Age-Dependent Radial Increases in Wood Specific Gravity of Tropical Pioneers in Costa Rica

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ABSTRACT

Wood specific gravity is the single best descriptor of wood functional properties and tree life-history traits, and it is the most important variable in estimating carbon stocks in forests. Tropical pioneer trees produce wood of increasing specific gravity across the trunk radius as they grow in stature. Here, we tested whether radial increases in wood specific gravity were dependent on a tree's diameter or its age by comparing trees of different diameters within cohorts. We cored trunks of four pioneer species in naturally regenerating, even-aged stands in the lowland, wet forests of Costa Rica. For each core, specific gravity was determined for 1-cm radial wood segments, pith to bark. Increases across the radius were evident in all four species studied, and in four different stands for one species. For any given species in a given stand, the rate of radial increase in specific gravity as a function of radial distance from the pith was greater in smaller diameter trees. As the trees in a stand represent a colonizing cohort, these results strongly suggest that the radial increases in specific gravity in lowland pioneers are associated with tree age, not with tree diameter. Furthermore, the specific gravity of the outermost wood was not associated with tree radius, further negating size dependence. One consequence of these results is that species-specific biomass estimates for trees in secondary forests are likely to be confounded by age, as diameter alone may be a poor indicator of specific gravity in individual trees for pioneers of tropical wet forests.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp

Key words: biomass; *Bursera simaruba*; *Heliocarpus appendiculatus*; *Ochroma pyramidale*; *Trema micrantha*.

WOOD SPECIFIC GRAVITY (SG) is the single most important predictor of wood strength properties for both dry and green wood. SG predicts various mechanical properties because it represents allocation to structure—namely, dry biomass per unit volume of live wood. It has been described as a 'unique integrator' of tree properties because wood performs several essential functions in plants—mechanical support, transport, and storage (Chave *et al*. 2009). As such, wood SG is associated with tree growth rates and tree survivorship (Wright *et al*. 2007, Poorter *et al*. 2008), probably for structural reasons in wet forests, and possibly for plant hydraulic reasons in tropical dry forests (Borchert 1994). Chave *et al*. (2009) have suggested the existence of a 'wood economics spectrum' that parallels the clustering functions of foliage in the 'leaf economics spectrum' (Wright *et al*. 2004). In addition, SG is the primary variable in the estimation of biomass to assess world carbon stocks (Brown & Lugo 1992; Fearnside 1997; Chave *et al*. 2005; Nogueira *et al*. 2005, 2007, 2008a, b; Malhi *et al*. 2006; Keeling & Phillips 2007; Baker *et al*. 2009). Despite recent interest in wood as a functional trait, little is known about SG variation within individual trees, especially in tropical pioneers where within tree variation is extraordinary.

Pioneer species of tropical, lowland, wet forests exhibit large SG increases across the tree radius from pith to bark, sometimes over 100 percent, although fewer than 20 pioneer species have been studied (Whitmore 1973; Wiemann & Williamson 1988, 1989a, b; Omolodun *et al*. 1991; Butterfield *et al*. 1993). Similar, albeit more modest, increases occur in tropical pioneer species of lowland dry forests (Baraja-Morales 1987; Wiemann & Williamson 1989a, b). Among temperate hardwoods such dramatic changes in specific gravity are unknown, although small radial increases may be associated with the transition from juvenile to mature wood and radial decreases are evident in the transition from heartwood to sapwood of some hardwoods (Zobel & Sprague 1998). The exaggerated increases in SG for tropical pioneers morphologically comprise a gradual anatomical shift in the proportion of parenchyma that develops into fibers and a shift in the anatomy of fibers themselves (Butterfield *et al*. 1993, McDonald *et al*. 1995). These changes complicate estimation of forest biomass, especially in secondary forests that regenerate following deforestation in the tropics (Fearnside 2005, Nogueira *et al*. 2008a). They also add a new dimension to species-specific analysis of SG as a functional trait because pioneers must be characterized by an equation that represents the change in SG across the radius, not by a single SG value.

Two adaptive functions of the radial shift in SG have been proposed. The first maintains that radial increases in wood SG concentrate denser wood at greater distances from the neutral axis of the stem (the pith in a symmetrical tree), resulting in a stronger, more rigid stem from a limited amount of material (Niklas 1997,

1998). The argument originates from the strong positive relationships between wood SG and most wood strength properties (Forest Products Laboratory 1999, Chave *et al.* 2009). Strengths generally increase as a power function of SG with an exponent ≥ 1 although the modulus of rupture's exponent is < 1 (Forest Products Laboratory 1999). If wood strength depends on SG, then radially increasing SG results in cylinders of increasing strength (Schniewind 1962). Pioneer species compete for full sunlight in an emerging canopy by initially allocating resources to stature at the cost of strength and then gradually increasing strength. Presumably, this changing allocation involves some risk, namely structural failure. Structural failure in the form of trunk breakage has been shown to occur more frequently in tropical trees with lower specific gravities, and tree mortality rates are inversely related to their specific gravities (Putz *et al.* 1983, King *et al.* 2006, Chao *et al.* 2009).

An alternative interpretation of the radial shift is that changes in xylem composition and fiber anatomy associated with increased SG prevent cavitation during hydric stress, as shown by Hacke *et al.* (2001) for an array of temperate woody plants. In a tropical dry forest, higher SG is associated with trees that develop very low water potentials (Borchert 1994), so the radial increase could be an adaptation to increased water stress with greater tree size.

One important question arising from earlier work on tropical woods is whether the radial increases in SG are associated with tree age or with tree size (de Castro *et al.* 1993). Hypothetically, SG increases that are a function of age would produce a different pattern than increases that are a function of diameter (Fig. 1). Trees of a given age but of different diameters should have radial increases of the same magnitude, despite different diameters, if the radial increase is a function of age; for example, the three solid lines in Figure 1 have different slopes, but the same starting SG and the same ending SG. On the other hand, trees of a given age but different diameters should have radial increases of different magnitudes but the same slope, if the radial increase is a function of tree size; for example, the three dashed lines in Figure 1 partially overlap and have the same starting SG but different ending SG.
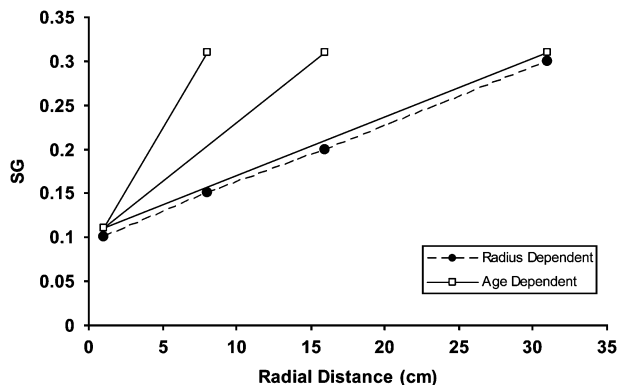

FIGURE 1. Hypothetical model of radial changes in wood specific gravity (SG) for three trees each of two cohorts, each with a different radius for radius-dependent SG (solid circles, dashed lines) and for age-dependent SG (open squares, solid lines).

Age vs. size dependence of the increases in SG also reflects a genetic vs. environmental control of the SG increases. SG is a highly heritable trait in the few species that have been studied (Daniel *et al.* 1979, Cornelius 1994), so age-dependent SG increases may also be controlled genetically. The alternative, size-dependent SG increases, presumes an environmental control as most size variation within a species is environmental.

Unfortunately, tree age is usually not known and cannot be determined from ring counts for most tropical wet forest trees, although there are exceptions (*e.g.*, Worbes 1989). Here, we compare SG increases among trees of the same age but of different diameters. Individuals of the same age can be found in plantations or in even-aged natural stands. A colonizing cohort of pioneers harbors individuals of different diameters but the same approximate height (Fig. S1A) due to differential success of individual trees in the same stand. To date, SG increases for individuals in a cohort have been reported for only two tropical species, *Joannesia princeps* Vell., grown in plantations in Brazil (de Castro *et al.* 1993) and *Melia azedarach*, a dry forest species in Thailand (Nock *et al.* 2009). We present results for four species from six naturally regenerating even-aged stands in Costa Rica. The four species are among the predominant pioneers of tropical wet forest in Central America.

METHODS

The stands sampled were located in the Atlantic lowlands (10–11° N, 84–84° W; < 100 m asl) of Costa Rica, where annual rainfall is *ca* 400 cm with no severe dry season. The driest month receives 15 cm of precipitation while the wettest month receives 48 cm (Sanford *et al.* 1994). Temperatures are relatively constant, with the coldest month averaging 25°C and the warmest month, 27°C (Sanford *et al.* 1994). The ages of two of the six stands studied were known accurately because the trees colonized clearcuts at the Organization for Tropical Studies' La Selva Biological Station: trees in the Succession Plots were 4 yr 5 mo old and those in the Cacao Plantation were 4 yr 11 mo old at the time they were sampled. Two other stands, Pueblo Nuevo and El Tigre, regenerated following clearcuts 6 yr before our sampling, so the trees were 5–6 yr old. The ages of the trees in the two remaining stands, La Guaria and Cahuita, were not known, although the species' uniform canopy heights indicated that the trees were even aged.

In each stand, trees were selected arbitrarily to reflect the range of available diameters of trees of the same height. Trees near the edges of each stand were excluded because they experienced different light regimes and often exhibited eccentric growth. At the time of sampling, the diameter at breast height (dbh = 1.4 m) of each tree was measured with a diameter tape without complications from buttresses. The species sampled, *Ochroma pyramidale* (Cav. ex Lam.) Urban (Bombacaceae), *Heliocarpus appendiculatus* Turcz. (Tiliaceae), *Bursera simaruba* (L.) Sarg. (Burseraceae) and *Trema micrantha* (L.) Blume (syn. *Trema integerrima* (Beurl.) Standley) (Ulmaceae), had been shown in prior studies to exhibit large radial increases in wood SG (Wiemann & Williamson 1988, 1989a). *Ochroma* was sampled in four stands, whereas the other three

species were sampled in only one stand each, yielding seven species–stand combinations (Table 1).

Pith-to-bark wood samples were taken with a 12-mm diam. increment borer (Figs. S1B, C) and the extracted cores were examined to verify that they reached the tree pith (Fig. S1C). Wood cores were sealed individually in plastic tubes to prevent drying and then transported to the lab at La Selva Biological Station where they were cut into 1-cm segments measured from the pith. The green volume of each segment was determined by water displacement (Wiemann & Williamson 1988) (Fig. S1D). Then, the segments were oven-dried at 100–105°C for 1–2 d before weighing on an electronic balance. Basic SG of each segment was calculated as its oven dry weight divided by the weight of water displaced by its green volume.

The basic specific gravities of the first three 1-cm segments closest to the pith were averaged to estimate the inner wood specific gravity (SG_i). Similarly, the basic specific gravities of the three segments closest to the bark were averaged to estimate outer wood specific gravity (SG_o). Three segments were used instead of one because a single segment often gives an erratic estimate, as the first and last segments are adjacent to the pith and the phloem, respectively (Wiemann & Williamson 1988). The innermost wood may also contain juvenile wood or primary xylem.

Linear least squares regression of basic SG of each segment as a function of its distance from the pith was performed for each tree, after checking for linearity. Only trees with significant ($P \leq 0.05$), positive regressions of SG on radial distance were considered further, as the purpose of the study was to explain radial increases in those trees that exhibited them. The regression parameters were averaged to characterize each species–stand combination as in prior studies (Wiemann & Williamson 1988, 1989a, b).

To test the dependence of SG on diameter and on age two differentiating criteria were employed (de Castro *et al.* 1993): (1) Is the slope of the regression of SG on radial distance steeper for smaller trees, as it would be for age dependence but not for radius dependence? and (2) Is the outer wood specific gravity (SG_o) higher in larger radius trees, as it would for radius dependence but not for age dependence (Fig. 1)?

RESULTS

Regression of SG on radial distance proved to be significant with a positive slope for 77 of the 115 trees sampled (Table 1). Most (37 of 38) trees without significant radial increases were small diameter individuals (dbh = 10–15 cm; Table 1), either *Ochroma* from the Cacao Plantation (24 of 34) or *Heliocarpus* from the Succession Plots (13 of 29). Prior studies have confirmed that the regressions are less likely to be significant for smaller diameter trees because larger diameters more fully revealed the radial increases and the SG of the inner few centimeters often shows no radial increase (Wiemann & Williamson 1988). Trees without significant regressions were excluded from further analysis.

Means of the slopes of the significant regressions of SG on radial distance ranged from 0.0066 SG/cm for *Bursera* at Cahuita to 0.0181 for *Ochroma* at Pueblo Nuevo (Table 1), and fell within the range of previously reported values for these species (Wiemann & Williamson 1988, 1989a). The four stands of *Ochroma* showed somewhat variable slopes of SG on radial distance, with La Guaria (0.0141) and Pueblo Nuevo (0.0181) being about double El Tigre (0.007) and the Cacao Plantation (0.0081), although the intercepts were quite similar for the four regressions (0.082–0.122; Table 1). For illustration, the individual tree regression lines of SG on radial distance are shown for the seven *Ochroma* at La Guaria (Fig. 2A) and the 19 *T. micrantha* at the Successional Plots (Fig. 3A).

The two test criteria to determine age dependence or radius dependence indicated that the radial increases in SG were mainly a function of age, not radius. For criterion 1, the slope of SG on radial distance was significantly steeper for smaller trees in six of the seven species–stand combinations, implying that age was determining SG (Table 1). The relationship of slope to radius is shown for *Ochroma* trees at La Guaria (Fig. 2B) and for *T. micrantha* at the Successional Plots (Fig. 3B). Regressions of slope on radius for the

TABLE 1. *Summary of regressions of SG on radial distance for the seven species–stand combinations. Columns are species, stand, total number of trees cored and their diameter range. For trees with significant radial increases (*P < 0.05*), sample size (*N*), dbh mean, SD and range, followed by means of their individual regression parameters of SG on radial distance (slope, intercept and coefficient of determination) are shown. Results of test criteria 1 and 2, respectively: slope regressed on radius and outer wood SG (*SG_o*) regressed on radius, in bold when *P < 0.05*.*

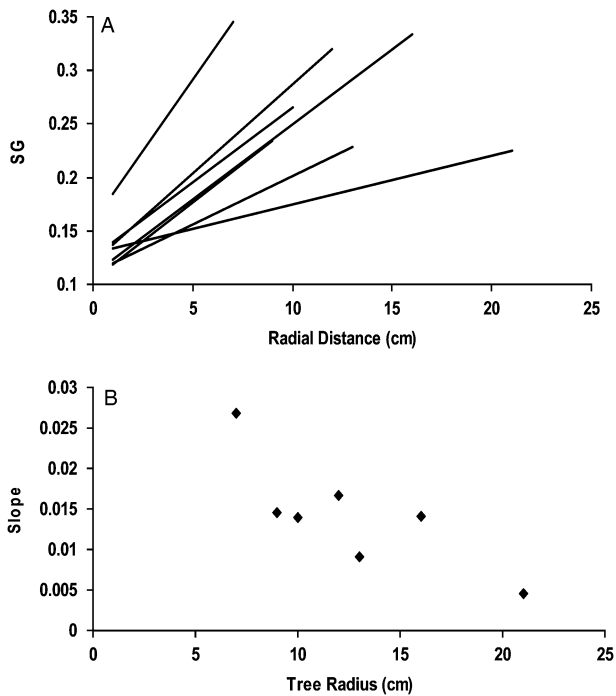| | | Total trees | | Trees with statistically significant radial increases | | | | | | | Criterion 1 | | Criterion 2 | |
| | | | | Tree dbh (cm) | | | Means for regressions | | | Slope on radius | | SG_o on radius | |
Species	Stand	Cored	dbh (cm)	N	Mean	SD	Range	Slope	Intercept	R^2	r	P	r	P
Bursera	Cahuita	6	47–90	6	67	16	47–90	0.0066	0.297	0.76	−0.83	**0.02**	−0.38	0.23
Heliocarpus	Succession Plots	29	10–32	16	20	6	10–32	0.0156	0.075	0.76	−0.62	**0.05**	+0.28	0.15
Trema	Succession Plots	20	10–34	19	23	5	14–34	0.0156	0.159	0.86	−0.69	**0.001**	+0.58	**0.01**
Ochroma	Cacao Plantation	34	10–41	10	28	7	16–41	0.0081	0.093	0.65	−0.69	**0.03**	−0.07	0.42
Ochroma	El Tigre	8	36–56	8	42	7	36–56	0.0070	0.102	0.70	−0.49	0.22	−0.15	0.36
Ochroma	La Guaria	7	18–49	7	33	10	18–49	0.0141	0.122	0.72	−0.82	**0.01**	−0.30	0.26
Ochroma	Pueblo Nuevo	11	26–54	11	35	9	26–54	0.0181	0.082	0.75	−0.84	**0.001**	−0.44	0.08

FIGURE 2. (A) Individual regression lines of SG on radial distance for seven *Ochroma pyramidale* trees at La Guaria and (B) slopes of the regressions plotted as a function of tree radius ($R^2 = 0.67$, $P = 0.01$).
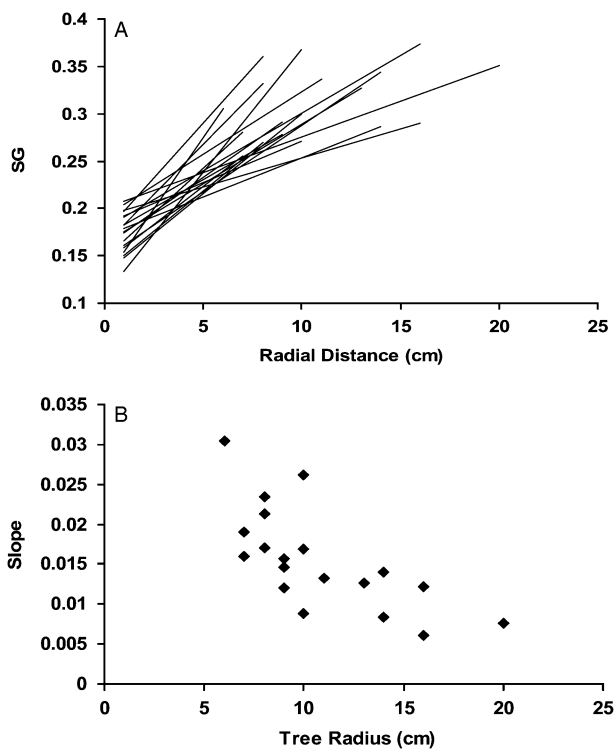

FIGURE 3. (A) Individual regression lines of SG on radial distance for 19 *Trema micrantha* trees at the Successional Plots and (B) Slopes of the regressions plotted as a function of tree radius ($R^2 = 0.48$, $P = 0.001$).

other five species–stand combinations (Table 1) were comparable, all of which were statistically significant ($P > 0.05$) except *Ochroma* at El Tigre ($P = 0.22$).

For criterion 2, SG_o was independent of radial distance in six of the seven species–stand combinations tested, implying that diameter was not determining SG (Table 1). Graphs of SG as a function of distance from the pith (Figs. 2A and 3A) generally conformed to the age-dependent model presented in Figure 1 except that there is considerable variation in the initial wood specific gravity.

For both test criteria one and two, we have shown the results of linear regressions on the untransformed data, although we considered several transformations as there was slight curvilinearity in some of the data (Figs. 2B and 3B). In general, the transformations did not improve the regressions or did so modestly for only a subset of the tests of a criterion. For example, the regression of slope on radius was improved slightly by an inverse function (1/slope vs. radius) for *T. micrantha* at the Successional Plots (R^2 of 0.48 increased to 0.58) and for *O. pyramidale* at La Guaria (R^2 of 0.67 increased to 0.70), but not for *O. pyramidale* at El Tigre (R^2 of 0.24 decreased to 0.00).

Finally, to illustrate the radial increases, we present graphs of SG as a function of radial distance for two trees each of six species–stand combinations. We arbitrarily chose one of the largest and one of the smallest trees that visually represented the changes in each species. Each graph shows radial changes for a large diameter and a small diameter tree (Fig. 4). In general, the graphs demonstrate steeper slopes in the smaller trees as well as the level of random variation.

DISCUSSION

The two models for regulating SG, age dependence and radius dependence, present contrasting mechanisms and therefore produce alternative testable hypotheses (Fig. 1). A species at a given site, however, could exhibit a mixture of the two responses, where specific gravity of the outer wood (SG_o) could be a function of both age and radius. It is equally possible that SG_o could be mainly a function of age in young trees and more a function of radius in older trees, as structural and physiological stresses change with age or size. Furthermore, different species could have different mechanisms controlling the radial shift in SG, given that there are different anatomical designs for achieving the radial shift in SG (Wiemann & Williamson 1988, 1989a, b; McDonald *et al.* 1995).

Looking for overall trends in these colonizing cohorts, however, revealed a common pattern wherein SG is determined by age, not by diameter, for the species, size classes and stands sampled. Trees of a cohort in a stand often produce inner wood (SG_i) that is somewhat variable, but the regression slopes are steeper for smaller diameter trees (Fig. 4). It is no surprise then that the outer wood (SG_o) is extremely variable given the initial variability in SG_i followed by variability in the rate of increase of SG with radial distance (the slope). The absence of a relationship of SG_o with radius is, of course, not as strong a confirmation of age dependence as the presence of steeper slopes on smaller trees because absence simply
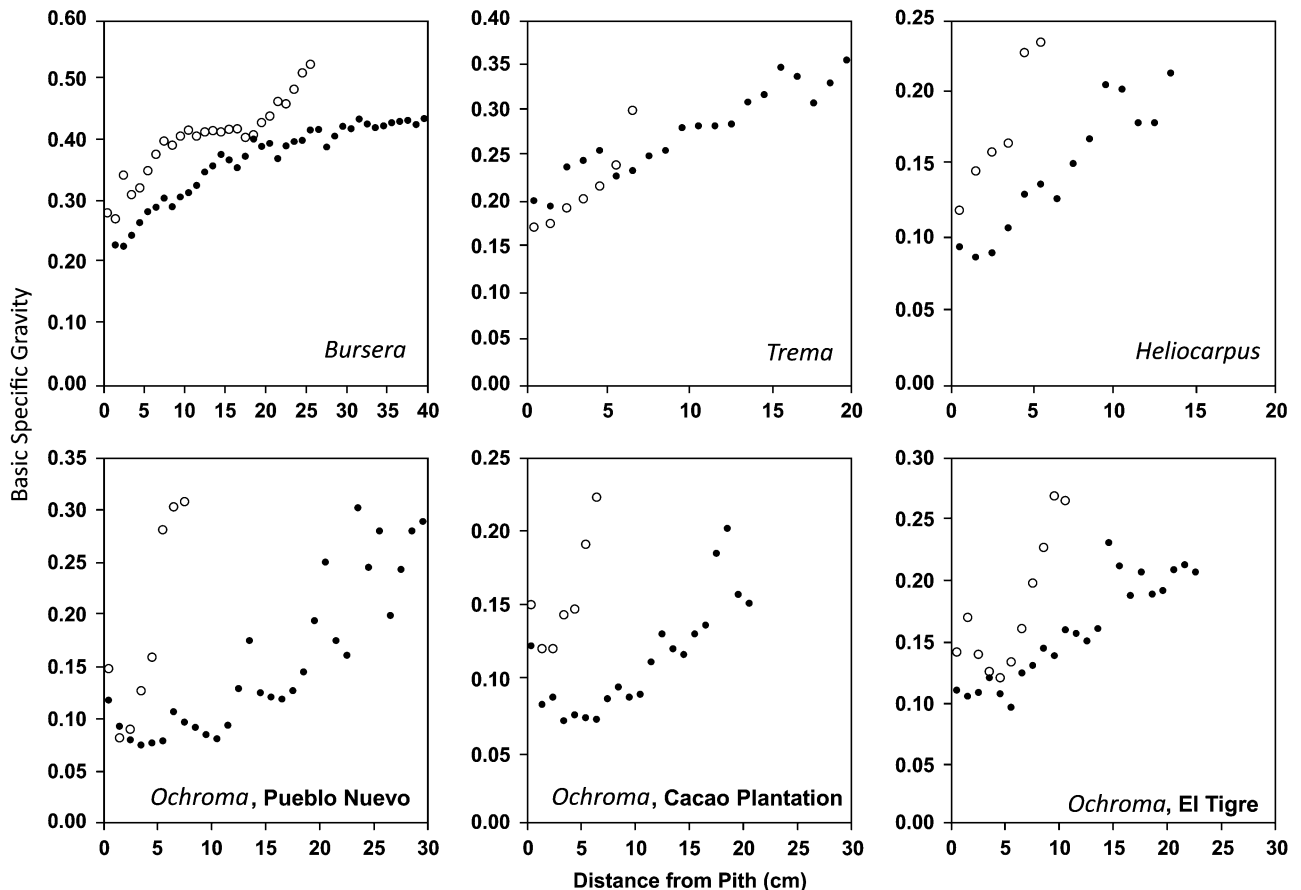
FIGURE 4. Wood SG as a function of radial distance for a large diameter tree (solid circles) and a small diameter tree (open circles) from six of the seven cohorts. Note that the slope of SG on radial distance is steeper for the smaller diameter tree in each stand.

means a null hypothesis could not be rejected. However, criterion 2 does allow rejection of size dependence in favor of age dependence.

In the two cases where our tests did not strictly confirm age dependence, there was no strong evidence in favor of size dependence. In the first of the two cases, *Ochroma* at El Tigre, the slope of SG on radius was negatively dependent on radius, as predicted by age dependence, but not significantly so ($P = 0.22$; Table 1). This leaves *Ochroma* with age-dependent radial increases at three sites, but not at El Tigre; perhaps the lack of significance was due to the limited variation in tree radii (CV = 16.4%) as our sample from that site included only large diameter trees (Table 1). In the second case (*T. micrantha*), the SG_o was significantly related to radius, supporting radius dependence, but the slope was even more strongly related to radius, supporting age dependence (Table 1); thus, *Trema* may be a species whose radial increases are dependent on both age and size.

The results here for natural stands of pioneers in Costa Rica parallel those from the only other such studies, where age dependence was established for *J. princeps* from plantations in Espirito Santo, Brazil (de Castro *et al.* 1993), and for *M. azedarach* L. from tropical dry forest in Thailand (Nock *et al.* 2009). The importance of age, not diameter, suggests that the control of SG during devel-

opment may be genetic, not environmental. Wood SG is a highly heritable quality in temperate and tropical hardwoods (Daniel *et al.* 1979, Cornelius 1994, Cavender-Bares *et al.* 2004), but no genetic tests have been performed to determine heritability of radial increases in SG exhibited by tropical trees.

The findings of age dependence in radial increases have a parallel in the radial increase at different heights up the bole, again implying genetic control of wood SG up the bole. Secondary xylem at different heights along the bole in *O. pyramidale* was time-dependent not radius-dependent, *i.e.*, wood produced at the same time along the bole had the same specific gravity regardless of height (Rueda & Williamson 1992). This pattern contrasts with that of juvenile wood that is always produced along the top of the growing axis. Unfortunately, outside of *Ochroma*, there have been no studies of the radial increase in SG at different heights for tropical pioneers.

If the radial shift in SG proves to be determined genetically and regulated developmentally by age, there are implications for the management of tropical hardwoods. For example, when seasoning wood, shrinkage is proportional to SG, so where SG changes rapidly across a radius, shrinkage does so likewise, producing warping during drying of lumber. Warping is a well-known problem of tropical hardwoods. To minimize warping, plantation managers

should grow trees as fast as possible, in essence reducing the slope of the SG shift over a given radius if the SG increase is a function of age. Alternatively, in tropical plantations, growing trees for posts and circular support columns, slower growth rates would yield more compact columns of comparable strength. More complex management schemes would emerge for veneer woods where rapid growth of a bole center (20 cm) might precede more moderate growth of a higher SG veneer at large diameters. Specialized uses such as artisan carvings often require pioneer species to be harvested before the trees' age and produce stronger, harder wood; for example, balsa (*O. pyramidale*) is harvested on a 4–6 yr rotation (Wiepking & Doyle 1944).

Age vs. size dependence of SG may also have dramatic effects for biomass estimations of different species. Traditional biomass estimates in the tropics have been based on tree diameter measurements coupled with a single mean SG per forest or mean SG values per species (Brown & Lugo 1992, Fearnside 1997, Baker *et al.* 2004). The error in such estimates caused by radial variation in SG among species, among individuals and within individuals can be substantial (Fearnside 1997, Woodcock 2000, Nogueira *et al.* 2008a, Nock *et al.* 2009). Tropical forests differ from their temperate counterparts in having species with extremely high- and low-density woods, and species with lower density woods tend to exhibit greater specific gravity increases across the radius (Wangaard 1951, Williamson 1984, Wiemann & Williamson 2002). Furthermore, tropical secondary forests contain a large proportion of pioneer species which show the most exaggerated SG shifts (Wiemann & Williamson 1988, Fearnside 1997). Consequently, Nelson *et al.* (1999) have recommended the use of species-specific biomass size equations for secondary species from tropical wet forests. Theoretically, if SG is radius-dependent, then biomass could be estimated precisely from diameter, but if SG is largely age-dependent, then species-specific biomass diameter relationships will have considerable 'unexplained' variance where age differences occur. In addition, biomass estimates may even require stand-specific equations because site factors often affect growth rates (Wiepking & Doyle 1944), and differential growth rates imply that trees of the same diameter on different sites will exhibit differences in biomass. In our study, *Ochroma* from four different stands in the Costa Rican lowlands showed quite different slopes for the regression of SG on radial distance. These pioneers are an important component of biomass in young secondary forests. In old growth stands where they regenerate only in gaps, pioneers will be minor contributors to biomass unless they remain as long-lived adults in the canopy like *Goupia glabra* Aubl. and *Laetia procera* (Poepp.) Eichler or as emergents like *Ceiba pentandra* (L.) Gaertn. (Turner 2001). Furthermore, long-lived pioneers which replace short-lived pioneers (Finegan 1996) appear to exhibit large radial increases in SG (Wiemann & Williamson 1989b).

One apparent aberration in the samples presented here was the lack of significant radial increases in 38 of 115 trees sampled. For this study, we intentionally selected trees over a range of diameters, small and large. Smaller diameter individuals often fail to yield significance because both the diameter range and the SG range are limited. In earlier studies aimed at documenting radial changes in SG, we sampled only large trees to witness the full range of SG changes (Wiemann & Williamson 1988); however, here our even-aged stands included many smaller trees, some of which did not show significant SG–radius relationships, perhaps due to their young age. The lack of significant increases was limited to the Succession Plots and the Cacao Plantation where plot ages are known to be < 5 yr. In many of our *Ochroma* cores, the first few centimeters of wood produced do not show an increase in SG the way the rest of the core does (Fig. 4). If the rest of the core is only a few cm as well, then any radial increase may not reach significance.

Our study here does not differentiate between the two adaptive hypotheses for the radial shift—mechanical structure vs. stem hydraulics. The tree species in our study, however, were located in the wet forest of Costa Rica's Atlantic lowlands, where cavitation is less likely, so we favor a structural interpretation for the radial increase in these stands. One of our species, *B. simaruba*, has a clean, straight bole in lowland wet forests, but it is a common colonizer in tropical dry forest, where it may be subject to cavitation. All four pioneers colonize forest clearings in the wet lowlands of Central America, and one species, *O. pyramidale*, extends into the Peruvian Amazon. Together with *Cecropia*, *Cavanillesia*, *Hampea*, *Heliocarpus* and *Schizolobium*, they epitomize the tropical pioneers' fugitive strategy—lightgap specialists with fast growth in stature, low wood SG, early reproduction and usually limited longevity (Williamson *et al.* 1998).

Given the attention devoted to wood SG as a prominent functional trait of trees, especially tropical trees, it is surprising that so little attention has been devoted to the radial shift in SG within tropical pioneers. If variation in SG among species is a result of adaptation, then variation across the radius must likewise be adaptive and serve one or more functions.

ACKNOWLEDGMENTS

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. (A) Even-age stand of *Ochroma* at Pueblo Nuevo; (B) G. B. Williamson coring a *Bursera* at Cahuita; (C) G. B. Williamson and M. C. Wiemann checking *Ochroma* core at Successional Plots; (D) M. C. Wiemann measuring core volume at La Selva Biological Station.

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LITERATURE CITED

BAKER, T. R., O. L. PHILLIPS, W. F. LAURANCE, N. C. A. PITMAN, S. ALMEIDA, L. ARROYO, A. DIFIORE, T. ERWIN, N. HIGUCHI, T. J. KILLEEN, S. G. LAURANCE, H. NASCIMENTO, A. MONTEAGUDO, D. A. NEILL, J. N. M. SILVA, Y. MALHI, G. LÓPEZ GONZALEZ, J. PEACOCK, C. A. QUESADA, S. L. LEWIS, AND J. LLOYD. 2009. Do species traits determine patterns of wood production in Amazonian forests? Biogeosciences 6: 297–307.

BAKER, T. R., O. L. PHILLIPS, Y. MALHI, S. ALMEIDA, L. ARROYO, A. DI FIORE, T. ERWIN, T. J. KILLEEN, S. G. LAURANCE, W. F. LAURANCE, S. L. LEWIS, J. LLOYD, A. MONTEAGUDO, D. A. NEILL, S. PATIÑO, N. C. A. PITMAN, J. N. M. SILVA, AND R. V. MARTÍNEZ. 2004. Variation in wood density determines spatial patterns in Amazonian forest biomass. Glob. Change Biol. 10: 545–562.

BARAJA-MORALES, J. 1987. Wood specific gravity in species from two tropical forests in Mexico. IAWA Bull. 8: 143–148.

BORCHERT, R. 1994. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. Ecology 75: 1437–1449.

BROWN, S., AND A. E. LUGO. 1992. Aboveground biomass estimates for tropical moist forests of the Brazilian Amazon. Interciencia 17: 8–18.

BUTTERFIELD, R. P., R. P. CROOK, R. ADAMS, AND R. MORRIS. 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.

DE CASTRO, F., G. B. WILLIAMSON, AND R. MORAES DE JESUS. 1993. Radial variation in the wood specific gravity of Joannesia princeps: The role of age and diameter. Biotropica 25: 176–182.

CAVENDER-BARES, J., D. D. ACKERLY, D. A. BAUM, AND F. A. BAZZAZ. 2004. Phylogenetic overdispersion in Floridian oak communities. Am. Nat. 163: 823–843.

CHAO, K. J., O. L. PHILLIPS, A. MONTEAGUDO, A. TORRES-LEZAMA, AND R. VASQUEZ MARTINEZ. 2009. How do trees die? Mode of death in northern Amazonia. J. Veg. Sci. 20: 60–268.

CHAVE, J., C. ANDALO, S. BROWN, M. A. CAIRNS, J. Q. CHAMBERS, D. EAMUS, H. FÖLSTER, F. FROMARD, N. HIGUCHI, T. KIRA, J.-P. LESCURE, B. W. NELSON, H. OGAWA, H. PUIG, B. RIÉRA, AND T. YAMAKURA. 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia 145: 87–99.

CHAVE, J., D. COOMES, S. JANSEN, S. L. LEWIS, N. G. SWENSON, AND A. E. ZANNE. 2009. Towards a worldwide wood economics spectrum. Ecol. Lett. 12: 351–366.

CORNELIUS, J. P. 1994. Heritabilities and additive genetic coefficients of variation in forest trees. Can. J. For. Res. 24: 372–379.

DANIEL, T. W., J. A. HELMS, AND F. S. BAKU. 1979. Principles of silviculture. McGraw-Hill Book Company, New York.

FEARNSIDE, P. M. 1997. Wood density for estimating forest biomass in Brazilian Amazonia. For. Ecol. Manage. 90: 59–87.

FEARNSIDE, P. M. 2005. Deforestation in Brazilian Amazonia: History, rates, and consequences. Cons. Biol. 19: 680–688.

FINEGAN, B. 1996. Pattern and process in neotropical secondary rain forests: The first 100 years. Trends Ecol. Evol. 11: 119–124.

FOREST PRODUCTS LABORATORY. 1999. Wood handbook—wood as an engineering material. General technical report FPL GTR-113. USDA Forest Service, Madison, Wisconsin.

HACKE, U. G., J. S. SPERRY, W. T. POCKMAN, S. D. DAVIS, AND K. A. MCCULLOH. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. Oecologia 126: 457–461.

KEELING, H. C., AND O. L. PHILLIPS. 2007. The global relationship between forest productivity and biomass. Glob. Ecol. Biogeog. 16: 618–631.

KING, D. A., S. J. DAVIES, S. TAN, AND N. S. M. NOOR. 2006. The role of wood density and stem support costs in the growth and mortality of tropical trees. J. Ecol. 94: 670–680.

MALHI, Y., D. WOOD, T. R. BAKER, J. WRIGHT, O. L. PHILIPS, T. COCHRANE, P. MEIR, J. CHAVE, S. ALMEIDA, L. ARROYO, N. HIGUCHI, T. J. KILLEEN, S. G. LAURANCE, W. F. LAURANCE, S. L. LEWIS, A. MONTEAGUDO, D. A. NEILL, P. N. VARGAS, N. C. A. PITMAN, C. A. QUESADA, R. SALOMÃO, J. N. M. SILVA, A. T. LEZAMA, J. TERBORGH, R. V. MARTINEZ, AND B. VINCETI. 2006. The regional variation of aboveground live biomass in old-growth Amazonian forests. Glob. Change Biol. 12: 1107–1138.

MCDONALD, S. S., G. B. WILLIAMSON, AND M. C. WIEMANN. 1995. Wood specific gravity and anatomy in Heliocarpus appendiculatus (Tiliaceae). Am. J. Bot. 82: 855–861.

NELSON, B. W., R. MESQUITA, J. PEREIRA, S. SOUZA, G. BATISTA, AND L. COUTO. 1999. Allometric regressions for improved estimates of secondary forest biomass in the central Amazon. For. Ecol. Manage. 117: 149–167.

NIKLAS, K. J. 1997. Size- and age-dependent variation in the properties of sap- and heartwood in black locust (Robinia pseudoacacia L.). Ann. Bot. 79: 473–478.

NIKLAS, K. J. 1998. The influence of gravity and wind on land plant evolution. Rev. Palaeobot. Palynol. 102: 1–14.

NOCK, C. A., D. GEIHOFER, M. GRABNER, P. J. BAKER, S. BUNYAVEJCHEWIN, AND P. HIETZ. 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, E. M., P. M. FEARNSIDE, AND B. W. NELSON. 2008a. Normalization of wood density in biomass estimates of Amazon forests. For. Ecol. Manage. 256: 990–996.

NOGUEIRA, E. M., P. M. FEARNSIDE, B. W. NELSON, R. I. BARBOSA, B. R. IMBROZIO, AND E. W. H. KEIZER. 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.

NOGUEIRA, E. M., P. M. FEARNSIDE, B. W. NELSON, AND M. B. FRANCA. 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: 119–135.

NOGUEIRA, E. M., B. W. NELSON, AND P. M. FEARNSIDE. 2005. Wood density in dense forest in central Amazonia, Brazil. For. Ecol. Manage. 208: 261–286.

OMOLODUN, O. O., B. E. CUTTER, G. F. KRAUSE, AND E. A. MCGINNES JR. 1991. Wood quality in Hildegardia barteri (Mast.) Kossern—an African tropical pioneer species. Wood Fiber Sci. 23: 419–435.

POORTER, L., S. J. WRIGHT, H. PAZ, D. D. ACKERLY, R. CONDIT, G. IBARRA-MANRÍQUEZ, K. E. HARMS, J. C. LICONA, M. MARTÍNEZ-RAMOS, S. J. MAZER, H. C. MULLER-LANDAU, M. PEÑA-CLAROS, C. O. WEBB, AND I. J. WRIGHT. 2008. Are functional traits good predictors of demographic rates? Evidence from five Neotropical forests. Ecology 89: 1908–1920.

PUTZ, F. E., P. D. COLEY, K. LU, A. MONTALVO, AND A. AIELLO. 1983. Uprooting and snapping of trees: Structural determinants and ecological consequences. Can. J. For. Res. 13: 1011–1020.

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

SANFORD, R. L., P. PAABY, J. C. LUVALL, AND E. PHILLIPS. 1994. Climate, geomorphology, and aquatic systems. In L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn (Eds). La Selva: Ecology and natural history of a neotropical rain forest, pp. 19–33. University of Chicago Press, Chicago, Illinois.

SCHNIEWIND, A. P. 1962. Horizontal specific gravity variation in tree stems in relation to their support function. For. Sci. 8: 111–118.

TURNER, I. M. 2001. The ecology of trees in the tropical rain forest, Cambridge University Press, Cambridge, UK.

WANGAARD, F. F. 1951. Tests and properties of tropical woods. Proc. For. Prod. Res. Soc. 5: 206–212.

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

WIEMANN, M. C., AND G. B. WILLIAMSON. 1988. Extreme radial changes in wood specific gravity in some tropical pioneers. Wood Fiber Sci. 20: 344–349.

WIEMANN, M. C., AND G. B. WILLIAMSON. 1989a. Radial gradients in the specific gravity of wood in some tropical and temperate trees. For. Sci. 35: 197–210.

WIEMANN, M. C., AND G. B. WILLIAMSON. 1989b. Wood specific gravity gradients in tropical dry and montane rain forest trees. Am. J. Bot. 76: 924–928.

WIEMANN, M. C., AND G. B. WILLIAMSON. 2002. Geographic variation in wood specific gravity: Effects of latitude, temperature, and precipitation. Wood Fiber Sci. 34: 96–107.

WIEPKING, C. A., AND D. V. DOYLE. 1944. Strength and related properties of balsa and quipo woods. Forest Products Laboratory, Madison, Wisconsin.

WILLIAMSON, G. B. 1984. Gradients in wood specific gravity of trees. Bull. Torrey Bot. Club 111: 51–55.

WILLIAMSON, G. B., R. C. G. MESQUITA, K. ICKES, AND G. GANADE. 1998. Estratégias de pioneiras nos Neotrôpicos. In C. Gascon and P. Moutinho (Eds). Floresta Amazônica: Dinâmica, Regeneração e Manejo, pp. 131–144. INPA, Manaus, Brazil.

WOODCOCK, D. 2000. Wood specific gravity of trees and forest types in the southern Peruvian Amazon. Acta Amazon. 30: 589–599.

WORBES, M. 1989. Growth rings, increment and age of trees in inundation forests, savannas and a mountain forest in the neotropics. IAWA Bull. 10: 109–122.

WRIGHT, I. J., D. D. ACKERLY, F. BONGERS, K. E. HARMS, G. IBARRA-MANRIQUEZ, M. MARTINEZ-RAMOS, S. J. MAZER, H. C. MULLER-LANDAU, H. PAZ, N. C. A. PITMAN, L. POORTER, M. R. SILMAN, C. F. VRIESENDORP, C. O. WEBB, M. WESTOBY, AND S. J. WRIGHT. 2007. Relationships among ecologically important dimensions of plant trait variation in seven neotropical forests. Ann. Bot. 99: 1003–1015.

WRIGHT, I. J., P. B. REICH, M. WESTOBY, D. D. ACKERLY, Z. BARUCH, F. BONGERS, J. CAVENDER-BARES, T. CHAPIN, J. H. C. CORNELISSEN, M. DIEMER, J. FLEXAS, E. GARNIER, P. K. GROOM, J. GULIAS, K. HIKOSAKA, B. B. LAMONT, T. LEE, W. LEE, C. LUSK, AND J. J. MIDGLEY. 2004. The worldwide leaf economics spectrum. Nature 428: 821–827.

ZOBEL, B. J., AND J. R. SPRAGUE. 1998. Juvenile wood in forest trees. Springer-Verlag, New York.