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ECOLOGICAL AND SYSTEMATIC WOOD ANATOMY OF ALSTONIA (APOCYNACEAE)

by

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SUMMARY

The wood anatomy is described of three sections of the genus *Alstonia*: sections *Alstonia*, *Monuraspermum*, and *Dissuraspermum*. The wood anatomical characters support the infrageneric classification on the basis of macropmorphological and pollen morphological features (Sidiyasa 1998). Vessel frequency, mean tangential vessel diameter, L/D ratio, ray frequency, presence or absence of laticifers, parenchyma distribution, fibre wall thickness, and fibre wall pitting are all, in various degrees, diagnostic to separate the light *Alstonia* timber group (= section *Alstonia*) from the heavy *Alstonia* group (including the other two sections studied). Sections *Monuraspermum* and *Dissuraspermum* can be separated on vessel frequency and mean tangential vessel diameter. Among the light *Alstonia* group, the swamp inhabiting species have lower multiseriate rays than the non-swamp species which presumably root in well-aerated soils. Vessel elements and fibres also tend to be shorter in material from swamps, but this difference is not statistically significant. This tendency is perhaps associated with the physiological drought induced by water-logged soils.

Key words: Vessel dimensions, laticifers, ray height, swamp species, light and heavy *Alstonia* groups, Pulai.

INTRODUCTION

Alstonia is the largest and most widespread genus of trees and shrubs in the subtribe Alstoniinae of the tribe Plumerieae of the Apocynaceae. Many of its species provide important timbers of commerce, and several species are used in traditional local medicine. The genus occurs in Central America, tropical Africa, and from the Himalayas and China to New South Wales in Australia, and has its centre of diversity in the Malesian region. The genus has recently been taxonomically revised (Sidiyasa 1998), and the present wood anatomical study was carried out as part of the morphological and anatomical analyses of variation within the genus. Five sections are currently recognised in *Alstonia*: sections *Alstonia, Blaberopus, Dissuraspermum, Monuraspermum*, and *Tonduzia*.

Table 1. Variation of selected wood anatomical characters of *Alstonia*.

	GR	SOL	RAD	CL	VF	VD	VL	L/D	IP	FL	FT	FPr	PD	PR	RF	RH	USR	LT	PC	NCC
Section *Alstonia*																				
A. actinophylla																				
Versteegh BW 66	–	10	70	20	8	106	695	6.5	4–5	1350	vt	+	±	+	7	435	1	+	–	–
A. angustiloba																				
BZFw 8018	+	8	67	25	4	107	1010	5.6	4–7	1570	vt	+	±	+	7	525	1	+	PR	17
KEPw 63545	+	4	64	32	5	154	840	6.9	5–7	1540	vt	+	±	+	6	450	1–2	+	–	–
A. boonei																				
INEAC 664,DF	–	4	80	16	5	162	1080	5.8	4–7	1740	vt	+	±	+	7	630	1–2	+	–	–
MAD–SJRw 47430	±	9	82	9	4	144	830	4.7	4–8	1400	vt	+	±	+	8	740	1–5	+	–	–
A. congensis																				
MADw 27091	–	21	65	14	4	116	785	5.7	4–7	1240	vt	+	±	+	7	800	1–2	+	PR	3
FHOw 818	±	8	52	40	5	149	1235	?	4–6	?	vt	+	±	+	8	650	1–4	+	–	–
A. iwahigensis																				
Ridsdale 1868	+	13	55	32	8	127	860	5.0	4–8	1550	vt	+	±	+	6	480	1–3	+	P	–
Sidiyasa 1116	±	11	45	43	6	91	960	7.5	4–10	1630	vt	+	±	+	6	450	1–3	+	P	–
AA 970	+	11	45	44	6	121	810	4.6	4–8	1410	vt	+	±	+	8	610	1	+	P	–
BZFw 13585	+	16	67	17	4	146	880	4.1	4–10	1670	vt	+	±	+	6	450	1–2	+	P	–
A. pneumatophora																				
Sidiyasa 1169	±	23	62	15	6	146	625	3.0	4–6	1380	vt	+	±	+	8	525	1	+	PR	20
(BZFw) E418	–	20	54	26	3	158	910	6.6	4–6	1420	vt	+	±	+	7	440	1	+	PR	19
Sidiyasa 1383	±	16	58	27	6	152	850	5.6	4–6	1340	vt	+	±	+	5	788	1	+	P	–
Sidiyasa 1381	±	17	49	33	5	120	710	4.7	4–5	1210	vt	+	±	+	6	455	1	+	–	–
A. rostrata																				
CAFw 12013	–	16	40	44	10	78	685	8.6	4–5	1430	vt	+	±	+	9	570	1–5	+	–	–
Gamble B–6750	±	12	63	25	15	76	770	10.7	4–6	1350	vt	+	±	+	8	565	1–7	+	PR	–
A. scholaris																				
van Balgooy 4809	–	10	50	40	4	154	930	6.1	4–6	1560	vt	+	±	+	6	740	1–2	+	PR	12
BZFw 25003	±	9	53	38	3	151	810	4.1	4–7	1420	vt	+	±	+	5	750	1–4	+	PR	4
Sidiyasa 1402	±	23	50	28	6	128	790	5.3	4–8	1410	vt	+	±	+	7	580	1–5	+	P	15
MADw 45148	–	14	78	8	3	172	840	3.5	4–6	1490	vt	+	±	+	6	830	1–6	+	P	–
AA 961	–	10	47	43	6	117	500	3.5	4–7	1110	vt	+	±	+	7	400	1–3	+	PR	10
A. spatulata																				
BZFw 22312	±	16	66	19	6	111	740	4.4	4–6	1170	vt	+	±	+	6	395	–	+	–	–
BZFw 13110	±	26	67	7	7	101	720	5.4	4–6	1330	vt	+	±	+	7	520	–	+	–	–

(Table 1 continued)

	GR	SOL	RAD	CL	VF	VD	VL	L/D	IP	FL	FT	FPr	PD	PR	RF	RH	USR	LT	PC	NCC
Section *Dissuraspermum*																				
A. costata																				
MADw 20623	±	30	67	3	100	46	620	9.8	3–4	1505	m–t	±	+	–	11	435	1–2	–	PR	24
MADw 29265	–	62	30	8	72	59	770	8.9	3–4	1500	m	±	+	–	11	425	1–2	–	PR	19
MAD–SJRw 24854	–	47	48	5	121	41	720	14.9	3–4	1360	m–t	±	+	–	12	415	1–5	–	–	16
MAD–SJRw 25481	–	44	49	7	110	49	870	14.8	3–4	1490	m–t	±	+	–	10	520	1–8	–	–	12
MAD–SJRw 26118	–	55	39	7	147	42	720	13.7	3–4	1300	m–t	±	+	–	13	535	1–10	+	PR	13
MAD–SJRw 28040	±	34	56	10	131	43	710	10.3	2.5–4	1430	m–t	±	+	–	12	435	1–4	–	PR	9
MAD–SJRw 28275	–	57	37	6	131	43	725	12.9	3–4	1270	m–t	±	+	–	11	400	1–4	–	PR	8
MAD–SJRw 28329	–	51	41	8	106	50	810	13.4	3–4	1500	m	±	+	–	12	400	1–3	–	PR	4
MAD–SJRw 28377	±	38	57	5	149	49	905	14.6	2.5–4	1530	m–t	±	+	–	13	660	1–12	–	PR	12
Section *Monuraspermum*																				
A. angustifolia																				
BZFw 6013	–	50	46	4	29	83	1000	9.8	4–5	1470	tm	±	+	–	9	315	1–11	–	P	16
BZFw 11044	–	37	58	5	30	91	890	9.7	3–5	1620	tm	±	+	–	11	320	1–11	–	P	8
BZFw 3365	–	32	56	12	34	72	940	10.7	3–5	1590	m–t	±	+	–	8	310	1–8	–	P	10
A. macrophylla																				
Ridsdale 1425A	±	39	57	5	49	88	760	10.6	3–5	1370	tm	±	+	–	10	300	1–10	–	PR	13
Ridsdale 1159	–	18	74	8	31	88	960	14.2	3–5	1480	tm	±	+	–	8	330	1–10	–	P	5
Jacobs 8668	–	57	41	2	61	51	790	11.6	4–5	1400	tm	±	+	–	14	505	1–12	–	–	–
NGF 15481	–	28	71	1	53	88	930	8.8	3–5	1590	tm	±	+	–	9	445	1–6	–	PR	13
Hoogland 8901	–	34	56	10	53	83	1320	12.5	4–5	1830	tm	±	+	–	7	455	1–8	–	P	8
A. spectabilis																				
Sidiyasa 1101	±	45	49	6	45	59	820	10.8	3–4	1480	tm	±	+	–	9	320	1–12	–	PR	13
BZFw 3331	+	44	44	12	31	77	960	10.5	3–5	1580	m–t	±	+	–	12	390	1–15	–	P	13
BZFw 22100	–	13	76	11	37	88	1100	13.5	3–5	1750	m–t	±	+	–	8	345	1–8	–	PR	20

GR: growth rings present and distinct (+), indistinct (±), absent (–). — **SOL:** Percentage of solitary vessels. — **RAD:** Percentage of radial vessel multiples. — **CL:** Percentage of clustered vessels. — **VF:** Vessel frequency (per sq. mm). — **VD:** Average tangential vessel diameter (µm). — **VL:** Average vessel element length (µm). — **L/D:** Ratio vessel length / vessel diameter. — **IP:** Intervessel pit diameter (µm). — **FL:** Average fibre length (µm). — **FT:** Fibre wall thickness (µm) (m: medium, tm: thin to medium, vt: very thin, m–t: medium to thick). — **FPr:** Fibre pits in radial walls common (+), very few (±). — **PD:** Axial parenchyma diffuse and diffuse-in-aggregates predominant (+), few (±). — **PR:** Axial parenchyma reticulate predominant (+), absent (–). — **RF**: Ray frequency (per mm). — **RH:** Height of multiseriate rays (µm). — **USR:** Number of square or/and upright (marginal) cells in multiseriate rays. — **LT:** Latex tubes present (+), absent (–). — **PC:** Prismatic crystals present in axial parenchyma cells (P), in the ray cells (R), or absent (–). — **NCC:** Number of chambers per chain of prismatic crystals.

Wood anatomical data on *Alstonia* in the literature are mostly confined to a few economically important timber species, and usually scattered in limited papers and some books or atlases on wood anatomy for restricted geographical regions. The most important references are: Metcalfe & Chalk (1950), Gill et al. (1985), Martawijaya et al. (1986), Ilic (1987 and 1991), Soerianegara & Lemmens (1993). No wood anatomical descriptions are available for the numerous non-commercial species from mainland Asia and the Pacific Islands.

These earlier studies have demonstrated that among the timber producing genera of *Alstonia* there are two distinct groups: lightweight woods traded as 'Pulai' with thin-walled fibres (including *A. pneumatophora, A. scholaris*, and *A. spatulata*) and medium heavy woods traded as 'Hard Alstonia' with thick-walled fibres (including *A. macrophylla* and *A. spectabilis*).

In addition to the main systematic objective, the present wood anatomical study of *Alstonia* was undertaken to explore relationships that might exist between wood structure and ecological preference of the species. *Alstonia* lends itself well to such an analysis because some species are restricted to swampy areas, while most occur in areas on well drained soils.

MATERIAL AND METHODS

Unfortunately, two sections (section *Blaberopus*, which includes only shrubs or very small trees up to 5 m high, and section *Tonduzia*) could not be studied because no wood samples could be obtained. More than 80 wood samples were obtained from various institutes (see Acknowledgements), but only 44 were selected to be studied (cited in Sidiyasa 1998). The selection was based on the quality of samples (mature ones were favoured) and the possibility of verifying their botanical identity using herbarium vouchers. Some unvouchered samples had to be included because no others were available. Samples were mostly from mature trees. When possible more than one sample (up to 9 specimens in *A. costata*) per species were studied in order to cover at least part of the infraspecific variability.

Information on habitat of each sample was collected for the analysis of ecological trends. In case this information was not mentioned on the label, it was inferred from the collective floristic data (Sidiyasa 1998).

All selected samples were sectioned, macerated and prepared according to standard techniques described by Baas & Zhang (1986) for light microscopic analysis and scanning electron microscopic (SEM) observation.

The sequence adopted for the general survey of wood anatomical features and the characterisation of the sections follows a standard format presented in Baas & Zhang (1986), Baas et al. (1988), and Zhang & Baas (1992). The terminology, definitions, and measurements of quantitative features mainly follow the IAWA List (Wheeler et al. 1989). The ratio of vessel element length to vessel element diameter (L/D ratio) is used here according to Zhang & Baas (1992). The specimens studied are listed in Sidiyasa (1998) and Table 1. In view of the small infrasectional variation, no wood anatomical species descriptions are given.

WOOD ANATOMICAL FEATURES IN ALSTONIA

The following description presents a general wood anatomical survey of *Alstonia* based on the three sections studied. The diagnostic and the systematic value of various wood anatomical characters are also discussed, especially at sectional level. Table 1 summarises the most important characters that were observed in the present study. Variation of mean vessel frequency, tangential vessel diameter, L/D ratio, and ray frequency of each section is illustrated in Figure 40.

Growth rings

Growth rings in *Alstonia* are absent or indistinct, rarely distinct (Fig. 4–9). If present, they are usually marked by slightly thicker walls of radially flattened fibres in the latewood. Only in few samples the growth rings are marked by narrower latewood fibres and vessels and a slightly higher vessel frequency in the latewood (i.e., in Fig. 9). In some species of section *Alstonia* (e.g., *A. scholaris* and *A. angustiloba*), the growth rings may also be indicated by the presence of marginal parenchyma bands.

Vessels

Distribution and grouping (Table 1 and Fig. 1–9) — Only diffuse porosity was observed in *Alstonia*. This feature is also found in the other genera of Apocynaceae (Metcalfe & Chalk 1950; Martawijaya et al. 1986; Ilic 1991; Lemmens et al. 1995).

The vessels are solitary and in radial multiples, more rarely in clusters. The percentage of each category can sometimes be helpful in identification. In section *Alstonia*, the pattern is usually dominated by radial multiples (sometimes also by clusters in *A. rostrata* only). In the other sections the situation is different: in sections *Dissuraspermum* and *Monuraspermum*, either solitary vessels or radial multiples may be dominant.

The radial multiples in *Alstonia* consist of 2–8(–11) vessels, and the clusters (i.e., laterally adjoining radial multiples, cf. Fig. 7) consist of 3–9(–10) vessels. These values are not diagnostic.

Frequency and element size — Vessel frequency ranges from 3 / sq. mm in *A. pneumatophora* and *A. scholaris* to 149 / sq. mm in *A. costata*. This feature has a high diagnostic value for identification at the sectional level: in section *Alstonia*, the vessel frequency varies from 3 to 8(–15) / sq. mm (Fig. 4–9); in section *Monuraspermum* from 29 to 53(–61) / sq. mm (Fig. 2 & 3); and in section *Dissuraspermum* it varies from (72–)100 to 149 / sq. mm (Fig. 1). Average tangential vessel diameter ranges from 42 µm in *A. costata* to 172 µm in *A. scholaris*. There is a distinct correlation between vessel frequency and vessel diameter, the species with higher vessel frequency tend to have a narrower vessel diameter, and vice versa.

The solitary vessels are usually round to oval, but slightly angular vessels were also found in all species, especially in section *Alstonia*.

Average vessel element length varies from 500 µm in one specimen of *A. scholaris* to 1320 µm in *A. macrophylla*. This feature usually varies greatly within species or sections. The longest individual vessel elements (up to 1950 µm) can also be found in

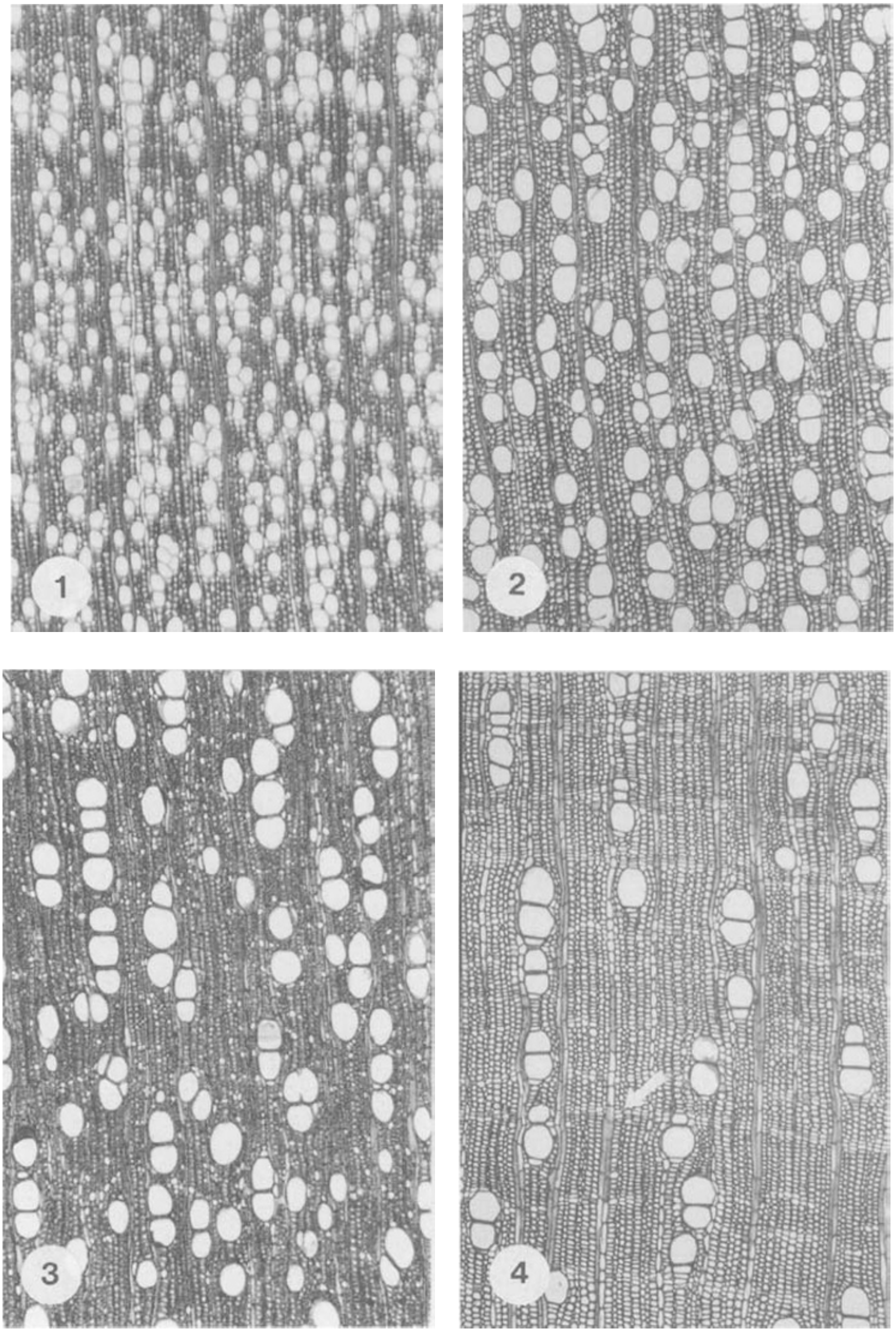

Fig. 1–4. Transverse sections (× 45) showing vessel distribution, grouping, and axial parenchyma predominantly diffuse and diffuse-in-aggregates (1–3), and axial parenchyma predominantly reticulate, showing vague ring boundaries (arrow) (4). – 1: *Alstonia costata* (MAD-SJRw 28329). – 2: *A. macrophylla* (Hoogland 8901). – 3: *A. angustifolia* (BZFw 11044). – 4: *A. rostrata* (CAFw 12013).

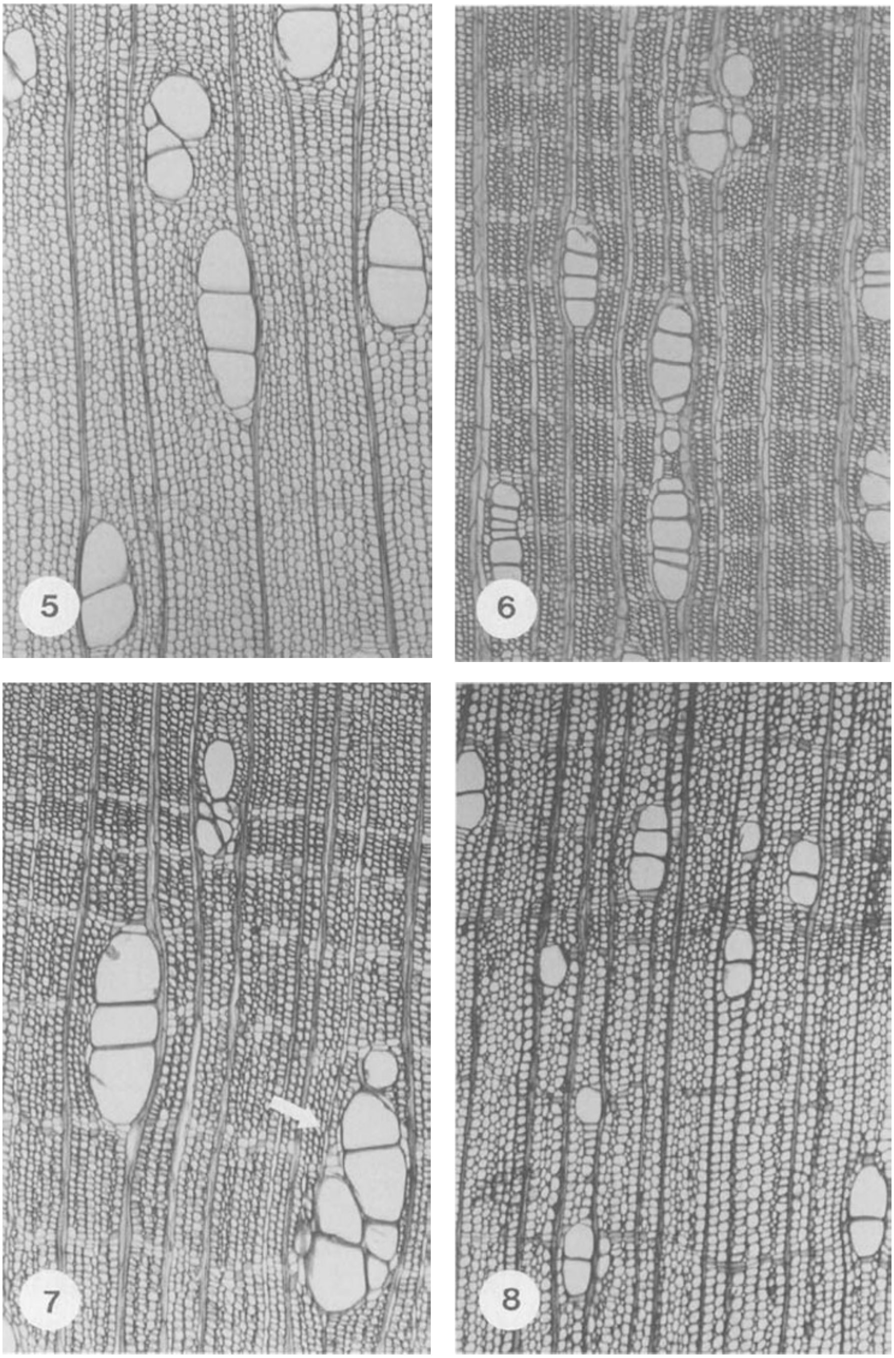

Fig. 5–8. Transverse sections (× 45) showing axial parenchyma reticulate. – 5: *Alstonia pneumatophora* (Sidiyasa 1383). – 6: *A. actinophylla* (Versteegh BW 66). – 7: *A. boonei* (MAD-SJRw 47430), note cluster of laterally adjoining radial multiples (arrow). – 8: *A. spatulata* (BZFw 13110).

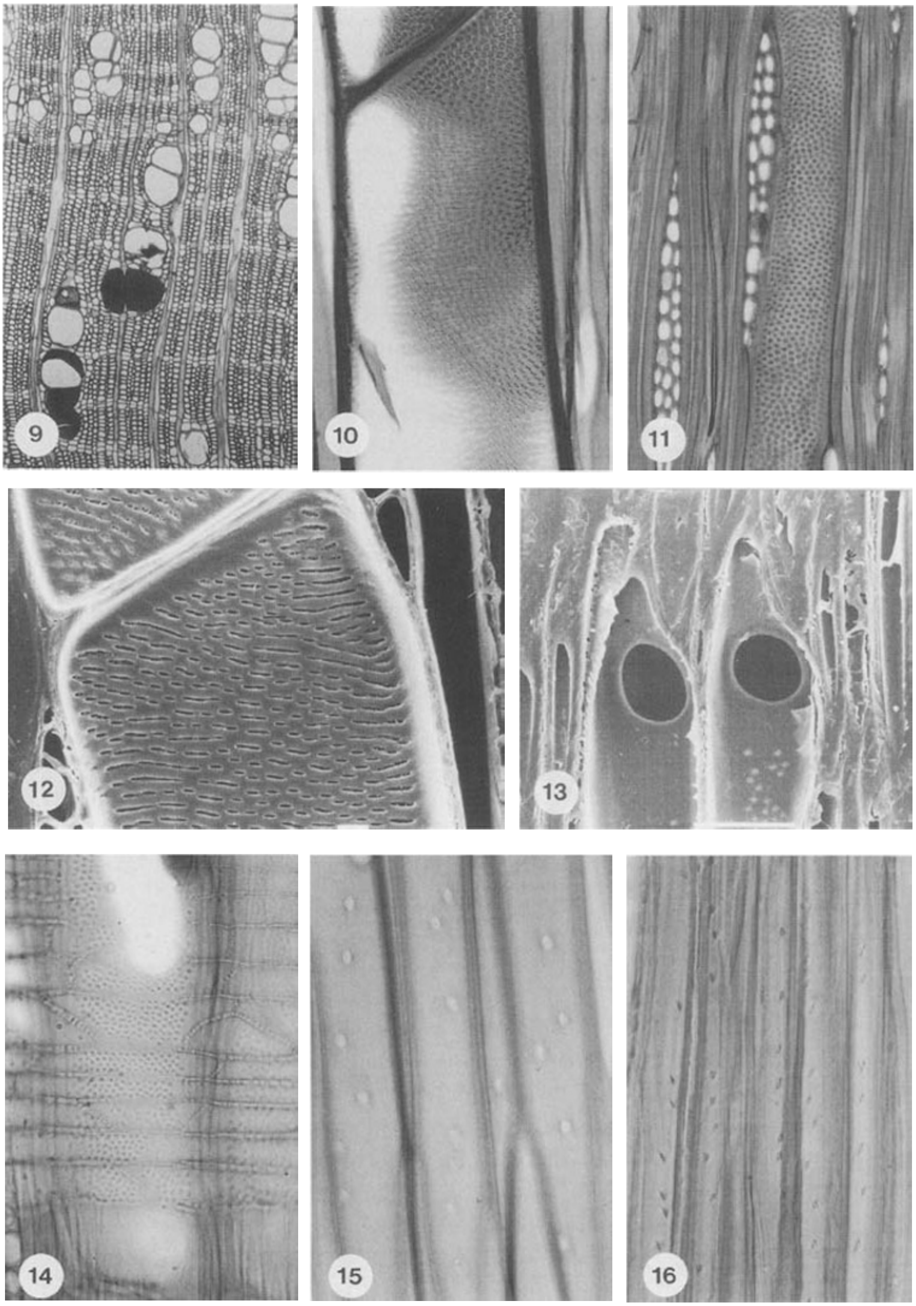

Fig. 9. *Alstonia scholaris* (Sidiyasa 1402), parenchyma reticulate, some vessels with deposits. — Fig. 10–12. Intervessel pits (10, 11, × 206; 12, × 495). – 10 & 12: *A. iwahigensis* (Sidiyasa 1116). – 11: *A. spectabilis* (BZFw 3331). — Fig. 13. Simple perforation (RLS, × 330): *A. macrophylla* (Hoogland 8901). — Fig. 14. Vessel-ray pits (RLS, × 206): *A. angustifolia* (BZFw 11044). — Fig. 15 & 16. Fibre pits (TLS, × 330). – 15: *A. rostrata* (CAFw 12013). – 16: *A. pneumatophora* (Sidiyasa 1383).

A. macrophylla, the shortest (only 170 µm long) in *A. costata*. Vessel element length has no diagnostic value at the species or section level in *Alstonia*.

Vessel wall thickness varies from (1.5–)2–8 µm. The species of section *Dissuraspermum* are usually characterised by vessel walls up to 4(–5) µm thick. It is a quite consistent wood anatomical feature for the section. In the other sections, vessel wall thickness varies greatly, from 2 to 8 µm.

Perforation plates (Fig. 13) — All species of *Alstonia* and all other tree genera of *Apocynaceae* have exclusively simple perforations (Metcalfe & Chalk 1950). The perforations are usually round, in oblique or more rarely in horizontal end walls.

Wall pitting (Fig. 10–12 & 14) — Intervessel pits in *Alstonia* are alternate and vestured (Fig. 10–12). Pit shape is characteristically round to oval and/or slightly polygonal. The horizontal diameter ranges from 2.5 to 8(–10) µm. The intervessel pit diameter is diagnostic for most of the sections. The smallest pits (2.5–4 µm) are found in section *Dissuraspermum*, medium sized ones (3–5 µm) in section *Monuraspermum* (Fig. 11), and the largest pits, 4–8(–10) µm, in section *Alstonia* (Fig. 10).

Pit apertures are mostly oval or narrowly elliptic, but circular apertures are also present especially in *A. rostrata*. In some species of section *Alstonia* (*A. scholaris, A. boonei,* and *A angustiloba*), coalescent apertures are sometimes present and give an impression of scalariform intervessel pit arrangement (Fig. 12). Coalescent apertures have not been observed in other sections of the genus *Alstonia*.

Vessel-ray (Fig. 14) and vessel-parenchyma pits are usually similar to the intervessel pits in arrangement, shape, size, and apertures, with the exception that they are sometimes more variable. They may be somewhat smaller or bigger and more clearly polygonal.

Helical thickenings — Helical thickenings are absent from the vessel elements in *Alstonia*.

Tyloses and deposits — Tyloses are always absent. Vessel deposits were observed in many species, but usually very few and only in some vessels.

Vestures — This feature is found in intervessel pits, vessel-ray pits, and in fibre pits. It is very difficult to observe the vestures with the light microscope, but they appear invariably present when using high magnifications with an oil immersion objective. With SEM, some variation of vestures can be recognised, mainly in density and morphology (Fig. 28–36).

Fibres (Fig. 15–19)

The fibres are non-septate and have distinctly bordered pits. The length of fibres and diameter of pits do not provide good characters for identification. The average length of fibres varies greatly, from 1110 to 1830 µm (full range: 520–2470 µm). The diameter of the fibre pits varies from 3 to 10 µm (but is mostly less than 8 µm). Fibre wall thickness (Fig. 17–19) and distribution of pits (Fig. 15 & 16, only for section *Alstonia*) are good characters to classify the woods into two groups (light and heavy).

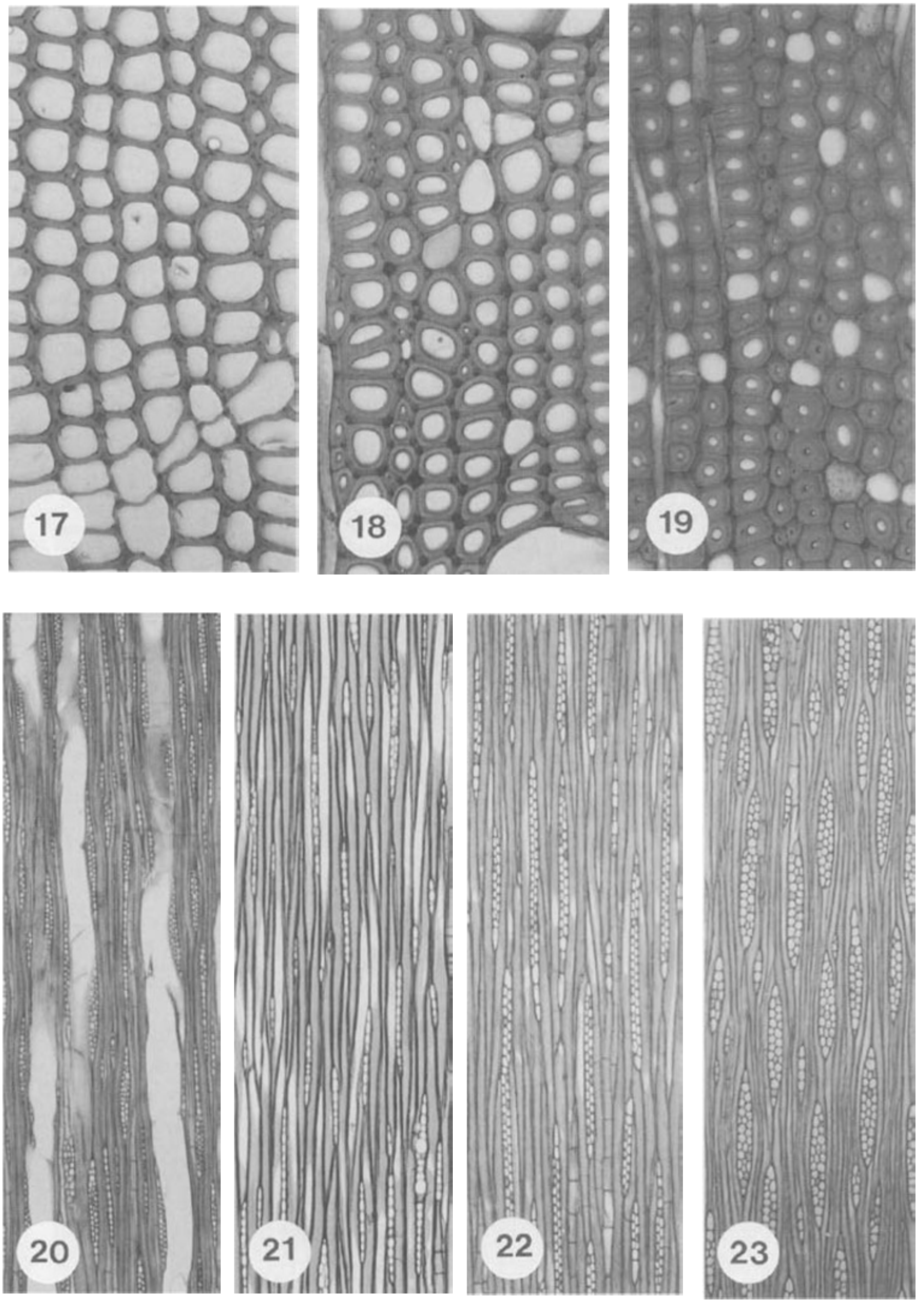

Fig. 17–19. Fibre wall thickness (× 287). – 17: Very thin walls in *Alstonia scholaris* (BZFw 25003). – 18: Very thin to medium thick walls in *A. macrophylla* (Hoogland 8901). – 19: Thick walls in *A. spectabilis* (BZFw 22100). — Fig. 20–23. Rays in tangential view (× 46). – 20: *A. macrophylla* (Ridsdale 1159). – 21: *A. pneumatophora* (BZFw = E 418). – 22: *A. boonei* (SJRw 47430). – 23: *A. actinophylla* (Versteegh BW 66).

These characters are mutually related. The woods of the light *Alstonia* group (section *Alstonia*) are characterised by very thin fibre walls and pits common in the radial walls; in contrast, the woods of the heavy *Alstonia* group (*Dissuraspermum* and *Monuraspermum*) have medium to very thick fibre walls and few or very few pits in both radial and tangential walls (Fig. 26 & 27, see arrows).

Axial parenchyma (Fig. 1–9)

This feature is of great diagnostic value. Two characteristic types of axial parenchyma distribution (both apotracheal) were observed in *Alstonia*: 1) predominantly reticulate in narrow bands and 2) diffuse and diffuse-in-aggregates. These characters are also correlated with those of the fibres that characterise the two groups (light and heavy) of *Alstonia*. The light *Alstonia* group (section *Alstonia*) has predominantly reticulate axial parenchyma (Fig. 4–9), while the heavy *Alstonia* group (the other two sections) has predominantly diffuse and diffuse-in-aggregates parenchyma (Fig. 1–3).

The reticulate pattern is usually in bands of 1–3 cells wide (up to 4 cells in *A. rostrata* only). The bands are usually wavy; the (almost) straight ones are marginal and form the (indistinct) growth ring boundaries. The other patterns of axial parenchyma distribution are scanty paratracheal and vasicentric. The latter pattern is usually very rare.

Axial parenchyma strand length varies from 3 to 15 cells, and is not of diagnostic value. This feature also varies greatly within the species or sections. In section *Alstonia*, the strands are mostly longer than in the other sections. The longest strands (up to 15 cells) are found in *A. congensis*, in the other sections they are usually less than 10 cells long.

Rays (Fig. 20–23)

In general, rays in *Alstonia* are similar in all species. The uniseriate and multiseriate forms [1–3(–4) cells wide] are found together, with a frequency of 5–15 (4–18)/mm. Usually, the species of section *Alstonia* have a lower frequency of rays compared with the other sections (see Table 1 & Fig. 40). Rays up to 4 cells wide are only found in *A. rostrata*.

The uniseriate rays are 1–23(–32) cells high, composed of weakly procumbent and upright or square cells. There are no distinct differences in number of cells between the species. The upright and/or square marginal cells of the multiseriate rays are more common in sections *Dissuraspermum* and *Monuraspermum* (Fig. 20 & 21), and less so in the other sections (Fig. 22 & 23).

Multiseriate rays vary from 60–1460 µm in height and are composed of procumbent body cells and (0–)1–15 rows of upright or square marginal cells. There is a great variation in the arrangement and number of the upright or square marginal cells, and this may be useful for identification. For instance, in *A. pneumatophora*, there is always only one row of upright marginal cells, and the mature wood of *A. spatulata* has procumbent cells only. In section *Monuraspermum*, there are up to 6 or more rows of square to upright marginal cells (up to 15 in *A. spectabilis*). Rays over 1 mm high are usually found in section *Alstonia*, the highest one is 1.5 mm tall.

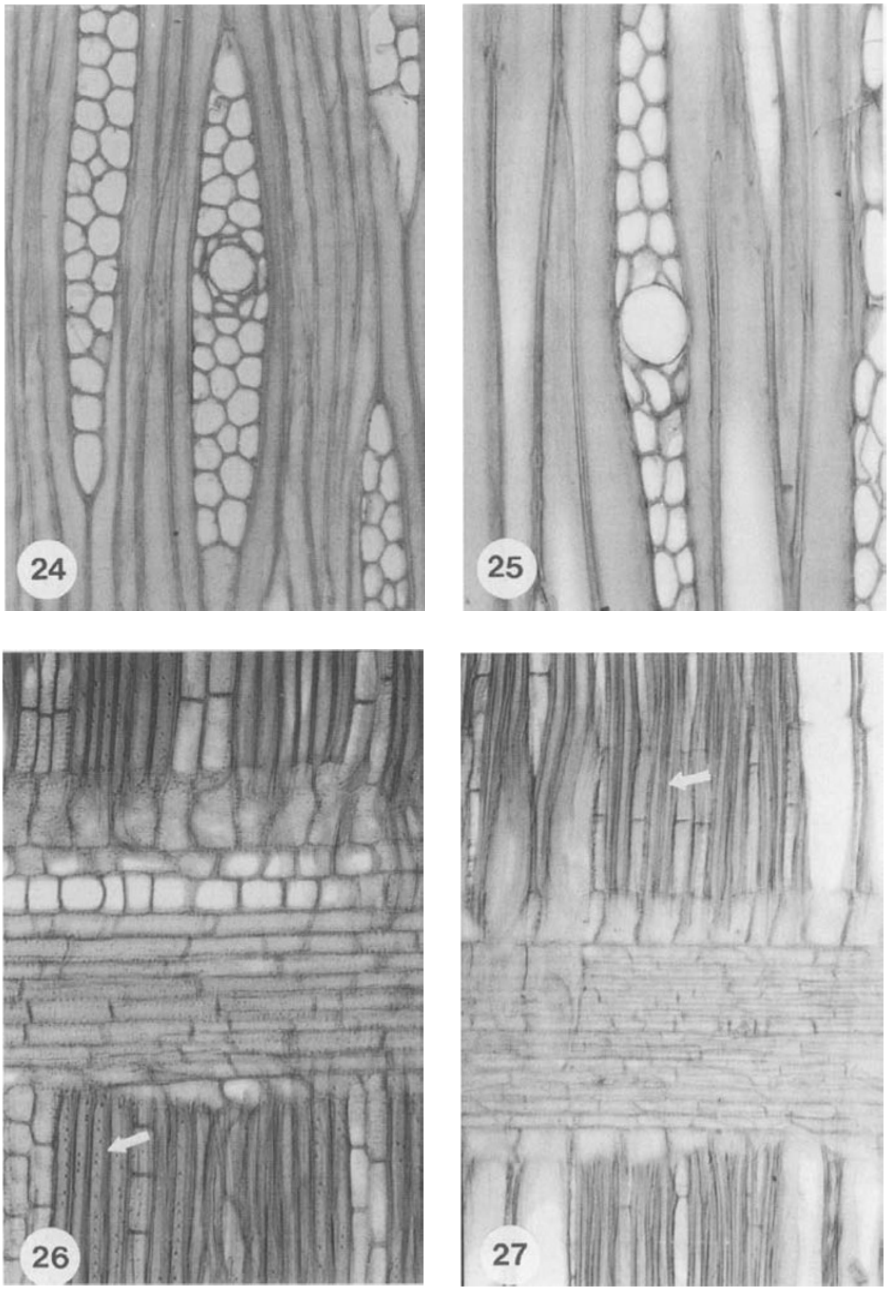

Fig. 24 & 25. Latex tubes (× 280). – 24: *Alstonia actinophylla* (Versteegh BW 66). – 25: *A. iwahigensis* (Sidiyasa 1116). — Fig. 26 & 27. Rays in radial view (× 108). – 26: Two rows of square and one row of upright marginal cells and pits in fibre walls very common (arrow) in *A. rostrata* (CAFw 12013). – 27: One row of upright marginal cells and very few pits in fibre walls (arrow) in *A. costata* (MAD-SJRw 28329).

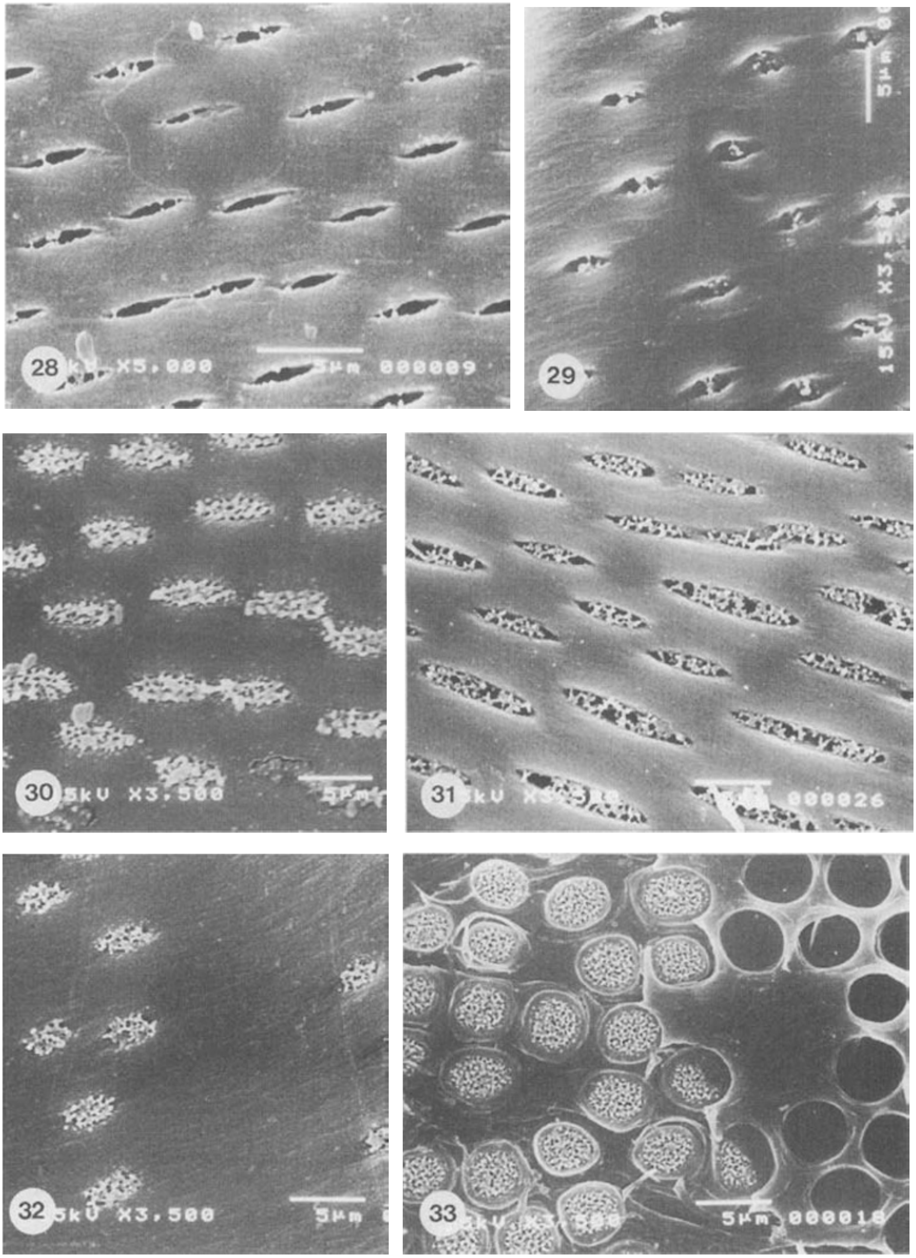

Fig. 28–33. Vestured intervessel pits (28–31, 33) and vessel-parenchyma pits (32) (28, × 3300; 29–33, × 2310). – 28: *Alstonia angustifolia* (BZFw 11044). – 29: *A. macrophylla* (Hoogland 8901). – 30 & 31: *A. scholaris* (van Balgooy 4809). – 32: *A. costata* (MAD-SJRw 28329). – 33: *A. rostrata* (CAFw 12013), split along the pit membrane (middle lamella).

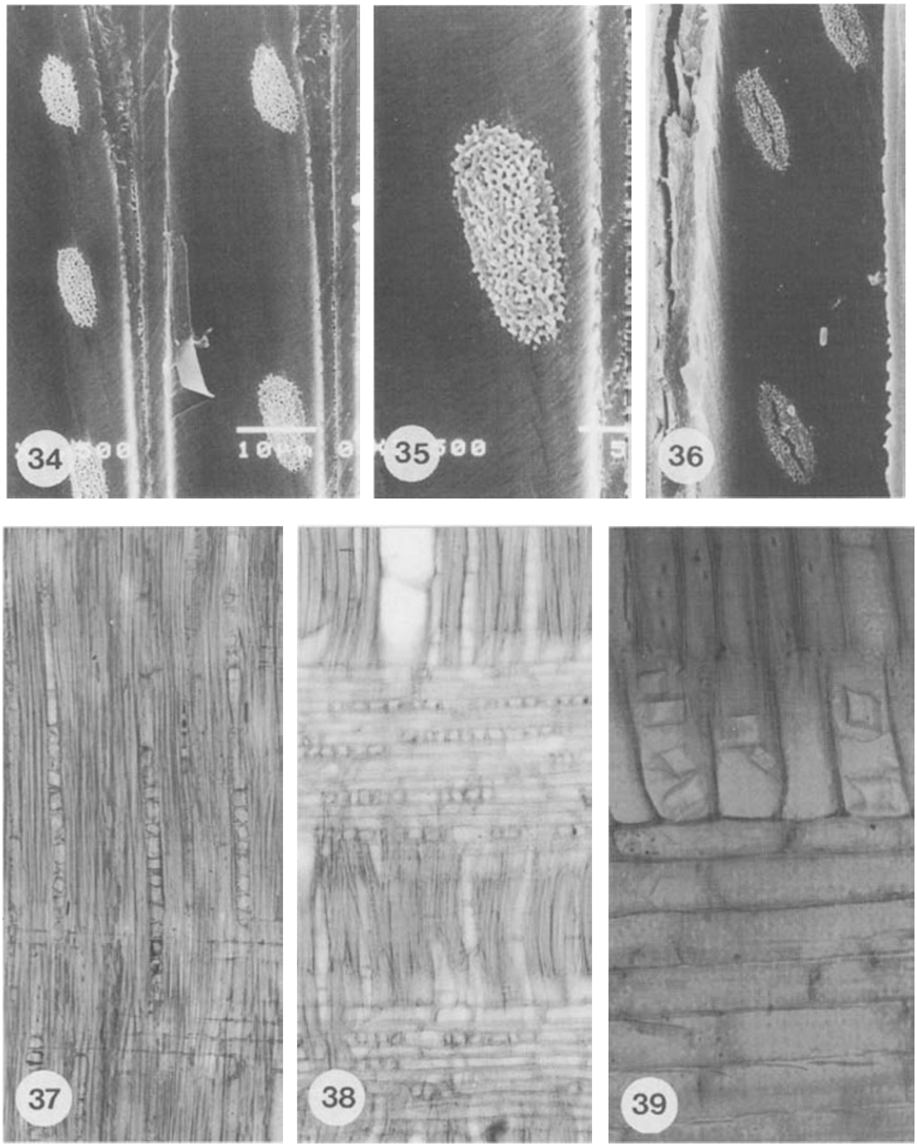

Fig. 34–36. Vestured pits in fibres (34, × 1260; 35, × 2940; 36, × 1680). – 34 & 35: *Alstonia iwahigensis* (Sidiyasa 1116). – 36: *A. rostrata* (CAFw 12013). — Fig. 37–39. Prismatic crystals (37 & 38, × 105; 39, × 262). – 37: In axial parenchyma cells in *A. macrophylla* (Havel & Kairo NGF 15481). – 38: In procumbent ray cells in *A. costata* (Craven & Schodde 198, MADw 29265). – 39: In upright chambered ray cells in *A. scholaris* (Ambriansyah & Arifin AA 961).

Latex tubes are mostly rounded or slightly oval and 20–55 µm in diameter (Fig. 24 & 25). This feature is always present and therefore diagnostic in section *Alstonia*. In section *Dissuraspermum*, latex tubes were observed only in one sample of *A. costata*. This is an exception for this section, and there is a possibility that the sample was mislabelled or misidentified.

Crystals (Fig. 37–39)

The only form of crystals observed in *Alstonia* is prismatic. They are present in chambered or non-chambered axial parenchyma cells and ray cells, but usually more common in axial parenchyma cells. The frequency and location of the prismatic crystals are variable, from very infrequent to abundant. In the abundant form, they usually form chains of up to 24 chambers. More than one crystal of about the same size or of two distinct different sizes per cell are sometimes present in square or upright marginal cells.

The prismatic crystals are absent from a number of specimens and species (mainly belonging to section *Alstonia*). Silica bodies are absent.

WOOD ANATOMICAL CHARACTERISATION OF THE SECTIONS

In the brief descriptions below, only the characters are mentioned that can be used to differentiate (at least to some extent) between the sections of *Alstonia*. For full details of character variation within and between species and sections see Table 1 and Sidiyasa (1998).

Section *Alstonia* R. Br.

Vessels 3–8(–15)/sq. mm, mostly in radial multiples of 2–7(–10) (40–82%), remainder solitary (8–26%) and in clusters of 3–8(–10) (7–44%), mean tangential diameter (76–)100–160 µm (range 30–250 µm). L/D ratio 3–10.7 (0.9–18(–37.4)). Intervessel pits 4–8(–10) µm in horizontal diameter. *Fibres* very thin-walled. *Axial parenchyma* predominantly apotracheal, reticulate, in bands of 1–3(–4) cells wide (usually wavy), sometimes discontinuous and tending to diffuse-in-aggregates, rarely diffuse; also in marginal bands up to 6 cells wide and scanty paratracheal, rarely vasicentric, in 3–15-celled strands. *Rays* 5–9 (4–11)/mm, multiseriate rays often with small *latex tubes* of 20–50 µm in diameter. *Prismatic crystals* usually present (not seen in *A. spatulata* and *A. boonei*).

Section *Dissuraspermum* (A. Gray) Benth.

Vessels (72–)100–149/sq. mm, mostly solitary (30–62%) and in radial multiples of 2–7(–10) (30–67%), remainder in oblique clusters (sometimes obscure) of 3–6(–9) (3–10%), mean tangential diameter 41–59 (20–85) µm. L/D ratio 8.9–14.9 (2.4–29.5). Intervessel pits (2.5–)3–4 µm in horizontal diameter. *Fibres* medium to very thick-walled. *Axial parenchyma* predominantly apotracheal, diffuse and diffuse-in-aggregates, and scanty paratracheal, rarely vasicentric, in 4–10(–13)-celled strands. *Rays* 10–13 (8–15)/mm, *latex tubes* absent (except in one specimen, where they are 25–35 µm in diameter and of common occurrence). *Prismatic crystals* abundant.

Table 2. Selected wood anatomical characters in the light *Alstonia* group (section *Alstonia*) with information on habitat.

	A	B	C	D	E	F	G
Species and specimens							
A. actinophylla							
Versteegh BW 66	ns	8	106	695	1350	7	435
A. angustiloba							
BZFw 8018	ns	4	107	1010	1570	7	525
KEPw 63545	ns	5	154	840	1540	6	450
A. boonei							
INEAC 664, DF	ns	5	162	1080	1740	7	630
MAD-SJRw 47430	ns	4	144	830	1400	8	740
A. congensis							
MADw 27091	ns	4	116	785	1240	7	800
FHOw 818	ns	5	149	1235	?	8	650
A. iwahigensis							
Ridsdale 1868	ns	8	127	860	1550	6	480
Sidiyasa 1116	ns	6	91	960	1630	6	450
AA 970	ns	6	121	810	1410	8	610
BZFw 13585	ns	4	146	880	1670	6	450
A. pneumatophora							
Sidiyasa 1169	sw	6	146	625	1380	8	525
(BZFw) E 418	sw	3	158	910	1420	7	440
Sidiyasa 1383	ns	6	152	850	1340	5	788
Sidiyasa 1381	sw	5	120	710	1210	6	455
A. rostrata							
CAFw 12013	ns	10	78	685	1430	9	570
Gamble B-6750	ns	15	76	770	1350	8	565
A. scholaris							
van Balgooy 4809	ns	4	154	930	1560	6	740
BZFw 25003	ns	3	151	810	1420	5	750
Sidiyasa 1402	ns	6	128	790	1410	7	580
MADw 45148	ns	3	172	840	1490	6	830
AA 961	ns	6	117	500	1110	7	400
A. spatulata							
BZFw 22312	sw	6	111	740	1170	6	395
BZFw 13110	sw	7	101	720	1330	7	520

Legend:
A = Habitat (ns = non swamp; sw = swamp).
B = Vessel frequency (per sq. mm).
C = Average tangential vessel diameter (µm).
D = Average vessel element length (µm).
E = Average fibre length (µm).
F = Ray frequency (per mm).
G = Height of multiseriate rays (µm).

Section ***Monuraspermum*** Monach.

Vessels 23–54/sq. mm, mostly in radial multiples of 2–8(–11) (41–74%) and solitary ((13–)18–57%), remainder in clusters of 3–7 (1–12%), mean tangential diameter 50–90 (20–140) µm. L/D ratio 8.8–14.3 (2.3–33.3). Intervessel pits 3–5 µm in horizontal diameter. *Fibres* usually medium thick-walled, sometimes very thick-walled. *Axial parenchyma* predominantly apotracheal, diffuse and diffuse-in-aggregates, and scanty paratracheal, rarely vasicentric, in 3–10-celled strands. *Rays* 7–11 (4–18)/mm, *latex tubes* absent. *Prismatic crystals* mostly abundant (except in one specimen).

RELATIONS BETWEEN WOOD ANATOMY AND HABITAT

In the following section the relationships between wood anatomy and the habitat factors swampy versus well-drained soils, are analysed.

Only the species of section *Alstonia* were analysed for correlations between wood anatomical characters and habitat, because within this section most samples are from trees, and all are from stems of over 10 cm in diameter, and species differ significantly in ecological preference for swamps or well-drained soils. A comparison of thin stems (< 10 cm in diameter) and thick stems in sections *Dissuraspermum* and *Monuraspermum* showed major effects of habit and stem size on the wood anatomical features analysed (Sidiyasa 1998).

The wood anatomical characters analysed are vessel frequency and diameter, vessel element length, ray frequency, and height of the multiseriate rays. Table 2 gives a complete list of all wood anatomical characters and other parameters analysed.

Analysis of variance (ANOVA) was used to calculate the significance levels of the correlations between wood anatomical characters and habitat. Partial correlation analysis was used to test the significance levels of mutual correlations between the wood anatomical characters.

The only significant differences in wood anatomy between the samples from swamps and well-drained soils in the light *Alstonia* group is in ray height; rays in trees growing in swamps are lower (Table 3). Fusiform elements (vessel elements and fibres) also tend to be shorter in the material from swamps, but this difference is not statistically significant.

Table 3. Average values ± standard deviation of quantitativewood anatomical features in the light *Alstonia* group in relation to habitat.

	swamp (n = 5)	non-swamp (n = 19)
Vessel frequency	5.4 ± 1.52	5.9 ± 2.84
Vessel diameter	127.2 ± 23.99	129.0 ± 28.25
Vessel element length	741.0 ± 104.18	850.5 ± 155.99
Fibre length	1302.0 ± 108.03	1456.1 ± 155.15
Ray frequency	6.8 ± 0.84	6.8 ± 1.08
Ray height*	467.0 ± 55.29	602.3 ± 139.57

Remarks: n = number of samples; * = significant at 0.05 level.

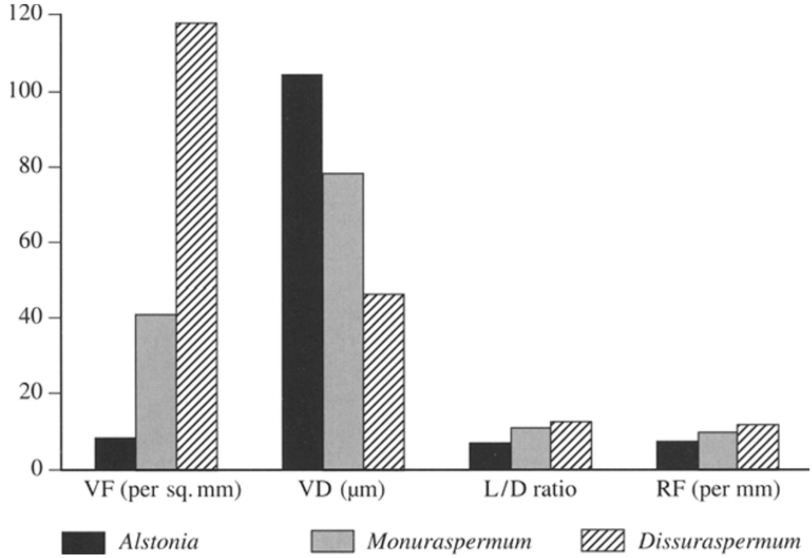

Fig. 40. Mean vessel frequency (VF), tangential vessel diameter (VD), L/D ratio, and ray frequency (RF) of sections *Alstonia, Monuraspermum*, and *Dissuraspermum*.

DISCUSSION

Systematic implications

The wood anatomical characters in *Alstonia* show a considerable amount of variation of a type which is often used in systematic wood anatomy and wood identification. They support the infrageneric classification (sections) recognised by Sidiyasa (1998) on the basis of macromorphological features. The species within a section have a similar wood anatomy, and are different from the species of the other sections. Due to the homogeneous characters within the sections, identification to the species level is impossible with wood anatomy. Figures 40 & 41 show the wood anatomical differences between the sections. Vessel frequency is the best character to recognise the sections: it increases markedly from section *Alstonia* (with the lowest frequency) to section *Dissuraspermum* (with the highest frequency).

The timbers of *Alstonia* in Southeast Asia have been classified in two groups (Soerianegara & Lemmens 1993) mainly based on fibre wall thickness and tangential vessel diameter. If we look at only these two features as the basis (key characters) in this classification, *A. rostrata*, formerly belonging to section *Winchia*, does not fit in. This species has more or less the same vessel diameter as species of section *Monuraspermum*, but it is characterised by very thin fibre walls. Due to this and some other supporting characters, we placed *A. rostrata* in the light *Alstonia* group (= Pulai group according to Soerianegara & Lemmens 1993), together with the other species of section *Alstonia*.

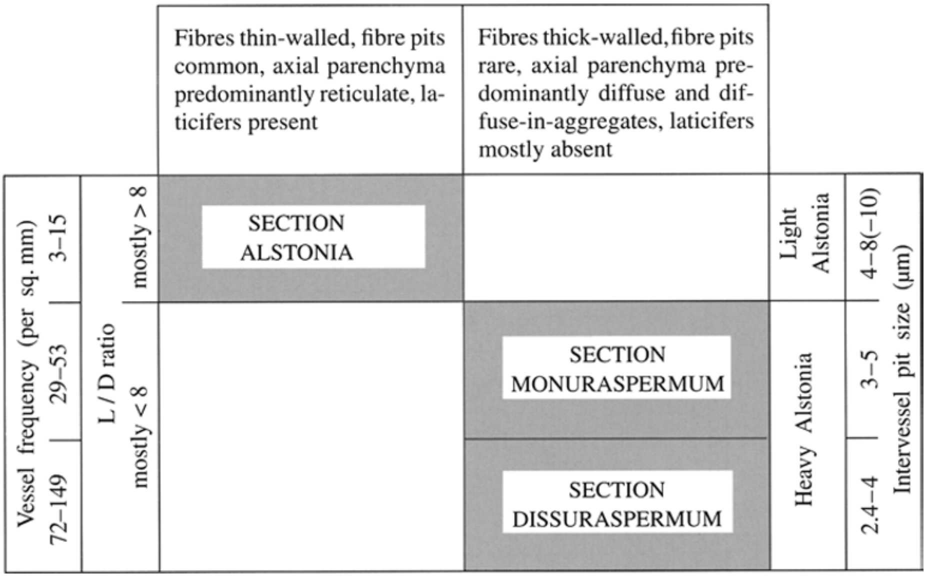

Fig. 41. Tentative 'block key' to the sections of the genus *Alstonia* based on wood anatomical characters.

Parenchyma distribution (see Fig. 1–9) is another important character in *Alstonia* that can be included as a key character for sectional classification. The predominantly reticulately banded type is characteristic for the light *Alstonia* group, while predominantly diffuse and diffuse-in-aggregates parenchyma is typical for the heavy *Alstonia* group (= hard *Alstonia* group according to Ilic 1991 and Soerianegara & Lemmens 1993). Ilic (1991) includes three species in this group: *A. brassii, A. glabriflora*, and *A. spectabilis*, of which the first two now are synonyms of *A. macrophylla* (Sidiyasa 1998).

Figure 41 summarises the numerous wood anatomical differences between light and heavy *Alstonia* on the one hand, and between all three sections available for wood anatomical study. Possibilities to differentiate between sections with relatively many quantitative wood anatomical features is quite unusual; in many woody families such differences are not even available to differentiate genera.

The CSIRO's macro key for hardwood identification (Ilic 1990) records that diffuse and diffuse-in-aggregates axial parenchyma is found rarely in *A. angustifolia*, while the diffuse-in-aggregates pattern is absent in *A. macrophylla*. This erroneous interpretation is understandable if these features are only studied with a hand lens. Parenchyma is often difficult to differentiate from the thin-walled fibres in light *Alstonia*. Ilic (1987) also recorded diffuse and diffuse-in-aggregates parenchyma for *A. actinophylla* but these features are never predominant in section *Alstonia* (cf. Fig. 6). However, most of the diagnostic characters illustrated by Ilic (1987, 1990, 1991) for *Alstonia* conform with the present results.

Soerianegara & Lemmens (1993) and Lemmens et al. (1995) noted that the light *Alstonia* closely resembles *Dyera*. Their wood anatomical description for *Dyera* looks very similar to that of *A. scholaris*. It differs only in axial parenchyma distribution, which, in *Dyera*, tends to be predominantly diffuse-in-aggregates or in short (discontinuous) tangential lines. In *D. costulata*, these lines are closely spaced and mostly only one cell wide and form a reticulate pattern (Martawijaya et al. 1986). A relationship between *Alstonia* section *Alstonia* and *Dyera* is also shown by macromorphological characters (Monachino 1949). The wood of *Alstonia* section *Alstonia* also resembles that of *Nerium, Stemmadenia, Ochrosia,* and *Tabernaemontana* due to the latex tubes in the rays (Metcalfe & Chalk 1950).

When the wood anatomical features are overlain on the cladogram for *Alstonia* based on an analysis of the macromorphological and pollen morphological diversity pattern (Sidiyasa 1998, Fig. 42), the following transformations can be hypothesised. The ancestral or the primitive characters of the genus are: thin or very thin fibre walls, wide and few vessels, laticifers present, fibre pits common in both radial and tangential walls, and reticulate parenchyma. Several of these features are common characters for the family Apocynaceae (see also Metcalfe & Chalk 1950). Only the first three of those characters show distinct transformations in the cladogram. These characters are found only in the outgroup and in section *Alstonia*. Thick-walled fibres, very infrequent tangential fibre pits, and the absence of laticifers are considered to be derived characters and synapomorphic for sections *Monuraspermum* and *Dissuraspermum*. Each of these sections has also two autapomorphies (see Fig. 42).

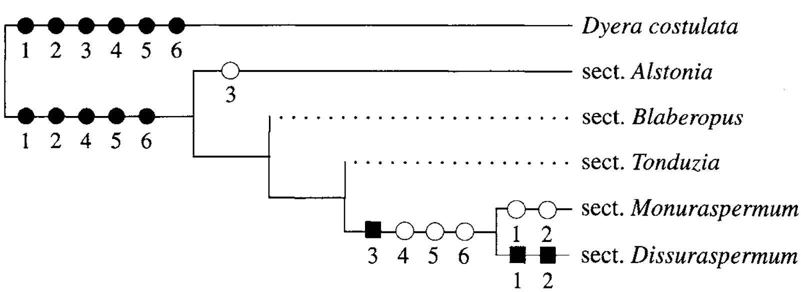

Fig. 42. Transformations of wood anatomical characters of the genus *Alstonia*.

1. Average vessel frequency: ● = 3–10(–15); % = 29–61; ■ = (72–)100–149.
2. Average vessel diameter: ● = (76–)92–162 µm; % = 49–91 µm; ■ = 41–59 µm.
3. Axial parenchyma: ● = densely reticulate and with short or discontinuous lines, mostly uniseriate; % = reticulate with mostly irregularly spaced bands, 1–3(–4) cells wide; ■ = predominantly diffuse and diffuse-in-aggregates.
4. Fibre walls: ● = thin or very thin; % = medium to thick.
5. Fibre pits: ● = common in both radial and tangential sections; % = very rare in tangential section.
6. Latex tubes or laticifers: ● = present; % = absent.

The irregularly spaced reticulate form of axial parenchyma cells in section *Alstonia* is an autapomorphy. This character is derived from very narrow bands (usually uniseriate lines) as found in *Dyera costulata,* which presumably developed into a slightly different form, predominantly diffuse and diffuse-in-aggregates, in sections *Monuraspermum* and *Dissuraspermum.* The uniseriate lines of axial parenchyma cells also occur in some species of *Cerberiopsis, Funtumia, Geissospermum, Parahancornia, Plumeria,* and *Vallaris* of the Apocynaceae (Metcalfe & Chalk 1950).

The sectional distinction by mean tangential vessel diameter is unexpected. The transformation from wide average diameters in section *Alstonia* to narrow in section *Dissuraspermum* is quite clear (see also Table 1). Section *Monuraspermum* is intermediate between these two sections. Ecological factors and tree size or shrub habit may have influenced this trend.

It is impossible to give the transformation of character states in sections *Blaberopus* and *Tonduzia* since no data are available. Based on the cladogram, they may be supported by the characters or character states which resemble those found in sections *Dissuraspermum* and *Monuraspermum,* because both sections are mostly comprised of shrubs and small trees.

Ecological trends and functional significance

Wood or secondary xylem provides a complex tissue for water transport, mechanical strength, and for metabolic processes such as storage and mobilisation of reserve carbohydrates and lipids (Zimmermann & Brown 1971; Zimmermann 1983; Baas 1986; Carlquist 1988). Ecological and evolutionary trends in vessel diameter, perforation plate type, vessel frequency, vessel member length, total vessel length, and fibre type have all been discussed in terms of their input to the safety and efficiency of water transport (Zimmermann & Brown 1971; Baas 1986). Both efficiency or maximal conductivity and safety are strongly related to vessel diameter and vessel frequency. Increased vessel diameter increases efficiency of water conduction dramatically, but at the same time it decreases safety (Zimmermann 1983).

In *Alstonia,* these functionally significant characters vary between groups or sections and ecological categories. In section *Alstonia* (light *Alstonia*), the diameter of the vessels is much wider (except in *A. rostrata*) and vessel frequency is lower than in the sections of the heavy *Alstonia* group (Fig. 40). However, species of both groups may grow together in the same type of habitat and in the same locality. Moreover, we did not find distinct differences within leaf morphology (e.g., leaf size and lamina thickness) between the *Alstonia* species from different ecological niches. Field observations backed by herbarium specimens substantiated the above general observation of species with contrasting woods and similar leaf texture growing side by side, e.g., *A. spectabilis* and *A. scholaris* in Central and Southeast Sulawesi, *A. angustifolia* and *A. iwahigensis* in Central Kalimantan (Sidiyasa 1998). This is suggestive of alternative strategies in xylem structure and function within *Alstonia*; one emphasising efficiency in water conduction (section *Alstonia,* except *A. rostrata*) and one favouring safety of conduction (the other sections). The exceptional condition in *A. rostrata* may be due to the fact that it usually occurs at higher altitudes than the other species of section *Alstonia.*

In the literature we could find no other reports for a correlation between swamp conditions and wood anatomy. However, water-logged conditions of the soil imply physiological drought, because water uptake is inhibited in the anaerobic root environment, and non-swamp habitats are assumed to have well-drained, well aerated soils, where there are no inhibitory factors for water uptake (Slatyer 1967). Taking this interpretation into account the ecological trends of *Alstonia* in relation to habitat partly conform to a general trend reported in other studies (especially Dickison et al. 1978; Baas et al. 1983; Carlquist & Hoekman 1985; Baas 1986; Baas & Zhang 1986; Zhang et al. 1992): xeric conditions are associated with shorter tracheary elements. However, the weak differences in vessel element and fibre length within section *Alstonia* are not statistically significant. Within several individual genera, relatively low rays have so far been found to be associated with high latitudes or large plant size, i.e., the tree habit (Baas 1973; Van der Graaff & Baas 1974; Zhang et al. 1992; Sidiyasa 1998). The functional significance of relatively low rays in swamp species, species from a cool microclimate, or large trees remains obscure.

In view of the presumed physiological drought associated with swampy soils, it is somewhat surprising that the more readily understandable functional features of the hydraulic system, viz. vessel diameter and vessel frequency, are not significantly affected by habitat in *Alstonia*.

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