EXTREME RADIAL CHANGES IN WOOD SPECIFIC GRAVITY IN SOME TROPICAL PIONEERS

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ABSTRACT

Twelve *Hampea appendiculata,* six *Heliocarpus appendiculatus,* and twelve *Ochroma pyramidale* trees from tropical wet forest in Costa Rica were sampled across their radii. Wood from all three species increased linearly in specific gravity from pith to bark. The magnitude of the increase was about 0.1 units of specific gravity per 10 cm of radius, although there were differences between the species and between trees within each species. All three species colonize clearings and disturbed sites, and these extreme changes in specific gravity may be associated with the pioneer habit in the wet forest.

Keywords: Wood specific gravity, within-tree variation, pioneer, succession, *Hampea appendiculata, Heliocarpus appendiculatus, Ochroma pyramidale.*

INTRODUCTION

Wood specific gravity is a measure of the amount of dry cell-wall material per unit volume of wood, and as such, is probably the single most important predictor of the properties of a wood. Strength; suitability as pulp; treatability with preservatives; dimensional stability; value as fuel; and acoustical, electrical, and thermal insulating properties are associated with specific gravity.

Understanding the variability of specific gravity is critical to the optimal utilization of wood. Among species, woods range in specific gravity from less than 0.05 for *Aeschynomene hispida* Willd. (Kanehira 1933) to 1.08 for *Dalbergia melanoxylon* G.&P. (Chudnoff 1979). Williamson (1984) found that between-species specific gravity variance was greater among tropical hardwoods than among temperate hardwoods, with extremely low and extremely high specific gravity woods being found mainly in the tropics. Variables such as growth rate, shade tolerance, seral stage, and climatic life zone are associated with differences in specific gravity between species, although the relationships are far from exact (Richards 1952; Williamson 1975; Chudnoff 1976; Hartshorn 1980). Among trees of the same species, environmental and genetic influences affect wood properties (Panshin and deZeeuw 1980). One of the primary environmental factors causing between-tree variability is availability of moisture (deZeeuw 1965). Howe (1974) found climate to have a pronounced effect on wood specific gravity among individual trees in three Costa Rican species; in one of these, *Cordia alliodora* (R.&P.) Cham., wood specific gravity of trees growing in tropical dry forest was 60% higher than in trees growing in tropical moist forest.

In addition to the differences between species and between trees of the same species, specific gravity may be highly variable within a tree. Specific gravity varies within growth rings, from pith to bark, and with height (Panshin and

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de Zeeuw 1980). Most specific gravity variation studies have been done on temperate zone trees and have reported pith to bark changes of less than 50% (Zobel and McElwee 1958; Hamilton 1961; Taylor 1968, 1973, 1979; Taylor and Wooten 1973). However, one exceptional report (Whitmore 1973) documented a 120% pith to bark increase in specific gravity in a 50-cm diameter balsa [*Ochroma pyramidale* (Cav. ex Lam.) Urban]. This extreme variability within balsa trees is well known to commercial producers of the wood. The highest quality, lightest grades of balsa are produced by fast-grown trees which are harvested on a 4- to 6-yr rotation; slower-grown wood and wood from older trees is of reduced value because it is denser (Wiepking and Doyle 1944).

Balsa's role as a pioneer species in the wet, tropical lowlands suggests a possible association of pioneer habit with extreme radial increase in wood specific gravity. The colonizing habit may combine rapid growth in stature with the production of a weak trunk early in development. Tropical colonizers have long been known to produce wood of low specific gravity (Richards 1952; Whitmore 1984). With gain in height, increase in specific gravity may be necessary to maintain structural stability. In order to investigate this hypothesis, we studied specific gravity variation in large trees of balsa and two other pioneer species of the wet tropics, *Hampea appendiculata* (Donn. Sm.) Standl. and *Heliocarpus appendiculatus* Turcz. The latter two species frequently co-occur with balsa in clearings and along forest edges. If balsa's increase in specific gravity with diameter has an ecological explanation, these species might be expected to exhibit similar patterns. The three species are fast-growing. Balsa trees may grow to 6 cm diameter and 5 m height in the first year, and commonly reach 60 cm diameter and 20 m height after seven years (Brush 1945). Specific growth rate data on the other two species are unavailable, but in Costa Rica, 4½ years after it had been cleared, one plot contained individuals of *Heliocarpus appendiculatus* that exceeded 20-cm diameter and *Hampea appendiculata* that exceeded 10-cm diameter (GBW unpublished data).

MATERIALS AND METHODS

Wood samples of *Hampea appendiculata, Heliocarpus appendiculatus,* and *Ochroma pyramidale* were collected from the region of Sarapiquí in Costa Rica. Sarapiquí has a mean temperature of 24 C and an average annual rainfall of 400 cm, with no real dry season. It is Tropical Wet Forest, according to Holdridge's (1967) Life Zone classification. The range in elevation of the collection sites is 30–50 m above sea level. In addition, one *Heliocarpus appendiculatus* (Tree No. 16) was sampled in the region of Guatuso, south of Cartago, Costa Rica, at an elevation of 1,500 m. This area is a Tropical Lower Montane Wet Forest, with an annual rainfall of 250 cm, a dry season of four months' duration, and an average annual temperature of about 15 C (Dulin 1982; Coen 1983; Hartshorn 1983; OTS 1985).

The diameter of each tree sampled was measured with a diameter tape at breast height or, when large buttresses were present, immediately above the buttresses. Radial (pith to bark) wood samples were obtained at the height of the diameter measurement, usually from a 12-mm diameter increment borer, but in some instances from a smaller (8-mm) borer or from strips cut from disks taken from felled trees. The three methods gave comparable results.

The radial samples were marked at 1-cm lengths measuring from the pith. In the few instances in which a core did not contain pith, distances from the pith were determined by examining the core at various places to estimate the point of convergence of the wood rays. This point was taken as the location of the pith, and from it distances to each 1-cm length were calculated. The 1-cm lengths were split into segments with a razor blade. Green volumes were determined by measuring the weight of water displaced by submerged segments. Subsequently, the segments were oven-dried for one or two days at 100–105 C and then weighed. Basic specific gravity was calculated for each segment by dividing the weight of the water displaced by the green sample into the weight of the oven-dry sample.

Wood specific gravity was plotted as a function of distance from pith for each tree sampled. Linear regressions and their coefficients of determination were calculated for each tree, and their values were averaged for each species. Additionally, specific gravity values of the three samples located nearest to the pith were averaged to give a measure of the specific gravity of the wood produced when a tree was young, and the values for the three samples nearest to the bark were averaged to give a measure of the specific gravity of the most recently formed wood.

RESULTS AND DISCUSSION

Plots of specific gravity versus distance from the pith for the largest diameter trees of *Hampea, Heliocarpus,* and *Ochroma* (Fig. 1) reveal a strong linear increase in specific gravity with distance from pith for each tree; the respective coefficients of determination are 0.84, 0.96, and 0.91. These three trees exhibit respective specific gravity increases of 110%, 330%, and 230%. The specific gravity increase exhibited in a single tree is a function of both its regression equation and of the size of the tree. The latter factor is important because specific gravity appears to continue to increase as the diameter of the trees increases (Fig. 1). At what diameter, if any, specific gravity would cease to increase is unclear.

The regression equations for the other, smaller diameter trees exhibit linear increases and coefficients of determination similar to those for the largest tree of each species (Table 1). For individual trees, doubling of specific gravity across the trunkwood is common in *Hampea* and *Ochroma,* and tripling is common in *Heliocarpus* (Table 1). The positive linear relationship of specific gravity as a function of distance from pith was strong in all but a few cases.

The regression equations for *Hampea, Heliocarpus,* and *Ochroma* show average increases in specific gravity, respectively, of 0.10, 0.10, and 0.07, per 10 cm of radius increase. Thus, the rate of increase in *Hampea* and *Heliocarpus* is larger than the increase in *Ochroma.* Information about relative growth rates of three species would be of value in interpreting the data. If specific gravity is strongly correlated to tree age, faster growth would tend to decrease the slope of the relation between specific gravity and distance from pith.

An analysis of covariance for each species reveals that in addition to the significant dependence of specific gravity on distance from pith ($P < 0.001$) there is significant variation among trees in specific gravity ($P < 0.001$) and in the slope of the specific gravity versus distance from pith relationship ($P < 0.001$). However, neither of the latter two factors was as important as distance from pith in explaining the variation in specific gravity. Therefore, it can be said that specific gravity in these three species is exceptionally dependent on distance from the pith, although there is some tree-to-tree variation.

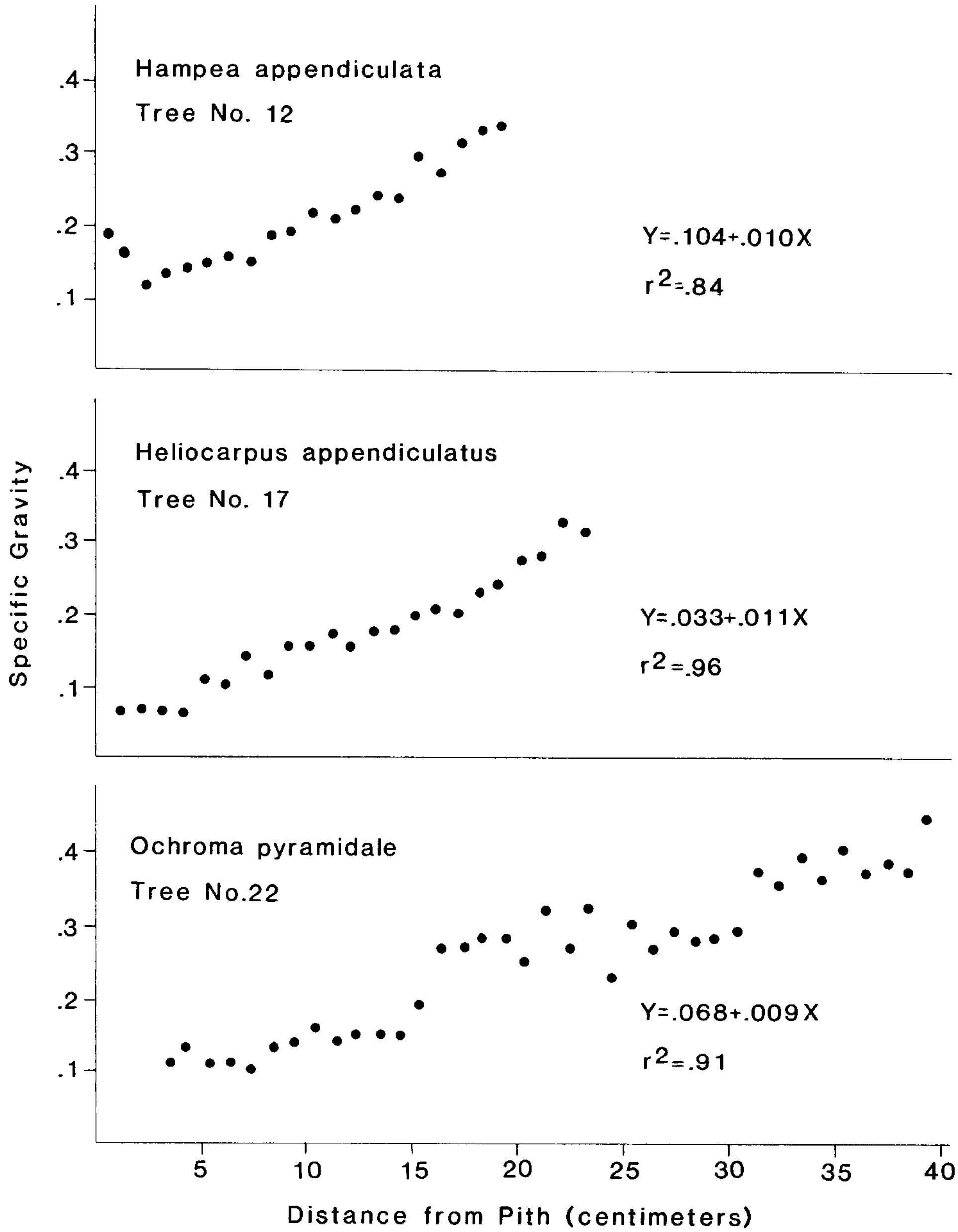

FIG. 1. Specific gravity as a function of distance from the pith for large trees of *Hampea, Heliocarpus,* and *Ochroma.* Tree numbers correspond to numbers in Table 1.

Hampea and *Heliocarpus* show linear increases in specific gravity similar to those shown by *Ochroma.* This suggests a connection between the ecological habit of pioneer species of the wet, tropical lowlands and the ability of these species to vary their wood specific gravity as they grow. Pioneers of the lowland tropics produce some of the lowest specific gravity woods in the world (Richards 1952; Whitmore 1984; Williamson 1984). In addition, they may be able to produce

TABLE 1. *Tree number, diameter, and specific gravity of the old wood (inner 3 cm), new wood (outer 3 cm), the new/old ratio, the regression equation of specific gravity (Y) on distance from pith (X), and the coefficient of determination (R^2) for individual trees and species averages.*

Species	Tree no.	Dia. (cm)	Specific gravity				
			Old	New	Ratio	Regression	R^2
Hampea	1	40	0.14	0.30	2.1	Y = 0.099 + 0.009X	0.80
	2	43	0.20	0.34	1.7	Y = 0.170 + 0.012X	0.84
	3	37	0.16	0.28	1.7	Y = 0.141 + 0.008X	0.88
	4	37	0.14	0.34	2.4	Y = 0.119 + 0.015X	0.99
	5	44	0.17	0.31	1.8	Y = 0.116 + 0.008X	0.68
	6	41	0.16	0.30	1.9	Y = 0.119 + 0.010X	0.87
	7	36	0.21	0.32	1.5	Y = 0.201 + 0.012X	0.85
	8	35	0.15	0.30	2.0	Y = 0.103 + 0.011X	0.81
	9	35	0.20	0.28	1.4	Y = 0.179 + 0.007X	0.68
	10	44	0.18	0.35	1.9	Y = 0.146 + 0.010X	0.82
	11	38	0.18	0.38	2.1	Y = 0.125 + 0.013X	0.86
	12	48	0.15	0.32	2.1	Y = 0.104 + 0.010X	0.84
	Average		0.17	0.32	1.9	Y = 0.135 + 0.010X	0.83
Heliocarpus	13	40	0.07	0.22	3.1	Y = 0.037 + 0.010X	0.84
	14	36	0.08	0.23	2.9	Y = 0.036 + 0.010X	0.82
	15	47	0.11	0.23	2.1	Y = 0.061 + 0.006X	0.79
	16	44	0.09	0.34	3.8	Y = 0.052 + 0.015X	0.98
	17	50	0.07	0.30	4.3	Y = 0.033 + 0.011X	0.96
	18	50	0.11	0.29	2.6	Y = 0.126 + 0.007X	0.90
	Average		0.09	0.27	3.0	Y = 0.057 + 0.010X	0.88
Ochroma	19	43	0.15	0.32	2.1	Y = 0.088 + 0.017X	0.83
	20	44	0.14	0.26	1.9	Y = 0.141 + 0.006X	0.65
	21	52	0.10	0.25	2.5	Y = 0.069 + 0.008X	0.84
	22	90	0.12	0.40	3.3	Y = 0.068 + 0.009X	0.91
	23	38	0.11	0.23	2.1	Y = 0.067 + 0.007X	0.72
	24	36	0.08	0.18	2.3	Y = 0.058 + 0.006X	0.78
	25	36	0.18	0.24	1.3	Y = 0.177 + 0.008X	0.72
	26	42	0.11	0.19	1.7	Y = 0.102 + 0.003X	0.37
	27	36	0.10	0.18	1.8	Y = 0.064 + 0.005X	0.53
	28	47	0.15	0.21	1.4	Y = 0.118 + 0.003X	0.46
	29	65	0.12	0.30	2.5	Y = 0.070 + 0.009X	0.80
	30	66	0.11	0.31	2.8	Y = 0.093 + 0.007X	0.93
	Average		0.12	0.26	2.2	Y = 0.093 + 0.007X	0.71

higher specific gravity wood as needed for structural stability. In the lush environment of tropical rainforests, pioneer tree species must compete for light with each other as well as with large herbaceous plants and sprawling lianas. Such an environment may have selected for allocation of resources toward rapid growth in stature, at the initial expense of strength, accompanied by the ability to increase the specific gravity of wood produced subsequently.

SUMMARY AND CONCLUSIONS

Three pioneer species from the wet, lowland tropics show extreme radial increases in specific gravity. The increases appear to be linear functions of distance from the pith, and result in tripling or quadrupling of specific gravity in large diameter trees. These results suggest that tropical colonizers, long known for producing wood of low specific gravities, are capable of increasing the specific gravity of the xylem produced as the trees increase in size. Consequently, the trees may be able to grow tall quickly when young and gradually adjust their trunkwood for structural stability as they reach maturity.

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