

WOOD QUALITY IN *HILDEGARDIA BARTERI* (MAST.)
KOSSERN—AN AFRICAN TROPICAL
PIONEER SPECIES¹

Olayinka O. Omolodun

Former graduate research assistant

Bruce E. Cutter

Associate Professor of Forestry
The School of Natural Resources
University of Missouri—Columbia
Columbia, MO 65211

Gary F. Krause

Professor of Statistics
College of Agriculture
University of Missouri—Columbia
Columbia, MO 65211

E. Allen McGinnes, Jr.

Professor Emeritus of Forestry
The School of Natural Resources
University of Missouri—Columbia
Columbia, MO 65211

(Received May 1990)

ABSTRACT

Hildegardia barteri (Mast.) Kossern is a fast-growing African tropical pioneer species that often colonizes open spaces and disturbed vegetation, forming almost pure stands extending over several hectares. The results of anatomical and specific gravity studies of *Hildegardia* grown on four different sites in southern Nigeria are presented. Fiber length and fiber and vessel element tangential diameters varied significantly among the four sites. Most anatomical features varied with distance from the pith. Height above ground was not a significant factor. Specific gravity varied with site, distance from the pith, and height above ground.

Keywords: Descriptive anatomy, cell dimensions, specific gravity, extractive content.

INTRODUCTION

In Nigeria's tropical lowland rainforest and savanna regions, over 560 tree species reach merchantable size (Keay 1959). However, only about a dozen species are actually utilized for commercial production. The rest are grouped as lesser-known or underutilized species and comprise about 95% of the productive hardwood forests (Yeom 1984). One of these underutilized species is *Hildegardia barteri* (Mast.) Kossern, a fast-growing pioneer species that often colonizes open spaces and disturbed vegetation, forming almost pure stands extending over sev-

¹ Paper No. 11,287 in the University of Missouri—Columbia's Agricultural Experiment Station Journal Series.

eral hectares. *Hildegardia* gains rapidly in stature, attaining heights of 30 m with girths of up to 3.6 m. A buttress may extend 5 m up the trunk. Early studies in Nigeria found that specific gravity ranged from 0.28 to 0.31, with tree moisture contents in excess of 200% (Keay and Onochie 1959). Therefore, no further exploration of wood properties and potential utilization was done.

Overexploitation of the major commercial species has provided an impetus for, and a renewed interest in, determining the fundamental properties and utilization potential of underutilized species such as *Hildegardia*. Accordingly, a study was designed to evaluate within-tree, between-tree, and among-site wood property variation in this species. This paper presents the results of anatomical and specific gravity studies of *Hildegardia* grown on different sites.

MATERIALS AND METHODS

Samples were collected from four sites in southwestern Nigeria (Fig. 1). Sites 1 and 2, located on the Oluwa and Akure Forest Reserves, were in the lowland rainforest zone. Sites 3 and 4, on the Olokemeji and Owo Forest Reserves, while also in the lowland rainforest, exhibited derived savanna vegetal structure due to earlier land-clearing efforts. Three trees from each site were selected for anatomical studies: one from the small diameter (<34 cm dbh) class, one from the medium diameter class (34–45 cm dbh) and one from the large diameter class (>45 cm dbh). Radial strips were cut from the base, middle, and top cross sections of each of these trees. A 2- × 2- × 2-cm block was obtained from each strip at (1) the pith region, (2) the region contiguous to the pith, (3) the arithmetic middle of the radial strip, and (4) a region adjacent to the bark. These blocks were then stored in FAA solution prior to sectioning or maceration.

Samples were softened in ethylenediamine (Carlquist 1982) prior to paraffin embedding and sectioning. Cross sections, 12 μm thick, and radial and tangential sections, 16 μm thick, were cut on a rotary microtome, mounted on glass slides using Haupt's adhesive (Bissing 1974), and stained using safranin/fast green.

A standard Jeffrey's solution (10% nitric acid and 10% chromic acid in water) was used to macerate already softened samples. The softened samples were placed in Jeffrey's solution for 45 min at 60 C. Macerated tissue was stained in safranin prior to mounting.

Fifty measurements were made for each parameter for each section. Fiber length and vessel member length were measured using an ocular micrometer, while fiber double-wall thickness, vessel diameter, and ray height (tangential section) were measured from projections onto a digitizing tablet. Vessel element length was defined as the end-to-end dimension of the cell including the caudate tips. Proportional volume of tissue types (vessels, fibers, rays, and axial parenchyma) was determined using the uniform grid method (Smith 1967). Fifty measurements were made here as well.

Specific gravity determination

In each compartment, two 8-mm increment cores were taken at dbh from 10 dominant or co-dominant trees. An additional dominant or co-dominant tree was felled, and 10 cm-thick cross sections were taken at 3-m intervals up the stem. Height and diameter measurements were made on all trees. Radial strips were cut from the cross sections and divided into 2- × 2- × 2-cm blocks for specific

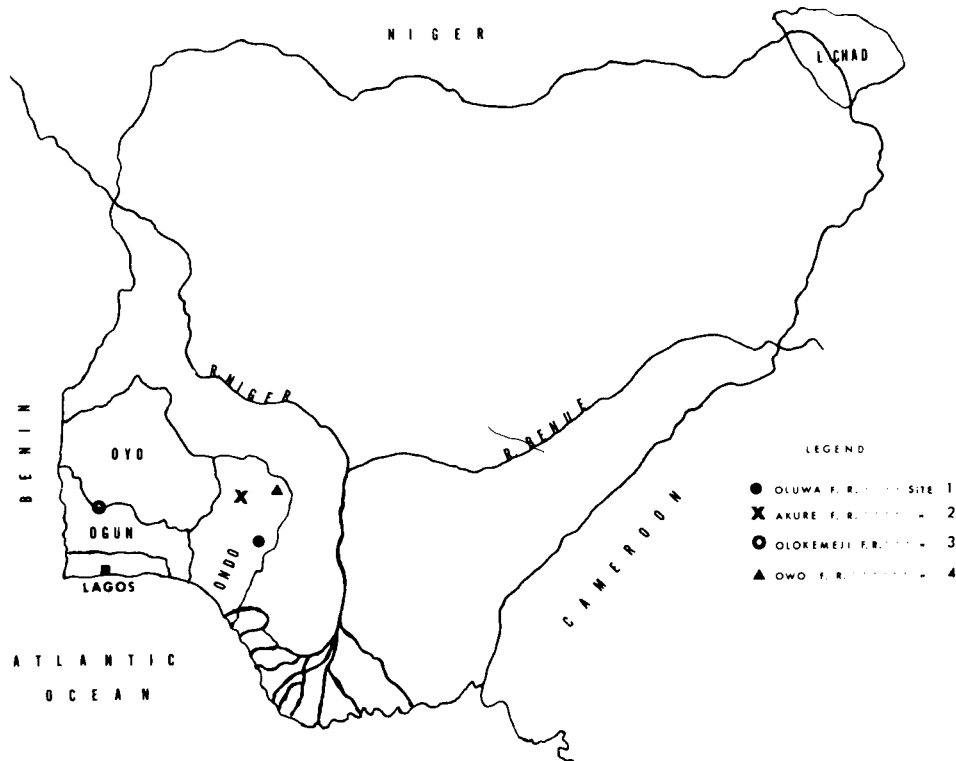


FIG. 1. Map of Nigeria showing locations of sample sites.

gravity measurements. This grouping was used in lieu of age groupings since annual rings were generally indistinct. These blocks were further categorized as inner blocks, the three cubes adjacent to the pith; outer blocks, the three cubes adjacent to the bark; and middle, the remainder of the blocks.

Specific gravity was measured using the maximum moisture content technique (Smith 1954). To establish the effect of extractives on specific gravity in this species, all block samples were extracted with methanol (48 h) and hot water (72 h) in a Soxhlet extraction apparatus. Oven-dry weights were obtained before and after extraction, while saturated weights were taken following the hot water extraction.

Site factor analyses

In each forest reserve, soil samples were obtained from three randomly chosen compartments. Twenty auger samples were taken in each compartment, and the soil was divided into three layers: I, the upper 0–15 cm; II, the middle 16–30 cm; and III, 31–45 cm deep. Rainfall data for the eight years prior to sampling were obtained from the Nigerian Meteorological Department.

Soil samples were analyzed for pH, P, K, Ca, Mg, and exchangeable Al. Potassium and Al levels were determined using flame emission spectrometry; Ca and Mg, using atomic absorption spectrometry; and P, using colorimetry (Brown and Rodriguez 1983).

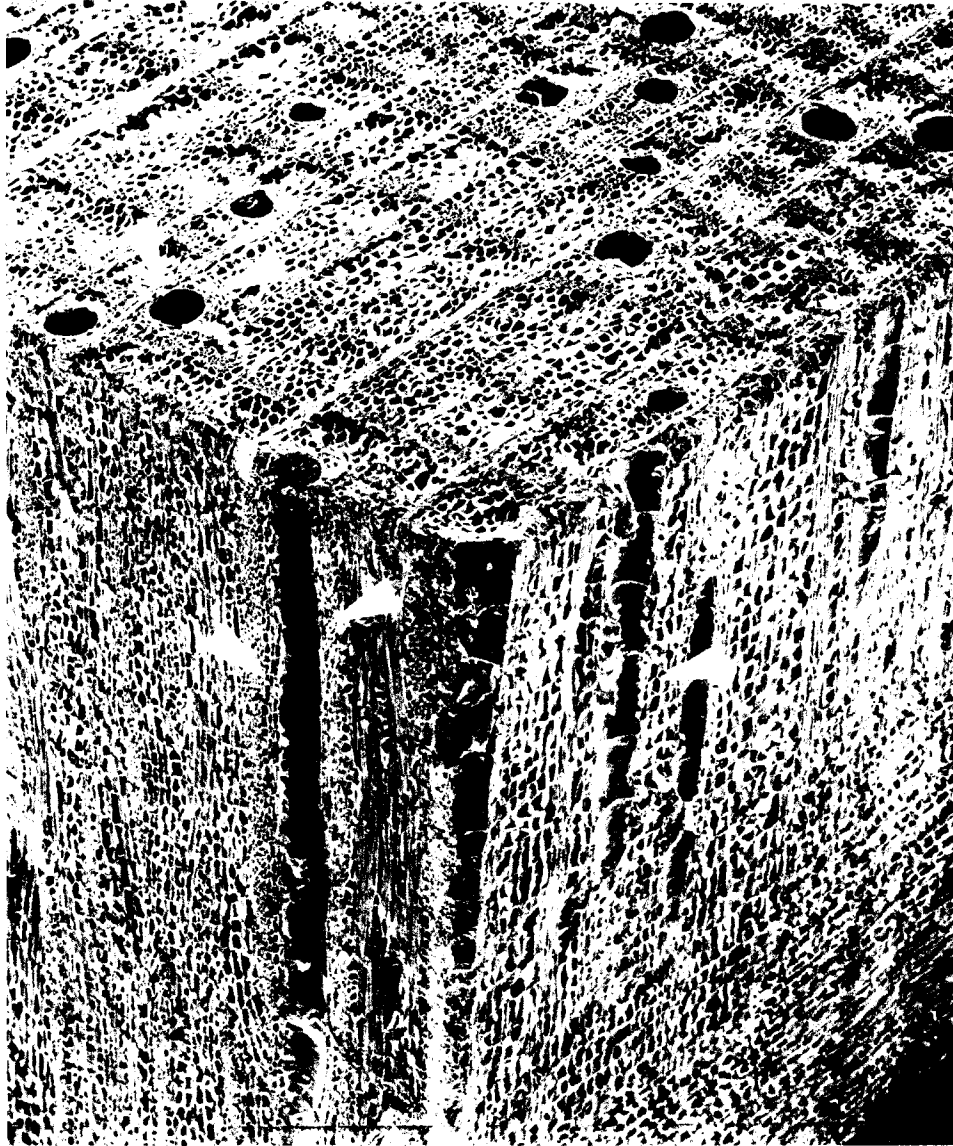


FIG. 2. SEM view of *H. barteri* showing vessels surrounded by axial parenchyma and ray cells ($\times 20$).

All data were analyzed using the General Linear Models Procedure (PROC GLM) in SAS (SAS Institute, Inc. 1985).

RESULTS AND DISCUSSION

Descriptive wood anatomy

The wood of *Hildegardia barteri* is diffuse-porous and the growth rings are generally indistinct, rendering tree age determination impracticable (Fig. 2). The wood is cream-colored, odorless, and soft. It is considered a sapwood tree (Bos-

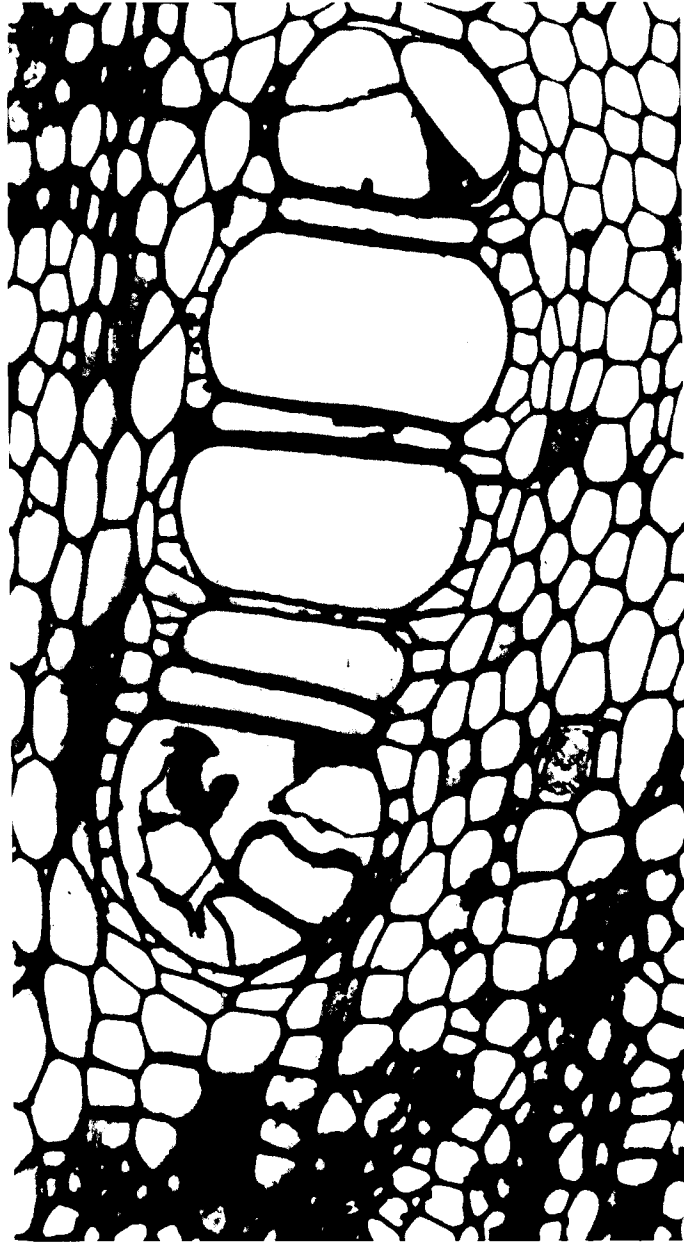


FIG. 3. Earlywood vessel chain ($\times 100$).

shard 1966). Microscopic examination revealed that the pores occurred in radial multiples of 2 to 3 and occasionally 4. The wood adjacent to the pith contained small pore chains, up to 10 cells long (Fig. 3). Perforation plates were simple-oblique (Fig. 4). Intervascular pit-pairs were alternate, averaging $4 \mu\text{m}$ in diameter. The vessel elements were short ($349 \pm 22 \mu\text{m}$ with a range of 303 to 420) and moderately wide (tangential diameter, $156 \pm 41 \mu\text{m}$, range from 86 to 245). The

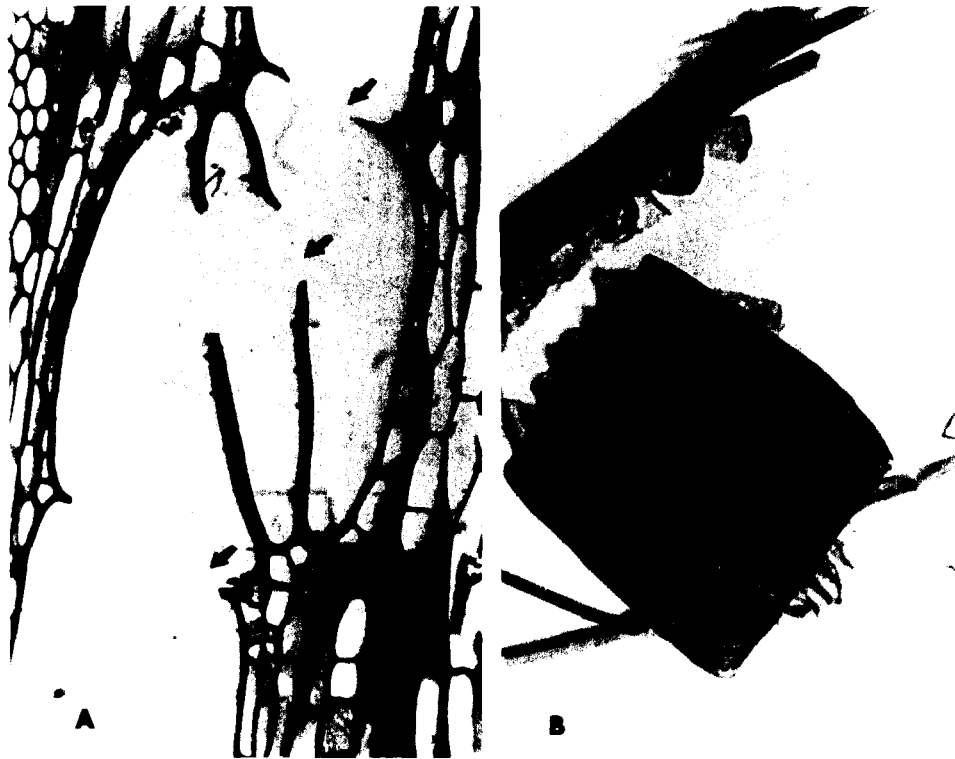


FIG. 4. A) Oblique view of a simple perforation plate ($\times 100$). B) Individual vessel element ($\times 100$).

vessels were devoid of cellular inclusions, but tyloses-like structures were observed in wood adjacent to the pith in a few trees from the Akure Forest Reserve.

The fibers (classified as libriform fibers) averaged 2.3 ± 0.3 mm in length (range from 1.5 to 2.9 mm), had an average tangential diameter of 15.8 ± 1.3 μm (range from 10 to 21.6), and had an average double cell-wall thickness (DWCT) of 8.7 ± 1.3 μm (range from 5.3 to 11.7) (Fig. 5). The fibers occurred in tangential bands 4 to 15 cells wide, alternating with the bands of axial parenchyma cells (Figs. 2, 6). In all trees, the fiber bands were narrowest at the pith and widest at the bark.

Hildegardia is characterized by abundant axial parenchyma occurring in tangential bands 4 to 15 cells wide. These cells decreased in abundance from pith to bark.

Rays were usually 5 to 8 cells seriate, occasionally up to 12 cells, and surrounded by sheath cells (Fig. 7). These rays were moderately high, with an average height of 1.9 mm. Uniseriate and biseriate rays, although present, were quite low and scattered.

Fibers comprised $16.8 \pm 5\%$ of the cross section, while vessels comprised $5.2 \pm 2\%$; rays, $24.9 \pm 6\%$; and axial parenchyma, $53.2 \pm 8\%$.

Rhomboidal crystals were numerous but confined to the wood adjacent to the pith. The crystals usually were found in axial parenchyma cells, but in the trees from Site 2, the Akure F.R., the crystals were also found in the ray parenchyma cells.

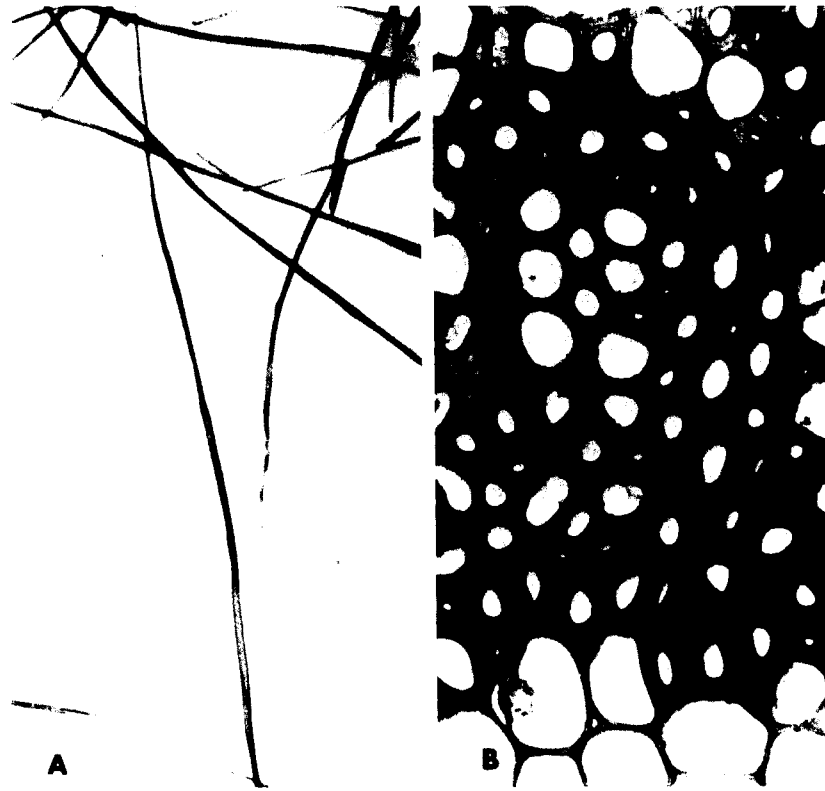


FIG. 5. Fibers as seen in: A) maceration ($\times 35$) and B) cross-section ($\times 100$).

Statistical analyses of anatomical variables

Analyses of variance results (Table 1) indicated that site and radial position in the cross section exerted significant influences on both cell dimensions and tissue types. Specifically, fiber length, fiber diameter, vessel element diameter, ray height, and fiber and vessel area changed significantly among sites; while fiber length, fiber diameter, fiber DCWT, vessel element length, vessel element diameter, and fiber and vessel area varied across the cross section (Table 2). The percentage of the cross section occupied by ray tissue was never significant, and this feature is not shown in Tables 1 and 2. For all the other variables examined, there were significant differences among trees within a site.

There are other variables that probably exert a marked influence on wood properties in *Hildegardia*. These include genetics, age, and growth rate to name a few. In this study, accurate plantation establishment dates did not exist, so any estimates of tree age and growth rate would be purely speculative. However, the fact that the site and tree factors were frequently significant suggests that a tree improvement program might be undertaken that would contribute significant (in the statistical sense) and real changes in selected or desired wood properties in *Hildegardia*. For example, *Hildegardia* is characterized by long fibers and short vessel elements. Bailey (1920) and Chalk and Chattaway (1934) have shown that

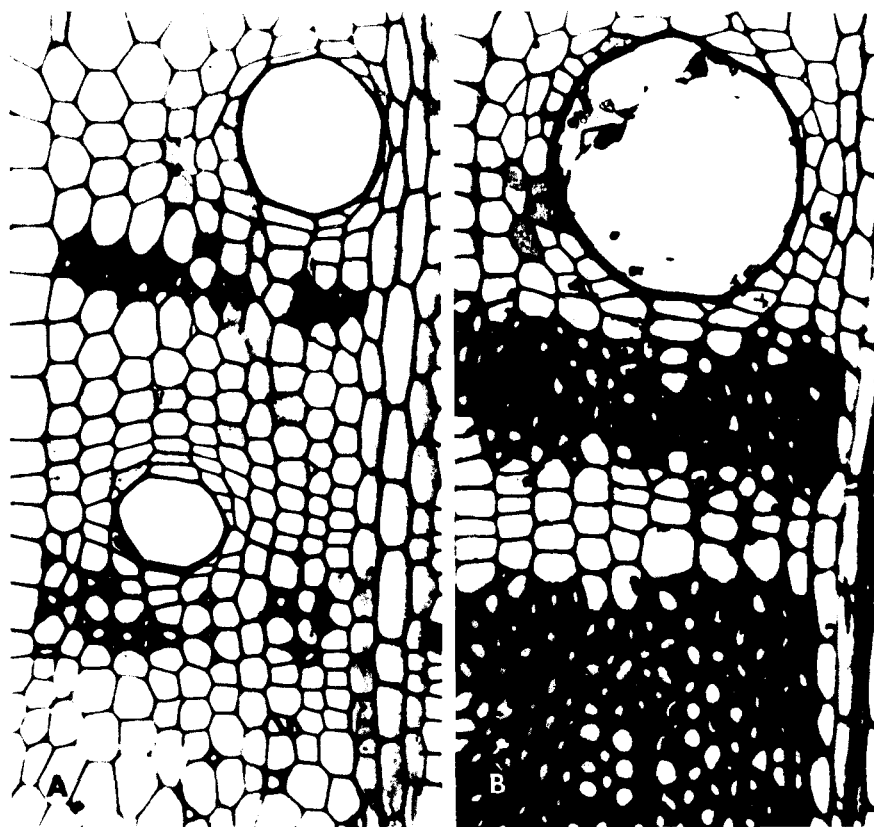


FIG. 6. Fiber-parenchyma bands as seen in cross section: A) near pith ($\times 100$); B) near bark ($\times 100$).

the length of vessel elements is approximately the length of the cambial initials and therefore may be assumed to be the original length of the fibers. According to Frost (1930), short vessel elements are more specialized as a rule than are long vessel elements. Therefore, greater elongation of fibers also reflects specialization (Baas 1976; Carlquist 1975, 1980). The ratio of fiber to vessel element length ranges from 1.1 to 9.5 in dicots (Chattaway 1936). In *Hildegardia*, the ratio is 6.6. The fact that there were differences in fiber lengths among the sites suggests that both genetics and site differences need to be more extensively evaluated for *Hildegardia*.

Statistical analyses of specific gravity and extractive content

The mean specific gravity of all the individual samples was 0.26 (oven-dry weight, green volume), with a standard deviation of 0.06 and a range from 0.11 to 0.57. When expressed on a tree basis, the mean was still 0.26 ± 0.041 , but the range was from 0.20 to 0.36. As indicated in Table 3, there were significant (at the 1% level) differences in specific gravity among sites, across radial sections, and among trees within a site, as well as a significant section \times height interaction. Again, other factors undoubtedly need to be examined to account fully for SG

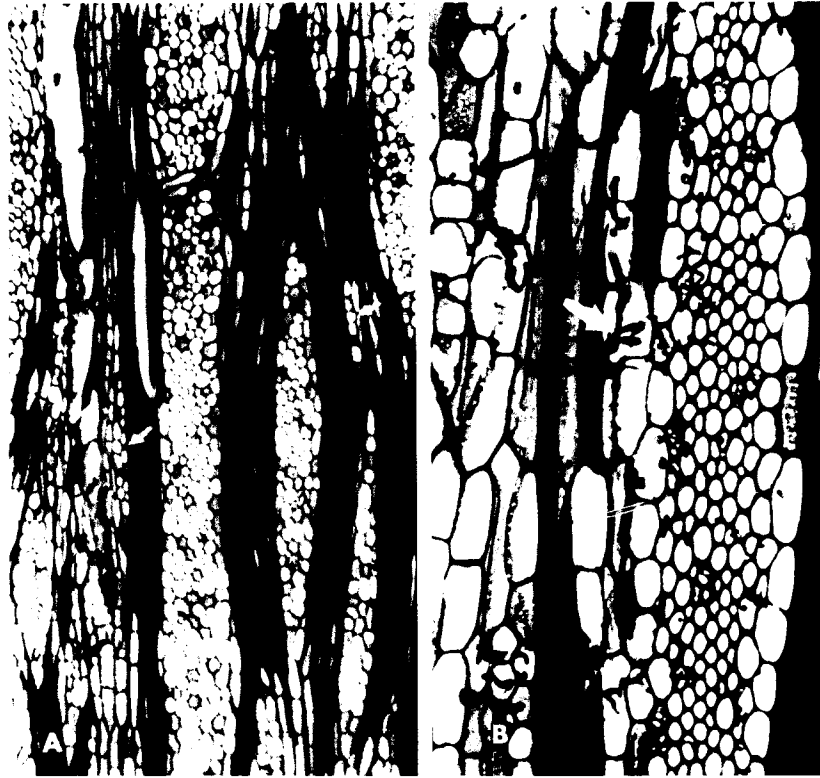


FIG. 7. Rays on the tangential surface showing: A) multiseriate rays and low uni- and biseriate rays (arrow) ($\times 35$); B) sheath cells surrounding a multiseriate ray with fungal hyphae (arrow) ($\times 100$).

variation in *Hildegardia*. The fact that several trees had specific gravity values above 0.30 suggests that genetic improvement of the species may be possible.

There were significant differences in the amount of both methanol and hot water extractives removed (Table 3). The numbers were confounded by the fact that all the samples from the Olokemeji Forest Reserve, Site 3, contracted a well-developed blue-stain fungal infection in the field sampling and transport process. This is felt to be the reason that the amount of hot water-soluble compounds was significantly less than the amount for the other sites. The decrease in SG (measured at dbh) amounted to about 10% overall for all sites. This is consistent with the results of other studies (Lee 1986; Olson and Carpenter 1985). The mean SGs for Sites 1 and 4, the Oluwa and Owo Forest Reserves, were significantly greater than those of Sites 2 and 3, the Akure and Olokemeji Forest Reserves (Table 4). Specific gravity varied among sites, radial position, and height. Specific gravity increased from pith to bark and, to a certain extent, with height. Hot water soluble extractives decreased with increasing height and increased from pith to bark.

The increase in SG from pith to bark appears to be directly tied to a change in tissue composition. Numerous past studies have reported an inverse relationship between fiber and vessel volume and this relationship's effect on specific gravity (Isebrands 1972; Olson and Carpenter 1985; Taylor and Wooten 1973; Vurdu

TABLE 1. Analysis of variance F-values for the anatomical elements.

Source	df	Fiber			Vessel element			Fiber area	Vessel area	Axial paren. area
		Length	Diameter	DCWT	Length	Diameter	Ray height			
Site	3	24.36**	20.24**	2.09	0.87	70.91**	4.95**	3.76*	1.68	1.89
Height	2	0.31	1.46	0.73	0.79	1.20	0.80	5.99**	6.21**	2.16
Site × height	6	0.39	2.81*	1.87	0.64	0.89	1.69	1.97	1.14	0.65
Radial section	3	33.13**	99.68**	15.50**	17.82**	216.29**	1.40	10.36**	18.27**	4.44*
Site × section	9	2.56*	1.53	0.98	1.57	2.98*	2.19*	2.28*	1.25	1.35
Section × height	6	0.38	1.34	1.59	1.06	0.68	0.35	2.89**	0.76	2.68*
Site × section × height	18	0.32	0.61	0.62	0.40	0.45	1.08	0.73	0.91	0.24
Tree (site)	8	5.16**	26.30**	4.62**	8.03**	9.67**	6.35**	2.44*	5.26**	3.38*
ANOVA Model R^2		0.74**	0.87**	0.59**	0.64**	0.92**	0.58**	0.64**	0.61**	0.49*

* Significant at the 5% level.

** Significant at the 1% level.

TABLE 2. Results of mean separation tests for selected anatomical parameters.¹

Source	Fiber			Vessel element		Ray height (mm)	Cross-sectional area		
	Length (mm)	Width (µm)	DCWT (µm)	Length (µm)	Diameter (µm)		Fiber (%)	Vessel (%)	Area (%)
Site									
Oluwa	2.32a	15.6a	8.5a	347.6a	139.7a	1.94a	17.7a	5.5a	50.9a
Akure	2.17b	16.0a	8.7ab	347.4a	139.0a	1.91a	15.1b	4.7b	54.6a
Olokemeji	2.25a	14.9b	8.6a	348.3a	180.6b	2.01a	17.8a	5.2ab	53.0a
Owo	2.49c	16.7c	9.1b	353.1a	168.1c	1.76b	16.4ab	5.3ab	54.1a
Radial section									
Pith	2.11a	13.8a	7.8a	334.2a	112.7a	1.84a	14.4a	6.6a	54.1ab
Inner	2.26b	15.2b	8.5b	344.4b	143.2b	1.87a	15.5a	4.2b	56.2a
Middle	2.39c	16.8c	9.1c	356.1c	176.7c	1.96a	18.6b	4.2b	51.6ab
Outer	2.47d	17.5d	9.4c	361.1c	194.9d	1.95a	18.5b	5.6c	50.8b

¹ Those means within a factor followed by the same letter are not significantly different at the P ≥ 0.05 level.

and Bensed 1980). There was a significant negative correlation between fiber and vessel volume in this study as well ($r = -0.38$).² However, the relationship between fiber volume and parenchyma volume ($r = -0.67$) apparently exerts a greater influence on specific gravity in this species. Our studies showed that increased fiber volume and wider fiber bands from pith to bark are paralleled by decreased axial parenchyma volume and narrower parenchyma bands. The fibers also increased in size and wall thickness from pith to bark (Table 2). The proportion of cross-sectional area occupied by axial parenchyma volume decreased from pith to bark as well. Wood improvement breeding programs aimed at reducing the proportion of parenchymatous tissue in *Hildegardia* might be expected to result in increased fiber production and therefore, higher specific gravity.

As noted, specific gravity increased from pith to bark (inner to middle to outer samples) (Table 3). Generally the densest wood was the outer wood at all height levels (Table 5). Wiemann and Williamson (1987, 1989a, b) and Whitmore (1973) observed that SG increased linearly with distance from the pith in fast-growing

² All correlations are significant at the 5% level.

TABLE 3. Analysis of variance F-values for SG and extractive content.

Source	df	F-values		
		SG	MeOH	Hot water
Site	3	16.33**	56.74**	117.41**
Height	4	2.84*	0.80	41.01**
Radial section	2	56.01**	2.45	14.02**
Site × section	6	3.24**	7.77**	11.92**
Site × height	12	1.84*	1.22	3.93**
Section × height	8	5.29**	3.38**	9.90**
Site × section × height	24	0.55	0.60	0.98
Tree (site)	32	9.99**	8.85**	20.64**
ANOVA model R ²		0.568**	0.557**	0.761**

* Significant at the 5% level.

** significant at the 1% level.

TABLE 4. Results of mean separation tests for specific gravity and extractive content.¹

Source	Specific gravity	MeOH (%)	Hot water (%)
Site			
Oluwa	0.277a	1.7a	5.9a
Akure	0.251b	1.2b	6.7b
Olokemeji	0.246b	2.0c	3.8c
Owo	0.263c	1.2b	7.2d
Height			
0 meters	0.254a	1.6a	7.3a
3	0.255a	1.5a	6.3b
6	0.261ab	1.6a	5.7c
9	0.257a	1.6a	5.3d
12	0.270b	1.5a	4.7e
Radial section			
Inner wood	0.243a	1.6a	5.4a
Middle wood	0.249a	1.5a	6.2b
Outer wood	0.285b	1.5a	6.1b

¹ Those means followed by the same letter are not significantly different at the $P \geq 0.05$ level.

tropical pioneer tree species. For tropical wet forest pioneers, Wiemann and Williamson (1987) reported increases ranging from 90 to 270%. However, the percentages of increase observed in *Hildegardia* from inner to outer samples are considerably lower than Wiemann and Williamson observed in any of their studies. In only one tree, a 44-cm-diameter tree on Site 3, did the increase exceed 100% (Table 6). The range in percent increase was from 0 to 129%, and the overall simple correlation (r) with actual tree diameter was 0.66, significant at the 5% level.

When specific gravity was expressed as a function of the fractional distance from the pith, specific gravity increased linearly from pith to bark as well. Simple linear regression equations for individual *Hildegardia* trees in this study had a wide range in the degree of linearity, as expressed by r^2 , which varied from 0.004 to 0.93 (Table 6). When all trees on all sites were regressed as a group, the results were less than encouraging (Table 7, Eq. 1). This was at least partially due to the fact that the trees on the Akure and Olokemeji sites had significantly lower means than the trees from the other two sites (Table 1).

One of the other problems in dealing with data such as these is the fact that each tree is an individual and, apparently, genotypically and phenotypically different from its neighbor. To overcome this problem, the specific gravity data were

TABLE 5. Specific gravity as functions of height and radial position. Means for all trees from all sources.

Height (m)	Radial position		
	Inner	Middle	Outer
0	0.211	0.252	0.298
3	0.235	0.246	0.284
6	0.243	0.252	0.288
9	0.257	0.241	0.274
12	0.269	0.259	0.283

TABLE 6. Relationship between tree diameter and specific gravity. The regression equation is of the form $Y = \text{Intercept} + [\text{Slope} \times (X)]$ where X is the fractional distance from pith.

Site	Tree No.	DBH (cm)	Specific gravity		Percent increase	Intercept	Slope	r^2
			Inner	Outer				
Oluwa	1	31	0.200	0.200	0	0.205	0.003	0.004
	2	27	0.250	0.290	56	0.204	0.290	0.66
	3	24	0.221	0.355	61	0.177	0.029	0.84
	4	27	0.186	0.279	50	0.171	0.011	0.71
	5	36	0.235	0.335	42	0.197	0.017	0.85
	6	29	0.230	0.284	23	0.212	0.011	0.82
	7	31	0.236	0.308	31	0.213	0.011	0.53
	8	38	0.202	0.370	83	0.177	0.019	0.84
	9	36	<u>0.249</u>	<u>0.276</u>	<u>11</u>	<u>0.231</u>	<u>0.005</u>	<u>0.24</u>
Site mean			0.224	0.311	40	0.199	0.014	0.61
Akure	10	51	0.212	0.302	43	0.201	0.008	0.89
	11	48	0.182	0.245	35	0.159	0.007	0.55
	12	33	0.184	0.240	30	0.155	0.009	0.45
	13	28	0.187	0.308	65	0.123	0.030	0.64
	14	48	0.261	0.337	29	0.227	0.007	0.54
	15	38	0.207	0.298	44	0.171	0.011	0.66
	16	30	0.183	0.256	40	0.162	0.012	0.59
	17	38	0.165	0.297	80	0.135	0.020	0.48
	18	34	<u>0.198</u>	<u>0.242</u>	<u>22</u>	<u>0.173</u>	<u>0.009</u>	<u>0.48</u>
Site mean			0.198	0.281	43	0.167	0.013	0.61
Olokemeji	19	52	0.162	0.211	30	0.140	0.013	0.46
	20	39	0.205	0.329	60	0.175	0.018	0.91
	21	39	0.146	0.266	82	0.119	0.017	0.94
	22	44	0.153	0.351	129	0.129	0.020	0.89
	23	26	0.248	0.272	10	0.229	0.006	0.20
	24	41	0.132	0.239	81	0.100	0.015	0.86
	25	42	0.189	0.316	67	0.158	0.016	0.87
	26	50	0.227	0.429	89	0.174	0.022	0.93
	27	53	<u>0.258</u>	<u>0.386</u>	<u>50</u>	<u>0.230</u>	<u>0.013</u>	<u>0.86</u>
Site mean			0.191	0.311	66	0.162	0.015	0.77
Owo	28	59	0.322	0.407	26	0.326	0.005	0.43
	29	30	0.222	0.248	12	0.216	0.004	0.14
	30	32	0.253	0.285	13	0.237	0.005	0.20
	31	32	0.207	0.294	42	0.174	0.013	0.67
	32	30	0.217	0.260	20	0.203	0.007	0.80
	33	31	0.188	0.244	30	0.167	0.011	0.82
	34	40	0.249	0.270	8	0.242	0.002	0.21
	35	27	0.205	0.294	43	0.165	0.022	0.91
	36	32	<u>0.224</u>	<u>0.308</u>	<u>38</u>	<u>0.196</u>	<u>0.017</u>	<u>0.92</u>
Site mean			0.232	0.290	26	0.214	0.010	0.56

standardized. Standardization is a technique that is used widely in dendrochronology (Fritts 1976). There are a number of standardization techniques used in dendrochronological studies. In this case, we standardized by dividing each value for a given tree by the mean specific gravity for that tree. This gives an overall mean for each tree of 1.00 and, for our purposes, provides an excellent comparative method to see if trends are being developed. While the coefficients of determi-

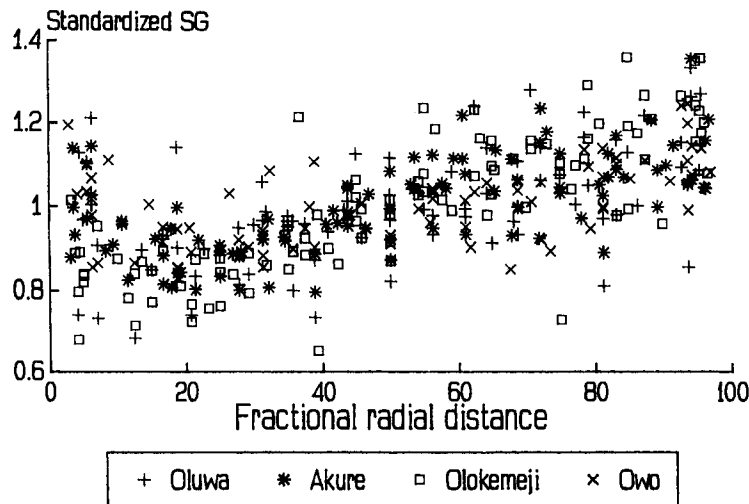


FIG. 8. DBH standardized specific gravity for the four different sites plotted against percentage of distance from the pith.

nation improved markedly (Table 7, Eq. 2), the results still suggest that a simple straight line increase from pith to bark may not be entirely satisfactory. Plots of the data indicated that the sample of wood immediately adjacent to the pith was appreciably higher than many of the other samples (Fig. 8). The data sets were therefore reduced by disregarding this sample in each tree, and the resulting equations are shown as Eqs. 3 and 4 in Table 7. Undoubtedly, better fits of the data could be obtained using some type of curvilinear equation. However, the question then becomes an exercise in statistical/mathematical expertise and manipulations rather than one of basic wood quality behavior.

Site factor relationships

The two major site factors influencing tree growth in this (and other) region(s) are the rainfall regime and the soils (Jacoby 1989). All four sites were in the lowland rainforest area, even though the lengths of the rainy season varied from 9 months in the Oluwa and Akure Forest Reserves to 8 months in the Olokemeji and Owo Forest Reserves (Table 6). Total annual and mean monthly rainfalls were greater in the former reserves as well. The soils in the Oluwa, Akure, and

TABLE 7. Regression equations for specific gravity (SG) and standardized specific gravity (SSG) as a function of distance from pith.

Simple linear, full data set		
(1)	$SG = 0.2299 + 0.00075 (\text{Radius } \%)$	$r^2 = 0.167$
(2)	$SSG = 0.859 + 0.0028 (\text{Radius } \%)$	$r^2 = 0.378$
Simple linear, reduced data set		
(3)	$SG = 0.2176 + 0.00093 (\text{Radius } \%)$	$r^2 = 0.206$
(4)	$SSG = 0.809 + 0.0035 (\text{Radius } \%)$	$r^2 = 0.491$

TABLE 8. Site means for soil, rainfall, and tree size.

Soil layer	Oluwa			Akure			Olokemeji			Owo		
	I	II	III	I	II	III	I	II	III	I	II	III
pH	5.2	5.1	4.9	6.8	6.2	6.5	7.1	7.0	7.2	6.4	5.9	5.7
Al (lb/A)	38	118	202	4.5	4.6	3.6	2.5	1.9	1.7	6.1	37	54
P (lb/A)	10.7	11.7	7.7	27.3	16.3	23.0	41.7	34.7	41.7	16.3	13.7	9.3
Ca (lb/A)	760	400	330	5,403	3,313	3,087	2,433	1,820	1,777	2,897	1,250	1,241
Mg (lb/A)	98	50	55	334	208	192	235	184	217	406	205	187
K (lb/A)	181	184	119	202	106	125	151	137	137	356	268	198
Mean annual rainfall (mm)	1,553			1,478			1,255			1,304		
Mean monthly rainfall (mm)	123.7			123.2			104.2			108.5		
Rainy period (>40 mm/month)	9			9			8			8		
Tree diameter (cm)	31			41			42			38		
Tree height (m)	17.9			19.7			22.3			14.9		

Owo Forest Reserves were acidic, with soil pH decreasing from layer I to Layer III. The soil at Olokemeji Forest Reserve was neutral to slightly alkaline in the three layers sampled. Exchangeable Al levels increased with depth in the Oluwa and Owo Forest Reserve soils, while Al levels decreased with depth at the other two sites. As might be expected, there was a significant correlation ($r = -0.84$ to -0.99) between soil pH and Al levels. A more intensive site and soil sampling scheme would have been desirable, but was not feasible given budget and time constraints.

Tree diameter was positively correlated with soil pH ($r = 0.93$ to 0.99) and negatively correlated with exchangeable Al ($r = -0.84$ to -0.95). Tree height also correlated positively with soil pH ($r = 0.50$ to 0.73).

The analyses of variance had indicated that there were significant differences among sites for many of the variables tested (Tables 1 and 3). The poorest sites (from a soil chemistry standpoint) were the Oluwa and Owo Forest Reserves. These sites had the highest mean SG (0.277 and 0.263, respectively), as well as the longest fibers and the highest proportion of cross-sectional area occupied by fibers (Table 2). However, for the most part, the proportion of variance accounted for by site appeared to be relatively small. This suggests that genetics and cambial age exerted a greater influence on *Hildegardia*'s growth and wood quality insofar as this study was concerned.

REFERENCES

- BAAS, P. 1976. Some functional and adaptive aspects of vessel member morphology. *Leiden Bot. Ser.* 3:157-181.
- BAILEY, I. W. 1920. The cambium and its derivative tissue. II. Size variation of cambial initials in gymnosperms and angiosperms. *Am. J. Bot.* 7:355-367.
- BISSING, D. R. 1974. Haupt's adhesive mixed with formalin for affixing paraffin sections to slides. *Stain Technol.* 49:116-117.
- BOSSHARD, H. H. 1966. Notes on the biology of the heartwood formation. *IAWA Bull.* 1:1-14.
- BROWN, J. R., AND R. R. RODRIGUEZ. 1983. Soil testing in Missouri: A guide for conducting soil tests. Missouri Cooperative Extension Service. University of Missouri and Lincoln University.
- CARLQUIST, S. 1975. Ecological strategies of xylem evolution. University of California Press, Berkeley, CA. 259 pp.
- . 1980. Further concepts in ecological wood anatomy, with comments on recent work in wood anatomy and evolution. *Aliso* 9(4):499-553.
- . 1982. The use of ethylenediamine in softening hard plant structures for paraffin sectioning. *Stain Technol.* 57:311-317.
- CHALK, L., AND M. M. CHATTAWAY. 1934. Measuring the length of vessel members. *Trop. Woods* 40:19-26.
- CHATTAWAY, M. M. 1936. Relation between fiber and cambial initial length in dicotyledonous woods. *Trop. Woods* 46:16-20.
- FRITTS, H. C. 1976. *Tree rings and climate*. Academic Press, New York. 567 pp.
- FROST, F. H. 1930. Specialization in secondary xylem of dicotyledons. I. Origin of vessel. *Bot. Gaz.* 89:67-94.
- ISEBRANDS, J. G. 1972. The proportion of wood elements within eastern cottonwood. *Wood Sci.* 5(2):139-146.
- JACOBY, G. C. 1989. Overview of tree-ring analysis in tropical regions. *IAWA Bull.* n.s. 10(2):99-108.
- KEAY, R. W. J. 1959. *An outline of Nigerian vegetation*. Government Printers, Lagos, Nigeria.
- , AND C. ONOCHIE. 1959. *Nigerian trees, vol. I*. Government Printers, Lagos, Nigeria.
- LEE, C. H. 1986. A note on the effect of alcohol-benzene extractives on juvenile wood specific gravity in red pine. *Wood Fiber Sci.* 18:376-381.

- OLSON, J. R., AND S. B. CARPENTER. 1985. Specific gravity, fiber length, and extractive content of young *Paulownia*. *Wood Fiber* 17:428–438.
- SAS INSTITUTE, INC., 1985. SAS user's guide: Statistics. Version 5 Edition. SAS Institute, Inc., Cary, NC. 956 pp.
- SMITH, D. M. 1954. Maximum moisture content method for determining specific gravity of small wood samples. USDA Forest Service. Forest Prod. Lab. Tech. Rept. No. 2014. 8 pp.
- . 1967. Microscopic methods for determining cross-sectional cell dimensions. USDA Forest Service. Research Paper FPL-79.
- TAYLOR, F. W., AND T. E. WOOTEN. 1973. Wood property variation of Mississippi delta hardwoods. *Wood Fiber* 5:2–13.
- VURDU, H., AND D. W. BENSEND. 1980. Proportions and types of cells in stems, branches and roots of European black alder (*Alnus glutinosa* L. Gaertn.). *Wood Sci.* 13(1):36–40.
- WHITMORE, J. L. 1973. Wood density variation in Costa Rican balsa. *Wood Sci.* 5(3):223–229.
- WIEMANN, M. C., AND G. B. WILLIAMSON. 1987. Extreme radial changes in wood specific gravity in some tropical pioneers. *Wood Fiber Sci.* 20:344–349.
- , AND ———. 1989a. Radial gradients in the specific gravity of wood in some tropical and temperate trees. *Forest Sci.* 35:197–210.
- , AND ———. 1989b. Wood specific gravity gradients in tropical dry and montane rain forest trees. *Amer. J. Bot.* 76(6):924–928.
- YEOM, F. B. C. 1984. Lesser-known tropical wood species: How bright is their future? *Unasylva* 36(145):3–16.