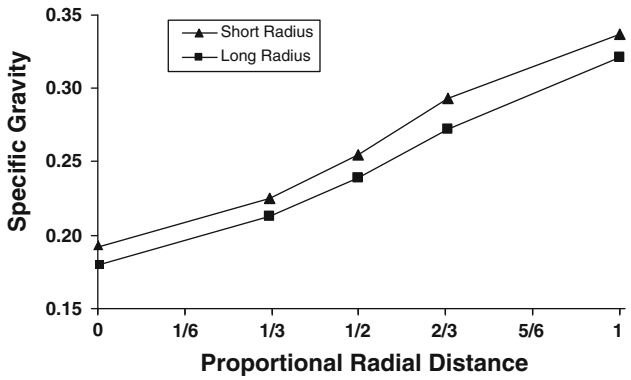


**Fig. 3** Mean wood specific gravity in eccentric trees from the short radius (*triangles*) and the long radius (*squares*), at proportional distances (0–1) along the radii

significant, with $X$ explaining 67% of the variation in $Y$ ($R^2 = 0.67$, $P < 0.0001$; slope ± SE was 1.67 ± 0.22; intercept ± SE was 0.72 ± 0.29).

This result provides support for age-dependence of wood SG. Does the increased slope along the short radius of eccentric trees compensate for the decreased radius? Short radius SG means were slightly larger than long radius means, although not necessarily significantly so (Fig. 3). At proportional distances 0, 1/3, 1/2, 2/3 and 1, the respective, calculated *P*-values were 0.002, 0.16, 0.09, 0.01, and 0.03 (paired *t* tests, $df = 29$); with a Bonferroni correction for five comparisons, only the means at 0 and 2/3 of the radii would be significantly different at $P = 0.05$ (Bonferroni $P = 0.05/N$ comparisons). The paired differences (mean ± SE) at proportional distances from 0 to 1.0 were quite small: 0.013 ± 0.004, 0.012 ± 0.009, 0.016 ± 0.009, 0.021 ± 0.008, and 0.016 ± 0.007. The short and long radius means shown at proportional distances in Fig. 3 were highly correlated ($R = 0.999$). By comparison, the SG values at successive proportional points on either radius were highly significantly different by paired *t* tests (Bonferroni corrected $P < 0.002$ in all eight cases).

## Discussion

A tree's allocation to height is fixed by its biomass, form factor (height/diameter ratio) and SG. Although form can change slightly, species differences in SG generally reflect differences in height for a given biomass. For example, for a given biomass, an *Ochroma pyrami*dale (Cav. ex Lam.) Urb. with a mean SG of 0.20 should be approximately 2.5 times the size (total wood volume) of a *Pentaclethra macroloba* (Willd.) Kuntze with a mean SG of 0.50. Parallel to species' differences in SG, the radial changes in SG allow pioneers to grow faster, earlier in life and more

slowly later as adults. In the example above, the *Ochroma* with a mean SG of 0.20 actually produced wood of SG = 0.13 as a young sapling, and subsequently wood SG increased gradually to SG = 0.26 at the outermost wood of this 55 cm dbh tree. In essence, for a unit of biomass produced, the tree produced wood volume twice as fast initially. Of course, the shift in SG from lower to higher, within a tree or among species, involves a tradeoff between height growth versus wood strength—greater height at lower SG invokes greater risk of structural failure.

The question here is how SG is controlled in species that exhibit radial increases. Potentially, SG could be determined by tree size through some inducible mechanism such as stress or strain that changes with size. Alternatively, SG could be determined by age through ontogenesis. Given that size increases with age, either mechanism could produce the desired effect of increasing SG during the lifetime of the tree. Prior to this study, two experimental methods have been proposed to evaluate the dependence of SG on age versus size (Castro et al. 1993): (1) compare SG changes in trees of different ages, but the same size, and (2) compare SG changes in trees of different sizes, but the same age. The former method has never been used, but the latter has been performed successfully with *Joannesia princeps* Vell. in a Brazilian forest plantation (Castro et al. 1993) and with cohorts of four pioneer species in naturally regenerating stands in Costa Rica (Williamson and Wiemann 2010b). Both studies revealed patterns that supported age-dependent, not size-dependent, SG determination.

A third method arises where trees exhibit annual growth rings, such that radial SG and age can be determined for natural stands. Regression models of SG with a combination of variables including size, age and their interaction can be evaluated statistically. However, applicability of regression rests on the degree of independence of age and size in order to estimate their relative contributions in explaining variation in SG. Nock et al. (2009) applied this method successfully to demonstrate that age explained more variation in SG than did size of *Melia azedarach* L. in Thailand.

The study of eccentric trees provides a novel methodology to evaluate size versus age-dependence. The eccentrics method supports the conclusion of prior approaches that age is more important than size in SG determination. As the method is different from others, it contributes robustness to the conclusion.

Although this conclusion is tempered by the small dataset of 30 trees from 12 species, the method of comparing age-dependence versus size-dependence of the radial shift in SG offers a unique metric where trees can be bored bark-to-pith-to-bark, and if trees are eccentric. Although eccentricity is difficult to discern prior to boring, it was surprisingly common in our dataset, although it varied among individuals (Table 1). The ratio of the long radius to the short radius was a minimum at 1.04 for a 47 cm dbh *Heliocarpus appendiculatus* Turcz. and a 56 cm dbh *Liriodendron tulipifera* L. and a maximum at 2.38 for a 29 cm dbh *Cecropia peltata* L. (Table 1). Of the 30 trees, 23 had one side at least 10% longer than the other; however, only five trees had one side more than 50% longer than the other (Table 1). Eccentricity measured here may underestimate the maximal difference in each tree because we did not necessarily core the trees along the axis of maximal eccentricity, as that position was unknown to us. However, we doubt that eccentricity was much greater than that registered here because trees whose trunks appeared elliptical externally were bored along the long axis as practice has proven that hitting the pith is more likely on this axis.

Most of the eccentric trees excluded from the analysis were from biomes that show little or no radial increases in SG. The 24 trees that failed to produced significant increases included six from tropical dry forests, five from tropical montane forests, 10 from temperate forests, and three from tropical lowland wet forests. Temperate species, tropical montane species and species exclusive to tropical dry forests rarely shows large radial increases in SG (Wiemann and Williamson 1989a, b). The three lowland wet forest trees that were excluded for lack of significant radial increases in SG actually had the three most eccentric trunks—an *Apeiba aspera* Aubl. with a ratio of radii of 3.7, a *Ceiba pentandra* (L.) Gaertn. with a ratio of 3.1, and an *O. pyramidale* with a ratio of 2.9. Thus, it appears that our regression criterion ($P \leq 0.01$) for inclusion in the analysis dataset excluded the most eccentric trees from the original dataset. The three trees share two characteristics: (a) each had a very short radius with a very steep increase in SG, and (b) each had a very long radius with a very shallow or no increase in SG. As the wood produced on the short radius was much higher in SG than the wood on the long radius, they deviate from the general model of age-dependent radial increases presented here.

A detailed look at the regression line in Fig. 2 reveals both supportive and contrary elements for the age-dependent model of radial increases in SG. First, the line neatly intersects the expected concentric origin of the ratios (1, 1) with an observed point of (0.97, 1.00). Second, the regression explains 2/3 of the variation in the ratio of slopes ($R^2 = 0.67$). However, the observed ratio of slopes of 1.67 is significantly larger than the expected slope of 1.00 ($F$ test, $df$ 1,28, $F = 9.05$, $P < 0.006$). Finally, there appear to be eccentricity differences among species which might lead to different responses; for example, *Hampea* appears to exhibit less eccentricity and less variation in the ratio of the slopes than *Ochroma* and *Heliocarpus* (Table 1). With larger datasets, regressions could be run for species separately and analysis of covariance employed to compare species' responses.

One might argue that the results here are trivial because what happens on one side of tree must happen on the other side, based on the assumption of radially symmetrical growth processes. However, differential xylem production occurs and produces the eccentricities in radii. Furthermore, it can be accompanied by differential SG production as shown by the three exceptionally eccentric trees described above. Other processes, such as branch development, flowering and fruiting, can also occur differentially on sides of a trunk. Likewise, trees on slopes compensate with differential xylem development on upslope and downslope radii, and species with incomplete rings exhibit growth on one side and not at all on the other, alternating through the years. Thus, trees are not required to grow and develop equally around the bole. Given eccentric production of xylem on opposite sides of a tree, the quality of that xylem in terms of anatomy and SG would not necessarily be the same. In fact, the greater the eccentricity, the more we might anticipate differences. But wood produced at the same time, on opposite sides of the tree, differs little in SG. We conclude that radial variation in SG in eccentric trees appears to support age-dependence not size-dependence. This result concurs with the few previous studies on age versus size-dependence of the radial shift in SG, and it validates that conclusion from an alternative methodology.

Finally, it is noteworthy that age-dependence of radial increases in SG reinforces the characterization of SG change per unit of time, not per unit of size. For example, SG changes per year would be similar whether a species grew slowly or rapidly during the year, but SG changes per cm of radius, as determined here, would vary. This conclusion is problematic for future research as many tropical wet forest species do not exhibit annual rings. However, additional clarity may be forthcoming where tropicals exhibit both SG increases and annual rings (e.g. Nock et al. 2009).

**Acknowledgments** This research was supported by the U.S. National Science Foundation (DEB-0639144) and the Michaux Fund of the American Philosophical Society. Sayra Navas, Ana Gómez, Sonia Vargas, Toni Soto and Jacqueline Henrot helped in extracting and measuring the cores. Luis Poveda and Nelson Zamora confirmed the species' identifications. We gratefully acknowledge the cooperation of the Organization for Tropical Studies.

## References

Baker TR, Phillips OL, Malhi Y, Almeida S, Arroyo L, DiFiore A, Erwin T et al (2004) Variation in wood density determines spatial patterns in Amazonian forest biomass. Glob Change Biol 10:545–562

Baker TR, Phillips OL, Laurance WF, Pitman NCA, Almeida S, Arroyo L, DiFiore A et al (2009) Do species traits determine patterns of wood production in Amazonian forests? Biogeosciences 6:297–307

Brown S, Lugo AE (1992) Aboveground biomass estimates for tropical moist forests of the Brazilian Amazon. Interciencia 17:8–18

Butterfield RP, Crook RP, Adams R, Morris R (1993) Radial variation in wood specific gravity, fiber length and vessel area for two Central American hardwoods: *Hyeronima alchorneoides* and *Vochysia guatemalensis*: natural and plantation-grown trees. IAWA Bull 14:153–161

Castro F, Williamson GB, 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

Chave J, Andalo C, Brown S, Cairns MA, Chambers JQ, Eamus D, Fölster H et al (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia 145:87–99

Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE (2009) Towards a worldwide wood economics spectrum. Ecol Lett 12:351–366

Fearnside PM (1997) Wood density for estimating forest biomass in Brazilian Amazonia. For Ecol Manage 90:59–87

Keeling HC, Phillips OL (2007) The global relationship between forest productivity and biomass. Glob Ecol Biog 16:618–631

Malhi Y, Wood D, Baker TR, Wright J, Phillips OL, Cochrane T, Meir P et al (2006) The regional variation of aboveground live biomass in old-growth Amazonian forests. Glob Change Biol 12:1107–1138

Nock CA, Geihofer D, Grabner M, Baker PJ, Bunyavejchewin S, Hietz P (2009) Wood density and its radial variation in six canopy tree species differing in shade-tolerance in Western Thailand. Ann Bot 104:297–306

Nogueira EM, Nelson BW, Fearnside PM (2005) Wood density in dense forest in central Amazonia, Brazil. For Ecol Manage 208:261–286

Nogueira EM, Fearnside PM, Nelson BW, Franca MB (2007) Wood density in forests of Brazil's 'arc of deforestation': implications for biomass and flux of carbon from land-use change in Amazonia. For Ecol Manage 248:19–135

Nogueira EM, Fearnside PM, Nelson BW (2008a) Normalization of wood density in biomass estimates of Amazon forests. For Ecol Manage 256:990–996

Nogueira EM, Fearnside PM, Nelson BW, Barbosa RI, Imbrozio BE, Keizer WH (2008b) Estimates of forest biomass in the Brazilian Amazon: new allometric equations and adjustments to biomass from wood-volume inventories. For Ecol Manage 256: 1853–1867

Poorter L, Wright SJ, Paz H, Ackerly DD, Condit R, Ibarra-Manríquez G, Harms KE et al (2008) Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. Ecology 89:1908–1920

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

Whitmore JL (1973) Wood density variation in Costa Rican balsa. Wood Sci 5:223–229

Wiemann MC, Williamson GB (1988) Extreme radial changes in wood specific gravity in some tropical pioneers. Wood Fiber Sci 20:344–349

Wiemann MC, Williamson GB (1989a) Radial gradients in the specific gravity of wood in some tropical and temperate trees. For Sci 35:197–210

Wiemann MC, Williamson GB (1989b) Wood specific gravity gradients in tropical dry and montane rain forest trees. Am J Bot 76:924–928

Williamson GB, Wiemann MC (2010a) Measuring wood specific gravity…correctly. Am J Bot 97:519–524

Williamson GB, Wiemann MC (2010b) Age-dependent radial increases in wood specific gravity of tropical pioneers. Biotropica 42:590–597

Wright IJ, Ackerly DD, Bongers F, Harms KE, Ibarra-Manriquez G, Martinez-Ramos M, Mazer SJ et al (2006) Relationships among ecologically important dimensions of plant trait variation in seven neotropical forests. Ann Bot 99:1003–1015