

WOOD ANATOMICAL VARIATION IN RELATION TO LATITUDE AND ALTITUDE

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SUMMARY

The wood anatomical variation within 17 eurytherm hardwood genera in relation to altitude and latitude has been studied using wood samples from 52 species. With increasing latitude a miniaturization of secondary xylem elements (shorter vessel members, narrower vessels, shorter and sometimes narrower fibres, lower rays) is reported, together with an increase in vessel frequency and frequency and expression of helical thickenings to the vessel walls. Increasing altitude has similar but much weaker effects, and none on vessel grouping or helical thickenings. The number of bars per perforation plate in genera with partly or exclusively scalariform perforations is in general not correlated with altitude or latitude. In the softwood genus *Podocarpus* tracheid length and diameter and ray height decrease with increasing altitude. An analysis of the wood anatomical variation within 2 species with a wide latitudinal and 5 with a wide altitudinal range did not reveal correlations between the above mentioned features and latitude or altitude. The results are discussed with reference to previous interpretations of latitudinal and altitudinal variation in wood (Baas, 1973), stressing the significance for phylogenetic wood anatomy.

INTRODUCTION

In a survey of the wood anatomical range in the genus *Ilex*, the second author found a correlation between a number of characters and latitude and altitude of provenance of the species involved (Baas, 1973). In comparing species from the tropics with species from subtropical or temperate regions, vessel member length, vessel diameter, number of bars per perforation, and fibre length decreased with increasing latitude, whilst vessel frequency, degree of vessel grouping, and frequency and size of bordered pits on the tangential fibre

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walls increased. Occurrence and distinct presence of helical thickenings to the vessel and fibre walls was for a great deal restricted to material from subtropical to temperate latitudes. In comparing species from the tropical lowland with those from tropical montane regions, a similar but much weaker 'effect' was found with increasing altitude, except for the features helical thickening and fibre pitting. Additional evidence on *Prunus*, *Symplocos*, *Viburnum*, and *Hydrangea*, together with data from the literature (for a rather elaborate discussion see Baas, 1973) suggested that the findings for *Ilex* presented an example of a general trend in widespread genera, of relevance for ecological and phylogenetic wood anatomy.

The present study was undertaken in order to collect additional data on more genera and to test the general validity of the suggestions mentioned above. From 17 dicotyledonous genera (belonging to 14 families), the wood of 52 species was studied in order to examine latitudinal and altitudinal variation within genera. This was also done for one gymnospermous genus. In order to see whether any of the trends can also be traced within eurytherm species, 40 specimens were studied of 5 species with a wide latitudinal or altitudinal range. This was considered to be of crucial importance for tracing back the origin of the anatomical variation on the genus level. The results are presented in tables, diagrams, and additional notes.

MATERIALS AND METHODS

Wood samples used are from the wood collection of the Rijksherbarium and from other wood collections indicated according to Stern (1967). Not all the material studied was vouched. Almost all material was from stems or branches exceeding 5 cm diameter. Wood anatomical features were studied in transverse, tangential, and radial sections and macerations. The latter were prepared according to Franklin's method (Anonymous, 1968). Means and ranges for vessel member length, tangential vessel diameter, number of bars per perforation, tangential fibre diameter, fibre length, and ray height are based on at least 25 measurements. Vessel frequency and vessel grouping were determined in at least 5 square millimetres. Vessel frequency has not been recorded for ring-porous woods; for semi-ring-porous woods the values are based on counts in all representative zones of the growth ring.

LIMITATIONS OF THIS STUDY

Unless stated otherwise, the material studied was derived from peripheral parts of stems or branches with a diameter of at least 5 cm. For *Ilex* this gave a sufficient guarantee that vessel member length had become more or less stable (Baas, 1973). Further changes beyond this diameter may of course occur, and other sources of within-a-tree variation may also have influenced our results. However, we believe that such variation cannot have influenced the general trends, derived from many species and wood samples.

The botanical identity of the material may be uncertain for those specimens which were unvouched and for the vouched specimens of genera in need of a taxonomic revision. However, the wood anatomical character complex suggested that no major misidentifications had occurred.

The material studied has mainly been selected on one criterion only: the availability of wood specimens in the Rijksherbarium collection or in some other institutional wood collections. This implies that our data for each individual genus are too limited for drawing conclusions for the genus as a whole, because the number of species studied was too low. Only after combining the data on all species and genera, some reliability of altitudinal and latitudinal trends can be expected.

RESULTS

Latitudinal and altitudinal trends within genera

In table I data are given on vessel frequency, percentage of solitary vessels, tangential vessel diameter, presence or absence of helical thickenings, mean vessel member length, number of bars per perforation, mean fibre length, tangential fibre diameter, and mean ray height for 17 genera with a wide altitudinal and/or latitudinal range. Localities of provenance have been grouped into zones as follows:

Latitudinal lowland zones (below 1000 m alt.):

Zone I (L I) Tropical, 0° — $23^{\circ} 30'$

Zone II (L II) Subtropical, $23^{\circ} 30'$ — 35°

Zone III (L III) Warm temperate, 35° — 45°

Zone IV (L IV) Temperate, 45° — 60° .

Tropical altitudinal zones:

Zone I (A I) 0—1000 m at 0° latitude to 0 m at $23^{\circ} 30'$ latitude (this zone coincides with zone L I, and has been referred to in table I as zone AL I).

Zone II (A II) 1000—1700 m at 0° latitude to 0—500 m at $23^{\circ} 30'$ latitude

Zone III (A III) 1700—2600 m at 0° latitude to 500—1200 m at $23^{\circ} 30'$ latitude

Zone IV (A IV) 2600—4000 m at 0° latitude to 1200—2400 m at $23^{\circ} 30'$ latitude.

Latitudinal zones I, II, III, and IV can be regarded as having more or less similar temperature regimes as altitudinal zones I, II, III, and IV, resp., except for seasonality (Van Steenis, 1962).

Of some specimens no exact data on latitude and/or altitude were available. In those cases the altitudinal or latitudinal zone had to be chosen somewhat arbitrarily and was based on the distribution of the species as given in floristic and taxonomic literature. For instance *Rhamnus prinoides* from East Africa has been assigned to zone I in table I, but its distribution is from 1000—3000 m in Kenya. Our data of *Styrax argenteus* and *S. glabratus* were insufficient to decide whether our specimens should be placed in altitudinal zone I or II. In the table they have been included in zone I. For the other material more precise data on latitude and altitude of provenance can be found under the notes at the end of this paper. As will become clear from the results any possible mistakes on *Rhamnus* and *Styrax* can only negatively have influenced the trends we found.

In order to compare the data on all genera studied, the highest quantitative value for any character within a genus has been considered to be 1, all lower values having been expressed in fractions of 1. In fig. 1 and 2 these values for vessel frequency, vessel diameter, vessel member length, number of bars per perforation, fibre length, and ray height are given in frequency diagrams for the different altitudinal and latitudinal zones. In fig. 3 and 4 the means of the relative quantitative values are given. Vessel frequency (Vf) has been plotted as $1/Vf$ for reasons of comparison.

From table I and fig. 1—4 it becomes clear that species from temperate latitudes, if compared with their tropical relatives, possess more vessels per surface area, narrower vessels, shorter vessel members, shorter fibres, and lower rays. These differences are also present, though to a much lesser extent, if one compares tropical montane with tropical lowland species. The values for number of bars per perforation are, however, erratic if we compare the average values for different latitudinal and altitudinal zones in fig. 3 and 4.

Table I. Variation in 9 wood anatomical features within genera in relation to latitudinal and altitudinal distribution. Mean values are given in μm . (See also notes on specimens studied on p. 000; for explanation of altitudinal and latitudinal zones see text, p. 000). S = vessel perforations exclusively simple.

Species studied	A Altitudinal and Latitudinal Zone	B Vessel frequency	C % of solitary vessels	D Tangential vessel diameter	E Helical thickenings	F Vessel member length	G Number of bars per perforation	H Fibre length	I Tangential fibre diameter	J Ray height
<i>Acacia</i>										
<i>cyanophylla</i>	L II	22	35	108	—	210	S	680	13	170
<i>mangium</i>	AL I	10	69	152	—	380	S	900	15	140
<i>Ailanthus</i>										
<i>altissima</i>	L IV				+	370	S	820	18	300
<i>integrifolia</i>	AL I				—	840	S	1620	29	1280
<i>Cryptocarya</i>										
<i>caloneura</i>	AL I	5	59	170	—	610	S	1200	55	480
<i>minutifolia</i>	A IV	14	42	90	—	490	S	900	28	210
<i>Diospyros</i>										
<i>amboinensis</i>	AL I	9	22	96	—	660	S	1340	12	370
<i>virginiana</i>	L III	14	50	115	—	380	S	1270	19	240
<i>Drypetes</i>										
<i>lateriflora</i>	L II	72	17	51	—	950	2.1	1700	18	730
<i>diversifolia</i>	L II	123	7	43	—	620	1.3	1420	14	340
<i>gossweileri</i>	AL I	11	12	115	—	980	0.1	2490	20	790
<i>spec.</i>	AL I	26	11	80	—	970	0.9	1690	17	550
<i>Elaeocarpus</i>										
<i>dolichostylus</i>	AL I	5	71	152	—	760	S	1200	26	330
<i>japonicus</i>	L II	104	30	54	++	720	S	1200	16	470
<i>robustus</i>	AL I	12	35	142	—	830	S	1410	17	660
<i>spec.</i>	A IV	28	38	85	—	640	S	890	17	510
<i>Erythrina</i>										
<i>crista-galli</i>	L IV	2	81	120	—	150	S	790	18	680
<i>variegata</i>	AL I	0.6	30	250	—	290	S	1900	18	870
<i>Eurya</i>										
<i>acuminata</i>	AL I	62		69	—	1700	74	2220	27	630
<i>obovata</i>	A III	95		60	—	1760	79	2240	26	670
<i>tigang (1200 m alt.)</i>	A II	52		66	—	1600	65	2080	25	770
<i>tigang (3250 m alt.)</i>	A IV	93		65	—	2000	61	2270	25	1200
<i>Fagraea</i>										
<i>salticola</i>	A IV	14	54	83	—	400	S	910	18	360
<i>gracilipes</i>	AL I	5	29	161	—	540	S	1780	22	1080
<i>Gordonia</i>										
<i>excelsa</i>	AL I	16	87	99	—	1760	15	2630	35	510
<i>lasianthus</i>	L II	140	57	49	+	1330	28	1670	21	290
<i>papuana (740 m alt.)</i>	AL I	67	81	73	—	1900	15	2800	30	430
<i>papuana (30 m alt.)</i>	AL I	55	91	74	—	1820	16	2630	34	410
<i>spec.</i>	A IV	34	86	86	—	1470	20	2320	22	510
<i>Magnolia</i>										
<i>acuminata</i>	L III	82	46	76	—	520	0	1070	18	210
<i>drymifolia</i>	AL I	8	85	112	—	980	5.2	1650	21	390
<i>kobus</i>	L IV	76	47	43	—	440	0.2	900	17	200
<i>splendens</i>	A II	14	54	105	—	1010	6.8	1710	23	410
<i>tripetala</i>	L IV	176	36	47	—	600	4.4	1000	17	280

Species studied	A	B	C	D	E	F	G	H	I	J
Pisonia										
ambigua	L II			81	—	230	S	750	13	200
cuspidata	AL I			65	—	230	S	570	10	210
macranthocarpa	AL I			58	—	150	S	570	11	170
olfersiana	L II			70	—	250	S	860	16	200
rotundata	L II			57	—	180	S	510	14	140
sandwicensis	AL I			56	—	140	S	640	12	
Rhamnus										
catharticus (Netherl.)	L IV			78	++	240	S	670	11	130
catharticus (Flor.)	L II			63	++	290	S	850	10	130
prinoides	AL I			125	+	490	S	850	15	370
Rhus										
glabra	L IV	50	29	57	+	250	S	460	14	210
taitensis	AL I	6	82	112	—	520	S	890	14	290
vernix	L IV	57	36	72	+	260	S	330	14	180
Streblus										
glaber (alt. 750 m)	AL I	5	54	164	—	660	S	1970	16	510
glaber (alt. 15 m)	AL I	5	48	171	—	700	S	1880	18	500
urophyllus	A IV	8	28	88	—	370	S	970	11	250
Styrax										
argenteus	AL I	24	15	84	—	1010	7.4	1500	20	590
glabratus	AL I	28	29	83	—	1160	7.3	1700	22	660
japonicus	L IV	62	8	37	—	790	11	1030	17	240
obassia	L IV	50	26	36	—	600	11	1030	16	300
Weinmannia										
blumei	AL I	38		84	—	1200	10	1450	22	520
trichosperma	L III	106		48	—	700	16	1050	20	270
spec.	A IV	84		65	—	770	7	1050	19	400

Drypetes, *Gordonia*, *Styrax*, and *Weinmannia* show some increase in number of bars with increasing latitude or even altitude, *Magnolia*, on the other hand, shows the reverse.

The data on vessel grouping are not entirely conclusive for establishing general trends. Out of 9 diffuse-porous genera with a wide latitudinal distribution and with some degree of vessel grouping, 5 show a higher degree of vessel grouping (lower percentage of solitary vessels) in their species from more temperate latitudes, for 3 the reverse holds true, and 1 genus is more or less indifferent in this respect. For *Ailanthus* with its complicated vessel arrangement in the temperate species, and of which no % of solitary vessels is given in table I, vessel grouping is also stronger in the temperate representative. In 6 diffuse-porous genera with a wide altitudinal range, 3 show an increase in vessel grouping with increasing altitude, 1 shows the reverse, and 2 genera are indifferent. Perhaps we may anticipate a weak general trend for more pronounced vessel grouping in the temperate and also montane species, but more data are obviously needed. For *Ilex* only a weak latitudinal trend could be established (Baas, 1973).

The species from temperate latitudes of *Ailanthus*, *Elaeocarpus*, *Gordonia*, and *Rhus* show helical thickenings, whilst they are absent from the tropical species. In the temperate *Rhamnus catharticus* nearly all vessels possess helical thickenings, in contrast to 12 % of the vessel elements only in the tropical *Rhamnus prinoides*. In both species all tracheids have helical thickenings.

If we compare the general trends apparent from the diagrams with the altitudinal and latitudinal variation within the individual genera (table I) it becomes clear that most

Fig.1 Distribution of relative quantitative values over latitudinal lowland zones

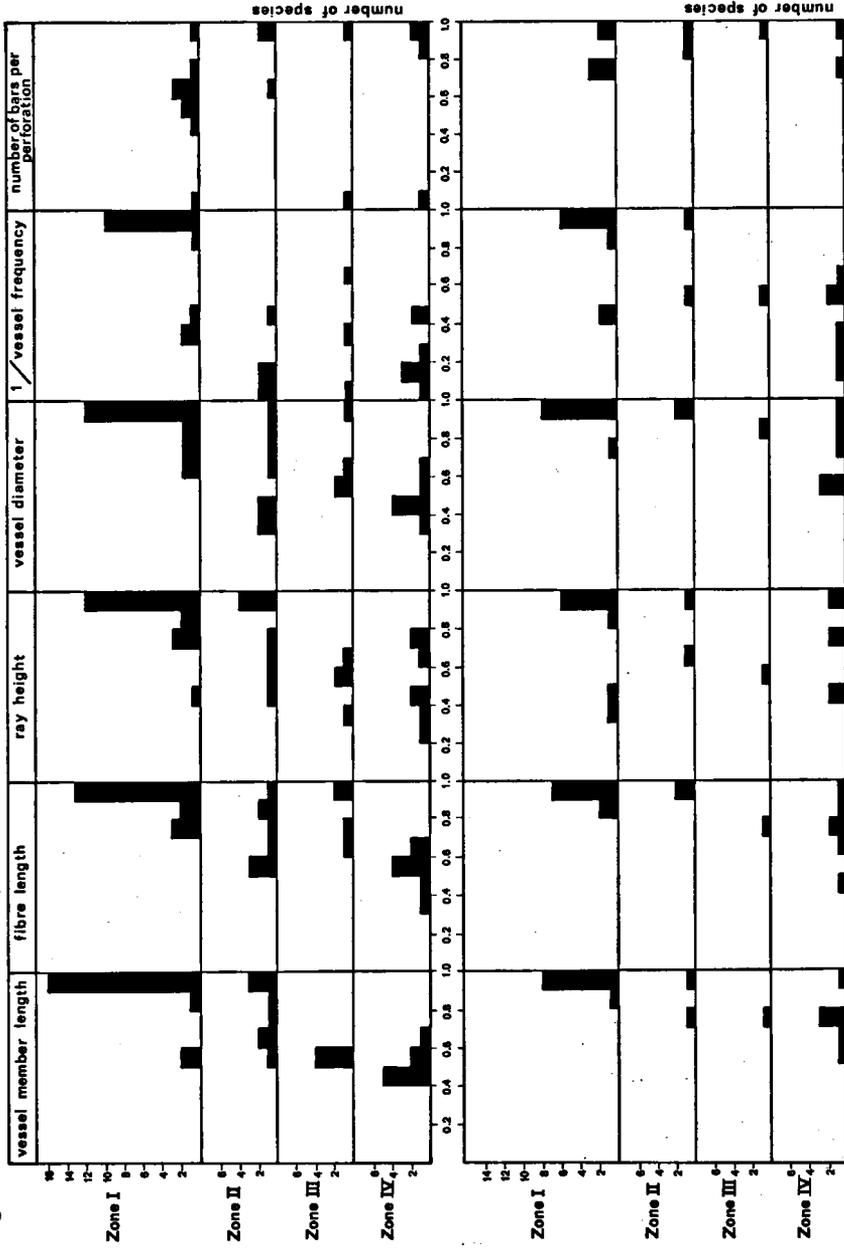


Fig.2 Distribution of relative quantitative values over tropical altitudinal zones

relative quantitative values

Fig.3 Average relative values for different latitudinal lowland zones (I, II, III, IV)

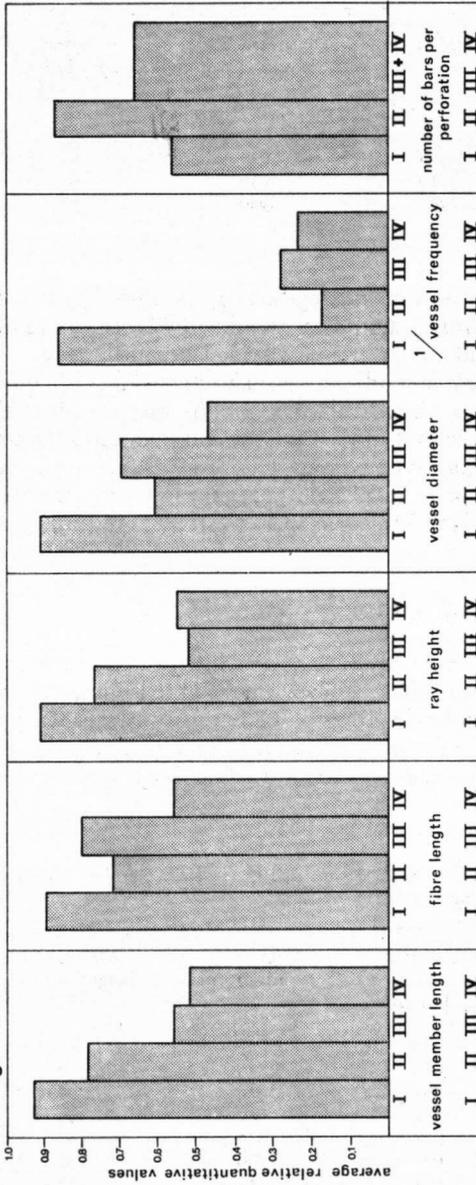


Fig.4 Average relative values for different tropical altitudinal zones (I, II, III, IV)

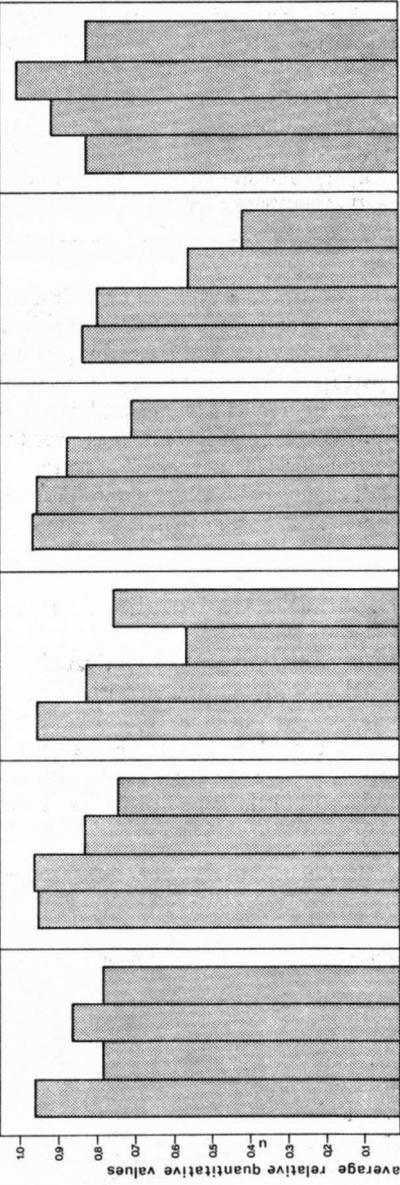


Table II. Altitudinal variation in some Podocarps

Species studied	altitude in m	mean tracheid length in μm	mean ray height in μm
<i>Decussocarpus wallichianus</i> (= <i>Podocarpus blumei</i>)	8	5020	103
<i>Podocarpus neriifolius</i>	10	4830	90
<i>Podocarpus bracteatus</i>	2780	2980	60

genera contribute with most of their characters to these trends. They are absent, however, from *Eurya* and *Pisonia*. In *Eurya* this involves altitudinal trends; in *Pisonia* latitudinal trends, but the material from this genus did not cover a very wide latitudinal range.

Apart from the 17 hardwood genera, one softwood genus was also studied for altitudinal variation in tracheid length and ray height. From table II it appears that the montane *Podocarpus* specimen has much shorter tracheids than the two lowland Podocarps (*Decussocarpus wallichiana* is very close to *Podocarpus*: synonymous with *Podocarpus blumei*). The latitudinal effect also exists within *Podocarpus*, because Patel (1967) gave low average values for tracheid length in temperate New Zealand *Podocarpus* species (3480—1130 μm).

Latitudinal and altitudinal variation within species

Melia azedarach, widely cultivated, was the only species of which we had sufficient material to study latitudinal variation. Mean vessel member length, fibre length, and ray height are given in table III and vessel member length is plotted in fig. 5. Other features were not recorded for this species because of its ring porosity. In spite of a considerable variation there is no correlation with latitude. A specimen of *Melia dubia* from Zaire is entirely within the range of *Melia azedarach*.

Table III. Latitudinal variation in some features of *Melia azedarach* (one specimen of *M. dubia* has been included for comparison)

Provenance	Latitude	Mean vessel member length in μm	Mean fibre length in μm	Mean ray height in μm
Surinam	c. 4° N	300	850	320
N. Borneo	6° N	290	1020	290
New Caledonia	c. 22° S	390	1040	390
Egypt	c. 27° N	330	850	200
Florida	c. 28° N	190	560	190
Florida	28° N	420	910	370
Florida	30° N	330	870	340
Cyprus	c. 35° N	270	590	220
Japan	36° N	340	750	230
<i>Melia dubia</i> : Zaire	c. 8° S	350	840	290

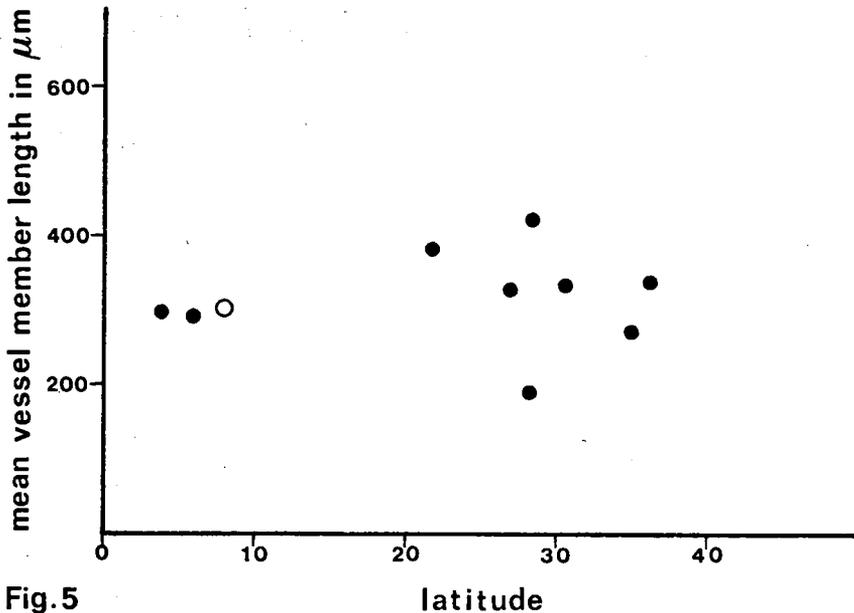


Fig. 5 Vessel member length and latitude in *Melia azedarach* (●) and *Melia dubia* (○).

Of *Rhamnus catharticus* (see table I) two specimens were available, one from the Netherlands and a cultivated one from Miami, Florida. Here the values for the subtropical specimen hardly deviate from those for the temperate one.

By courtesy of Mr. J. Womersley from the Division of Botany at Lae, Papua New Guinea, we received a wealth of specimens enabling the study of altitudinal variation within species of *Pittosporum*, *Calophyllum*, and *Schuurmansia* with a very wide altitudinal range. The results are given in table IV and are also pictured in fig. 7 for vessel member length in *Schuurmansia*. In *Pittosporum ferrugineum* there is no correlation between altitude and the wood anatomical characters analysed, and the variation is quite small in the 9 specimens from altitudes between sea level and 2667 m. Of the other *Pittosporum* species only montane specimens were available and they do not differ considerably in their wood anatomy from *P. ferrugineum*. The same holds more or less true for *Calophyllum pauciflorum*, *C. papuanum* falling completely within the range of the former species as far as longitudinal dimensions are concerned. For *Schuurmansia hemmingsii* of which 13 specimens were studied, again no correlation between anatomical features and altitude could be established. In *Clethra canescens* from the Philippines any correlation between vessel member length and altitude is also absent (table V).

DISCUSSIONS

Infrageneric trends

From the results it follows that latitude is in general much more strongly correlated with wood structure than is altitude. Most emphasis will therefore be put on latitudinal variation. In genera of which only material from tropical to subtropical zones was available latitudinal trends are weakest or wholly absent (e.g. in *Pisonia*). In *Drypetes* not all species

Table IV. Altitudinal variation within some species from New Guinea. Mean values are given in μm . (Ray height not recorded for *Schuermansia henningsii*, because of frequent fusions by sheath and tail cells.)

Specimens studied	A altitude in m	B vessel frequency	C tangential vessel diameter	D vessel member length	E fibre length	F ray height
<i>Calophyllum papuanum</i> Laut.						
NGF 7277	579	3.9	178	740	1055	230
NGF 2452	792	7.1	174	870	1210	140
<i>Calophyllum pauciflorum</i> A. C. Smith						
NGF 1011	180	8.1	137	840	1240	270
NGF 20203	1981	6.0	145	1110	1390	210
Hoogland 5946	2210	6.1	137	710	990	220
NGF 20753	2819	7.3	125	740	1080	190
<i>Pittosporum ferrugineum</i> Ait. f.						
NGF 1592	0	58	69	690	930	440
Hoogland 3403	10	34	79	720	1020	380
NGF 2417	120	49	71	860	1030	440
Schodde 2827	457	40	79	840	1050	360
Schodde 2895	457	60	61	780	1070	230
Schodde 2855	610	34	88	780	1070	370
NGF 1107	1829	25	76	860	1090	460
Hoogland & Schodde 7326	2591	34	74	710	960	420
NGF 30125	2667	35	67	770	990	320
<i>Pittosporum pullifolium</i> Burk.						
NGF 4453 (var. <i>ledermannii</i>)	1829	48	45	620	770	250
Hoogland & Pullen 7081	2896	38	69	780	940	230
Hoogland & Pullen 5528	3048	30	66	850	1060	290
<i>Pittosporum ramiflorum</i> Zoll.						
NGF 4460 (var. <i>praegnans</i>)	1829	29	68	710	1000	220
Hoogland & Schodde 6961	2286	37	66	690	940	380
NGF 40675 (var. <i>praegnans</i>)	2515	33	83	800	1180	610
Schodde 2030	2667	42	74	810	1020	450
NGF 28294 (var. <i>praegnans</i>)	2820	26	84	860	1140	490
<i>Schuermansia henningsii</i> K. Schum.						
Hoogland 3507	150	16	97	1010	1310	
NGF 40163	150	15	120	870	1240	
NGF 1336	457	30	101	970	1350	
Schodde 2232	823	16	99	980	1370	
NGF 5457	884	13	106	780	1390	
NGF 5458	884	22	98	770	1030	
NGF 1035	1829	20	81	1020	1360	
NGF 5159	2134	14	128	820	1330	
NGF 11337	2286	13	92	990	1320	
Hoogland & Pullen 5432	2338			720	1300	
NGF 28217	2591	11	88	680	940	
Schodde 2035	2667	14	88	720	1130	
Hoogland 6128	2743	11	109	810	1290	

or characters studied conform to the trend. Other genera generally follow the trends outlined in fig. 3, but may be exceptional for odd characters. It should be stressed that such exceptions to the rule are only to be expected with a material like wood, the variability of which may be due to a great number of factors other than temperature as related to latitude of provenance.

Table V. Altitudinal variation in some features of *Clethra canescens* from the Philippines

Material studied	Vessel member length in μm	Number of bars per perforation
var. <i>novoguineensis</i> alt. 600 m	120—1000—1700	15—32—41
var. <i>luzonica</i> alt. 2300 m	730—1220—1850	21—47—66
var. <i>luzonica</i> alt. 2620 m	450—1040—1390	24—41—52

The differences generally existing between species from higher latitudes and those from the tropics can be classified as follows:

1. Longitudinal dimensional effects: shorter vessel members, shorter fibres, and lower rays in the more temperate species.
2. Transverse dimensional effects: narrower vessels and sometimes narrower fibres in the more temperate species.
3. Higher vessel frequency in temperate species.
4. A stronger expression of growth ring boundaries (see notes on p. 116) and a tendency to ring porosity in some genera.
5. More frequent occurrence and stronger expression of helical thickenings in temperate species.

Vessel member length, fibre length, and ray height are positively correlated. Only for ray height the correlation sometimes breaks down. In most cases one may speak of inter-dependently varying features. This can be demonstrated in *Melia*, where the large amount of variation in these features, though mutually closely related, is not correlated with latitude (fig. 6). Vessel member length can be considered as a valid measure for cambial initial length, and it is most likely that the longitudinal effects find their origin in shorter fusiform and ray initials in the cambium of temperate species.

As for the transverse dimensional effects in vessels, which have only been determined in diffuse and semi-ring-porous species, there may be two underlying phenomena: less expansion of the cambial initials during vessel maturation and/or a smaller diameter of the cambial initials in temperate species. That the latter phenomenon at least plays some part in the transverse dimensional effects, becomes likely if we consider that often fibre diameter also decreases with increasing latitude. The increase in vessel frequency in temperate species may partly be due to a decrease in transverse dimensions of the cambial elements resulting in a higher number of elements per transverse surface area. However, this can only partly account for the great differences in vessel frequency that sometimes exist between temperate and tropical-lowland species.

The finding that helical thickenings are more in evidence in subtropical and temperate species of *Ailanthus*, *Elaeocarpus*, *Gordonia*, *Rhamnus*, and *Rhus* than in their tropical relatives is a further confirmation of a general trend shown by Baas (1973). That this trend can also be demonstrated in representative samples of woody floras has been discussed before (Kanehira, 1921; Baas, 1973). In addition to the high percentage of genera with spiral thickenings in the predominantly temperate floras of Europe, the U.S.A., and Japan (38—60%) we can now also add a percentage of 35—45 for a temperate flora from the Southern Hemisphere: New Zealand (data generously put at our disposal by B. G. Butterfield and B. A. Meylan). For tropical floras this percentage is 15 or lower. It is noteworthy that in many cases helical thickenings are restricted to narrow vessels. In *Ailanthus*,

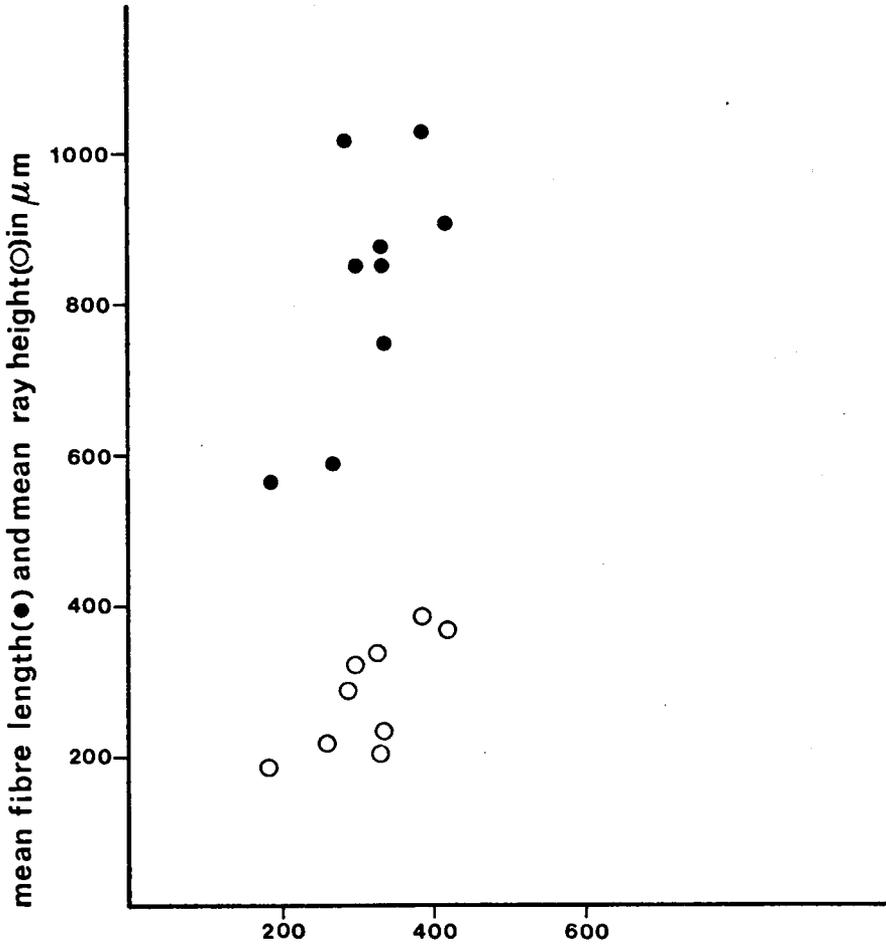


Fig.6 mean vessel member length in μm

Correlations between fibre length, ray height, and vessel member length in *Melia azedarach*.

glandulosa for instance the width of the vessels as studied in macerations is strongly correlated with the occurrence of helical thickenings, vessels with helical thickenings measuring about 10—50 μm , whilst vessels without helical thickenings range in diameter from 40—260 μm . Since the former range of vessel diameter does not occur in the tropical *Ailanthus integrifolia*, it is not amazing that this species does not show helical thickenings. The same holds true for *Rhus* and probably for numerous other genera. This leads to the suggestion that the occurrence or the expression of helical thickenings in those genera which have the genotypic ability to form them can partly be interpreted as a secondary effect related to the degree of expansion of vessels during maturation. This is supported by the fact that often helical thickenings are better developed in or sometimes even entirely restricted to the narrow tips (tails) of vessel members as compared with the parts of a higher diameter. One could imagine that the 'low concentration' of protoplasmic material in strongly

expanded elements constitutes a limiting factor for the formation of tertiary wall thickenings. This hypothesis should be tested in ultrastructural studies.

In conclusion we may summarize the wood anatomical trends from tropical to temperate species of the same genus as a 'miniaturization' of the wood elements and, what may partly be interpreted as a secondary effect, an increase in occurrence and expression of helical thickenings.

Altitudinal variation generally follows the latitudinal trends, but with much weaker effects. Presence or expression of helical thickenings show no altitudinal trends (this agrees more or less with what the second author found in *Ilex*). In *Eurya* the trends seem sometimes reversed and the number of exceptions to the altitudinal trends are in general higher than to the latitudinal trends (see table III).

A number of trends mentioned above have also been recorded in the literature for other genera and taxa of higher rank (Baas, 1973; Carlquist, 1966; Dadswell & Ingle, 1954). Carlquist (1966, 1970) and Novruzova (1968) found parallel trends when comparing plants from mesic with plants from dry habitats. In the paper on *Ilex* (Baas, 1973) the trend for tropical lowland species to have more numerous bars than temperate and tropical montane species, constituted a great problem if accepted as example of a general trend. This idea had found support in similar findings for *Symplocos* and *Viburnum*. The present data on 6 more genera with scalariform perforations, however, indicate that no such a general trend exists. In *Drypetes*, *Gordonia*, *Styrax*, and *Weinmannia* the number of bars increases with increasing latitude, in *Magnolia* it decreases more or less. For *Eurya* no relationship can be found between altitude and number of bars per perforation.

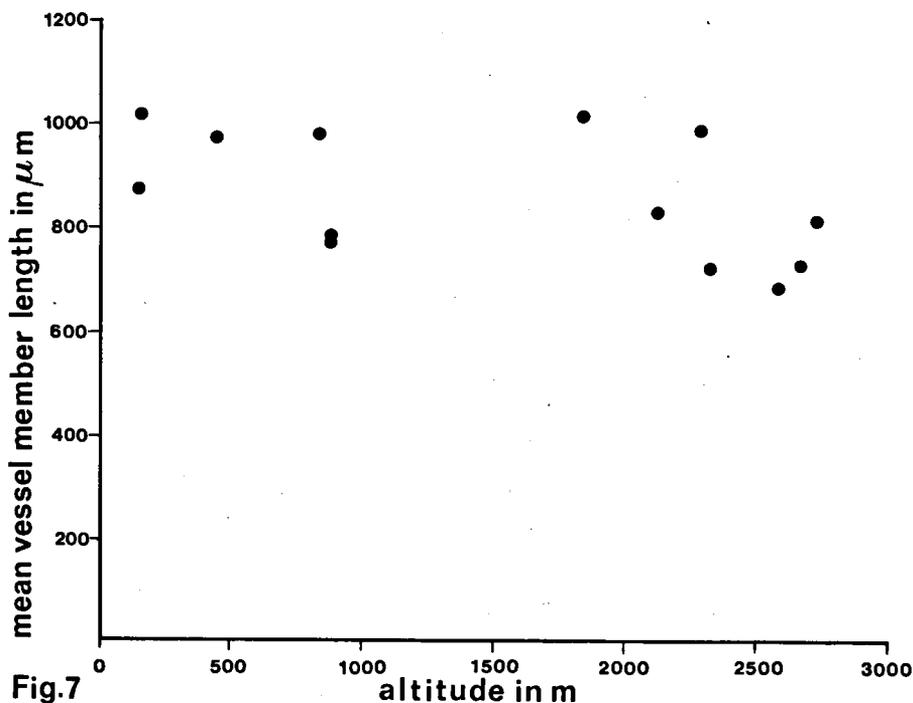


Fig. 7

Vessel member length and altitude in *Schuurmansia henningsii*.

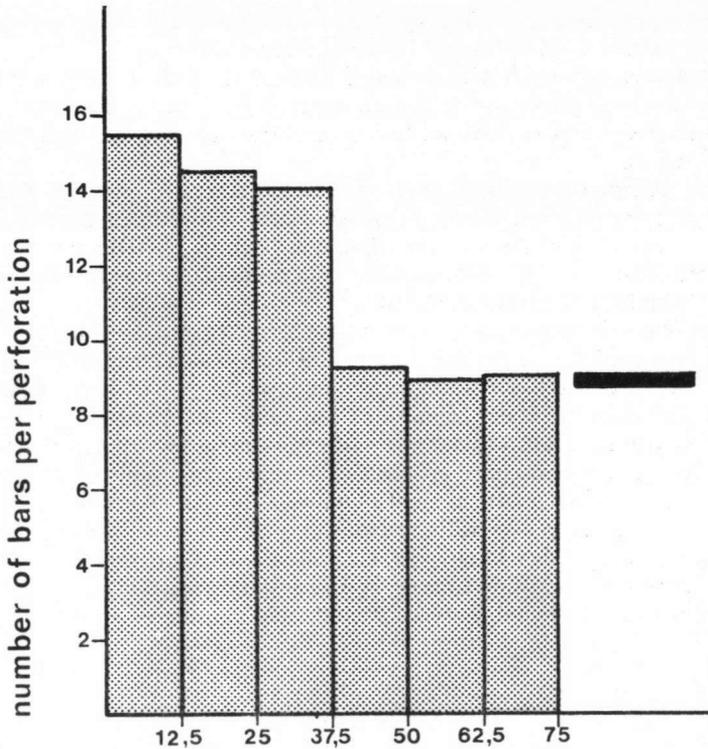


Fig.8 diameter size classes in μm

Vessel diameter and number of bars per perforation in late wood of *Styrax obassia*. Black bar gives value for early wood.

From the literature we can derive some more conflicting examples supporting the view that no general latitudinal or altitudinal trends for number of bars per perforation exist (Dadswell & Ingle, 1954, for *Nothofagus*; Tabata, 1964, on *Betula*; Versteegh, 1968, for *Litsea* and *Cinnamomum*; Baas, 1969, on *Platanus*; Baas, 1973 on *Ilex*, *Symplocos*, *Vaccinium*, *Viburnum*, and *Hydrangea*). In a number of examples where number of bars per perforation increases with higher latitudes, this seems to be due to a higher number in the narrow late-wood vessels (*Styrax*, *Drypetes*, *Nothofagus*). Fig. 8 illustrates the correlation between vessel diameter and number of bars per perforation in the late wood of *Styrax obassia*. For *Magnolia kobus* this phenomenon also exists, but this does not alter the fact that this species has a much lower value than the tropical *Magnolia* species.

Obviously more studies are needed before we can be certain about the absence of any correlation between ecological factors and elaboration or reduction in perforation plates, but the data available at present suggest at most a minor role of such factors.

Intraspecific variation

The wood anatomical variation within species of *Calophyllum*, *Clethra*, *Melia*, *Pittosporum*, *Rhamnus*, and *Schuermansia* is not correlated with altitude or latitude (see tables)

This unexpected discrepancy between data on variation on the genus level and on the species level resp. calls for some comment. Hunter & Goggans (1969) and Dinwoodie (1963) found latitudinal correlations in accordance with our generic trends for fibre length in Sweetgum (*Liquidambar styraciflua*) and for tracheid length in Sitka Spruce (*Picea sitchensis*), and Dinwoodie could demonstrate that the differences in Sitka Spruce from different latitudes had become genetically fixed. For *Rhamnus* and *Melia* we used wood samples of cultivated species and the lack of any correlation between latitude and dimensions of wood elements may be due to genetically fixed differences in the planting material from different provenances, unknown to us. The lack of any altitudinal correlation within the New Guinea species may be due to the fact that temperature as related to altitude has not been a 'limiting' factor in the processes involved in the expression of certain quantitative xylem characters. Sastrapradja & Lamoureux (1969) were also unable to demonstrate a correlation between altitude and wood anatomical features in *Metrosideros polymorpha*. They only found an unclear tendency for rapidly growing plants from wet sites to have slightly bigger xylem elements than slowly growing plants from dry sites. Novruzova (1968) and Greiss (1939) stress the influence of water supply on certain wood anatomical characters; xeric conditions having similar effects in the species they studied as high altitudes or latitudes within genera examined by us. Unfortunately, data on rainfall and soil drainage are insufficient for all the material studied by us, and we can therefore only tentatively suggest that ecological factors other than temperature may have been limiting in the wood anatomy of the species with a wide altitudinal range. A similar reasoning might be used in accounting for the exceptions to the rule on the genus level. The fact that below the species level no correlations with latitude or altitude could be traced, may also be used as an argument to consider the random genetical variation below the species level of more significance than any ecologically controlled variation. The long term selection process that may result in a differentiation into various geographically separated species may also lead to the correlations between certain wood anatomical features and latitude and/or altitude we found within genera. This suggestion breaks down in those cases (e.g. *Melia azedarach*) where infraspecific variability equals or approximates infrageneric variability.

In conclusion we have to admit that the infraspecific variation found by us in a number of species does not shed any light on the problem of how to interpret the general latitudinal and altitudinal trends within genera.

GENERAL CONCLUSIONS

The data presented here enable us to adjust some of the conclusions and throw new light on some of the problems discussed in a previous paper (Baas, 1973). The correlation between xylem element size and latitude, and to a lesser extent also between xylem element size and altitude within genera has to be accepted as a general rule, valid in taxonomically widely unrelated groups. If we combine this with the reports in literature of an important correlation between rainfall and xylem element dimensions, we can only conclude that climatic factors such as temperature and water supply play an important role in the determination of xylem element size, probably through a long term process involving many generations of trees. Shortening of vessel elements in the evolution of woody plants is one of the corner stones of the generally accepted trends in wood specialization, and one may hypothesize that climatic factors have played a directing influence in these trends. We can, however, not imagine that such a major climatic influence has resulted in the unidirectional phylogenetic trends, the irreversibility of which has mostly been

accepted as a dogma by students of wood phylogeny (e.g. Bailey, 1953). Tracheids and vessel members probably have been and are able to shorten and elongate under the influence of changing climates in past and present. That this reversibility would be so important as to blur completely the very strong shortening of elements which must have taken place in phylogeny (Bailey & Tupper, 1918) we do not believe. The present data only indicate that we must even be more cautious than Bailey told us to be in using vessel member length as an indicator of phylogenetic specialization.

The results on number of bars per perforation have removed some of the paradoxes on occurrence and frequency of scalariform perforations in tropical and temperate floras (Baas, 1973). The lack of general altitudinal and latitudinal trends for this character implies that our results are neutral with regard to the phylogenetic importance usually attached to this character.

As a final conclusion we would like to stress the importance of ecological considerations for the evaluation of wood anatomical characters in taxonomic and phylogenetic studies, and the need for further analyses of the type presented here.

NOTES ON THE GENERA, SPECIES, AND SPECIMENS STUDIED

In this section locality and collection data of the specimens studied are listed, together with some notes on the wood anatomy of the genera involved. Because most of the genera have been described wood anatomically in Metcalfe & Chalk (1950) or elsewhere, we have not included detailed descriptions. The anatomical notes are usually restricted to vessel distribution and some miscellaneous characters of relevance for the interpretation of our results in table I—V.

Acacia (*Leguminosae*)

Material studied: *A. cyanophylla* Lindl., Morocco, lat. c. 26° N, *Backhuys s.n.* (diam. 3.5 cm). *A. mangium* Willd., West New Guinea, lat. c. 1° S, alt. 60 m, BW 2196.

Growth rings are faint to distinct. The vessels are diffuse, solitary and in short radial multiples. Parenchyma is much more abundant in *A. cyanophylla* than in *A. mangium*. The former species was collected in a very dry habitat.

Ailanthus (*Simaroubaceae*)

Material studied: *A. integrifolia* Lam., West New Guinea, lat. c. 0°, alt. 50 m, BW 12467. *A. altissima* Swingle (= *glandulosa* Desf.), The Netherlands, lat. 52° N, cult. U 14421 (Uw).

The vessel distribution in *A. altissima* is very different from that in *A. integrifolia*. *A. integrifolia* is a diffuse-porous species without distinct growth rings. The vessels are infrequent and wide, solitary and in short radial multiples, rarely in clusters with some accompanying narrow vessels. *A. altissima*, on the other hand, is ring-porous with vessels of two distinct sizes: large early wood vessels solitary and in short radial multiples, rarely in clusters together with some narrow vessels, and narrow late-wood vessels in conspicuous clusters. Because of these fundamental differences in vessel distribution and grouping, vessel frequency and vessel diameter has not been listed in table I.

Calophyllum (*Guttiferae*)

Material studied: See herbarium numbers listed in table IV; all material is from East New Guinea (LAEw).

Growth rings are very faint to absent in all specimens studied. The vessels are almost exclusively solitary and arranged in an oblique to radial pattern, the expression of which is rather variable.

Clethra (*Clethraceae*)

Material studied: *C. canescens* Bl., Philippines; var. *luzonica* (Merr.) Sleum., lat. 16° N, alt. 2300 m, *Jacobs* 7517; *ibid.*, lat. 16° N, alt. 2620 m, *Jacobs* 7199. var. *novoguineensis* (Kanch. & Hatus.) Sleum., lat. 15° N, alt. 600–700 m, *Jacobs* 7899.

Growth rings are faint in all specimens studied of this diffuse-porous species. The vessels are mostly solitary, very rarely in short multiples.

Cryptocarya (*Lauraceae*)

Material studied: *C. caloneura* (Scheff.) Kosterm., West New Guinea, lat. 2° S, alt. 75 m, *BW* 9387. *C. minutifolia* C. K. Allen, East New Guinea, lat. 6° S, alt. 2940 m, *Kalkman* 4790.

Growth rings are present in these diffuse-porous woods. The vessels are solitary and in radial multiples.

Diospyros (*Ebenaceae*)

Material studied: *D. amboinensis* Bakh., West New Guinea, lat. 2° S, alt. 50 m, *BW* 9079. *D. virginiana* L., U.S.A., Virginia, lat. c. 38° N, *USw* 3418 (= *Uw* 7316).

In the tropical *D. amboinensis* growth rings are indistinct; in the semi-ring-porous *D. virginiana* they are distinct. The vessels are solitary and in radial multiples.

Drypetes (*Euphorbiaceae*)

Material studied: *D. diversifolia* Krug. et Urb., U.S.A. Florida, lat. c. 25° N, *USw* 20866 (= *Uw* 10192). *D. gossweileri* S. Moore, Zaire, lat. c. 3° S, *IF* 5213 (from Museum of Central Africa, Tervuren). *D. lateriflora* Krug. et Urb. (= *D. crocea* Poit.), U.S.A., Florida, lat. c. 25° N, *A. F. Wilson F.* 20 (= *Uw* 10193). *D. spec.*, West New Guinea, lat. c. 0° S, alt. sea level, *BW* 12440.

In the two tropical species growth rings are faint; in the subtropical species they are distinct. The vessels are solitary and in radial multiples. Only a small percentage of the vessel perforations is scalariform: 2 % in *D. spec.*; 4 % in *D. gossweileri*, 14 % in *D. latiflora*, and 17 % in *D. diversifolia*. The average values in table I are calculated for all vessel perforations, including the simple ones with no bars.

Elaeocarpus (*Elaeocarpaceae*)

Material studied: *E. dolichostylus* Schlechter, West New Guinea, lat. 1° S, alt. 40 m, *BW* 9324. *E. japonicus* Sieb., Japan, Nagasaki, lat. 33° N, *Regel* 92. *E. robustus* Roxb., India, Darjeeling, lat. c. 23° N, *Mawson* 96. *E. spec.*, East New Guinea, lat. 6° S, *Kalkman* 4961.

In the two species from New Guinea growth rings are absent or faint, in the other species they are distinct. The vessels are diffuse, solitary and in radial multiples, rarely in clusters.

Erythrina (*Leguminosae*)

Material studied: *E. crista-galli* L., The Netherlands, lat. 52° N, cult., *UN* 103 (*Uw*, diam. 2.5 cm). *E. variegata* L. var. *orientalis* L., West New Guinea, lat. 1° S, alt. 2 m, *BW* 7658.

Growth rings are absent in the tropical specimen, distinct in the temperate one. The vessels are diffuse, solitary and in radial multiples.

Eurya (*Theaceae*)

Material studied: *E. acuminata* DC., Java, lat. 7° S, alt. c. 1000 m, *Koorders 15296* (RTIw). *E. obovata* Korth., Java, lat. 7° S, alt. 2230 m, *Koorders 8161* (RTIw). *E. tigan* K. Schum. & Laut., West New Guinea, lat. 2° S, alt. 1220 m, *Van Royen 3699*. *E. cf. tigan* K. Schum. & Laut., East New Guinea, lat. 6° S, alt. 3150 m, *Kalkman 5162*.

Growth rings are very faint in the material studied. The vessels are diffuse, mainly solitary, but also in short radial multiples.

Fagraea (*Loganiaceae*)

Material studied: *F. gracilipes* A. Gray, West New Guinea, lat. 2° S, alt. 70 m, *BW 8103*. *F. salticola* Leenh., East New Guinea, lat. c. 6° S, alt. 2700 m, *Kalkman 4901*.

Growth rings are absent from the two specimens studied. The vessels are diffuse, solitary and in radial multiples.

Gordonia (*Theaceae*)

Material studied: *G. excelsa* Bl., Sumatra, lat. c. 1° S, alt. 660 m, *bb 3030* (∴ for wood sample series *bb 2860*, RTIw). *G. lasianthus* L., U.S.A., lat. c. 30° N, *USw 3428* (= *U 7319*, Uw). *G. papuana* Kobuski, West New Guinea, lat. c. 1° S, alt. 740 m, *BW 7970*; *ibid.*, alt. 30 m, *BW 11798*. *G. spec.*, Philippines, lat. 16° N, alt. 2300 m, *Jacobs 7421*.

Growth rings are faint to absent in the tropical species, distinct in *G. lasianthus*. The vessels are diffuse, solitary and in some radial multiples.

Magnolia (*Magnoliaceae*)

Material studied: *M. acuminata* L., U.S.A., lat. c. 39° N, *USw 5844* (= *U 7442*, Uw). *M. drymifolia* Dandy, Sabah, lat. 5° N, alt. below 1000 m, *SAN 73446*. *M. kobus* DC., The Netherlands, lat. 52° N, cult. *UN 353* (Uw). *M. splendens* Urb., Puerto Rico, lat. 18° N, alt. 700–800 m, *MADw* ('*Puerto Rico 8*'). *M. tripetala* L., The Netherlands, lat. 52° N, cult. *UN 354* (Uw).

Growth rings are distinct in the temperate species, faint to absent in the tropical ones. Vessels are diffuse, solitary, in radial multiples and occasionally in clusters. The vessel perforations are almost exclusively simple in *M. acuminata* (only one scalariform perforation observed in 200 vessel members); 5 % of the perforations are scalariform in *M. kobus*; the other species have exclusively scalariform perforations.

Melia (*Meliaceae*)

Material studied: *M. azedarach* L., Cyprus, lat. c. 35° N, *FHOW 3898*; Egypt, lat. c. 27° N, *RTIw 4184–2350*; Florida, lat. c. 38° N, cult. *USw 11021* (= *U 8511*, Uw); *ibid.*, lat. 30° N, *SJRw 48929* (*MADw*); Japan, var. *japonica* (G. Don) Makino, lat., c. 36° N, *WLw 1742*; New Caledonia, lat. 22° S, *WLw N.C. 89*; Sabah, lat. 5° N, alt. 200–300 m, *SAN 26392*; Surinam, lat. c. 4° S, alt. probably low, *Lindeman 5765* (= *U 3928*, Uw). *M. dubia* Cav. (= *M. bombo* Welw.), Zaire, lat. c. 8° S, *Donis 1771* (= *IF 9809* from Museum of Central Africa, Tervuren).

Growth rings are distinct in all specimens studied. The wood of *M. azedarach* is ring-porous, that of *M. dubia* is semi-ring-porous. Some of the large early wood vessels are accompanied by narrow vessels, forming small clusters. In the late wood of *M. azedarach* the vessels are very narrow and clustered in an ulmiform pattern. In *M. dubia* clustered late

wood vessels are absent. All the narrow vessel elements have helical thickenings, in the wide vessels they may be present or absent. Vessel frequency and vessel diameter have not been listed because of the vessel dimorphism reported above (see table III).

Pittosporum (*Pittosporaceae*)

Material studied: See herbarium numbers listed in table IV; all material is from East New Guinea (LAEw).

Growth rings are faint or absent in the material studied. The vessels are diffuse, solitary and in radial multiples.

Pisonia (*Nyctaginaceae*)

Material studied: *P. ambigua* Heimerl, Brasil, Santa Catarina, lat. c. 26° S, alt. 200 m, Reitz & Klein 4695 (=MADw 18111). *P. cuspidata* Heimerl, Guyana, lat. c. 5° N, Forest Dept. 5387 (=FHOw 14975). *P. macranthocarpa* J. D. Smith, Colombia, lat. 11° N, alt. 200 m, SJRW 20989 (MADw). *P. olfersiana* Link, Klotsch & Otto, Brasil, Santa Catarina, lat. c. 26° S, Reitz 15015 (=U 6399, Uw, diam. 4 cm). *P. rotundata* Griseb., U.S.A., Florida Keys, lat. c. 25° N, Stern 3054 (=MARYw 1943, Maryland). *P. sandwicensis* Hillebrand, Hawaii, lat. c. 20° N, Carlquist 1985 (=U 16301, Uw, diam. 7 × 4 cm).

In the tropical material growth rings are absent to faint, in the subtropical *P. ambigua* and *P. olfersiana* they are distinct. The vessels are present in clusters on the abaxial side of the included phloem which is of the foraminiate type. Because of this uneven distribution, no data on vessel frequency and % of solitary vessels have been listed in table I.

Podocarpus & Decussocarpus (*Podocarpaceae*)

Material studied: *Podocarpus bracteatus* Bl., East New Guinea, lat. c. 6° S, alt. 2780 m, Kalkman 5189. *Podocarpus neriifolius* D. Don, West New Guinea, lat. 1° S, alt. 10 m, BW 943. *Decussocarpus wallichianus* (Presl) De Laub. (= *Podocarpus blumei* Endl.), West New Guinea, lat. 2° S, alt. 8 m, BW 11121.

Growth rings are rather distinct and closely spaced in the three specimens studied. Whether one regards *Decussocarpus* as a genus separate from *Podocarpus* is a matter of taxonomic opinion. The two taxa are very close, also wood anatomically, and a comparison of tracheid length and diameter, and ray height with reference to altitudinal distribution was therefore considered to be justified (see table II).

Rhamnus (*Rhamnaceae*)

Material studied: *R. catharticus* L., U.S.A., Florida, lat. 25° N, Scott 58 (WLw); The Netherlands, lat. 52° N, Ter Laak 127 (WLw). *R. prinoides* l'Hérit., East Africa, lat. tropical, Schlieben s.n., Reinbeck 1742 (=U 15801, Uw).

Growth rings are very faint in *R. prinoides*, distinct in *R. catharticus*. The vessels are arranged in a conspicuous dendritic pattern, and data on vessel frequency and % of solitary vessels have therefore been omitted from table I.

Rhus (*Anacardiaceae*)

Material studied: *R. glabra* L., U.S.A., Wisconsin, lat. c. 45° N, MADw 24969. *R. taitensis* Guill., West New Guinea, lat. c. 2° S, alt. 100 m, BW 9221. *R. vernix* L., The Netherlands, lat. 52° N, cult. UN 279 (Uw).

Growth rings are very faint in the diffuse-porous *R. taitensis*. In *R. glabra* and *R. vernix* the wood is ring-porous and growth rings are very distinct. Vessels are solitary in radial multiples and in clusters. The degree of clustering is much stronger in the temperate species.

Schuurmansia (*Ochnaceae*)

Material studied: See herbarium numbers listed in table IV; all material is from East New Guinea (LAEw).

Growth rings are faint to absent in the material studied. The vessels are diffuse, solitary and in radial multiples.

Streblus (*Moraceae*)

Material studied: *S. glaber* (Merr.) Corn., West New Guinea, lat. c. 1° S, alt. 750 m, *BW 9107*; *ibid.*, lat. c. 2° S, alt. 15 m, *BW 11165*. *S. urophyllus* Diels, East New Guinea, lat. c. 6° S, alt. 2990 m, *Kalkman 4938*.

Growth rings are faint to fairly distinct in the material studied. The vessels are diffuse, solitary and in radial multiples.

Styrax (*Styracaceae*)

Material studied: *S. argenteus* Presl, Panama, lat. c. 8° N, *Stern, Eyde & Ayensu 1993* (=U 14829, Uw). *S. glabratus* Scott, Surinam, lat. c. 4° N, *Schultz 7142* (=U 4907, Uw). *S. japonicus* Sieb. et Zucc., The Netherlands, lat. 52° N, cult. *UN 412* (Uw). *S. obassia* Sieb. et Zucc., The Netherlands, lat. 52° N, cult. *UN 188* (Uw).

Growth rings are present in all species studied. The tropical species are diffuse-porous, the temperate species semi-ring-porous. The vessels are solitary and in radial multiples. Vessel clusters only occur in the late wood of the temperate species.

Weinmannia (*Cunoniaceae*)

Material studied: *W. blumei* Planch., West New Guinea, lat. c. 2° S, alt. 75 m, *BW 5891*. *W. trichosperma* Cav., Chile, lat. c. 41° S, *Grijpsma s.n.* (WLw.) *W. spec.*, East New Guinea, lat. c. 6° S, alt. 3140 m, *Kalkman 4860*.

Growth rings are distinct in *W. trichosperma*, fairly distinct in *W. spec.*, and very faint in *W. blumei*. The vessels are diffuse and nearly all solitary.

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