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VARIATION IN WOOD ANATOMY OF SPECIES WITH A DISTRIBUTION COVERING BOTH RAIN FOREST AND SAVANNA AREAS OF THE IVORY COAST, WEST-AFRICA

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Summary. The variation in wood anatomy within 30 hardwood species, each with a distribution covering both rain forest and savanna areas of the Ivory Coast, Africa, has been studied. Compared to specimens from the rain forest, material from the savanna tends to have more wood ray tissue (rays are higher, wider, and more numerous) and slightly more vessel tissue (vessels are more numerous and wider, although they are often composed of shorter vessel members). Within any one species the total amount of axial wood parenchyma in the material from both areas is practically constant. The results are discussed with reference to latitudinal variation and major trends of phylogenetic wood specialization.

INTRODUCTION

An important factor for the identification of wood samples is to know where the material concerned comes from. It often appears that there is considerable variation in wood anatomy between samples of a particular species from different origins, as has been pointed out by a number of authors (Carlquist, 1966, 1975; Baas, 1973). These authors compared either different species of the same genus, or a single species with a large natural area of distribution, originating from different latitudes. Variation in wood anatomy in relation to altitude has been studied by, among others, Versteegh (1968) and van der Graaff & Baas (1974). The observed differences, affected by environmental conditions were discussed from a phylogenetic point of view. In relation to the results found by the above mentioned authors, an investigation was made of anatomical characteristics of the secondary xylem of Angiosperms which occur in two regions of the Ivory Coast in which the environment is very different, viz. in the coastal rain forest and in the seasonally dry inland savanna. The differences in altitude and latitude (five to six degrees north and nine to ten degrees north, respectively) between the two locations, is slight. Only some 30 of the 780 species collected by Versteegh and Den Outer in the Ivory Coast in 1969, appeared to be suitable for this study. So the aim of the present study is to investigate a number of species from several families, common to two different environments, in this way eliminating the effects of phylogenetic drift and concentrating on environmental effects.

MATERIALS AND METHODS

Wood samples used were from the Versteegh and Den Outer collection, Ivory Coast (1969). All the material studied had been catalogued. Almost all the material was collected from stems at breast height and immediately fixed in FAA.

Transverse, radial and tangential sections varying in thickness from 10–20 μm, were made with a sledge microtome. Maceration was performed according to Jeffrey (Johansen, 1940). All sections were embedded in Kaiser's gelatin-glycerin (Johansen, 1940). Means and ranges of the number of wood rays per mm in the tangential direction, ray height and width, radial vessel diameter, and vessel member length, are based on at least twenty measurements. Vessel member length was measured excluding the tails, from the middle of one perforation plate to that of the next one. The authors are aware that vessel member lengths, measured in this way are not comparable with measurements including the tails, but it is felt that, for any functional consideration, the length of the body of the element is more significant than the total vessel member length. Vessel frequency and vessel grouping were determined over an area at least 20 square mm in size. The percentage of the axial system occupied by axial wood parenchyma, was estimated on a transverse section of the sample. For our research in tropical woody species we have used the definition of tracheids and libriform fibres given by Moll & Janssonius (1906–1936), Janssonius (1940) and Reinders (1935). Wood rays were classified according to Kribs (1935).

We realize that the material, originating from two different areas but in each case from the same species, is not entirely comparable in some cases, because it was collected from trees with a different diameter at breast height. Also the variability within the individual trees may have had some disturbing effect on the results obtained. Furthermore the number of investigated species is far from numerous.

RESULTS

The results are given in three tables: Table 1, information on rays; Table 2, information on vessels; Table 3, information on parenchyma and on miscellaneous features. The species investigated are arranged alphabetically within a family; the families are arranged according to the classification of Engler (1964).

From Tables 1–3, the following generalized trends can be deduced. Specimens from the savanna possess more ray tissue than specimens of the same species from the rain forest. The wood rays of the savanna material are higher in most cases (60% higher, 33% lower, and 7% equal). Furthermore they are also wider (63% wider, 20% smaller, and 17% equal) and more numerous (50% more, 20% less, and 30% equal). Also, the total amount of the cross section occupied by vessels is somewhat greater in the savanna material. This is caused by the fact that the vessels are wider (63% wider, 30% smaller, and 7% equal), whereas at the same time the number per square mm is slightly larger

SYMBOLS AND ABBREVIATIONS USED IN TABLES 1, 2, AND 3

+	= present	PC	= axial wood parenchyma
–	= absent	R	= species from rain forest
±	= scarcely present	raf.	= raphid
I	= uniseriate rays and multiseriate rays with long uniseriate tails	S	= species from savanna
II	= uniseriate rays and multiseriate rays with short uniseriate tails	sep. l	= septate wood fibre
III	= only uniseriate rays present	sm.	= paratracheal parenchyma on all sides of the vessel, less than three cells wide
br.	= paratracheal parenchyma on all sides of the vessel, three or more cells wide	sm½	= paratracheal parenchyma only half around the vessel, less than three cells wide
br.½	= paratracheal parenchyma only half around the vessel, three or more cells wide	sm.tg.b.	= apotracheal parenchyma in small tangential bands
br.tg.b.	= apotracheal parenchyma in broad tangential bands	t	= fibre-tracheids
dbh	= diameter at breast height	term.	= terminal apotracheal parenchyma
diff.	= diffuse apotracheal parenchyma	tg.b.	= apotracheal parenchyma in tangential bands
He	= heterogeneous wood rays	u	= upright wood-ray cell
Ho	= homogeneous wood rays	V + 0 number	= number of the wood sample and corresponding herbarium material of the Versteegh and den Outer collection, Ivory Coast, West-Africa, 1969
l	= libriform fibres	WR	= wood-ray parenchyma
(l+)	= a small number of libriform fibres present		
p	= procumbent wood-ray cell		

Table 1

Specimens studied	forest type and V+0 number	dbh cm	wood rays					
			average number per tangential mm	maximum height (average) µm	maximum width µm	maximum number (average) of rows	cell type	ray type
Cleistopholis patens (Benth.)	R 76	30	3	1240(705)	240	10(6-7)	p(+u)	Ho II
Engl. et Diels (Annonaceae)	S 302	20	3	2100(1030)	300	15(8-9)	p(+u)	Ho II
Berlinia tomentella Keay	R 183	40	8	440(245)	40	3(1-2)	p(+u)	Ho I
(Caesalpiniaceae)	S 284	40	11	480(200)	45	3(2)	p(+u)	Ho I
Baphia pubescens Hook.f.	R 34	10	5	1650(600)	75	8(5-6)	p	Ho II
(Papilionaceae)	S 316	20	6	1830(725)	95	9(5-6)	p	Ho II

Pterocarpus santalinoides L'Hér.	R 104	80	11	230(200)	30	2(1)	p	Ho III
ex DC. (Papilionaceae)	S 487	15	12	220(180)	30	2(1)	p	Ho III
Campylospermum glaberrimum (P.	R 146	4	14	2800(1430)	100	7(5)	p+u	He II
Beauv.) Farron (Ochnaceae)	S 537	2	18	3000(1430)	100	7(5)	p+u	He II
Harungana madagascariensis Lam.	R 57	25	9	1050(215)	60	5(3)	p+u	He II
ex Poir. (Hypericaceae)	S 314	15	8	1030(220)	70	6(3-4)	p+u	He II
Smeathmannia pubescens Soland.	R 92	5?	12	4700(4500)	70	3(1-2)	u	Ho I
ex R.Br. (Passifloraceae)	S 540	10	13	6800(5650)	80	4(1-2)	u	Ho I
Trema orientalis (L.) Bl.s.l.	R 584	20?	7	1400(475)	60	5(3-4)	p+u	He II
(Ulmaceae)	S 277	7	10	1800(610)	45	3(1-2)	p+u	He I
Ficus congensis Engl.	R 158	30	5	1440(540)	175	11(4-5)	p+u	He II
(Moraceae)	S 348	30	4	2240(790)	110	9(5)	p+u	He II
Strychnos usambarensis Gilg	R 677	12	6	4000(540)	80	6(4-5)	p+u	He II
(Loganiaceae)	S 539	4	10	3500(790)	70	6(3-4)	p+u	He II
Holarrhena floribunda (G.Don)	R 631	15	8	590(200)	40	3(2-3)	p(+u)	He I
Dur.et Schinz var.floribunda	S 322	15	8	700(245)	45	4(3-4)	p+u	He I
(Apocynaceae)								
Rauvolfia vomitoria Afzel.	R 86	6	7	850(575)	40	5(3-4)	p+u	He I
(Apocynaceae)	S 287	7	4	950(550)	60	6(4-5)	p+u	He I
Canthium subcordatum DC.	R 5	20	8	1400(625)	80	6(4-5)	p+u	He II
(Rubiaceae)	S 318	10	7	3200(810)	120	8(5-6)	p+u	He II
Gaertnera paniculata Benth.	R 141	10	10	1800(680)	80	6(3-4)	p+u	He I
(Rubiaceae)	S 330	15	12	4800(1540)	100	5(3-4)	p+u	He I
Morinda lucida Benth.	R 28	25	7	1150(490)	100	6(3-4)	p+u	He II
(Rubiaceae)	S 320	25	7	1600(625)	100	6(3-4)	p+u	He II
Nauclea latifolia Sm.	R 65	10	13	1830(585)	50	5(2-3)	p+u	He I
(Rubiaceae)	S 296	10	16	3100(610)	70	3(2-3)	p+u	He I
Oxyanthus unilocularis Hiern	R 251	10	19	2000(855)	70	6(3-4)	p+u	He I
(Rubiaceae)	S 293	10	19	5370(1130)	70	6(3-4)	p+u	He I
Pavetta cf.corymbosa (DC.)F.N.	R 32	10	18	3050(605)	30	3(1-2)	p+u	He I
Williams (Rubiaceae)	S 459	4	20	2500(560)	30	4(1-2)	p+u	He I

Table 1 (*continued*)

Specimens studied	forest type and V+O number	dbh cm	wood rays: average number per tangential mm	maximum height (average) µm	maximum width µm	maximum number (average) of rows	cell type	ray type
Harrissonia abyssinica Oliv.	R 208	6	10	2600(545)	40	3(1-2)	p+u	He I
(Simarubaceae)	S 334	10	12	2000(510)	45	3(1-2)	p+u	He I
Carapa procera DC.(Meliaceae)	R 704	30	6	1600(540)	100	6(3-4)	p+u	He II
	S 344	40	6	2700(575)	175	8(6-7)	p+u	He II
Trichilia monadelpha (Thonn.)	R 17	25	8	700(340)	40	3(2)	p(+u)	He II
J.J.de Wilde (Meliaceae)	S 323	50	8	670(270)	50	4(2-3)	p(+u)	He II
Spondias mombin L.	R 73	35	4	2100(830)	200	9(5-6)	p+u	He II
(Anacardiaceae)	S 518	15	4	1650(600)	160	5(4-5)	p+u	He II
Paullinia pinnata L.	R 106	5	16	3250(1000)	90	9(4)	p+u	He II
(Sapindaceae)	S 526A	4	16	1800(630)	90	8(4)	p+u	He II
Christiana africana DC.	R 214	6	7	2270(490)	100	5(3-4)	p+u	He II
(Tiliaceae)	S 534	10	9	1800(430)	120	6(4-5)	p+u	He II
Sterculia tragacantha Lindley	R 109	60	3	2500(1175)	300	14(10)	p+u	He II
(Sterculiaceae)	S 336	25	3	2700(1580)	325	17(10)	p+u	He II
Antidesma membranaceum M.A.	R 19	15	14	2250(810)	75	5(3-4)	p(+u)	He II
(Euphorbiaceae)	S 278	8?	12	2400(1120)	60	5(3-4)	p(+u)	He II
Antidesma venosum Tul.	R 162	5	14	2500(1610)	70	3(2)	p+u	He I
(Euphorbiaceae)	S 527	6	12	2500(1400)	150	7(3-4)	p+u	He II
Bridelia micrantha (Hochst.)	R 14	25	7	540(420)	90	6(4-5)	p+u	He II
Baill. (Euphorbiaceae)	S 275	10	9	1050(535)	75	5(3)	p+u	He I
Phyllanthus discoideus (Baill.)	R 228	10	9	2500(765)	65	6(4-5)	p+u	He II
M.A. (Euphorbiaceae)	S 442	20	10	2500(1050)	130	10(5)	p+u	He II
Kigelia africana (Lam.) Benth.	R 601	10	4	390(150)	40	3(2)	p	Ho II
(Bignoniaceae)	S 283	15	5	320(150)	80	5(3-4)	p	Ho II

Table 2

Specimens studied		vessels: average number per square mm	radial pore multiple	pore cluster	tylosis	simple perforation plates	maximum diameter (average) µm	range of vessel member length (average) µm
Cleistopholis patens (Benth.)	R	2	+	±	-	+	250(145)	180-500 (350)
Engl. et Diels (Annonaceae)	S	1	+	±	-	+	210(160)	160-400 (320)
Berlinia tomentella Keay	R	6	+	±	-	+	280(160)	150-350 (230)
(Caesalpiniaceae)	S	6	+	±	-	+	200(115)	200-350 (280)
Baphia pubescens Hook.f.	R	5	+	±	-	+	140(90)	150-240 (210)
(Papilionaceae)	S	16	+	±	-	+	180(100)	120-270 (210)
Pterocarpus santalinoides L'Hér.	R	6	+	+	-	+	180(110)	270-180 (230)
ex DC. (Papilionaceae)	S	6	+	+	-	+	160(95)	240-150 (210)
Campylospermum glaberrimum(P.	R	95	±	-	-	+	50(35)	210-590 (350)
Beauv.) Farron (Ochnaceae)	S	135	±	-	-	+	55(35)	200-420 (330)
Harungana madagascariensis Lam.	R	4	±	-	+	+	270(190)	150-350 (250)
ex Poir. (Hypericaceae)	S	7	±	-	+	+	270(205)	120-410 (240)
Smeathmannia pubescens Soland.	R	22	+	+	-	+	130(75)	260-950 (570)
ex R.Br. (Passifloraceae)	S	22	+	+	-	+	130(80)	530-1120(750)
Trema orientalis (L.) Bl.s.l.	R	17	+	±	+	+	200(115)	320-550 (430)
(Ulmaceae)	S	23	+	±	+	+	150(80)	150-380 (210)
Ficus congensis Engl.	R	2	+	±	-	+	250(145)	180-325 (180)
(Moraceae)	S	3	+	±	-	+	350(235)	300-500 (350)
Strychnos usambarensis Gilg	R	55	+	+	-	+	230(160)	170-350 (270)
(Loganiaceae)	S	96	+	+	-	+	105(65)	120-350 (230)
Holarrhena floribunda (G.Don)	R	26	+	±	-	+	120(90)	210-540 (340)
Dur.et Schinz var.floribunda	S	32	+	±	-	+	100(60)	170-590 (350)
(Apocynaceae)								

Table 2 (*continued*)

Specimens studied		vessels					
	average number per square mm	radial pore multiple	pore cluster	tylosis	simple perforation plates	maximum diameter (average) µm	range of vessel member length (average) µm
Rauvolfia vomitoria Afzel. (Apocynaceae)	R 50	±	±	-	+	75(60)	150-480 (350)
	S 70	±	±	-	+	110(80)	145-530 (350)
Canthium subcordatum DC. (Rubiaceae)	R 23	+	+	-	+	190(135)	410-740 (610)
	S 39	+	+	-	+	180(105)	290-450 (590)
Gaertnera paniculata Benth. (Rubiaceae)	R 28	+	+	-	+	90(50)	180-590 (380)
	S 16	+	+	-	+	130(85)	410-820 (590)
Morinda lucida Benth. (Rubiaceae)	R 7	+	+	-	+	210(125)	230-590 (370)
	S 6	+	+	-	+	240(140)	145-380 (280)
Nauclea latifolia Sm. (Rubiaceae)	R 6	+	+	-	+	260(130)	260-820 (460)
	S 4	+	+	-	+	300(180)	325-650 (480)
Oxyanthus unilocularis Hiern (Rubiaceae)	R 110	+	±	-	+	60(40)	360-780 (550)
	S 120	+	±	-	+	60(40)	240-860 (440)
Pavetta cf.corymbosa (DC.)F.N. Williams (Rubiaceae)	R 115	±	-	+	+	75(40)	190-690 (440)
	S 155	±	-	-	+	65(35)	160-730 (430)
Harrissonia abyssinica Oliv. (Simarubaceae)	R 25	+	±	-	+	140(95)	180-560 (370)
	S 32	+	±	-	+	140(70)	180-380 (310)
Carapa procera DC. (Meliaceae)	R 8	+	±	-	+	190(100)	230-440 (350)
	S 8	+	±	-	+	200(130)	120-440 (290)
Trichilia monadelpha (Thonn.) J.J.de Wilde (Meliaceae)	R 8	+	+	-	+	180(95)	210-590 (400)
	S 15	+	±	-	+	200(115)	120-470 (290)
Spondias mombin L. (Anacardiaceae)	R 7	+	+	-	+	300(120)	180-530 (330)
	S 5	+	±	-	+	230(150)	180-650 (360)
Paullinia pinnata L. (Sapindaceae)	R 18	+	-	-	+	230(105)	120-380 (280)
	S 18	±	-	-	+	250(115)	120-470 (300)

Christiana africana DC. (Tiliaceae)	R	30	+	±	-	+	120(70)	180-350 (260)
	S	20	+	±	-	+	140(75)	230-330 (280)
Sterculia tragacantha Lindley (Sterculiaceae)	R	3	+	±	-	+	380(220)	290-470 (380)
	S	3	+	+	-	+	300(180)	230-470 (370)
Antidesma membranaceum M.A. (Euphorbiaceae)	R	40	+	+	-	+	110(70)	260-750 (410)
	S	25	+	+	-	+	120(80)	410-590 (480)
Antidesma venosum Tul. (Euphorbiaceae)	R	50	+	±	-	+	60(50)	410-1120(760)
	S	70	+	±	-	+	90(60)	150-740 (410)
Bridelia micrantha (Hochst.) Baill. (Euphorbiaceae)	R	11	+	+	-	+	150(80)	120-410 (230)
	S	9	+	±	-	+	170(110)	200-620 (360)
Phyllanthus discoideus (Baill.) M.A. (Euphorbiaceae)	R	17	+	±	-	+	135(80)	240-760 (560)
	S	10	+	±	-	+	175(105)	350-530 (440)
Kigelia africana (Lam.) Benth. (Bignoniaceae)	R	7	±	±	-	+	140(100)	130-240 (200)
	S	6	±	±	-	+	160(125)	90-200 (140)

Table 3

Specimens studied		axial wood parenchyma: apotracheal	paratracheal	% PC of the axial system in cross section	main axial system	spiral thickenings	crystals	further observations
Cleistopholis patens (Benth.)	R	+(sm.tg.b.)	+(sm.)	20	1	-	±	
Engl. et Diels (Annonaceae)	S	+(sm.tg.b.)	+(br.)	15	1	-	-	
Berlinia tomentella Keay	R	+(diff.+br.tg.b.)	+(br.)	40	1	-	+(in PC)	
(Caesalpiniaceae)	S	+(diff.+br.tg.b.)	+(br.)	30	1	-	+(in PC)	
Baphia pubescens Hook.f.	R	+(br.tg.b.)	+(br.)	45	1	+	+(in PC)	
(Papilionaceae)	S	+(br.tg.b.)	+(br.)	35	1	-	+(in PC)	
Pterocarpus santalinoides L'Hér.	R	+(diff.)	+(sm.)	15	1	-	+(in PC)	storied
ex DC. (Papilionaceae)	S	+(tg.b.)	+(sm.)	25	1	-	+(in PC)	storied
Campylospermum glaberrimum (P.	R	±(diff.)	±	5	1+t	+	+(in WR)	broad aggregate rays
Beauv.) Farron (Ochnaceae)	S	±(diff.)	±	5	1+t	+	+(in WR)	broad aggregate rays
Harungana madagascariensis Lam.	R	+(tg.b.)	±	10	1	-	±	vascular tracheids
ex Poir. (Hypericaceae)	S	+(tg.b.)	±	15	1	-	±(in PC)	vascular tracheids
Smeathmannia pubescens Soland.	R	+(diff.)	+(sm½)	30	1	+	+(in WR)	{ slime cells in wood rays;
ex R.Br. (Passifloraceae)	S	+(diff.)	+(sm½)	30	1	+	+(in WR)	some scalariform perforation plates
Trema orientalis (L.) Bl.s.l.	R	±(diff.)	±	<5	1	-	-	
(Ulmaceae)	S	±(diff.)	±	<5	1	-	-	
Ficus congensis Engl.	R	+(tg.b.)	+(br.)	50	1	-	+(in PC)	
(Moraceae)	S	+(tg.b.)	+(br½)	30	1	-	±	
Strychnos usambarensis Gilg	R	+(tg.b.)	+(br.)	40	1	-	+	aggregate rays
(Loganiaceae)	S	+(tg.b.)	+(br.)	25	1+t	-	+	aggregate rays
Holarrhena floribunda (G.Don)	R	+(diff.)	±	<5	1+t	-	+(in PC)	
Dur.et Schinz var.floribunda (Apocynaceae)	S	+(diff.)	±	<5	1+t	-	+(in PC)	slightly ring-porous

Rauvolfia vomitoria Afzel.	R	+(diff.)	+(sm.)	40	1+t	-	+(in WR)	
(Apocynaceae)	S	+(diff.)	±	20	t	-	+(in WR)	
Canthium subcordatum DC.	R	+(diff.)	±	10	t	+	-	
(Rubiaceae)	S	+(diff.)	±	10	t	+	-	
Gaertnera paniculata Benth.	R	+(br.tg.b.)	±	40	1+t	+	-	
(Rubiaceae)	S	+(br.tg.b.)	±	30	1+t	+	-	
Morinda lucida Benth.	R	+(br.tg.b.)	±	45	1	-	±(raf.in PC)	
(Rubiaceae)	S	+(br.tg.b.)	±(sm.)	60	1	±	±(raf.in PC)	
Nauclea latifolia Sm.	R	+(diff.+tg.b.)	±	30	t	-	-	
(Rubiaceae)	S	+(diff.+tg.b.)	±	30	t	-	-	
Oxyanthus unilocularis Hiern	R	±(term.)	±	5	t	+	-	
(Rubiaceae)	S	±(term.)	±	5	t	+	-	
Pavetta cf.corymbosa (DC.)F.N.	R	±(diff.)	±	<5	(1+)t	+	-	pith flecks
Williams (Rubiaceae)	S	±(diff.)	±	<5	(1+)t	+	-	
Harrissonia abyssinica Oliv.	R	±(diff.)	±	<5	1	+	+(in WR)	
(Simarubaceae)	S	±(diff.)	±	<5	1	+	+(in WR)	pith flecks
Carapa procera DC.(Meliaceae)	R	+(diff.)	+	8	1	+	+(in WR)	
	S	+(diff.)	+	8	1	-	+(in WR)	
Trichilia monadelpha (Thonn.)	R	+(diff.)	+(br.)	10	1	+	+(in PC)	pith flecks
J.J.de Wilde (Meliaceae)	S	+(diff.)	+(br.)	10	1	+	+(in PC)	
Spondias mombin L.	R	±(diff.)	+(sm.)	5	1	-	+(in WR) }	horizontal resin ducts in
(Anacardiaceae)	S	±(diff.)	+(sm.)	5	1	-	+(in WR)	wood rays
Paullinia pinnata L.	R	±(diff.)	+(sm.)	<5	1	-	+(PC+WR)	broad aggregate rays
(Sapindaceae)	S	±(diff.)	+(sm.)	<5	1	-	+(PC+WR)	broad aggregate rays
Christiana africana DC.	R	+(br.tg.b.)	+(sm½)	35	1	+	+(in WR)	weakly storied
(Tiliaceae)	S	+(br.tg.b.)	+(sm½)	25	1	+	-	storied
Sterculia tragacantha Lindley	R	+(diff.)	+(br.)	50	1	-	-	
(Sterculiaceae)	S	+(diff.)	+(br.)	50	1	-	+(in WR)	
Antidesma membranaceum M.A.	R	±(diff.)	±	<5	1	-	-	
(Euphorbiaceae)	S	±(diff.)	±	<5	1	-	-	

Table 3 (*continued*)

Specimens studied	axial wood parenchyma: apotracheal	axial wood parenchyma: para-tracheal	axial wood parenchyma: % PC of the axial system in cross section	main axial system	spiral thick-enings	crystals	further observations
Antidesma venosum Tul. (Euphorbiaceae)	R ±(diff.)	±	2	sep.l.	-	-	
	S ±(diff.)	±	2	sep.l.	-	-	
Bridelia micrantha (Hochst.) Baill. (Euphorbiaceae)	R +(diff.+term.)	+(sm½)	30	±sep.l.	-	+(in PC)	
	S +(term.)	+(sm½)	8	±sep.l.	-	+(in PC)	
Phyllanthus discoideus (Baill.) M.A. (Euphorbiaceae)	R ±(diff.)	±	2	1	-	+(in WR)	
	S ±(diff.)	±	2	1	-	+(in WR)	
Kigelia africana (Lam.) Benth. (Bignoniaceae)	R ±(br.tg.b.)	+(br.)	25	1	-	-	
	S +(br.tg.b.)	+(br.)	45	1	-	-	

(47% more, 33% less, and 20% equal). Also vessel member length tends to be shorter in samples collected in the savanna (57% shorter, 36% longer, and 7% equal). The total amount of axial wood parenchyma in material from both areas, is practically the same.

The differences between the values measured for the savanna and rain forest material were tested with the Wilcoxon signed rank test, with an one-sided significance level of 0.05. The differences are significant for the maximum and average height of the wood rays, the maximum width and maximum number of rows of the wood rays, the average number of wood rays per tangential mm, and for the average number of vessels per square mm. The differences in vessel diameter and vessel member length are not statistically significant, so that we can only deduce weak tendencies from our results for these characters.

DISCUSSION

In the present study we have tried to eliminate the effects of phylogenetic drift on the structure of the secondary xylem, and concentrate on environmental effects. We investigated species common to two different environments, both within a single area of distribution. Still some of the variations in wood anatomy reported above may concern characteristics which are regarded as an indication of phylogenetic specialization. Trends of evolution based mainly on anatomical investigations of woods of temperate regions as well as economically important tropical trees from the lowlands, were established by, among others, Bailey & Tupper (1918), Bailey (1920, 1953), Frost (1930a, 1930b, 1931), Kribs (1935), Barghoorn (1940, 1941a, 1941b), Tippo (1946), Carlquist (1966, 1975). Some of these specialization trends are:

(a) short vessel elements with broad diameter, circular in cross section are derived from long, narrow vessel elements, angular in cross section;
(b) vessel elements with simple perforation plates or multiple perforation plates with a few bars are derived from multiple perforation plates with numerous bars;
(c) a decrease of size and frequency of bordered pits on fibre walls means specialization, which means that evolution has proceeded from tracheids to fibre-tracheids to wood fibres (libriform);
(d) homogeneous, narrow, low wood rays are derived from heterogeneous, broad, high ones.

Baas (1973) concludes from his own data that within taxa (genera) the longer vessel members are found in the tropical lowland species, the shorter vessel members in the species from temperate regions. Also, that in tropical lowlands the xylem vessels are fewer but wider than in temperate regions. This applies not only for species from temperate regions, but to a certain extent, also for tropical high montane species. In this respect tropical montane species are more similar to temperate species, than tropical lowland species. Also van der Graaff & Baas (1974) reported that with increasing latitude a decrease in size of secondary xylem elements (shorter vessel members, narrower vessels, lower rays) together with an increase in vessel frequency is obtained. Increasing altitude has similar but much smaller effects. Versteegh (1968) on the other hand found that mountain species show less specialized characters, viz. fibre-tracheids and/or scalariform perforation plates are common, whereas in the lowland species fibre-tracheids are usually replaced by libriform fibres and scalariform perforations are completely wanting.

The difference in latitude between the rain forest and savanna areas in the Ivory Coast, is small. Unfortunately, we did not have detailed metereological data at our disposal. Apparently the differences in temperature between the two localities are very slight. So the influence of the degree of latitude as reported by van der Graaff & Baas (1974) will be minute. If this influence is present after all it may account for the shorter vessel members and for the increased number of vessels per square mm, though both changes were not very pronounced. It could not apply to the more distinct phenomena such as the wider vessels in the savanna material and their higher, wider, and more numerous wood rays.

It is a generally accepted view that increase in vessel diameter and decrease in ray height may be interpreted as specialization, but many authors are aware of the fact that these changes may easily be affected by environmental conditions (Metcalfe & Chalk, 1950). Added to this it has been demonstrated (den Outer, 1967) that, within the same species, the reduction of the rays runs parallel with the differentiation of the axial system. The above mentioned trends for vessel member length and number of bars per perforation plate, on the other hand, have often been regarded as more stable, irreversible, evolutionary processes.

The discussion may serve to illustrate that several sources of variation, viz. phylogenetic specialization, within-tree variation and ecological influences may affect results on genera and families of woody dicotyledons. The differences between savanna and rain forest trees from the same species reported here, must be largely attributed to different environmental conditions. At present, it is impossible to interprete the differences, viz. more ray tissue and slightly more vessel volume in the savanna material, in a functional or adaptive sense.

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