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Radial and Vertical Wood Specific Gravity in *Ochroma pyramidale* (Cay. ex Lam.) Urb. (Bombacaceae)[1]

Ricardo Rueda

Departamento de Biología, Universidad Nacional Autónoma de Nicaragua, León, Nicaragua and Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, U.S.A.
and
G. Bruce Williamson
Department of Botany, Louisiana State University, Baton Rouge, Louisiana 70808, U.S.A.

ABSTRACT

Radial (pith-to-bark) wood samples from *Ochroma pyramidale* sampled at breast height and at subsequent five meter height intervals were analyzed to determine basic specific gravity. Specific gravity increased linearly with radial distance at any given height. In multiple regressions both radial distance and height proved to be equally important independent variables in explaining variation in specific gravity. However, when radial distance was measured centripetally (bark-to-pith) rather than centrifugally (pith-to-bark), the importance of height diminished drastically. These results suggest that the secondary xylem produced at any one time along the bole exhibits the same specific gravity. This time-constant model is contrasted with the alternative extreme, the radius-constant model, where xylem at a given radial distance (pith-to-bark) would exhibit the same specific gravity. Both models present alternative developmental patterns for tropical wet forest species which commonly exhibit increases in specific gravity with distance from the pith.

RESUMEN

Muestras de madera de la médula a la corteza de *Ochroma pyramidale,* obtenidas a la altura del pecho y a intervalos de cinco metros a lo largo del fuste principal, fueron analizadas, determinándose así su gravedad especifica. La gravedad específica aumentó linealmente de Ia médula a Ia corteza en las diferentes alturas muestreadas. En múltiples regresiones, tanto Ia distancia de Ia médula a La corteza como la altura demostraron ser variables independientes, de igual importancia para explicar Ia variación en gravedad especifica. Sin embargo, cuando la gravedad específica se midió de la corteza a Ia médula y no a Ia inversa, la importancia de altura disminuyó significativamente. Estos resultados sugieren que el xilema secundario producido a un mismo tiempo a lo largo del fuste principal tiene una misma gravedad específica sin importar Ia distancia de este a La médula. Este modelo de tiempo constante se contrapone al modelo de radio constante, en el cual el xilema localizado a una misma distancia de la médula tendría una misma gravedad especifica. Ambos modelos representan patrones alternativos de desarrollo para especies del bosque húmedo tropical que frecuentemente muestran incremento en gravedad específica con el aumento de Ia distancia de Ia médula.

Key words: Costa Rica; Ochroma pyramidale; *radial growth; tropical wet forest; wood specific gravity.*

THE SPECIFIC GRAVITY OF TRUNKWOOD reflects important life history attributes of arboreal species. Trees with wood of low specific gravity usually grow rapidly (Wiemann & Williamson 1988), require full sunlight (Williamson 1975), reproduce at an early age (Williamson 1975) and are subject to snapping of the bole (Putz 1983). Species in successional sequences often are ranked in order of increasing wood specific gravity. In addition, specific gravity has important practical applications. It is related to wood attributes such as cutting forces required in machining, dimensional stability, mechanical strength, paper-forming properties, shrinkage, treatability with preservatives, value as fuel, as well as acoustical, electrical, and thermal insulating properties (Chudnoff 1984). As a result, wood specific gravity is the single most important index to the potential use of a species.

Wood specific gravity is extremely variable among species, ranging from 0.05 for *Aeschynomene hispida* Willd. to 1.08 for *Dalbergia melanoxylon* G. & P. (Kanehira 1933). Differences in specific gravity among species are more pronounced in the tropics than in the temperate zone (Howe 1974, Williamson 1984, Wiemann & Williamson 1989a). Moreover, due to environmental and genetic influences, wood specific gravity varies among trees of

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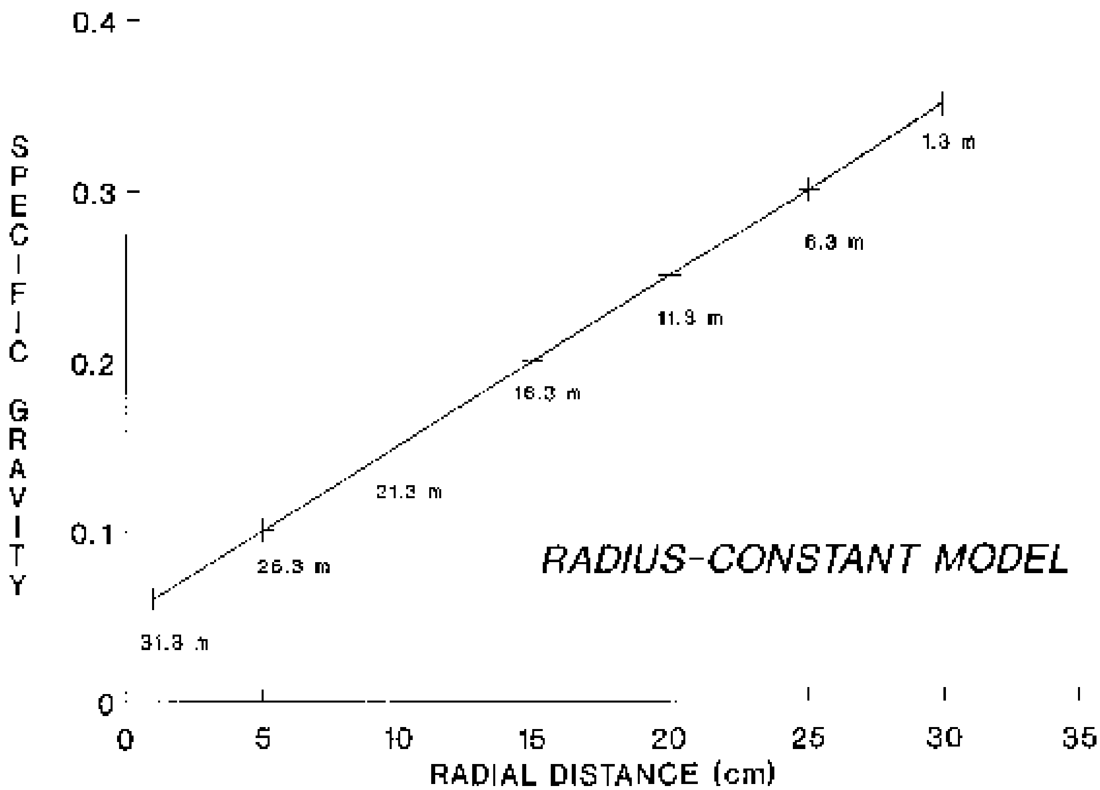

FIGURE 1. Wood specific gravity as function of radial distance from pith at heights from 1.3 m to 31.3 m, for the radius-constant model. Points indicate the bole radius at each height.

the same species; however, temperate tree species have sufficiently consistent specific gravities that each is characterized by a narrow range of values (Panshin & DeZeeuw 1980).

Exceptional variation in wood specific gravity has been documented within trees in the humid tropics (Whitmore 1973; Wiemann & Williamson 1988, 1989b). Whitmore (1973) first documented radial increases in *Ochroma pyramidale.* Wiemann and Williamson (1988) suggested that the radial increase in wood specific gravity in this species is related to its role as a pioneer in the wet lowland tropics. *Ochroma pyramidale* is a fast growing species, capable of reaching 6 cm dbh and 5 m in height in the first year and 60 cm dbh and 20 m in height in 20 years (Brush 1945). Wood with very low specific gravity is produced in the first few years, followed by wood of higher specific gravity as more structural support is needed (Wiemann & Williamson 1988). Pith-to-bark increases may reach 200 percent in pioneer species in lowland rain forests. Variation in specific gravity with height may also be important (Panshin & DeZeeuw 1980), although what little information exists for tropical species is often anecdotal (Greenhouse 1935).

In the present study we investigated the radial changes in specific gravity in *Ochrorna pyramidale* as a function of height on the trunk. This is the first study of vertical variation in the radial increase in wood specific gravity. We examined the radial increase in specific gravity at 5 m height intervals. Statistically, we tested whether specific gravity varied as a function of radial distance and as a function of height. Two models of the interaction of height and radial variation are proposed, based on preliminary data of one *Ochroma pyramidale* and one *Cecropia obtusifolia* Bertol. (Wiemann, pers. comm.). The radius-constant model assumes that all wood produced at a given radius, regardless of height, has the same specific gravity (Fig. 1). If radial distance is measured centrifugally (pith-to-bark), then a linear regression of specific gravity on radial distance and height would find distance, but not height, to be a significant independent variable. Alternatively, the time-constant model assumes that all wood produced at a given time, regardless of height, has the same specific gravity (Fig. 2). If radial distance is again measured centrifugally (pith-to-bark), then a linear regression of specific gravity on radial distance and height would find both distance and height to

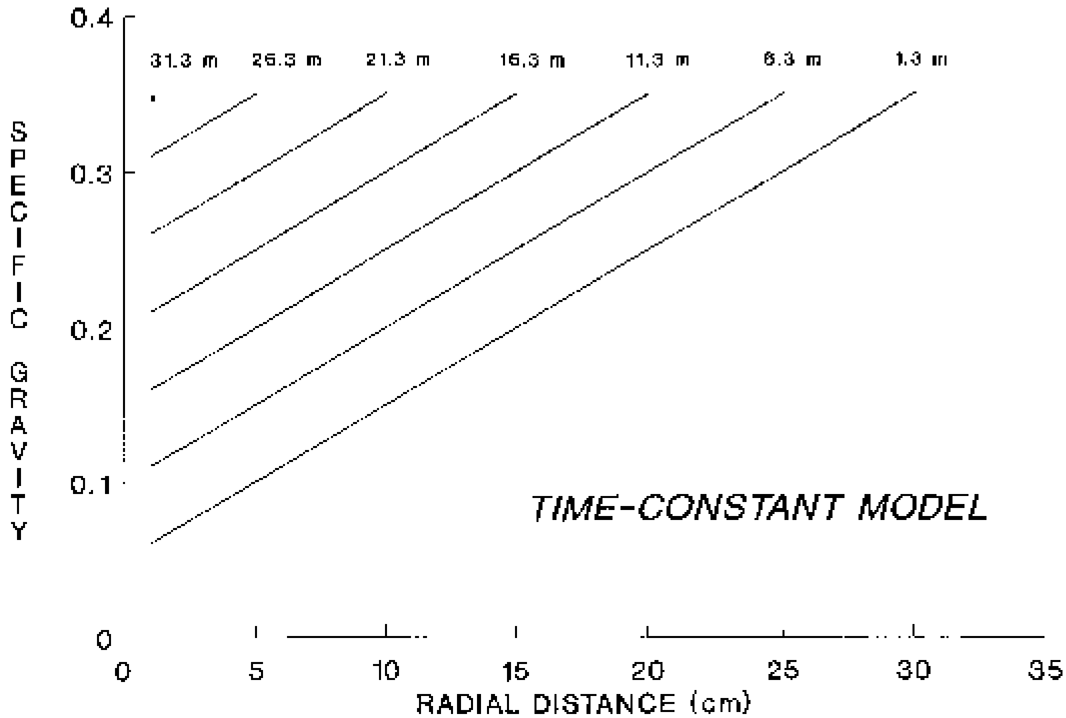

FIGURE 2. Wood specific gravity as function of radial distance from pith at heights from 1.3 m to 3 1.3 m, for the time-constant model (right).

be significant independent variables. However, if radial distance is measured centripetally (bark-to-pith), then a linear regression on radial distance and height will find radial distance, but not height, to be a significant independent variable.

Although the radius-constant and the time-constant models are only two of an infinite number of possible interactions of radial distance and height in determining specific gravity, they represent two testable models that may embody the biological limits of the interactions.

METHODS

The study area was dominated *by Ochroma pyramidale* trees that had colonized a cacao plantation, abandoned in August of 1984. The site, known previously as 'Hunter's Point," lies at the confluence of the Rìo Sarapiquì and the Rio Puerto Viejo (10°26'N, 83°59'W) in the Atlantic lowlands of Costa Rica. The elevation of the site is 35 m, and it is part of the Anexo Las Vegas at La Selva Biological Station, operated by the Organization for Tropical Studies (OTS). The region has an annual mean temperature of 24°C with a monthly range of 20-30°C. Rainfall is 400 cm per year, without a marked dry season (Hartshorn 1983).

In March 1991, *7* radial wood samples were obtained at different heights along the central axis from each of 10 trees: the first at breast height (1.30 m) and the others at subsequent 5 m height intervals to the top of the tree. Sometimes the seventh sample was taken at less than a 5 m interval where trees were shorter than 31.3 m. An increment borer of 12 mm diameter was used to obtain core samples at each height, except at the top of the tree, where a piece (1 cm long) was manually cut from the stem. Stem diameters at each sampling point were measured with a diameter tape. The trees sampled were very similar in size, ranging from 30 to 35 m in height and from 39 to 56 cm dbh. All trees had been cut one week prior to collection of the wood cores.

In most cases the pith was evident in the increment core. If it was not, distance from the pith was estimated by extrapolating along the rays. If the increment borer missed the projected pith by more than 1 cm, the tree was bored again. Each' wood sample from an increment boring was marked at 1 cm lengths, numbered from the pith to the

TABLE I. *Significance levels for overall regression and for each independent variable from linea regressions of specific gravity on different Sets of independent variables. Sample size is 887 wood segments from seven heights on ten trees.*

Overall		P for independent variable (ni = not included in the model)		
r^2	P	Centrifugal RD	Centripetal RD	Height
0.07	0.00	0.00	ni	ni
0.27	0.00	ni	0.00	ni
0.07	0.00	ni	ni	0.00
0.27	0.00	0.00	ni	0.00
0.27	0.00	ni	0.00	0.59
0.29	0.00	0.00	0.00	0.00

bark, and then cut into segments with a razor blade. The volume of each segment was determined by water displacement: the 1 cm segments were mounted at the end of a dissecting needle and then submerged in water in a beaker placed on an electronic balance, where the mass of the water displaced equals the green volume of the sample. Subsequently, these segments were oven-dried for 24 hr at 1 00—! 10°C to drive off all water and then weighed on the same balance. The specific gravity was obtained by dividing the mass of the sample when dry (moisture content 0%) by the mass of the water displaced by the sample when green, *i.e.*, basic specific gravity, as traditionally defined (Panshin & DeZeeuw 1980).

Wood specific gravity data were analyzed as the dependent variable through multiple regression analysis on the two independent variables, radial distance and height. Regressions were performed separately for radial distance measured centrifugally and centripetally, and the results compared to the radius-constant and time-constant models.

RESULTS

In the regression analysis, there were statistically significant specific gravity increases from pith to bark for every tree. These results confirm previous conclusions that wood specific gravity in *Ochrorna pyramidale* increases linearly from pith to bark (Whit-more 1973, Wiemann & Williamson 1988).

The relationship of the radial increase with height proved more complex. Initially a variety of linear regression models were explored to explain the variance in specific gravity for the pooled data from the 10 trees (Table 1). Independent variables used in the models included centrifugal radial distance, centripetal radial distance, and height. The three independent variables were intercorrelated as follows: centrifugal and centripetal distances *(r*=-0.40), centrifugal distance and height *(r*=-0.47) and centripetal distance and height *(r* = —0.47). In the regressions, centrifugal distance alone explained only 7 percent of the variance in specific gravity; whereas, centripetal distance alone explained 27 percent (Table 1). Height alone explained only 7 percent, but height and centrifugal distance included together explained 27 percent. However, when height was included with centripetal distance, there was no increase over the 27 percent variance already explained by centripetal distance. Finally, when centrifugal and centripetal distances are included with height, only a nominal increase from the 27 percent to 29 percent explained variance is encountered. Thus, centripetal distance is the most important independent variable, and after its incorporation in the model, the other independent variables explain little additional variance in specific gravity.

Individually, most trees followed the patterns evident in the joint data. For 9 of the 10 trees specific gravity was a positive function of both centrifugal radial distance and height (Table 2). Subsequent review of the data for the exceptional tree (Table 2, tree #8) revealed no increase in specific gravity with height from 1.3 m to 21.3 m, but wood in the highest two samples (26.3 m and 31.3 m) exhibited higher specific gravities than wood from the lower five samples. In contrast, when radial distance was measured centripetally, the relative importance of height in the regressions decreased markedly (Table 2). For example, means of the regression coefficients over all 10 trees revealed that the height coefficient in the centripetal model was less than 1 percent of the height coefficient in the centrifugal model (see mean' line, Table 2). Both the centrifugal and centripetal models achieved nearly the same mean r^5, 0.43 and 0.44; therefore, the variances explained by height and radial distance in the two models were about equal although the relative size of the coefficients changed notably. Thus, the time-constant model appeared to be a much better expression of the specific gravity variation in *Ochroma pyramidale* than the radius-constant model. These results from individual trees paralleled those from the joint regression where all 887 samples from the 10 trees are pooled ('joint" line, Table 2).

The time-constant model predicts that wood produced at any given time has the same specific gravity along the entire trunk. Specific gravity varies at different heights for a given distance from the

TABLE 2.

Result of linear regressions of wood specific gravity as a function of radial distance from the pith and height for 10 Ochroma pyramidale. *Separate regressions are shown for radial distance measured centrifugally (pith-to-bark) and centripetally (bark-to-pith). Sample size* (N) *is the number of wood segments. All 20 regressions were statistically significant at P = 0.00.*

	Centrifugal radius distance					Centripetal radius distance			
Tree	*N*	Inter—cept	Distance	Height	r^2	Inter—cept	Distance	Height	r^2
1	91	0.076	0.0054	0.0029	0.44	0.207	—0.0053	0.0008	0.42
2	109	0.055	0.0035	0.0036	0.50	0.165	—0.0034	0.000	0.47
3	102	0.082	0.0030	0.0019	0.24	0.164	0.0023	—0.0008	0.15
4	100	0.07	0.0042	0.0026	0.44	0.192	—0.0044	—0.0010	0.48
5	96	0.063	0.0056	0.0034	0.46	0.216	0.0053	—0.0014	0.42
6	76	0.063	0.0033	0.0032	0.66	0.135	—0.0032	0.0009	0.63
7	89	0.081	0.0016	0.0059	0.46	0.129	—0.0020	0.0044	0.47
8	77	0.094	0.0045	0.0076	0.37	0.179	—0.0052	—0.0023	0.46
9	76	0.086	0.0014	0.0021	0.30	0.121	—0.0014	—0.0008	0.29
10	73	0.080	0.0047	0.0039	0.46	0.179	—0.0060	0.0015	0.58
Ten tree Mean	89	0.075	0.0035	0.0022	0.43	0.169	— 0.0039	0.00001	0.44
Joint	887	0.076	0.0035	0.0029	0.27	0.166	—0.0034	0.0002	0.27

pith, but not a given distance from the bark. As further confirmation of the time-constant model, regressions of specific gravity on centrifugal radius distance were calculated from the joint data for each height and plotted (Fig. 3) for visual comparison to the two models (Fig. I and 2). Only the 1.3 m height regression falls out of place relative to the predictions of the time-constant model.

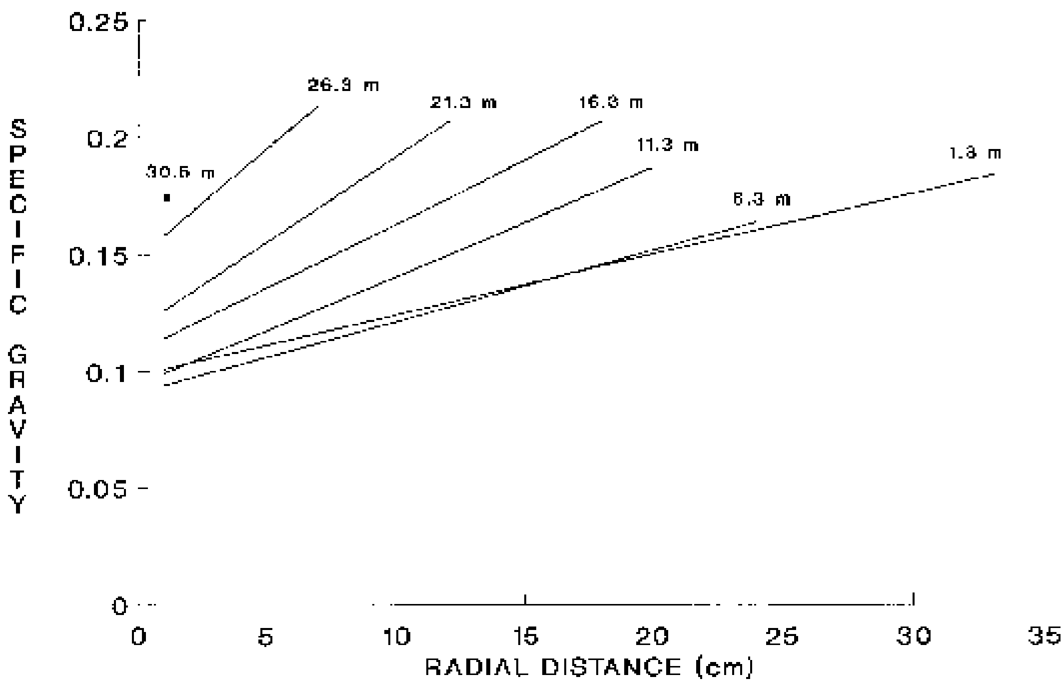

FIGURE 3. Actual regression lines of specific gravity on centrifugal radial distance, for ditferent heights (m) from 10 *Ochroma pyramidale*

DISCUSSION

In competitive environments where pioneers such as *Ochroma pyramidale* colonize, rapid growth in height may be the critical response to competition for light. *Ochroma pyramidale* grows rapidly in the first years by allocating resources to low specific gravity wood. As the tree grows taller, the specific gravity of the wood produced increases, concommitant with the increased need for structural support. The increase in specific gravity appears to continue even in very large trees, no matter how far this wood is from the pith. In Costa Rica, Whitmore (1973) and Wiemann and Williamson (1988) found the specific gravity increased radially by 100-200 percent. After 4—6 years *Ochroma pyramidale* growth slows and the wood loses commercial value as it becomes denser (Wiepking & Doyle 1944). In fact, wood producers harvest trees in a 4—6 year cycle in order to take advantage of the low specific gravity of the young wood (Wiepking & Doyle 1944).

The exact adaptive significance of the radial shift in specific gravity is still subject to considerable speculation. The current hypothesis is that the radial increase in specific gravity allows a species to put more biomass into height than girth when young, associated with a tradeoff in structural support for improved competition for light (Wiemann & Williamson 1989b). However, this hypothesis does not explain why the radial increase is absent from temperate trees and less prevalent in tropical dry and montane forests than in tropical wet forests, unless competition for light is more intense in the wet forests. Even within tropical wet forests the radial shift is more exaggerated in pioneers and gap colonizers than in mature forest dominants and middle strata species. However, some gap species, such as *Ceiba pentandra* (L.) Gaertn., exhibit a marked radial shift and become emergents of the mature forest. Interpretation of the radial shift is difficult in the context of little available knowledge of forest regeneration in the tropics.

The relationship between the radial shift and height may provide some clues to the importance of structure in the radial shift. For example, between models of the radial shift, the radius-constant model would provide greater allocation of wood to height with greater risk of structural failure than the time-constant model, given the same diameter. However, these differences may be minor relative to the overall adaptations associated with the radial shift. If so, the radius-constant and time-constant models may simply be alternative evolutionary avenues to the same ecological end. Obviously, study of more species is needed. In *Ochroma pyramidale,* the wood produced at any given time is generally of the same specific gravity. This result was evident in both regression analysis and visual comparison to the time-constant model. Only between 1.3 m and 6.3 m was there little support for the time-constant model. This absence of a difference at the lower heights may be a reflection of the rapid height growth of young saplings. Within the second year of life, it is common for saplings to elongate from 1—2 m to 4—8 m. In this case the time-constant and radius-constant models may be nearly indistinguishable. Therefore, the two models could be improved by including rates of height growth of the species under study.

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