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RADIAL WOOD ALLOCATION IN *SCHIZOLOBIUM PARAHYBA*[1]

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- *Premise of the study:* Pioneer species of tropical trees allocate wood specific gravity (SG) differently across the radius. Some species exhibit relatively uniform, low SG wood, whereas many others exhibit linear increases in SG across the radius. Here, we measured changes in SG across the radius of *Schizolobium parahyba* (Fabaceae-Caesalpinioideae), a wide-ranging, neotropical pioneer, used extensively in land reclamation and forest restoration in Brazil.
- *Methods:* Pith-to-bark radial wood cores were extracted with increment borers from 42 trees at five sites, in Central and South America. Cores were cut into 1-cm segments whose specific gravities were determined and analyzed via linear and nonlinear regression. Wood specific gravity, very low initially at 0.15-0.20, doubled or tripled across the tree radius to 0.45-0.65 for large adults.
- *Key results:* Unlike linear increases in other tropical pioneers, the increases in *Schizolobium* were nonlinear (convex up). At one site with even-aged trees, the magnitude of the radial increase was similar in all trees, despite a 4-fold difference in diameter among trees, implying that the radial increases in *Schizolobium* were regulated by tree age, not by tree size.
- *Conclusions:* This unique pattern of development should provide an extended period of growth when SG is low, facilitating hyper-extension of the bole, at some risk of structural failure. Later in growth, the SG rate of increase accelerates, reinforcing what was a precarious bole. Overall, these results suggest a third model for xylem allocation in tropical trees, a model that may be associated with monopodial stem development and limited life span.

Key words: age-dependence; pioneers; radial variation; *Schizolobium parahyba*, size-dependence; specific gravity; succession; wood allocation; wood density.

The diversity of tropical trees has captivated botanists for centuries. Woods of different species, not only differ in appearance, but also in functional traits—density, porosity, and strength—characteristics that relate to various plant functions such as support and conduction. The specific gravity (SG) of wood is a species' trait that integrates mechanical strength properties and sometimes efficiency of conduction and resistance to embolism (Chave et al., 2009; Zanne et al., 2010). In addition, where light is limiting, growth rates and mortality rates are often inversely related to species' wood specific gravities; thus, fast growing pioneers exhibit low SG wood relative to mature forest species (Kraft et al., 2010; Wright et al., 2010).

The utility of SG as a functional trait presumes that it varies less within a species than across species. This assumption has generally proven true, as many species exhibit relatively uniform SG wood; thus species' specific gravities are regularly used to estimate global carbon stocks of forests, and sometimes to project species' demographic and successional traits (Fearnside, 1997, van Gelder et al., 2006). However, very large linear increases in SG across the diameter of a tree have been discovered in some tropical species (Wiemann and Williamson, 1988, 1989a; Amorim, 1991; Rueda and Williamson, 1992; Butterfield et al., 1993; de Castro et al., 1993; Omolodun et al., 1991; Hernandez and Restrepo, 1995; Parolin, 2002). Some pioneer species of lowland wet forests exhibit linear increases of 200–300% (Wiemann and Williamson, 1989a).

The developmental model for such pioneers is a gradual transition from fast to slow growth in height, concomitant with the transition from low SG to high SG wood as a tree gains in stature and age. This tradeoff between wood SG and wood volume translates into a functional tradeoff in tree strength and tree size. It is most apparent as a linear increase in SG across the tree radius. In a recent survey of tropical wet forest trees, 123 of 128 individuals showed a linear relationship of SG with radial distance, whereas curvilinear changes in SG were rare and regarded as aberrant (Wiemann and Williamson, in press).

Here, we report that *Schizolobium parahyba* (Vell.) S. F. Blake, a rapidly growing pioneer of the neotropics, exhibits significant radial increases that are distinctly and consistently curvilinear (convex up). This is the first report of large curvilinear increases in radial SG in any tree species, tropical or otherwise. Curvilinear increases in SG invoke an alternative growth model in which the increases in wood SG are very slow early in development and quite sharp as a tree matures.

MATERIALS AND METHODS

Study Species*—Schizolobium parahyba* is an important neotropical pioneer (Record, 1925; Poorter, 1999) ranging from Mexico to southern Brazil. It is characteristic of lowland, semideciduous tropical forest, being briefly deciduous and flowering during the dry season (Marcati et al., 2008). *Schizolobium* has been planted extensively in reforestation projects in aseasonal as well as seasonal sites, from the Amazon Basin south to São Paulo, because it is tolerant

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of mild droughts, has low nutrient requirements, and grows quickly (Carvalho, 1994; Rosales et al., 1999; Fredericksen and Pariona, 2002; Lisi et al., 2008; Iwakiri et al., 2010). Unlike many legumes used in reclamation projects, it does not nodulate and fix nitrogen (Siviero et al., 2008). Limited to high light environments, it occurs naturally in large forest gaps and does not survive in the shade (Poorter and Hayashida-Oliver, 2000). In anthropogenic landscapes, it frequents ruderal habitats, abandoned pastures, and roadsides (Fredericksen and Pariona, 2002).

Seeds of *Schizolobium*, at 2.0 g oven dry weight, are unusually large for a pioneer plant (Ibarra-Manríquez and Oyama, 1992; Souza and Válio, 2001; Daws et al., 2007; Bentos et al., 2008) and for a wind-dispersed legume (Oliveira and Pereira, 1984; Augspurger, 1986). The large seeds allow *Schizolobium* to germinate and establish in pastures where grasses preclude establishment of small-seeded pioneers. The seeds are a major component of Scarlet Macaw diets in Mexico (Renton, 2006).

The wood of *Schizolobium* is light and is used in particle board, plywood, and furniture (Carvalho, 1994, Bortoletto and Belini, 2003; Iwakiri et al., 2010; Siviero et al., 2008), although its mechanical properties are relatively low (Torelli and Gorisek, 1995). Despite extensive reports on its uses and properties over the last century (e.g., Record, 1925, Marcati et al., 2008), there is no mention of radial variation in its wood, whose specific gravity (SG) is cited as 0.30 in the Amazon (Fearnside, 1997) and as 0.35 in Central America (Rosales et al., 1999). Rosales et al. (1999) did report a range in wood SG of 0.28-0.45, variability they attributed to site differences.

***Wood sampling*—**Bark-to-pith wood samples were collected from five different sites in Costa Rica and Brazil. The largest dataset included 15 trees of *Schizolobium parahyba* from a forestry trial near Porto Seguro in the Estação Ecológica do Pau Brasil in the southern portion of the state of Bahia, Brazil (6°44' S/39°25' W). Trees in the forestry trial constituted an even-aged cohort that was maintained free of interspecific, but not intraspecific, competition (Fig. 1A). The second site was a nearby second growth stand at the same station. These trees were not necessarily the same age, so we refer to them as uneven-aged, although young second-growth stands often have even-aged cohorts of pioneers (Williamson and Wiemann, 2010b). *S. parahyba* shared the stand with a variety of other species, all about the same height (Fig. 1B). As there were no small diameter *S. parahyba* trees in the second growth stand, the trees exhibited little variation in diameter relative to the forestry trial (Fig. 1).

Trees of *Schizolobium parahyba* were sampled from a variety of second growth patches at three other sites: (1) along the Golfito airstrip on the southwest side of Costa Rica (8°39' N / 83°11' W); (2) in Brazil near Linhares in the Forest Reserve of the Companhia Vale do Rio Dôce in the state of Espirito Santo (19°07' S/40°03' W); and (3) in Ilha do Cardoso State Park in the state of São Paulo (25°04' S/47°55' W). The trees do not represent even-aged individuals or even a single, regenerating cohort.

Recent nomenclature (Barneby, 1996; Lewis, 2010) considers *Schizolobium parahyba* to be a single species ranging from Central America through southeastern Brazil, although the species distribution is interrupted twice, first by the Andes and again by dry forest between the Amazon Basin and the Brazil's Matas Atlanticas (Barneby, 1996; Canchignia-Martínez et al., 2007). These geographic disjunctions seem to be the basis for the two subspecies, one widespread, *Schizolobium parahyba* var. *parahyba* and the other endemic to Amazonia, *Schizolobium parahyba* var. *amazonicum* (Huber ex Ducke) Barneby (Lewis, 2010). Beyond the range differences, there are few documented differences between the subspecies. Trees sampled for this study did not have floral material available to collect with the wood samples. The forestry trial at Porto

Fig. 1. *Schizolobium*, a light-barked, tall, pioneer species, growing near Porto Seguro, Brazil; (A) in a forestry trial; and (B) in a mixed species second growth stand. Note the extreme diameter variation of trees about the same height in the forestry trial and the absence of small diameter *Schizolobium* in the second growth stand.

Seguro was labeled "*S. amazonicum*", corresponding to the Amazonian subspecies, although it was growing in the region of *S. parahyba* var. *parahyba*. Seeds and diaspores from all five sites sampled here appeared the same, consistent with the single species taxonomy. One modern genetic study supports a single species with disjunction of the subspecies across the Andes (Canchignia-Martínez et al., 2007).

At each site, trees were sampled as they were encountered while walking through the secondary forests or the forestry trial to obtain as broad a range of sizes as existed at each site. Some preference was given to sampling larger diameter trees as they more fully reveal radial variation in SG. Trees that were leaning, crooked, or oddly shaped were excluded as their wood often reflects past injury or abnormal stress.

Wood samples were extracted from each tree with a 12-mm diameter increment borer, and the extracted cores were examined to verify that they reached the tree pith. Cores were then sealed individually in plastic tubes to prevent damage and drying, before being transported to a nearby laboratory where they were cut into 1-cm segments measured from the pith after removal of the bark. Most of the cores hit the pith on the first or second boring. For a few that did not quite reach the pith, the radial distance assigned to the innermost 1-cm piece was estimated from convergence of the wood rays. Wood grain sometimes shifted the cutting blade, resulting in pieces slightly longer or shorter than 1.0 cm, so the green volume of each piece was measured accurately using water immersion, as described elsewhere (Wiemann and Williamson, 1988, 1989a). The pieces were then dried at 103°C to constant weight (24-48 hours) and subsequently weighed on a top-loading balance. Basic SG of each piece was calculated as ovendry weight/green volume/density of water (Williamson and Wiemann, 2010a).

Statistical analysis of specific gravity increases—For each tree, the relationship of SG on radial distance was tested via two models: linear regression and nonlinear regression using the reciprocal linear function from Statistix 9.0 (Analytical Software, Tallahassee, Florida, USA). Both linear and reciprocal linear functions require estimation of only two parameters. In the linear model, wood SG increases linearly with radial distance (r) measured from the pith, such that

$$SG = a + b * r \quad \text{(Eq. 1)}$$

where "a" is the intercept or SG at the pith and "b" is a positive slope. In the reciprocal linear model, the SG is the multiplicative inverse of a linear function of distance (or put another way, where 1/SG is a linear function of distance), such that

$$SG = 1 / (j + k * r) \quad \text{(Eq. 2)}$$

where "j" and "k" are, like "a" and "b", two constants estimated from the dataset.

For each tree, the two models were compared through their residual mean squares (RMS), where a lower RMS implies a better fit. RMS values rank models the same as Akaike's Information Criterion (AIC) when the number of parameters estimated is the same for both models. Also for the linear model, we show the *P*-value for significance of a slope different from zero ($b \neq 0$). No comparable *P*-value can be calculated directly for the reciprocal model, as there is no least squares solution.

Size- vs. age-dependence of radial increase—For trees in the even-aged stand (the forestry trial at Porto Seguro), the radial change was evaluated for size- or age-dependence by converting the radial distance to proportional distance (dividing the distance from pith to a segment by the pith-to-bark distance). As a result, the radial distances of all pieces of each core were scaled from 0 to 1.00. Trees in the forestry trial, all the same age and about the same height, were extremely variable in diameter, the result of intraspecific competition for light (Fig. 1A). If radial change in SG is determined by size (size-dependence), even-aged trees of different diameters should exhibit individual curves of SG on true distance that would be aligned; so proportional scaling would tend to disalign them somewhat. In contrast, if SG is determined by age (age-dependence), the curves of even-aged trees should be out of alignment due to size differences but proportional scaling should tend to align them. Degree of alignment for the even-aged trees was assessed visually in graphs and quantitatively by combining the entire dataset with all pieces and computing the linear and reciprocal linear regressions on true distance and then repeating both regressions on proportional distance.

RESULTS

Schizolobium parahyba from Porto Seguro exhibited SG increases across the radius that were statistically significant by linear regression in 20 of the 22 trees (Table 1). The two exceptions (Table 1, trees 157 and 164) had positive radial increases in SG, but fell short of significance ($P = 0.07$ and $P = 0.27$, respectively), possibly due to their small radii (7 and 4 cm, respectively). Overall, the radial increases appeared curvilinear in a convex or cup-shaped form as exemplified by trees 152 and 155 (Fig. 2), both with very good linear regressions and even better nonlinear fits. The reciprocal linear functions provided improved fits as evidenced graphically (Fig. 2) and by reduced residual mean squares (Table 1). In fact, the residual mean square for the reciprocal linear model was less than that of the linear model for each of the 22 trees (Table 1). The reciprocal linear regressions produced convex curves for trees in the forest trial and for trees in the second growth stand at Porto Seguro (Fig. 3A and 3B).

The reciprocal linear function is characterized by the two coefficients "j" and "k". At the pith (r = 0), the wood specific gravity is given by SG = 1/j, so "j" is the inverse of "a" in the linear function. A value of j = 5.00 at the pith indicates an initial SG of 1/5 or 0.20 (Table 1). The coefficient "k" reflects how fast the SG increases with radial distance, similar to "b" in the linear function. As the value of the term "(j + k*r)" decreases proportionally with radial distance, SG increases with acceleration as it is the multiplicative, not the additive, inverse of "(a + b*r)". The result is a convex form that more closely fits the actual data than does the linear model for *Schizolobium* (Fig. 2). These coefficients "j" and "k" (Table 1) are strongly, but not perfectly, correlated with coefficients "a" and "b" from the linear function SG = a + b*r across the 22 trees at Porto Seguro ($R = -0.93$ for "a" and "j"; $R = -0.94$ for "b" and "k").

There are two simple ways to combine the data from the 22 trees to characterize radial change in *Schizolobium parahyba* at Porto Seguro. First, the coefficients can be averaged across trees. These results are shown for even-aged and uneven-aged trees separately and for all 22 trees combined (Table 1). Alternatively, the individual pieces combined into one dataset can be analyzed for a best fit by linear and reciprocal linear regressions. The linear all-pieces regressions exhibited reduced coefficients of determination (data not shown), suggesting added variability when the regression dataset included more than one tree (Table 1). This statistical contradiction—decreased fit with larger sample size—results from different trees accelerating upward in SG at different radial distances (Fig. 3A). For even-aged trees, the all-pieces regressions were greatly improved when SG is regressed on proportional distance instead of true distance (Fig. 3, Table 1). This improvement is evident through reduced RMS for even-aged (0.0035 to 0.0017) but not for uneven-aged trees (0.0013 to 0.0017) (Table 1). The all-pieces regressions weight pieces equally, so larger trees, having more 1-cm radial pieces, are more heavily weighted.

The forestry-trial trees provided an opportunity for additional analysis with regard to size- vs. age-dependence of the radial increases in SG. Despite large differences in radius (4-23 cm), the even-aged trees seem to start around a common SG (0.16-0.26) and all accelerate to a higher SG (0.37-0.57), suggesting that the radial changes are age-dependent (Fig. 3A). Age-dependence is supported graphically for the trees as the radial changes are more similar to one another after the transformation of true distance (Fig. 3A) to proportional distance (Fig. 3C).

TABLE 1. Results of linear regression and reciprocal linear regression of radial increases in SG for 15 even-aged trees in the forestry trial and 7 uneven-aged trees from a nearby secondary forest for *Schizolobium parahyba*. N = number of 1-cm pieces in each radial core. Coefficients "a" and "b" for the linear regression with the significance value (*P*), followed by coefficients "j" and "k" for the reciprocal linear function. The reciprocal linear function is a better fit than the linear function because it has a smaller residual mean square (RMS) for each tree. Below the data for individual regressions, the all-pieces regression shows the coefficients of the overall regressions of pieces of all trees, on true distance and on proportional distance, for the even-aged trees, uneven-aged trees and both groups combined. Finally, the tree mean ±SE regression coefficients are presented.

		Linear function SG = a + b*r				Reciprocal linear function SG = 1/(j + k*r)		
Tree No.	N	a	b	*P*	RMS	j	k	RMS
Even-aged								
150	23	0.20	0.010	0.0001	0.0012	4.54	−0.11	0.0009
151	16	0.18	0.011	0.0002	0.0016	5.42	−0.18	0.0010
152	11	0.19	0.026	0.0004	0.0026	4.81	−0.28	0.0011
153	14	0.15	0.017	0.0002	0.0021	5.96	−0.27	0.0012
154	18	0.21	0.012	0.0002	0.0029	4.63	−0.14	0.0020
155	23	0.19	0.010	0.0001	0.0018	4.96	−0.12	0.0009
156	18	0.20	0.013	0.0001	0.0017	4.58	−0.14	0.0011
157	7	0.21	0.027	0.07	0.0036	4.78	−0.36	0.0027
158	6	0.21	0.053	0.03	0.0042	4.32	−0.47	0.0017
159	7	0.22	0.032	0.04	0.0037	4.52	−0.37	0.0021
160	14	0.22	0.014	0.0001	0.0018	4.30	−0.15	0.0015
161	20	0.22	0.008	0.0001	0.0014	4.50	−0.11	0.0010
162	11	0.21	0.014	0.002	0.0012	4.67	−0.19	0.0008
163	7	0.24	0.022	0.02	0.0011	4.08	−0.24	0.0007
164	4	0.26	0.034	0.27	0.0023	4.07	−0.42	0.0018
Uneven-aged								
165	18	0.20	0.010	0.0001	0.0006	4.64	−0.12	0.0004
166	14	0.16	0.020	0.0001	0.0028	5.49	−0.26	0.0012
167	18	0.20	0.011	0.0001	0.0006	4.59	−0.13	0.0004
168	12	0.19	0.011	0.001	0.0009	4.97	−0.16	0.0008
169	22	0.20	0.012	0.0001	0.0008	4.38	−0.11	0.0007
170	13	0.17	0.011	0.0001	0.0005	5.72	−0.20	0.0003
171	15	0.21	0.013	0.0001	0.0007	4.36	−0.14	0.0006
All-Pieces Regressions								
Even-aged	199	0.24	0.008	0.0001	0.0036	4.01	−0.08	0.0035
Uneven-aged	112	0.19	0.012	0.0001	0.0013	4.54	−0.12	0.0013
All Trees	311	0.22	0.010	0.0001	0.0029	4.18	−0.10	0.0028
All-Pieces, Proportional Distance								
Even-aged	199	0.20	0.20	0.0001	0.0022	5.72	−2.45	0.0017
Uneven-aged	112	0.19	0.20	0.0001	0.0019	4.76	−2.35	0.0017
All Trees	311	0.20	0.20	0.0001	0.0021	4.73	−2.41	0.0017
Tree Means ± SE								
Even-aged	15	0.21 ± 0.006	0.020 ± 0.003			4.68 ± 0.13	−0.24 ± 0.03	
Uneven-aged	7	0.19 ± 0.008	0.012 ± 0.001			4.88 ± 0.20	−0.16 ± 0.02	
All Trees	22	0.20 ± 0.005	0.018 ± 0.002			4.74 ± 0.11	−0.21 ± 0.02	
ANOVA: even/uneven-aged		*P* = 0.16	*P* = 0.13			*P* = 0.39	*P*=0.13	
		$F_{(1,20)}$ = 2.55	$F_{(1,20)}$ = 4.35			$F_{(1,20)}$ = 0.76	$F_{(1,20)}$= 2.55	

Furthermore, the all-pieces regression of SG on proportional distance was a much better fit than the all-pieces regression on true distance (Table 1), again suggesting that proportional distances aligned SG values better than true distances.

Schizolobium parahyba from the other three sites also exhibited large radial increases in SG as evidenced by 20 highly significant results for linear regressions and for reciprocal linear regressions (Table 2). The best-fit model (indicated by the arrows in Table 2) was reciprocal linear in 11 of the 20 trees and linear in 9 of 20 trees, determined by the lowest RMS. However, best-fit models were not split evenly among the three sites, as reciprocal linear proved best in 3 of 4 trees at Ilha do Cardoso, 5 of 8 trees at Linhares, but only 3 of 8 trees at Golfito. These differences in best-fit models were not reflected in site differences in the coefficients of the two models, as there were no significant differences among the three sites for "a" (ANOVA, $F_{(2, 17)} = 0.14$, $P = 0.87$) or "b" ($F_{(2, 17)} = 0.98$, $P = 0.39$) of the linear model, nor for "j" ($F_{(2, 17)} = 1.25$, $P = 0.31$) or "k" ($F_{(2, 17)} = 0.10$, $P = 0.90$) of the reciprocal linear model.

When the two Porto Seguro collections are included with the other three sites, an analysis of variance across all five sites revealed significant variation in the intercept coefficient "a" for the linear model ($F_{(4,37)} = 4.76$, $P = 0.003$, $df = 4$, PROC MIXED, SAS 9.1 (SAS Institute, Inc., Cary, North Carolina, USA)). Pair-wise comparisons of LSMeans with the Tukey-Kramer adjustment for multiple comparisons showed that the Porto Seguro forestry trial had an intercept significantly larger than either Golfito ($t = 3.29$, $df = 1$, $P = 0.02$) or Linhares ($t = 3.58$, $df = 1$, $P = 0.008$). There was no significant variation in coefficient "b" among the five sites ($F_{(4,37)} = 1.48$, $P = 0.23$). The reciprocal linear model showed parallel results in comparisons of the coefficients. Coefficient "j" exhibited significant variation among the five sites ($F_{(4,37)} = 4.12$, $P = 0.007$) and pairwise comparisons of LSMeans showed a difference between the Porto Seguro forestry trial and Linhares ($t = 3.88$, $df = 1$, $P = 0.004$), but not Porto Seguro forestry trial and Golfito. Coefficient "k" did not show significant variation among sites ($F_{(4,37)} = 0.63$, $P = 0.65$). The Porto Seguro forestry trial and Linhares

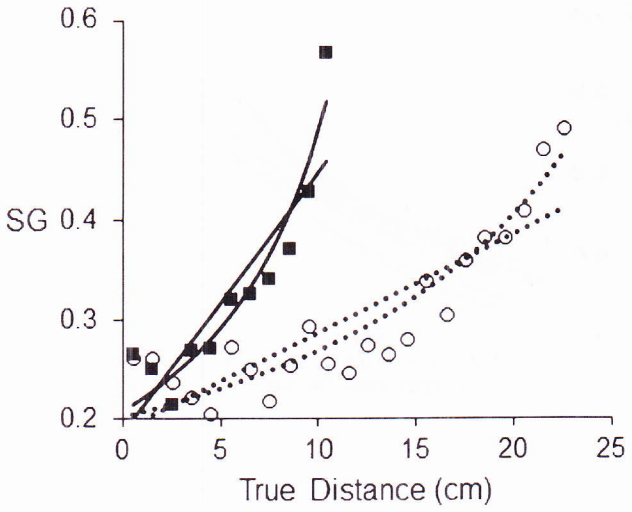

Fig. 2. Wood specific gravity (SG) across the radius of two *Schizolobium* trees from the forestry trial near Porto Seguro, Brazil. Points represent actual data and lines are linear and reciprocal linear regressions for tree #152 (solid squares and lines) and for tree #155 (open circles and dotted lines).

represented the extremes in the intercepts (coefficient "j") in the regressions based on means of the regression coefficients from each site (Fig. 4).

DISCUSSION

Extreme radial increases in tropical trees were first documented for one species, *Ochroma pyramidale* (Cav. ex Lam.) Urban, almost forty years ago (Whitmore, 1973). The number of internationally published studies on radial variation in tropical trees has increased by about twenty and the number of species studied has advanced to about 100 (Amorim, 1991; Rueda and Williamson, 1992; Butterfield et al., 1993; de Castro et al., 1993; Omolodun et al., 1991; Hernandez and Restrepo, 1995; Williamson et al., 1998; Parolin, 2002; Woodcock, 2000; Woodcock et al., 2000; Nock et al., 2009; Velásquez et al., 2009; Wiemann and Williamson, 1988, 1989a, 1989b, in press; Williamson and Wiemann, 2010b, 2011). While some of these species exhibit radial increases in SG in excess of 100%, no case has been documented of a curvilinear radial increase, as shown here for *Schizolobium parahyba*.

Characterizing curvilinear radial increases—Any of a number of nonlinear functions can describe the convex increase in SG in *Schizolobium*. We experimented with several and chose the reciprocal linear function because its parameters are relatively easy to interpret and compare. The pattern of RMS values was usually better with the reciprocal linear function than the linear function, but the pattern of residuals for a few trees showed a linear best fit whereas several others suggested a need for a function even more curved than reciprocal linear model (data not shown).

Another logical option is the extension of the linear function to second and third order polynomials. When we tested these polynomials, the cubic term was never statistically significant, while the quadratic term was included in most cases, but not all. One problem with the inclusion of the quadratic term was the tendency for the curve to be somewhat "J" shaped, because the second order polynomial characterizes a parabola. Raw data for some trees exhibited a small dip just away from the pith (see Fig. 2), so the parabola fit them, but many trees exhibited SG that increased monotonically with radial distance. Furthermore, the coefficients of the quadratic equation were difficult to interpret biologically, as the signs of the second-order term changed from tree to tree. Another common model, the exponential function ($SG = ae^{br}$), worked reasonably well in characterizing curvilinear changes in *Schizolobium*, but not quite as well as the reciprocal linear function. As yet, we have no a priori biological basis to justify one model vs. another.

Pioneer wood allocation models—Pioneers in closed canopy forests, temperate or tropical, generally exhibit low SG wood relative to nonpioneer species (Williamson, 1975; Wright et al., 2007). Here we ask how SG varies across the radius in pioneers. For many tropical montane and dry forest species, SG is relatively uniform across the radius (Model I). Production of lower SG wood usually allows faster growth because for any given biomass, SG should be inversely proportional to wood volume. The volume/SG tradeoff, in itself, does not result in a loss of mechanical support as the increased volume could be allocated to greater diameter if height were fixed. However, models assuming greater diameters at a fixed height (Anten and Schieving, 2009; Larjavaara and Muller-Landau, 2010) fail to recognize that the SG/volume tradeoff is accompanied by a diameter/height tradeoff, i.e., the extra wood volume generated by a lower SG is not allocated just to thicken the same column, but rather to increase all column dimensions (King, 1991; King et al., 2006). Because the increased volume is allocated to stature, not just diameter, pioneer boles are less stiff and more prone to snapping than comparable boles of higher SG wood. The SG/volume tradeoff swaps mechanical strength for size. In Model I, SG is uniform across the tree radius, so species with low SG wood attain size more rapidly than trees with high SG but at a cost of reduced mechanical support. The reduced support remains the same as the pioneer tree grows as long as its form and its SG remain the same.

In contrast, many tropical pioneers do not exhibit uniform SG across the radius (Fig. 4). The most prevalent pattern is SG that increases more or less linearly across the radius (Model II). Initially, these trees produce very low SG wood, sometimes leaving parenchyma cells undifferentiated in the xylem (McDonald et al., 1995; Wiemann and Williamson, in press). Then, as new xylem is added, support increases because increasingly higher SG wood is produced in cylinders further from the pith. Developmentally, relative growth rate is likely to be highest early in life, gradually, but steadily diminishing as higher SG of new xylem implies reduced volumetric gains.

In the case of *Schizolobium*, the unique feature of the SG increase is its convex upward, curvilinear shape (Model III). SG increases at less than a linear rate early in development, but accelerates as the tree grows. Given the wood volume/SG tradeoff, Model III trees can be expected to grow very quickly in height, but at much greater risk of structural failure than pioneers with linear increases in SG. Specific adaptations in tree architecture such as monopodial stems and symmetrical form may partially offset the risk of stem collapse or bending failure. Later in development, these adaptations may be unnecessary after SG has accelerated and stabilized tree structure.

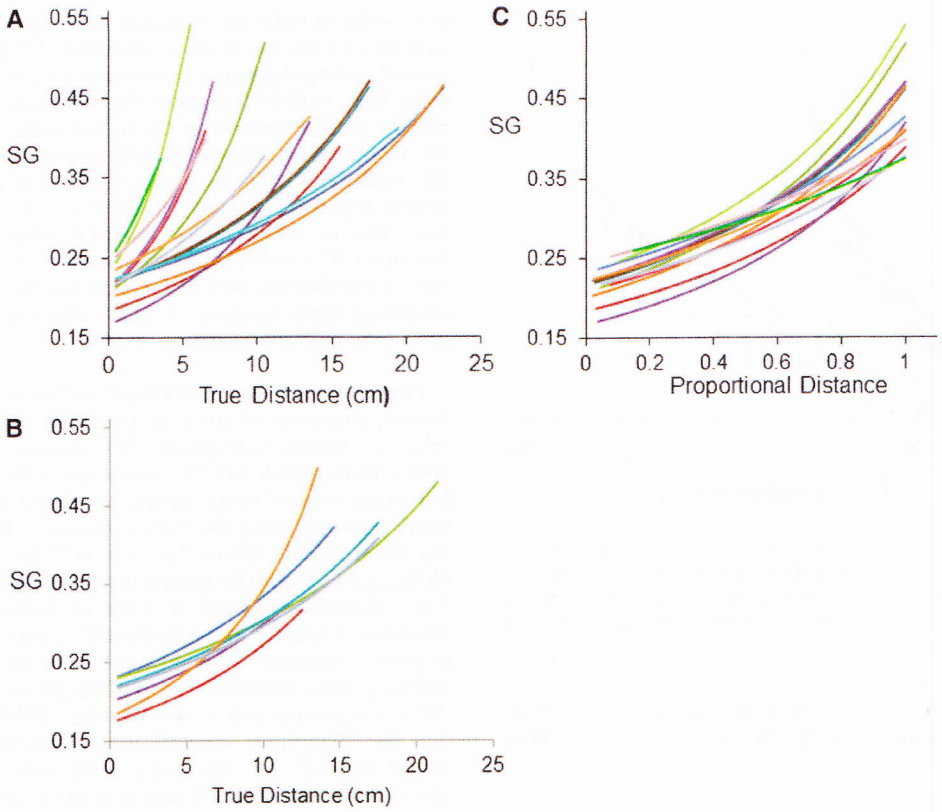

Fig. 3. Wood specific gravity across the true radial distance as modeled by the reciprocal linear regression for *Schizolobium parahyba*: (A) for 15 trees from the forestry trial; (B) for 7 trees from the nearby second growth stand; and (C) for the 15 trees from the forestry trial replotted as a function of proportional radial distance. The latter (C) aligns the curves better than true distance (A).

Schizolobium does exhibit risk-reducing architecture when it is young. It has a monopodial form during early growth with large compound leaves, 1-2 m long, originating around a single bole, hence the English common names, "Mexican Fern Tree" and "Brazilian Fern Tree". Even so, *Schizolobium* is highly vulnerable to wind damage, especially during the first three years of growth (Rondon, 2002). Growth is very rapid with plantation seedlings reaching 20 m tall and 20 cm dbh in only 60 mo when widely spaced (Rosales et al., 1999; Rondon, 2002). In a growth trial outside Manaus, Brazil, *Schizolobium* reached 15 m tall in four years, triple the height of *Ceiba pentandra* (L.) Gaertn., a well known pioneer with linear increases in SG (Wiemann and Williamson, 1989a; Rossi et al., 2003). Maximum height in a Bolivian forest was recorded at 35 m, somewhat taller than other co-occurring pioneers (Rozendaal et al., 2006). Large *Schizolobium* trees exhibit a branched, open crown, not a monopodium.

Given that radial variation in SG is a function of age, not size in *Schizolobium*, then tree size will be limited by growth rate, not time. For example, the self-thinning trees in the forestry trial grew more slowly than the second growth trees at the other four sites (Fig. 4). As SG cannot continue to rise indefinitely, growth of a Model III species may be limited to some maximum age by the accelerating SG (Fig. 2). In general, fast-grown individuals will reach large diameters while slow-grown trees reach only small diameters, but all will accelerate SG on the same time schedule. Slow-grown individuals will never catch up to the diameters of fast-grown trees, regardless of time, because the radial shift in SG occurs regardless of size. Presumably, reproduction completely replaces growth at some age. *Schizolobium* appears to be one of the short-lived tropical pioneers (sensu Finegan, 1996) as it disappears from successional sequences in about 20 yr (Peña-Claros, 2003).

How does the nonlinear radial increase in SG of *Schizolobium parahyba* compare to SG of other tropical trees? For graphical comparison (Fig. 4), we show its radial increase with the radial SG patterns of four common pioneers: Two from tropical-dry forests characteristic of Model I, *Enterolobium cyclocarpum* (Jacq.) Griseb. and *Pseudobombax septinatum* (Jacq.) Dugand; and two from tropical-wet forests characteristic of Model II, *Ochroma pyramidale* and *Trema micrantha* (L.) Blume (data from Wiemann and Williamson, 1988, 1989a, 1989b). In general, growth rates of trees can be predicted from wood SG (Wright et al., 2010), but only if they have similar growth models, as illustrated for *Enterolobium* vs. *Pseudobombax* (Model I) or for *Ochroma* vs. *Trema* (Model II).

Allocation of resources from rapid height growth when young to production of stronger wood as a place in the canopy is attained may have evolved in response by some shade-intolerant tropical trees to intense competition for light. Survival of young trees depends primarily on obtaining adequate light, but older trees require stems constructed strongly enough to support greater mass and larger crowns. Concentration of dense wood at a great distance from the neutral axis of a stem (the

TABLE 2. Results of linear regression and reciprocal linear regression of radial increases in SG for trees at three sites, Ilha do Cardoso, Linhares, and Golfito. Coefficients "a" and "b" for the linear regression with the significance value (*P*), followed by coefficients "j" and "k" for the reciprocal linear function. Arrows point to the best-fit model, determined by the smallest residual mean square (RMS). Below the data for individual trees, the all-pieces regression shows the coefficients of the overall regressions of pieces of all trees on true distance for trees at the three sites. Finally, the tree mean (±SE, SE) regression coefficients for each site are presented.

		Linear function SG = a + b*r					Reciprocal function SG = 1/(j + k*r)		
Tree Number	N	a	b	*P*	RMS		j	k	RMS
Cardoso									
60	11	0.12	0.020	0.0001	0.0002	←	6.56	−0.35	0.0003
23	20	0.17	0.013	0.0001	0.0014	→	5.19	−0.16	0.0008
24	14	0.14	0.024	0.0001	0.0009	→	5.50	−0.27	0.0006
59	17	0.23	0.009	0.0001	0.0013	→	4.27	−0.10	0.0012
Linhares									
48	40	0.16	0.006	0.0001	0.0016	→	5.53	−0.09	0.0010
50	26	0.17	0.009	0.0001	0.0005	→	5.04	−0.10	0.0002
X1	16	0.12	0.009	0.0001	0.0002	←	7.11	−0.22	0.0003
X2	10	0.13	0.017	0.0001	0.0003	→	6.80	−0.38	0.0002
X3	9	0.12	0.023	0.0001	0.0001	←	6.74	−0.44	0.0003
X4B	31	0.18	0.006	0.0001	0.0003	→	4.92	−0.07	0.0002
X5	20	0.14	0.013	0.0001	0.0014	→	5.81	−0.18	0.0010
X7B	19	0.16	0.010	0.0001	0.0002	←	5.44	−0.14	0.0060
Golfito									
175	20	0.10	0.019	0.0001	0.0010	←	5.81	−0.20	0.0012
177	29	0.08	0.016	0.0001	0.0016	←	5.52	−0.13	0.0035
178	17	0.10	0.027	0.0001	0.0009	←	5.31	−0.22	0.0017
179	23	0.24	0.007	0.0001	0.0010	←	3.88	−0.06	0.0011
180	11	0.13	0.014	0.0001	0.0005	→	6.89	−0.34	0.0003
181	9	0.17	0.028	0.0026	0.0022	→	5.19	−0.35	0.0014
182	17	0.26	0.005	0.0002	0.0004	→	3.79	−0.05	0.0003
183	20	0.12	0.015	0.0001	0.0007	←	5.25	−0.14	0.0015
All-Pieces Regressions									
Cardoso	62	0.18	0.014	0.0001	0.0019		4.79	−0.14	0.0020
Linhares	170	0.18	0.006	0.0001	0.0016		4.90	−0.07	0.0019
Golfito	146	0.17	0.013	0.0001	0.0034		4.52	−0.10	0.0043
All-Pieces, Proportional Distance									
Cardoso	62	0.17	0.224	0.0001	0.0020		5.20	−2.85	0.0017
Linhares	170	0.15	0.214	0.0001	0.0018		5.56	−3.03	0.0017
Golfito	146	0.15	0.294	0.0001	0.0034		5.10	−3.00	0.0037
Tree Means ± SE									
Cardoso	4	0.16 ± 0.023	0.016 ± 0.003				5.38 ± 0.47	−0.22 ± 0.06	
Linhares	8	0.15 ± 0.008	0.012 ± 0.002				5.92 ± 0.30	−0.20 ± 0.05	
Golfito	8	0.15 ± 0.024	0.016 ± 0.003				5.20 ± 0.36	−0.19 ± 0.04	

pith, in a symmetrical tree) may be an ideal means for constructing a strong, rigid stem from a given amount of material. Such a construction is also evident in arborescent palms of the wet tropics. Rich (1987) reported that the basic SG of inner stem tissue was 0.1 in *Iriartea gigantea* Wendl. ex Burret and 0.3 in *Welfia georgii* Wendl. ex Burret, but the basic SG of outer tissue in both species was 1.0.

While structural stability of wood may increase during development in species with increasing wood SG, structural risk may also vary. As a tree grows, it experiences different structural risks. In the understory, risk comes from falling debris such as palm leaves and dead branches. In the middle strata, risk is reduced from debris but enhanced by falling trees. Finally, in the canopy risk is reduced from falling debris and falling trees, but heightened by wind throw. Additionally, vine and epiphyte loads may alter structural risk during growth. Total structural risk at any time is the sum of several factors, and this sum may vary as the tree develops. It also may vary as surrounding vegetation changes. For example, species growing in pure successional stands in which tree heights are relatively even experience little risk from falling debris. Consequently, lower SG for an extended period in Model III trees may not entail greater risk, even though a tree is structurally less stable, if growth form helps mediate danger, as is the case of branchless, monopodial stems of *Schizolobium*. Unfortunately, little data are available on the sources of tree mortality at different sizes and under different growing conditions to make comparisons.

Discussion of wood SG, growth rates, structural stability, and risk presents an incomplete snapshot of a species' life-history as other functional traits contribute to success. *Schizolobium* has large seeds that allow it to establish quickly, even where ground cover and/or litter are relatively thick. For example, it recruits into managed pastures and airport grass strips in Costa Rica and southeastern Brazil, sites where potential small-seeded competitors, such as *Cecropia* species, are unable to establish. The added endosperm of the large seeds also fosters rapid growth in its first year, unlike small-seeded species. In forestry trials *Schizolobium* seedlings reached 3 m in height after one year, 13 m after two years and 18 m in height after five years (Rosales et al., 1999; Rondon, 2002). Therefore, speculation on growth rates based solely on wood SG may be misleading, as seed size may give *Schizolobium* a competitive edge over other pioneers, even those with lower wood SG. Its large seeds clearly facilitate its establishment

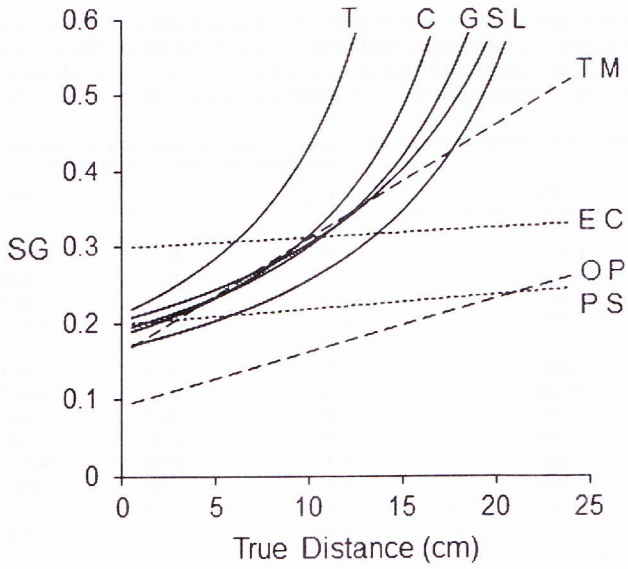

Fig. 4. Specific gravity trends for Model I (dotted lines), Model II (dashed lines), and Model III (solid lines). Straight lines are the linear regressions of SG on radial distance for *Ochroma pyramidale* = OP and *Trema micrantha* = TM for Model I, and *Pseudobombax septenatum* = PS and *Enterolobium cyclocarpum* = EC for Model II, from Costa Rica (Wiemann and Williamson 1988, 1989a, 1989b). Curved lines are *Schizolobium* from one forestry trial = T, and four second growth sites: Ilha do Cardoso, Brazil = C; Golfito, Costa Rica = G; Porto Seguro, Brazil = S; and Linhares, Brazil = L.

in restoration projects on intensively used, denuded areas (Siviero et al., 2008).

Forest ecologists have long recognized that wood SG is associated with other plant attributes and that lower SG woods characterize early successional or pioneer species and higher SG woods, more mature or climax species (Budowski, 1965; Daubenmire, 1974; Williamson, 1975; Swaine and Whitmore, 1988). In the last five years, wood SG has become increasingly topical as plant biologists searched for meaningful functional traits and attempted to unfold its ecological and evolutionary significance, especially in species-rich tropical forests where species life-history traits are relatively unstudied (Muller-Landau, 2004; Chave et al., 2006, 2009; King et al., 2006; van Gelder et al., 2006; Wright et al., 2007; Swenson and Enquist, 2007, 2008; Poorter et al., 2006). Wood SG has been associated with other functional traits such as growth rate, shade tolerance, maximum size, longevity, and light-compensation point, and tied as well, although less directly, to reproductive traits such as first age of reproduction, fecundity, seed size, seeds per fruit, and fruit size (Wright et al., 2007; Poorter et al., 2008). In many of these studies, wood SG has proven more predictive than other functional traits of demographic and successional characteristics. SG might prove even more useful if it were characterized by variation during ontogeny rather than just a single species' average. Obviously, many species can share a single mean SG value but still exhibit different SG developmental patterns, as shown here for *Schizolobium parahyba*. Analysis of wood during development helps define different life-history strategies within the framework now characterized as pioneers.

LITERATURE CITED

AMORIM, L. C. 1991. Estudo da biomassa aerea de floresta tropical umida de terra firme. Relatorio Final, Instituto Nacional de Pesquisas da Amazônica (INPA), Manaus, Amazonas, Brazil.

ANTEN, N. P. R., AND F. SCHIEVING. 2009. The role of wood mass density and mechanical constraints in the economy of tree architecture. *American Naturalist* 175: 250–260.

AUGSPURGER, C. 1986. Morphology and dispersal potential of wind-dispersed diaspores of neotropical trees. *American Journal of Botany* 73: 353–363.

BARNEBY, R. C. 1996. Neotropical Fabales at NY: Asides and oversights. *Brittonia* 48: 174–187.

BENTOS, T. V., R. C. G. MESQUITA, J. L. CAMARGO, AND G. B. WILLIAMSON. 2008. Reproductive phenology of Central Amazonia pioneer species in *Cecropia*-dominated secondary forests. *Tropical Conservation Science* 1: 186–203.

BORTOLETTO, G. JR., AND U. L. BELINI. 2003. Veneer and plywood production of guapuruvu wood (*Schizolobium parahyba* Blake) coming from a mixed plantation of Brazilian tree species. *Cerne* 9: 16–28.

BUDOWSKI, G. 1965. Distribution of tropical American rain forest species in the light of successional processes. *Turrialba* 15: 40–42.

BUTTERFIELD, R. P., R. P. CROOK, R. ADAMS, AND R. MORRIS. 1993. Radial variation in wood specific gravity, fibre length, and vessel area for two Central American hardwoods: *Hyeronima alchorneoides* and *Vochysia guatemalensis*. *IAWA Journal* 14: 153–161.

CANCHIGNIA-MARTÍNEZ, H. F., S. HERNÁNDEZ-DELGADO, M. GONZÁLEZ-PAZ, E. MOTTE, AND N. MAYEK-PÉREZ. 2007. Genetic relationships among *Schizolobium parahybum* (Vell.) Blake (Leguminosae) ecotypes from Ecuador and other countries. *Silvae Genetica* 56: 214–221.

CARVALHO, P. E. R. 1994. Espécies florestais brasileiras: Recomendaçoẽs silviculturais, potencialidades e usos da madeira. Empresa Brasileira de Pesquisa Agropecuária-Centro Nacional de Pesquisa de Florastas (EMBRAPA-CNPF), Colombo, Parana, Brazil; and Empresa Brasileira de Pesquisa Agropecuária-SPI (EMBRAPA-SPI), Brasília, Distrito Federal, Brazil.

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

CHAVE, J., H. C. MULLER-LANDAU, T. R. BAKER, T. A. EASDALE, H. TER STEEGE, AND C. O. WEBB. 2006. Regional and phylogenetic variation of wood density across 2456 neotropical tree species. *Ecological Applications* 16: 2356–2367.

DAUBENMIRE, R. F. 1974. Plants and environment: A textbook of plant autecology. 3rd edition. John Wiley, New York, New York, USA.

DAWS, M. I., C. BALLARD, C. E. MULLINS, N. C. GARWOOD, B. MURRAY, T. R. H. PEARSON, AND D. F. R. P. BURSLEM. 2007. Allometric relationships between seed mass and seedling characteristics reveal trade-offs for neotropical gap-dependent species. *Oecologia* 154: 445–454.

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.

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

FINEGAN, B. 1996. Pattern and process in neotropical secondary rain forests: The first 100 years. *Trends in Ecology & Evolution* 11: 119–124.

FREDERICKSEN, T. S., AND W. PARIONA. 2002. Effect of skidder disturbance on commercial tree regeneration in logging gaps in a Bolivian tropical forest. *Forest Ecology and Management* 171: 223–230.

HERNANDEZ, R. E., AND G. RESTREPO. 1995. Natural variation in wood properties of *Alnus acuminata* H.B.K. grown in Colombia. *Wood and Fiber Science* 27: 41–48.

IBARRA-MANRÍQUEZ, G., AND K. OYAMA. 1992. Ecological correlates of reproductive traits of Mexican rain forest trees. *American Journal of Botany* 79: 383–394.

IWAKIRI, S., F. ZELLER, J. A. PINTO, M. G. L. RAMIREZ, M. M. SOUZA, AND R. SEIXAS. 2010. Avaliação do potencial de utilização da madeira de *Schizolobium amazonicum* "Paricá" e *Cecropia hololeuca* "Embaúba" para produção de painéis aglomerados. *Acta Amazonica* 40: 303–308.

KING, D. A. 1991. Correlations between biomass allocation, relative growth rate and light environment in tropical forest saplings. *Functional Ecology* 5: 485–492.

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. *Journal of Ecology* 94: 670–680.

KRAFT, N. J. B., M. R. METZ, R. S. CONDIT, AND J. CHAVE. 2010. The relationship between wood density and mortality in a global tropical forest data set. *New Phytologist* 188: 1124–1136.

LARJAVAARA, M., AND H. C. MULLER-LANDAU. 2010. Re-thinking the value of high wood density. *Functional Ecology* 24: 701–705.

LEWIS, G. P. 2010. *Schizolobium in* Lista de espécies da flora do Brasil. Jardim Botânico do Rio de Janeiro, Brazil. Website *http://floradobrasil.jbrj.gov.br/2010/FB023142* [accessed 26 April 2012].

LISI, C. S., M. TOMAZELLO F., P. C. BOTOSSO, F. A. ROIG, V. R. B. MARIA, L. FERREIRA-FEDELE, AND A. R. A. VOIGT. 2008. Tree-ring formation, radial increment periodicity, and phenology of tree species from a seasonal semi-deciduous forest in southeast Brazil. *IAWA Journal* 29: 189–207.

MARCATI, R. C., C. R. D. MILANEZ, AND S. R. MACHADO. 2008. Seasonal development of secondary xylem and phloem in *Schizolobium parahyba* (Vell.) Blake (Leguminosae: Caesalpinioideae). *Trees (Berlin)* 22: 3–12.

MCDONALD, S. S., G. B. WILLIAMSON, AND M. C. WIEMANN. 1995. Wood specific gravity and anatomy in *Heliocarpus appendiculatus* (Tiliaceae). *American Journal of Botany* 82: 855–861.

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

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. *Annals of Botany* 104: 297–306.

OLIVEIRA, E. C., AND T. S. PEREIRA. 1984. Morfologia dos frutos alados em Leguminosae-Caesalpinoideae. *Martiodendron* Gleason, *Peltophorum* (Vogel) Walpers, *Sclerolobium* Vogel, *Tachigalia* Aublet e *Schizolobium* Vogel. *Rodriguesia* 36: 35–42.

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

PAROLIN, P. 2002. Radial gradients in the wood specific gravity in trees of the Central Amazonian floodplains. *IAWA Journal* 23: 449–457.

PEÑA-CLAROS, M. 2003. Changes in forest structure and species composition during secondary forest succession in the Bolivian Amazon. *Biotropica* 35: 450–461.

POORTER, L. 1999. Growth responses of 15 rain-forest tree species to a light gradient: The relative importance of morphological and physiological traits. *Functional Ecology* 13: 396–410.

POORTER, L., L. BONGERS, AND F. BONGERS. 2006. Architecture of 54 moist-forest tree species: Traits, trade-offs, and functional groups. *Ecology* 87: 1289–1301.

POORTER, L., AND Y. HAYASHIDA-OLIVER. 2000. Effects of seasonal drought on gap and understorey seedlings in a Bolivian moist forest. *Journal of Tropical Ecology* 16: 481–498.

POORTER, L., S. J. WRIGHT, H. PAZ, D. D. ACKERLY, R. CONDIT, G. IBARRA-MANRÍQUEZ, K. E. HARMS, ET AL. 2008. Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. *Ecology* 89: 1908–1920.

RECORD, S. J. 1925. *Schizolobium*: A promising source of pulpwood. *Tropical Woods* 1: 2–5.

RENTON, K. 2006. Diet of adult and nestling Scarlet Macaws in southwest Belize, Central America. *Biotropica* 38: 280–283.

RICH, P. M. 1987. Mechanical structure of the stem of arborescent palms. *Botanical Gazette (Chicago, Ill.)* 148: 42–50.

RONDON, E. V. 2002. Produção de biomassa e crescimento de árvores de *Schizolobium amazonicum* (Huber) Ducke sob diferentes espaçamentos na região de mata. *Revista Árvore* 26: 573–576.

ROSALES, L., F. S. WIJOYO, W. S. DVORAK, AND J. L. ROMERO. 1999. Parametros genéticos y variacion entre procedencias de *Schizolobium parahybum* (Vell.) Blake establecidas en Venezuela. *Foresta Veracruzana* 1: 13–18.

ROSSI, L. M. B., C. P. AZEVEDO, C. R. SOUZA, AND R. M. B. LIMA. 2003. Potential forest species for plantations in Brazilian Amazonia. Paper submitted to the XII World Forestry Congress, Quebec City, Canada. Website http://www.fao.org/docrep/article/wfc/xii/0537-b1.htm [accessed 26 April 2012].

ROZENDAAL, D. M. A., V. H. HURTADO, AND L. POORTER. 2006. Plasticity in leaf traits of 38 tropical tree species in response to light; relationships with light demand and adult stature. *Functional Ecology* 20: 207–216.

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.

SIVIERO, M. A., A. M. MOTTA, D. S. LIMA, R. R. BIROLLI, S. Y. HUH, I. A. SANTINONI, L. S. MURATE, ET AL. 2008. Interaction among N-fixing bacteria and AM fungi in Amazonian legume tree (*Schizolobium amazonicum*) in field conditions. *Applied Soil Ecology* 39: 144–152.

SOUZA, R. P. DE, AND I. F. M. VÁLIO. 2001. Seed size, seed germination, and seedling survival of Brazilian tropical tree species differing in successional status. *Biotropica* 33: 447–457.

SWAINE, M. D., AND T. C. WHITMORE. 1988. On the definition of ecological species groups in tropical rainforests. *Vegetatio* [*Plant Ecology*] 75: 81–86.

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

SWENSON, N. G., AND B. J. ENQUIST. 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.

TORELLI, N., AND Z. GORISEK. 1995. Mexican tropical hardwoods: Mechanical properties in green condition. *Holz als Roh- und Werkstoff [European Journal of Wood and Wood Products]* 53: 421–423.

VAN GELDER, H. A., L. POORTER, AND F. J. STERCK. 2006. Wood mechanics, allometry and life-history variation in a tropical rain forest tree community. *New Phytologist* 171: 367–378.

VELÁSQUEZ, J., M. E. TORO, L. GÓMEZ, F. M. TERZO, AND A. MÁRQUEZ. 2009. Patrón de variación axial y radial del peso específico en la madera de *Erisma uncinatum* Warm. *Interciencia* 34: 873–879.

WHITMORE, J. L. 1973. Wood density variation in Costa Rican balsa. *Wood and Fiber Science* 20: 223–229.

WIEMANN, M. C., AND G. B. WILLIAMSON. 1988. Extreme radial changes in wood specific gravity in some tropical pioneers. *Wood and Fiber Science* 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. *Forest Science* 35: 197–210.

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

WIEMANN, M. C., AND G. B. WILLIAMSON. 2012. Testing a novel method to approximate wood specific gravity of trees. *Forest Science* 58: in press.

WILLIAMSON, G. B. 1975. Pattern and seral composition in an old-growth beech-maple forest. *Ecology* 56: 727–731.

WILLIAMSON, G. B., R. C. G. MESQUITA, K. ICKES, AND G. GANADE. 1998. Estratégias de colonizaçion de ávores pioneiras nos Neotrôpicos. *In* C. Gascon and P. Moutinho [eds.], Floresta Amazônica: Dinâmica, regeneração e manejo, 131-144. Instituto Nacional de Pesquisas da Amazônica (INPA), Manaus, Amazonas, Brazil.

WILLIAMSON, G. B., AND M. C. WIEMANN. 2010a. Measuring wood specific gravity...correctly. *American Journal of Botany* 97: 519–524.

WILLIAMSON, G. B., AND M. C. WIEMANN. 2010b. Age-dependent radial increases in wood specific gravity of tropical pioneers in Costa Rica. *Biotropica* 42: 590–597.

WILLIAMSON, G. B., AND M. C. WIEMANN. 2011. Radial variation in wood specific gravity: Lessons from eccentrics. *Trees: Structure and Function* 4: 585–591.

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

WOODCOCK, D. W., G. DOS SANTOS, AND D. TAYLOR. 2000. The buttressed blue marble tree: Wood and growth characteristics of *Elaeocarpus angustifolius* (Elaeocarpaceae). *Annals of Botany* 85: 1–6.

WRIGHT, I. J., D. D. ACKERLY, F. BONGERS, K. E. HARMS, G. IBARRA-MANRÍQUEZ, M. MARTÍNEZ-RAMOS, S. J. MAZER, ET AL. 2007. Relationships among ecologically important dimensions of plant trait variation in seven neotropical forests. *Annals of Botany* 99: 1003–1015.

WRIGHT, S. J., K. KITAJIMA, N. J. B. KRAFT, P. B. REICH, I. J. WRIGHT, D. E. BUNKER, R. CONDIT ET AL. 2010. Functional traits and the growth mortality trade-off in tropical trees. *Ecology* 91: 3664–3674.

ZANNE, A. E., M. WESTOBY, D. S. FALSTER, D. D. ACKERLY, S. R. LOARIE, S. E. J. ARNOLD, AND D. A. COOMES. 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.