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Wood Anatomy of Mangrove Plants in Iriomote Island of Japan: a Comparison with Mangrove Plants from Lower Latitudes

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Abstract. Wood structure of five mangrove species collected from Iriomote Island, Okinawa Prefecture, i.e., *Bruguiera gymnorrhiza, Rhizophora stylosa, Kandelia candel, Sonneratia alba* and *Avicennia marina*, was investigated and compared with that of those species growing in lower latitudes. Results revealed that the plants from Iriomote Island differed from those in lower latitudes in the three aspects. First, the plants from Iriomote Island had some structural characters which were not found in the plants from lower latitudinal regions, such as short and wide vessel elements as in *B. gymnorrhiza*, vascular tracheids as in *R. stylosa*, septate fibers as in *K. candel*, heterocellular rays as in *S. alba*, and fine structure of sclereid bands as in *A. marina*. Second, the plants from Iriomote Island showed distinctive differences in a few structural characters such as vessel–ray and vessel–parenchyma pitting (bordered vs. simple or half–bordered) as in *B. gymnorrhiza*, vessel arrangement (predominantly in short radial multiples of 2–3 vs. solitary) as in *R. stylosa*, and perforation (simple vs. diverse) as in *S. alba*. Third, the plants from Iriomote Island tended to decrease average length of both vessel elements and fibers and to increase vessel diameter. The differences in these qualitative and quantitative characters between the plants from Iriomote Island and those from lower latitudes suggest that the mangrove species have a diverse structure of wood probably adapted to lower and higher latitudes.

Key words: Avicenniaceae, Iriomote Island, mangrove plants, Rhizophoraceae, Sonneratiaceae, wood anatomy.

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Mangroves are essentially the communities of various trees and shrubs in intertidal stripe of tropical zone. Individual mangrove species exhibit adaptations in diverse ways to mild tropical coastal habitats which can be well illustrated by their large scale of forests and high community productivities. Because of their importance in preservation for ecological equilibrium of coastal environment, the mangroves have attracted much attention of researchers since the 17th century. So far a lot of papers on mangrove plants have been published, which cover almost all aspects of ecology, physiology, anatomy, silviculture and utilization of them. Researches on wood anatomy of the mangroves can date back to the beginning of this century. Representative works include Panshin's (1932) investigation on the wood structure of mangrove species in Philippines. Marco (1935) and van Vliet (1976) dealt with wood structure of some mangrove species of Rhizophoraceae. Janssonius (1950) studied vessel characters of some Javan mangrove species. In addition, other reports were also published on wood structure of only selected mangrove species (e.g., Krishnamurthy and

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Sigamani, 1987; Metcalfe and Chalk, 1983; Rao and Prukayastha 1972, Rao *et al.*, 1987; Sun and Lin, 1997; van Vliet and Baas, 1984; Zamski, 1979). These researches have contributed to an increase of our knowledge of anatomical structures of mangrove woods and their peculiar adaptations to littoral habitats. However, almost all these earlier studies are based on materials collected from or growing in tropical regions.

Distribution of mangroves also extends towards higher latitudes into some areas of subtropical regions like Iriomote Island of Japan. Although sometimes they can still constitute a large-sized forest, they generally tend to have some variations in the size of forest, species composition, and the habits of plant body. These variations indicate to some extent the adaptations of this group of plants to an environment of higher latitudes, and are also expected to have a reflection in their wood structure. Therefore, researches on mangrove species growing in the subtropical regions of higher latitudes will lead to a comprehensive knowledge of wood anatomy of mangroves.

In this paper we presented the first report on wood anatomy of mangrove plants collected from Iriomote Island of Japan, i.e., in higher latitudes, and compared them with those from lower latitudes to clarify their differences in wood structure. Investigations were also focused on changes in structural characters during the thickening growth of their trunks and thus on adaptive changes in the mangrove species growing at higher latitudes.

Materials and Methods

Adult trees of the five following mangrove species collected at Iriomote Island, Okinawa Prefecture were used for this research: *Rhizophora stylosa* Griff., *Bruguiera gymnorrhiza* (L.) Lamk., and *Kandelia candel* (L.) Druce of Rhizophoraceae, *Sonneratia alba* J. Smith of Sonneratiaceae, and *Avicennia marina* (Frosk.) Vierh of Avicenniaceae. Wood samples for the examination of *B. gymnorrhiza, R. stylosa* and *K. candel* were collected from Funaura estuary (24°24′00″N; 123°49′00″E), and those for *S. alba* and *A. marina* from Shiiragawa estuary (24°19′00″N; 123°55′00″E). Sample discs with a diameter of 7–20 cm were cut out from the trunk at the height of 20 cm above the ground level and preserved in 50% ethanol for anatomical study.

Both sectioning and maceration methods were employed for the investigation of wood structure. For sectioning, several cubic blocks with a size of 2 cm × 2 cm × 2 cm were made out along the radius direction of sample discs. After having been softened in boiling water, they were sectioned in the transverse, tangential and radial direction with a sliding microtome. Sections were cut at 20 μm in thickness, stained in safranin O and fast green FCF, and dehydrated in an ethanol series, and permanently mounted for observation.

For maceration materials were taken out in individual slivers from different parts of the radius direction and kept in a mixture of one part of glacial acetic acid and one part of 6% hydrogen peroxide at 60°C for 36 hours. After that, the materials were washed by distilled water and stained with 1% aqueous safranin O solution, and macerated xylem cells were temporarily mounted for observation.

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Terminology followed the IAWA Committee (1989). Values for diameter, length, wall thickness etc. of xylem elements were respectively based on measurements of randomly selected 150–180 cells, and those for solitary rate, density of xylem constituents on measurements of 50–70 fields of view also selected at random.

Results and Discussion

Bruguiera gymnorrhiza

Wood diffuse-porous. Heartwood indistinct. Growth ring boundaries absent.

Vessels diffuse and sparse, 9–35 (average 17.2) per square mm, solitary (solitary rate up to 45%) or in short radial multiples of 2–3, rarely in clusters in inner wood (Fig. 1), but less solitary (about 28%), usually in radial multiples of 2–7 or in clusters in outer wood (Fig. 2). Vessels round, oval or rectangular in transverse section (Figs. 1, 2), 45–150 μm in tangential diameter and 1.5–3 μm in wall thickness.

Vessel elements 280–1050 μm long; perforation plates oblique, exclusively scalariform with 3–14 bars. Intervessel pits bordered, fine scalariform, densely arranged in transverse direction between the entire contact walls of neighbouring vessels. Three types of vessel elements distinguishable from shape and size. The first one long (more than 750 μm) and narrow (usually less than 70 μm in tangential diameter) with usually more than 10 bars in perforation plates; one or both tails tapering and long, and delicate annular or scalariform thickenings common in tails. The second one medium in size, 545–810 μm long and 88–106 μm wide with usually 6–10 bars; tails absent or short and blunt. The third type shortest (usually 300–415 μm long) but widest (usually 110–134 μm in tangential diameter) among these three types, elliptical or oval in outline; bars in perforation plates usually fewer than 5; tails absent or short and blunt. The first two types common in wood, but the third one few in quantity.

Imperforate tracheary elements composed of vascular tracheids, libriform fibers and gelatinous fibers. Vascular tracheids rare, 750–1200 μm long and less than 60 μm in diameter; delicate annular or helical thickenings present. Libriform fibers extremely abundant and constituting the ground mass of wood (Fig. 1), 460–2330 μm long, thick- to extremely thick-walled (5–12.5 μm) with few round simple pits; 2–4 septa common. Gelatinous fibers common in outer wood, diffuse or diffuse-in-aggregate among libriform fibers (Fig. 2).

Axial parenchyma rather rare, scanty to vasicentric paratracheal, rarely diffuse (Figs. 1, 2), and usually 5–8 cells per parenchyma strand. Vessel-parenchyma pits bordered, transversely-elongated elliptical, rarely round or elliptical, 9–30 μm in transverse diameter, and usually scalariform in arrangement (Fig. 6); unilaterally compound pitting between vessels and parenchyma (i.e., a vertically elongated parenchyma pit corresponding to 2–3 vessel pits) rarely present. Tannin-like particles common and solitary rhomboidal crystals sometimes present.

Rays multiseriate, 3–8 cells and 35–210 μm (average 88 μm) wide,

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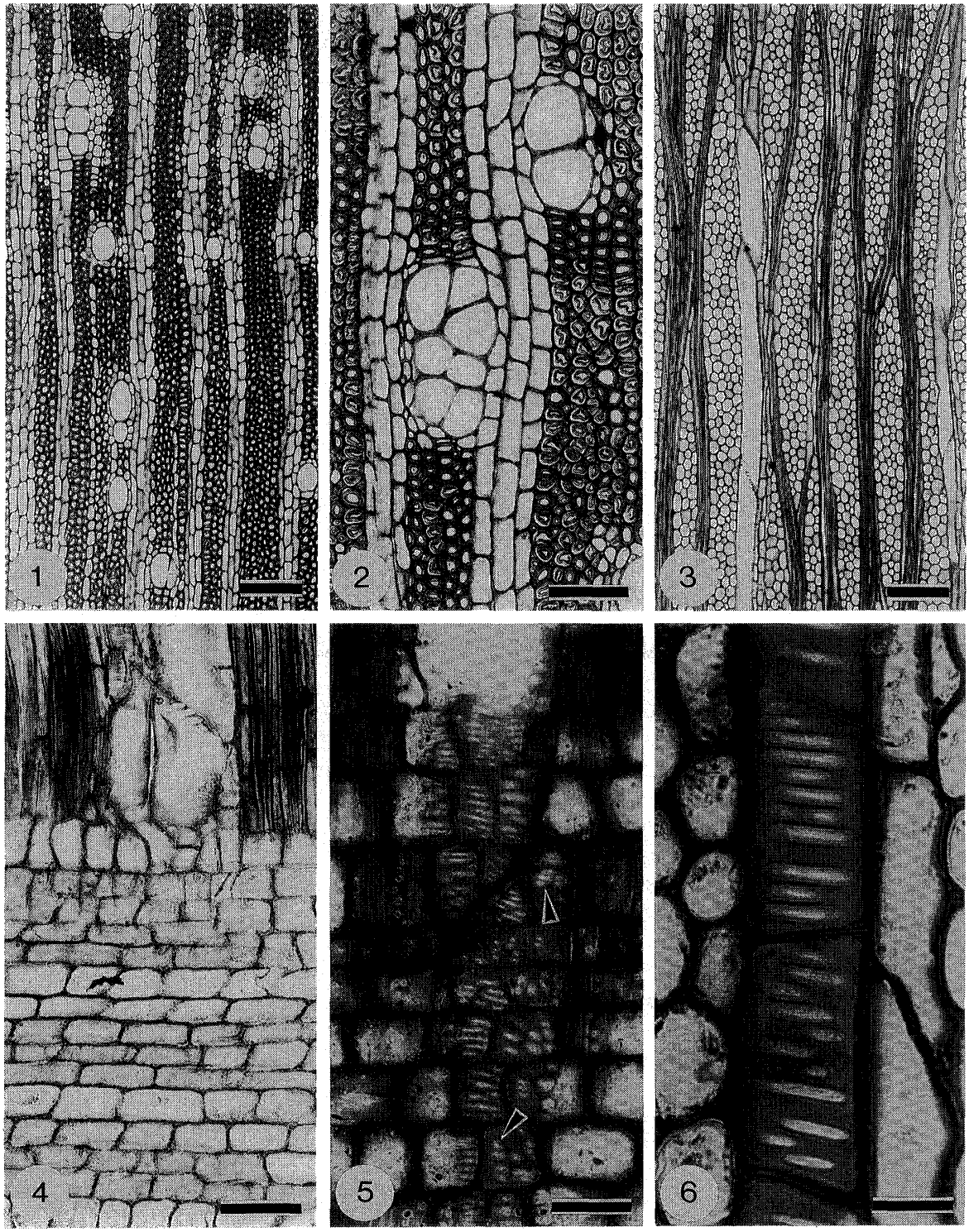

FIG. 1–6. *Bruguiera gymnorrhiza*. –1: TS, the inner wood, showing solitary vessels, short vessel multiples of 2–3 and scanty to vasicentric paratracheal axial parenchyma. –2: TS, the outer wood, showing a vessel cluster, axial parenchyma and diffuse–in–aggregate gelatinous fibers. –3: TLS, multiseriate rays. –4: RLS, heterocellular ray tissue, showing marginal row of upright cells and interspersing rows of procumbent cells. –5: RLS, vessel–ray pitting, showing usual bordered pits in regular or irregular longitudinal rows and unilaterally compound pits (arrowed). –6: TLS, scalariform or elliptical bordered vessel–parenchyma pits in a longitudinal row. Scale bar equals 200 μm in Figs. 1 and 3, 100 μm in Figs. 2 and 4, 50 μm in Fig. 5, and 25 μm in Fig. 6.

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550–4875 μm (average 2004 μm) high (Fig. 3), heterocellular with marginal rows of upright or square cells and numerous interspersing rows of procumbent cells and of square cells (Fig. 4). Vessel–ray pits bordered, elliptical or scalariform in outline, usually 6–27 μm in transverse diameter, in regular or irregular longitudinal rows and rarely in clusters; unilaterally compound pitting with a vertically elongated ray pit corresponding to 2–3 vessel pits common (Fig. 5). Solitary rhomboidal crystals and tannin–like particles present in ray cells.

Bruguiera gymnorrhiza is distributed in both tropical and subtropical regions, ranging from East Africa through Celyon and the Malay Archipelago to Micronesia and Polynesia, northward to the Ryukyu Islands and southward to tropical Australia (Tomlinson, 1994). van Vliet (1976) and Janssonius (1950) studied the wood structure of this species using collections from tropical regions. The present investigation showed that the plants from Iriomote Island differed from those of tropical regions in some important structural characters. Three types of vessel elements were distinguished in the plants from Iriomote Island according to their shapes and sizes. Among them, the short but wide vessel elements have not been reported in the plants from the other regions. Vascular tracheids which were not known in the plants from the other regions (van Vliet, 1976; Marco, 1935) were also observed in the plants from Iriomote Island although they were few in quantity. Tyloses reported in the tropical samples (van Vliet 1976) were not observed in our samples. Both vessel–ray and vessel–parenchyma pits were bordered in the plants from Iriomote Island, while they were almost simple, rarely half–bordered for the plants from the tropical regions. Gelatinous fibers were common in wood of this species. van Vliet (1976) reported their presence in the plants from some tropical regions but did not give notes on their exact distribution in wood. The present investigation revealed however that the gelatinous fibers were diffuse or diffues–in–aggregate among libriform fibers, and that they were confined to the outer wood and seldom present in inner wood.

The plants from Iriomote Island also differed from those of the tropical regions in some quantitative characters of cambial derivatives (Table 1). They generally had a greater variation range and mean value in tangential vessel diameter than the plants from the tropical regions, and also exhibited a greater variation range but a smaller mean value in vessel density and vessel element length. Therefore, although the plants from Iriomote Island all had a greater variation range in the quantitative characters of cambial derivatives, they tended to have a variation in wood structure, exhibiting the increase of average vessel diameter, the decrease of vessel number per unit area for conducting tissue, and the shortening of fibers for mechanical tissue.

Rhizophora stylosa

Wood diffuse–porous. Heartwood indistinct. Growth ring boundaries absent.

Vessels diffuse and sparse (Fig. 7), usually 40.6–54.3 per square mm in inner wood but 26–29 per square mm in outer wood; vessels arranged in short radial multiples of 2–3 (usually more than 90%) with few solitary vessels (average solitary rate 9.5%), round or oval in transverse section, 30–140 μm

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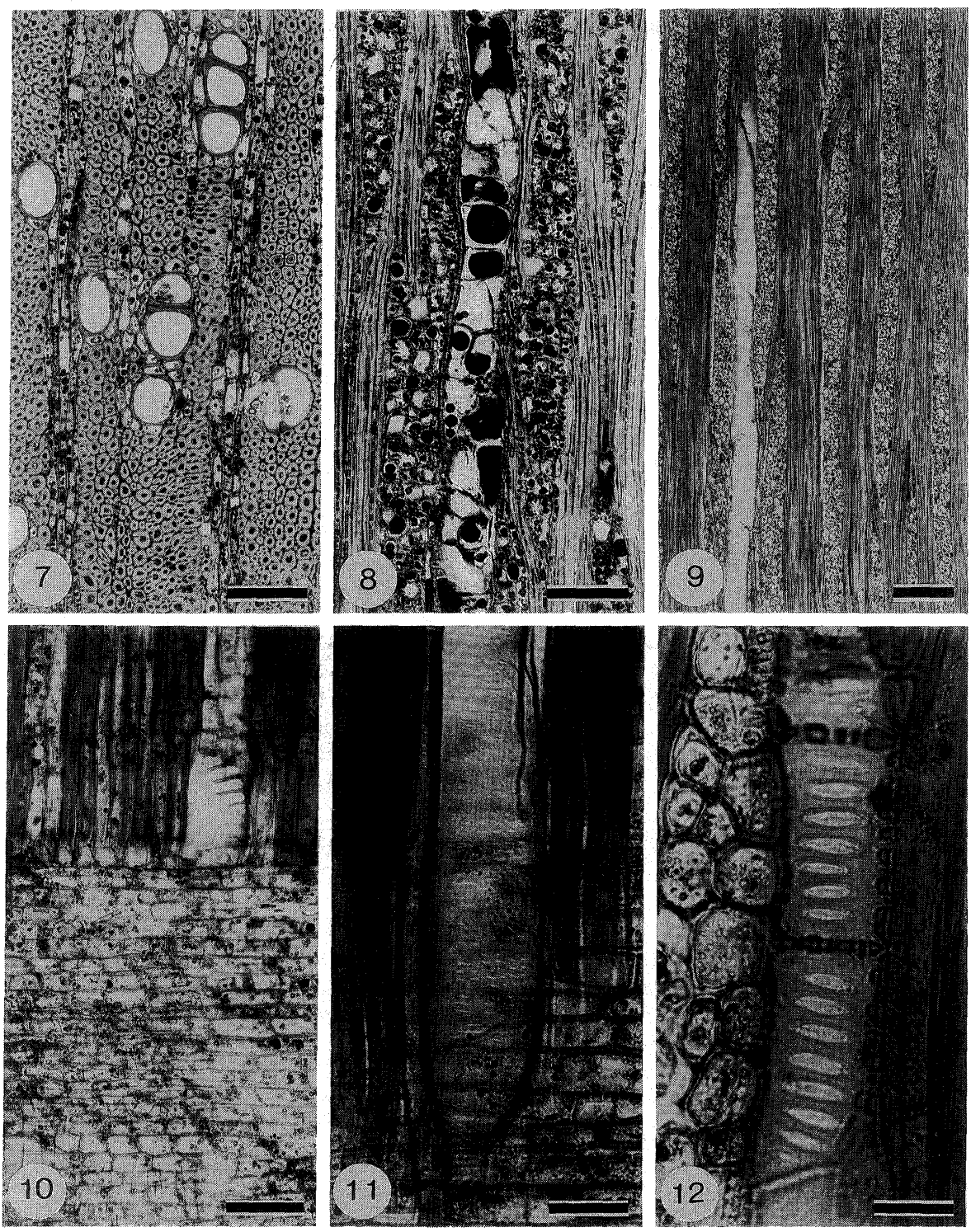

FIG. 7–12. *Rhizophora stylosa*. –7: TS, diffuse–porous wood, showing solitary vessels, short radial vessel multiples, scanty to vasicentric axial parenchyma and extremely abundant libriform fibers. –8: TLS, tyloses in a vessel of innermost wood, thin– or thick–walled and full of globular particles. –9: TLS, multiseriate rays. –10: RLS, heterocellular ray tissue with solitary rhomboidal crystals and globular particles. –11: RLS, bordered vessel–ray pits arranged regularly in both longitudinal and transverse directions. –12: TLS, bordered vessel–parenchyma pits in a longitudinal row. Scale bar equals 200 μm in Fig 9, 100 μm in Figs. 7, 8 and 10, 50 μm in Fig. 11, and 25 μm in Fig. 12.

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(average 92.7 μm) in tangential diameter and 2.2–3.3 μm in wall thickness. Vessel elements 310–1040 μm (average 678.1 μm) long; perforation plates oblique, exclusively scalariform with 3–9 (average 5.2) bars; tails usually blunt and short (less than 80 μm), rarely up to 120–240 μm long. Intervessel pits bordered, scalariform, densely arranged in transverse direction between the entire contact walls of neighbouring vessels. Tyloses common only in vessels of innermost part of wood, thin– or thick–walled, usually full of tannin–like particles of diverse sizes (Fig. 8); large rhomboidal crystals also present in tyloses.

Imperforate tracheary elements composed of vascular tracheids and libriform fibers. Vascular tracheids rather rare, vasicentric with helical thickening. Libriform fibers extremely abundant and constituting the ground mass of wood (Fig. 7), thick– to extremely thick–walled (5–13.8 μm) with some round simple pits, 620–2470 μm long and 15–32.5 μm in diameter. Small globular tannin–like particles common in narrow lumen of fibers.

Axial parenchyma extremely rare, scanty to vasicentric paratracheal (Fig. 7), usually 4–6 cells per parenchyma strand. Vessel–parenchyma pits bordered, transversely–elongated elliptical or scalariform, fewer in quantity but larger in size (usually 7.5–20 μm in transverse diameter), and usually arranged in one or two longitudinal rows (Fig. 12). Globular tannin–like particles of diverse sizes very common. Crystals not observed.

Rays multiseriate, 6–22 (average 10.5) per square mm, 2–6 cells and 20–100 μm (average 61.2 μm) wide, 110–5400 μm (average 1797.8 μm) high (Fig. 9), heterocellular with marginal rows of upright or square cells and interspersing rows of procumbent cells (Fig. 10). Vessel–ray pits bordered, round or elliptical, rarely transversely elongated, 4.5–10.5 μm in transverse diameter and arranged in regular rows in longitudinal direction or even in both transverse and longitudinal directions, rarely in irregular clusters (Fig. 11). Large solitary rhomboidal crystals and globular tannin–like particles of diverse sizes common in ray cells.

Rhizophora stylosa is a pantropical mangrove species which is mainly distributed from South India to the Eastern Pacific, southward to New South Wales, and westward to Indochina (Tomlinson, 1994). Although there were some investigations on wood structure of other species of *Rhizophora*, very little is known about the wood of this species even for the plants in tropical regions. The present study indicated that differences between the plants from Iriomote Island and those from Indonesia (van Vliet, 1976) existed in the following aspects. Tyloses, which were thin– or thick–walled and full of red globular tannin–like particles and sometimes solitary rhomboidal crystals, were very common in innermost wood but absent in outer wood in the plants from Iriomote Island. Few vascular tracheids with helical thickening wall were present around vessels in the plants from Iriomote Island. However, neither tyloses nor vascular tracheids were reported in those from Indonesia. Solitary vessels were few, only with an average rate of 9.5% in the plants from Iriomote Island, but were generally over 50% in those from Indonesia. As regards vessel–ray pitting, in the plants from Iriomote Island pits were bordered and arranged regularly in both longitudinal and transverse directions, and unilaterally compound pits were not observed. In the Indonesian plants, on the other hand, half–bordered to simple pits were

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present in addition to vertically unilaterally compound pits, and bordered pits were absent. Vessel–parenchyma pits were also bordered and arranged in one or two regular longitudinal rows in the plants from Iriomote island but half–bordered or simple and uniseriate, biseriate, scalariform or diffuse in arrangement in the Indonesian plants.

Concerning quantitative characters of cambial derivatives, the plants from Iriomote Island had a greater variation range and mean value than the Indonesian plants with respect to tangential vessel diameter, vessel density and vessel element length, but had a smaller mean value in fiber length despite its greater variation (Table 1).

Kandelia candel

Wood diffuse–porous. Heartwood indistinct. Growth ring boundaries absent.

Vessels diffuse, 26–99 (average 48.3) per square mm; solitary (solitary rate usually 14.3–20.1%) or in radial multiples of 2–3 (usually fewer than 5), rarely in clusters in inner wood (Fig. 13), but less solitary (solitary rate usually 6.2–9.9%), usually in radial multiples of 3–6 (sometimes up to 10) or in clusters of 4–10 in outer wood (Fig. 14). Vessels round, oval or square in transverse section, 32–91.2 μm (average 64.7 μm) in tangential diameter and 2.7–3.8 μm in wall thickness. Vessel elements 394.7–424.2 μm long; perforation plates oblique, exclusively scalariform with 4–9 (average 6.6) bars; tails absent or short, rarely long. Intervessel pits bordered, scalariform, densely arranged in transverse direction between the entire contact walls of neighbouring vessels.

Imperforate tracheary elements composed of libriform fibers and gelatinous fibers. Libriform fibers abundant (Fig. 14), 520–1620 μm (average 859.0 μm) long and 15–41.3 μm in diameter, mediately thick–walled (5–10 μm) with few round simple pits; one or two septa common. Gelatinous fibers rare, diffuse or diffuse–in–aggregate among libriform fibers in outer wood.

Axial parenchyma abundant, predominantly banded with 2–8 cells wide, rarely vasicentric and diffuse–in–aggregate (Figs. 13, 14), and usually 3–4 cells per parenchyma strand. Vessel–parenchyma pits (Fig. 18) bordered, round, oval, elliptical or transversely elongated, 7.5–15 μm in transverse diameter with apertures of diverse sizes; pits usually opposite, scalariform or in one or two longitudinal rows; unilaterally compound pitting with a vertically elongated parenchyma pit corresponding to 2–3 vessel pits rare. Rhomboidal crystals rare but tannin–like particles common in axial parenchyma cells.

Rays multiseriate (Fig. 15), 7–19 (average 11.2) per square mm, 2–9 cells and 15–225 μm (average 97.2 μm) wide, 120–3400 μm (average 1104.2 μm) high, heterocellular with marginal rows of upright and square cells and interspersing rows of procumbent cells and of square cells (Fig. 16). Vessel–ray pits (Fig. 17) bordered, round, oval or elliptical, rarely transversely–elongated, 4.5–12 μm in transverse diameter with apertures of diverse sizes; pits usually arranged in clusters or irregularly; unilaterally compound pitting with a vertically elongated ray pit corresponding to 2–4 vessel ones very rare. Tannin–like particles and rhomboidal crystals

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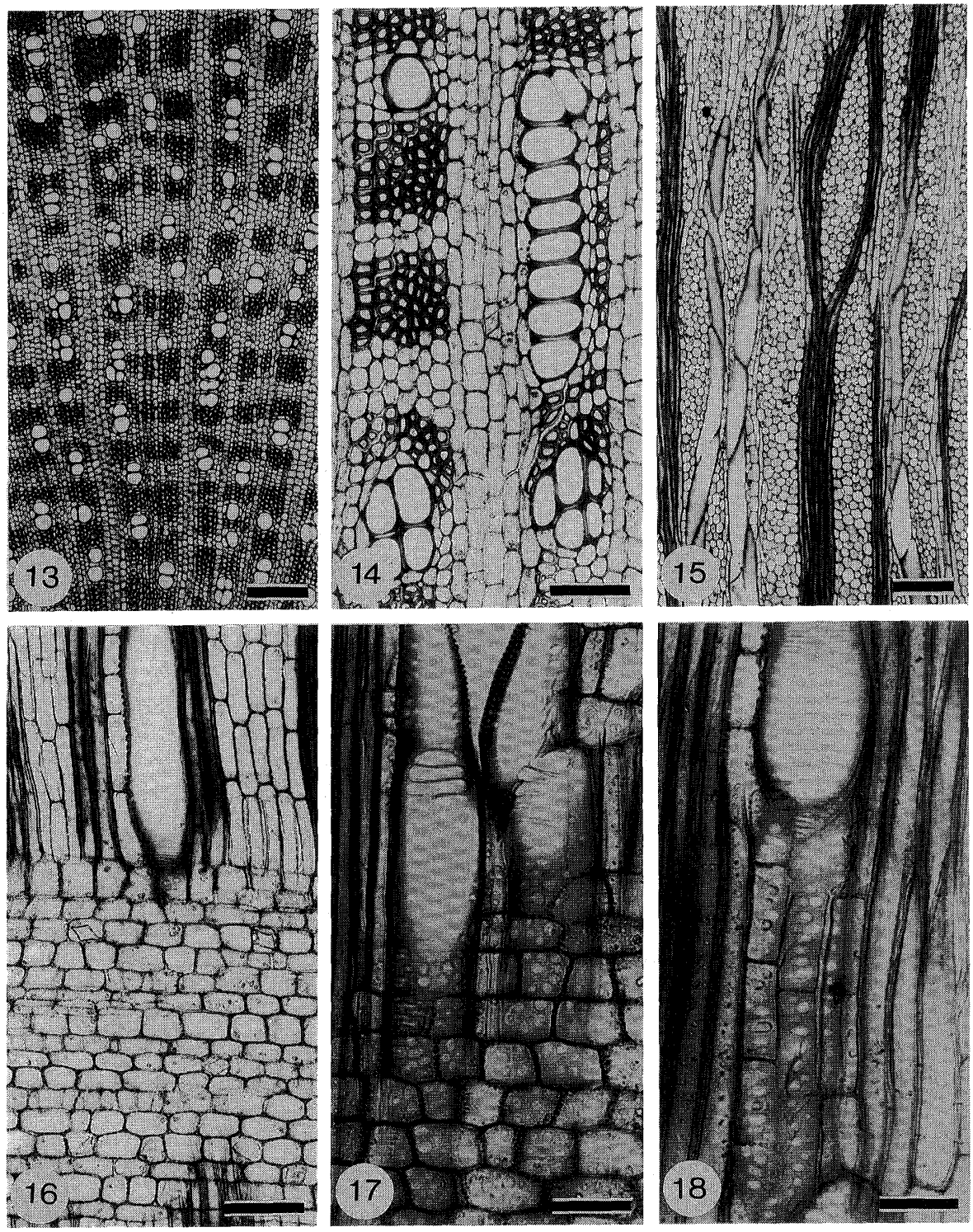

FIG. 13–18. *Kandelia candel*. –13: TS, the inner wood, showing solitary vessels, short radial vessel multiples and banded, vasicentric and diffuse–in–aggregate axial parenchyma. –14: TS, the outer wood, showing a long radial vessel multiple, vessel clusters and mediately thick–walled libriform fibers. –15: TLS, multiseriate rays. –16: RLS, heterocellular ray tissue with marginal row of upright cells and interspersing rows of procumbent cells and of square cells, solitary crystals also present. –17: RLS, bordered vessel–ray pits arranged irregularly or in clusters. –18: TLS, bordered vessel–parenchyma pits arranged in longitudinal rows. Scale bar equals 200 μm in Figs. 13 and 15, 100 μm in Figs. 14 and 16, and 50 μm in Figs. 17 and 18.

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common in ray cells.

Kandelia candel is one of a few cold-tolerant mangrove species. It is distributed from the Ganges Delta, Burma, through South Asia to South China and South Japan (Tomlinson, 1994). van Vliet (1976) and Cheng *et al.* (1992) investigated the wood structure of this species based on plants obtained from Malaya and South China, respectively. The present study showed that vessel arrangement varied according to the part in wood, and that vessels were usually arranged in radial multiples of 2–3 in inner wood but in radial multiples of 3–6 or in clusters in outer wood. That was not reported in the plants from both Malaya and South China. Solitary rate was lower (average 11.4%) in the plants from Iriomote Island as in those from South China, while it was much higher in the Malayan plants (22–66%). Storeyed vessel elements reported in the plants from South China were not found in those from Iriomote Island. Concerning vessel–ray and vessel–parenchyma pittings, in the plants from Iriomote Island bordered pits were opposite, scalariform or transitional between vessels and parenchyma, but diffuse or in clusters between vessels and rays. So-called unilaterally compound pitting was uncommon in both vessel–ray and vessel–parenchyma pits in the plants from Iriomote Island. However, in the Malayan plants pits between both vessel–ray and vessel–parenchyma were half-bordered to almost simple, arranged more or less reticularly between vessels and rays but uniseriate, biseriate, scalariform or diffuse between vessels and parenchyma; and unilaterally compound pits were also common. Tyloses reported in the plants from South China were not observed in those from Iriomote Island. Fibers with 1–2 septa were common in the plants from Iriomote Island but uncommon in the Malayan plants. Gelatinous fibers were rare in the plants from Iriomote Island but were not reported from the Malayan plants, while they were common in those from South China. Crystals were common in ray cells and also observed in axial parenchyma in the plants from Iriomote Island, but absent in those from the other two regions.

Concerning quantitative characters of some major cambial derivatives, the plants from Iriomote Island exhibited a greater mean value of tangential vessel diameter and vessel density, but a smaller mean value of vessel element length. Fibers were shorter in the plants from Iriomote Island than in those from both Malaya and South China (Table 1).

Sonneratia alba

Wood diffuse-porous. Heartwood indistinct. Growth ring boundaries usually absent despite the presence of several layers of radially flattened fibers in some parts.

Vessels (Figs. 19, 20) diffuse, 41–87 (average 59.9) per square mm, solitary (solitary rate usually 14.5–44.6%) or in short radial multiples of 2–3 (rarely over 5) or in clusters; vessels round, oval, rectangular or square in transverse section, 45–135 μm (average 85.3 μm) in tangential diameter and 1.5–2.2 μm in wall thickness. Vessel elements, 190–700 μm (average 395.3 μm) long; perforation plates simple in transverse or oblique end walls; short tails common, and long tapering tails present in some vessel elements of larger sizes. Intervessel pits crowded, alternate, rarely opposite in arrangement, round, oval, or elliptical in shape, 6–9 μm in transverse

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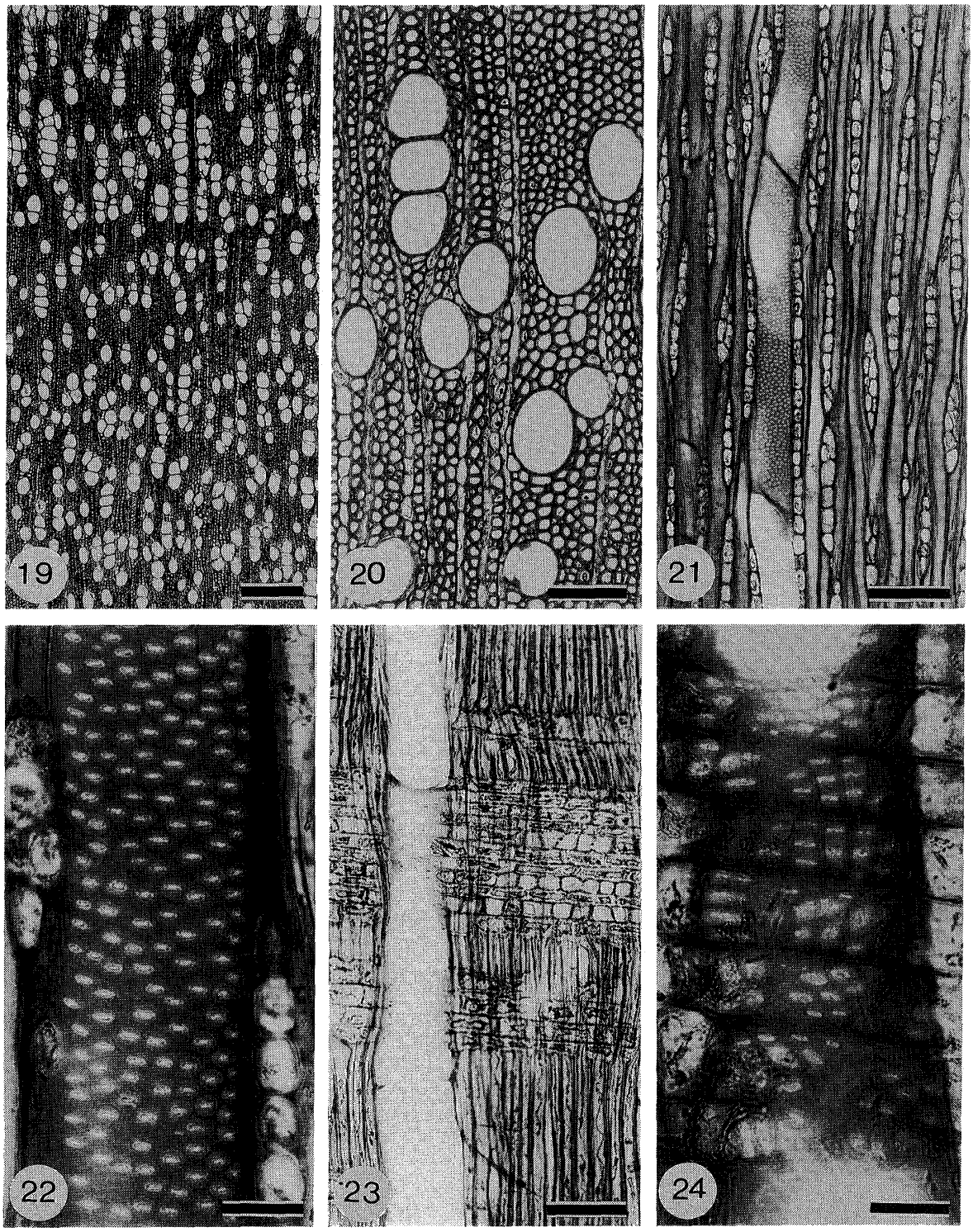

FIG. 19–24. *Sonneratia alba*. –19: TS, diffuse–porous wood, showing solitary vessels and radial vessel multiples. –20 TS, round to oval vessels and thin– to mediately thick–walled fibers. –21: TLS, uniseriate rays common and biseriate rays few. –22: bordered and vestured intervessel pits alternate. –23: RLS, heterocellular ray tissue with abundant solitary rhomboidal crystals and tannin–like particles. –24: RLS, bordered vessel–ray pits arranged irregularly or in clusters. Scale bar equals 400 μm in Fig. 19, 100 μm in Figs. 20, 21 and 23, and 25 μm in Figs. 22 and 24.

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diameter with narrow and transversely elongated apertures, bordered and vestured (Fig. 22).

Imperforate tracheary elements composed of libriform fibers and gelatinous fibers. Libriform fibers (Fig. 20) extremely abundant, 330–1300 μm (average 696.1 μm) long, 12.5–30 μm in tangential diameter, thin– to mediately thick–walled (1.25–5 μm) with very few simple pits; one or two (rarely three) septa common. Gelatinous fibers fewer, diffuse or diffuse–in–aggregate among libriform fibers.

Axial parenchyma absent.

Rays uniseriate, rarely biseriate or triseriate (Fig. 21), 67–140 (average 99.5) per square mm, 55–432.5 μm (average 203.6 μm) high, heterocellular with marginal rows of upright and square cells and interspersing rows of procumbent, upright and square cells (Fig. 23). Vessel–ray pits fewer and arranged irregularly or in clusters, bordered, round, oval or elliptical, rarely elongated, and 6–15 μm in transverse diameter (Fig. 24). Rhomboidal crystals and tannin–like particles abundant; 1 to 3 (rarely over 5) crystals in a ray cell also common.

Sonneratia alba is believed to be distributed most widely, ranging from East Africa and Madagascar to Southeast Asia, the Malay Archipelago to the Philippines, and tropical Australia to Micronesia, the Hebrides, and New Caledonia (Tomlinson, 1994). The wood structure of this species was studied by Rao *et al.* (1987) using plants from East India and Burma. Janssonius (1950) also dealt with some structural characters of vessels in Javan samples. Compared with these plants from lower latitudes, those from Iriomote Island usually did not have distinct growth rings, the presence of which was one of major characters of the Indian plants, although growth ring–like structure was sometimes present in some limited parts of wood. Perforation was always simple in the plants from Iriomote Island, but simple, reticulate or scalariform in those from India and Burma. Gelatinous fibers distributed diffusely or in diffuse–in–aggregate were common in the plants from Iriomote Island, but were not reported in those of the other two regions. Rays in the plants from Iriomote Island were heterocellular, consisting of marginal rows of upright and square cells and interspersing rows of procumbent, upright and square cells, but ray tissue in the Indian plants was homocellular with only procumbent cells.

Also differences in quantitative characters of some cambial derivatives were evident. The plants from Iriomote Island showed a tendency towards having smaller vessel diameter and shorter vessel element, but a greater vessel and ray density, compared to those from the other regions (Table 1).

Avicennia marina

Wood structure anomalous with included phloems and sclereid bands. Heartwood indistinct.

Cambium forming different tissues towards both sides: i.e., parenchyma band of 2–4 layers of cells towards the inside followed by relative amount of xylem tissue; sclereid band towards the outside also followed by the differentiation of parenchyma band where individual phloem strands were enclosed and arranged concentrically (Figs. 25, 28).

In transverse section, sclereid bands arranged concentrically and

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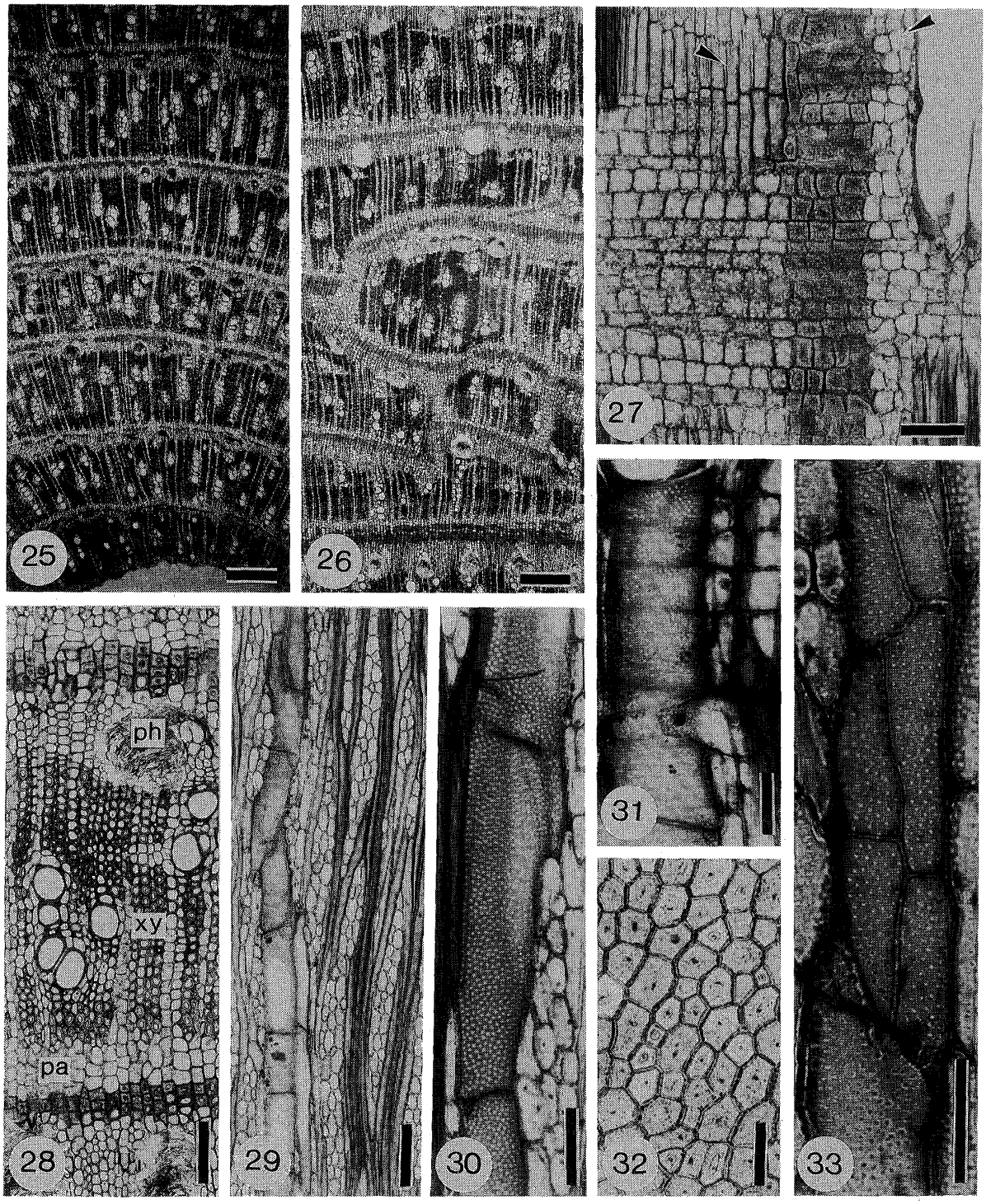

FIG. 25–33. *Avicennia marina*. –25: TS, concentric xylem tracts separated by sclereid bands. –26: TS, serious disturbance of concentric sclereid bands. –27: RLS, heterocellular rays blocked at sclereid band and parenchyma cells of different shapes in both sides of sclereid band (arrowed). –28: TS, tissue between two sclereid bands, showing xylem tract (xy), included phloems (ph) and parenchyma (pa) in both sides of xylem tract. –29: TLS, biseriate and triseriate rays. –30: TLS, bordered intervessel pits crowded and alternate. –31: RLS, bordered vessel–ray pits alternate, opposite or irregular in arrangement. –32: TLS, the tightly packed sclereids of diverse shapes and sizes. –33: TLS, bordered vessel–parenchyma pits crowded and alternate. Scale bar equals 400 μm in Figs. 25 and 26, 100 μm in Fig. 28, 90 μm in Figs. 27, 29 and 32, and 50 μm in Figs. 30, 31 and 33.

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composed of 2–4 (seldom over 6) layers of thick-walled sclereids, but also intermingled with parenchyma cells in few parts, especially where rays passed through. Individual sclereids in band tightly arranged without intercellular space, 20–30 μm, 25–40 μm and 25–62 μm in tangential, radial and vertical diameters respectively, usually square, rectangular, rarely round or oval in both transverse and radial sections (Figs. 27, 28), but polygonal, rectangular, round, oval or irregular in tangential section (Fig. 32). The regularly concentric sclereid bands also disturbed to different extent in few parts, and usually forming short and narrow branch bands in near parallel or slant ways to the concentric bands; but sometimes long and wide branch bands present and arranged in greater slant ways and almost extending to the neighbouring concentric bands; in rare cases, serious disturbance present in some part of several neighbouring bands and short segments of sclereid bands in diverse slant ways observed (Fig. 26).

Next to sclereid band, a parenchyma band of 2–4 layers of cells present in the outside (Fig. 28). These parenchyma cells square, rectangular, round or oval in transverse section, almost isometric and similar to the neighbouring sclereids in size and arrangement (Fig. 27), but thin-walled with many simple pits.

A tract of xylem tissue with the width of usually 0.8–1.2 mm in radial direction attached outwards the parenchyma band (Fig. 25). Xylem composed of vessels, libriform fibers, fiber-tracheids, axial parenchyma and rays. Vessels diffuse, 17–78 (average 35.2) per square mm, less solitary (average 11.9%), usually in radial multiples of 2–5 in narrower xylem tracts or narrower parts of xylem tracts, but in radial multiples of 4–10 or in clusters of over 5 in wider xylem tracts (Fig. 25). Vessels oval or round in transverse section, 22.5–92.5 μm (average 65.4 μm) in tangential diameter and 3–3.8 μm in wall thickness. Vessel elements 122.5–387.5 μm (average 266.0 μm) long; perforation plates transverse or a little oblique, exclusively simple; tails absent or short and blunt, and long tapering tails only present in narrower vessel elements. Intervessel pits crowded and alternate, bordered, round or oval, usually 1.5–3 μm in transverse diameter (Fig. 30).

Imperforate tracheary elements composed of libriform fibers and fiber-tracheids. Libriform fibers abundant (Fig. 28), 300–1130 μm (average 715.3 μm) long, 12.5–28.8 μm in diameter and mediately thick-walled (2.5–10 μm) with fewer simple pits; one or two septa common. Fiber-tracheids rare, vasicentric and similar to libriform fibers in size.

Axial parenchyma scanty to vasicentric paratracheal with a sheath of up to 2–5 layers of cells (Figs. 25, 26, 28), rarely diffuse or diffuse-in-aggregate; usually 2–3 cells per parenchyma strand. Vessel-parenchyma pits abundant, bordered, round or oval, usually 3–6 μm in transverse diameter, alternate and rarely opposite in arrangement (Fig. 33). Small rhomboidal crystals sometimes present.

Rays usually short in radial direction as a result of being bounded by sclereid bands (Fig. 27), but sometimes longer in those parts where parenchyma cells present in sclereid bands to lead to the connection of rays in neighbouring xylem tracts. Rays biseriate or triseriate, rarely uniseriate and multiseriate (Fig. 29), 47–76 (average 58.2) per square mm, 5–50 μm (average 21.4 μm) wide, 85–920 μm (average 338.5 μm) high,

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heterocellular with marginal rows of upright or square cells and interspersing rows of procumbent cells and of square or upright cells (Fig. 27). Vessel–ray pits similar to vessel–parenchyma pits in shape and size, but opposite, alternate or irregular in arrangement (Fig. 31). Rhomboidal crystals rare in ray cells.

Another parenchyma band attached to the outward side of xylem tract, and included phloems enclosed in this parenchyma band and concentrically arranged in strand (Figs. 25, 28).

The parenchyma bands 150–300 μm wide in radial direction and composed of 6–12 layers of cells except the strands of included phloems. These parenchyma cells different in shape from those in parenchyma band attached to the inward side of xylem tract. The former usually round, oval, rectangular and square in transverse section, and 15–32 μm in diameter but much longer (usually 87.5–125 μm) in vertical direction; the latter almost isometric with a diameter of usually 30–52 μm. (Figs. 27, 28).

Individual strands of included phloem oval, round or irregular in transverse section, 64–240 μm (usually 115–190 μm) in tangential diameter (Figs. 25, 26, 28), straight in longitudinal direction; tangential connections between neighbouring strands sometimes observed. The phloem strands usually destroyed and only empty cavities or disorganized tissue left; their fine structure indistinguishable by routine sliding sectioning.

Avicennia marina is widely distributed from East Africa and the Red Sea along tropical and subtropical coasts of the Indian Ocean to the South China Sea, throughout much of Australia into Polynesia, and south to the North Island of New Zealand (Tomlinson, 1994). Panshin (1932) and Krishnamurthy and Sigamani (1987) studied the wood samples of this species from the Philippines and South India respectively. However, sufficient information was still lacking for its wood structure. We showed that the samples from Iriomote Island had many distinct structures from those of lower latitudes. Three types of vessel arrangement were described for this species, but we showed for the first time that solitary vessels and short radial vessel multiples of 2–4 were often present in narrow xylem tracts or narrower parts of wide xylem tracts, and that long radial vessel multiples and vessel clusters of over 5 represented a major character of vessel arrangement in wide xylem tracts. Sclereid bands were also a structural character of this species. Panshin (1932) only described the structure of sclereids in transverse section, and pointed out the scattering distribution of sclereids in disorganized phloem tissue. The present study further revealed that sclereid bands were composed of tightly packed sclereids with diverse shapes and sizes to form a blockage of pure sclereids except in the parts connected to some rays where a few parenchyma cells still remained. Furthermore, branch bands of different lengths and angles from concentric sclereid bands were also found to extend into parenchyma, but no sclereids were observed in disorganized phloem tissue. Sclereids scattered in phloem cavity designated by Panshin (1932) are possibly the artifacts due to the process of sectioning. In addition to parenchyma within xylem tracts, there were also parenchyma attached to both the inside and the outside of xylem tract. The present study further showed their differences in structure. The inside parenchyma cells were almost isometric, but the outside ones longitudinally elongated. Besides

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TABLE 1. Comparisons in quantitative characters of some cambial derivatives among mangrove species distributed in different regions

Source	*Bruguiera gymnorrhiza*						*Rhizophora stylosa*	
	Present study	van Vliet (1976) Borneo	Australia	Philippines	East Africa	Janssonius (1950) Java	Present study	van Vliet (1976) Indonesia
Vessel element								
Tangential diameter (μm)	45–150 (98.8)*	71–122 (91)	75–110 (91)	63–110(97)	63–93 (80)	55–120	30–140 (92.7)	63–92 (74)
Density (/mm^2)	9–35 (17.2)	27–43 (34)	6–21 (17)	22–33(27)	23–46 (33)	(25)	17–78 (40.4)	15–19 (17)
Length (μm)	245–1210 (717.4)	660–1660 (1110)	920–1470 (1190)		630–1210 (930)		310–1040 (678.1)	320–840 (620)
Solitary rate (%)	6.7–66.7 (32.1)						3.3–25.7 (9.5)	
Bar number	3.5–16 (8.3)	8–14 (11)	8–15 (11)		6–13 (11)		3–9 (5.2)	4–8 (6)
Ray								
Height (μm)	550–4875 (2004.3)						110–5400 (1797.8)	
Width (μm)	35–210 (88.3)						20–100 (61.2)	
Density (/mm^2)							6–22 (10.5)	
Fiber								
Length (μm)	460–2330 (1178.1)	1290–2200 (1790)	1530–2160 (1810)		740–1630 (1290)		620–2470 (1270.8)	1020–1680 (1450)
Diameter (μm)	15.7–40 (27.4)						15–32.5 (25.2)	
Wall thickness (μm)	5–12.5 (8.8)						5–13.8 (9.9)	

*Number in parentheses indicates mean value or its range

TABLE 1. (continued)

Source	*Kandelia candel*			*Sonneratia alba*			*Avicennia marina*		
	Present study	van Vliet (1976) Malaya	Cheng (1992) China	Present study	Rao (1987) India	van Vliet (1984)	Present study	Krishnamurthy India (1987)	Panshin (1932) Philippines
Vessel element									
Tangential diameter (μm)	32–91.2 (64.7)	36–78 (52–62)		45–135 (85.3)	(95)	(120–160)	22.5–92.5 (65.4)	45–70 (50)	
Density (/mm^2)	26–99 (48.3)	23–42 (27–35)		41–87 (59.9)	(37)		17–78 (35.2)	30–70 (50)	
Length (μm)	230–500 (411.1)	230–670 (470–550)	340–700 (495)	190–700 (395.3)	(650)	(400–500)	122.5–387.5 (266.0)	125–395 (260)	170–350
Solitary rate (%)	1.9–30.6 (11.4)	22–66		14.5–44.6 (30.5)			9.5	34	
Bar number	4–9 (6.6)	4–11 (7)	(6–11)						
Ray									
Height (μm)	120–3400 (1104.2)		45–1617 (655–1361)	55–432.5 (203.6)			85–920 (338.5)	115–785 (355)	100–1200
Width (μm)	15–225 (97.2)		15–124 (81–95)				5–50 (21.4)	10–50 (25)	
Density (/mm^2)	7–19 (11.2)			67–140 (99.5)	(18)		47–76 (58.2)	40–55 (45)	
Fiber									
Length (μm)	520–1620 (859.0)	820–1230 (1040–1080)	780–1400 (1126)	330–1300 (696.1)			300–1130 (715.3)	520–900 (735)	700–1200
Diameter (μm)	15–41.3 (26.0)		(15–25)	12.5–30 (21.3)			12.5–28.8 (20.8)		20–24
Wall thickness (μm)	5–10 (6.1)			1.25–5 (3.1)			2.5–10 (5.7)		4–5

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libriform fibers, the only fiber type found in the Indian and Philippine plants, fiber–tracheids were also present, and septa were common in the plants of Iriomote Island. Rhomboidal crystals were observed in both axial parenchyma and rays of the plants from Iriomote Island, but they were reported only in rays of the philippine plants; crystals were absent in the Indian plants.

The plants from Iriomote Island also differed from those of the two lower latitudinal regions in quantitative characters of some cambial derivatives (Table 1). They generally had a tendency to vary in a greater range. Besides, vessels in plants from Iriomote Island had a larger diameter but lower density, although average vessel element length was almost the same as the Indian plants. As regards ray tissue, the plants from Iriomote Island exhibited much more quantity per unit area but smaller individual rays at average. Fibers were a little shorter in the plants from Iriomote Island than in those from the lower latitudes.

Conclusions

The five mangrove species investigated in this paper are essentially restricted to tropical regions of the Eastern Hemisphere: i.e., Australia, the Western Pacific, East Africa, India, Southeast Asia (Field, 1991; Lin, 1997; Tomlinson, 1994). However, they do not completely occur in the same regions and have different ranges of distribution. Iriomote Island of Japan is a high latitudinal region for mangrove distribution, and is also the northernmost or close to northern distribution limits for the five species. The comparisons in this present paper revealed that significant differences existed in both qualitative and quantitative characters of wood structure between plants of each species growing in lower latitudes (the Tropics) and those growing in higher latitudes (Iriomote Island in the Subtropics). They can be summarized as the following three aspects.

First, the plants from Iriomote Island had a few structural characters which were not reported in the plants from lower latitudes, such as short and wide vessel elements as in *Bruguiera gymnorrhiza*, vascular tracheids as in *Rhizophora stylosa*, septate fibers as in *Kandelia candel*, heterocellular rays as in *Sonneratia alba*, and fine structure of sclereid bands as in *Avicennia marina*. It is uncertain whether these structural characters are restricted to plants from Iriomote Island as well as to plants growing at higher latitudes, but at least this fact indicates that we require correction of our understanding of wood structure of mangroves. Also a more detailed investigation on plants growing from lower latitudes is still needed to confirm whether those structural characters are present or not.

Second, the plants from Iriomote Island showed distinctive differences from those of lower latitudes in some other structural characters, such as vessel–ray and vessel–parenchyma pitting (bordered vs. simple or half–bordered) as in *Bruguiera gymnorrhiza*, vessel arrangement (usually in short radial multiples of 2–3 vs. solitary) as in *Rhizophora stylosa*, and perforation (always simple vs. diverse) as in *Sonneratia alba*. These structural characters in plants from Iriomote Island might represent their adaptations in wood

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structure to a distinct environment at higher latitudes.

Third, a few quantitative characters related to cambial activities showed interesting differences between the plants from Iriomote Island and those from tropical regions. For instance, with the exception of vessel element length of *Rhizophora stylosa*, the plants from Iriomote Island tended to decrease average length of both vessel elements and fibers but to increase vessel diameter. The length of vessel elements is considered as a relatively exact indicator of the length of fusiform initials of vascular cambium (Bailey, 1920; Metcalfe and Chalk, 1983), and fiber length is also confirmed to be proportionally related to the length of fusiform initials (Spurr and Hyvärinen, 1954). Thus it seems likely that the mangroves have a tendency to shorten the length of fusiform initials at the regions of higher latitudes. In contrast, the plants from Iriomote Island had larger vessel diameter. Large vessels are certainly beneficial to a higher efficiency for water conduction. However, the enlargement of vessels in diameter make themselves to become weaker in resistance to collapse under high negative pressure in xylem of mangroves. Thus, through the shortening of vessel elements, vessels can improve mechanical strength so as to compensate themselves for disadvantages caused by enlargement of vessels. Thus, the quantitative character modifications, which were found in vessels of mangrove species in higher latitude, seem to reflect ecological evolution of xylem. However, an extensive investigation on tropical plants is still necessary prior to a final conclusion of this aspect.

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摘　　要

孫強・鈴木三男：マングローブ樹木の木材構造とその高緯度への適応形態

琉球列島から九州にかけては熱帯性のマングローブ樹木がもっとも高緯度まで生育している地域のひとつで，太平洋における分布北限地となっている。しかし，日本産の試料に基づいた木材構造の報告はこれまでにない。本研究ではこれらのマングローブ樹木の木材構造を記載し，同一種の熱帯域の標本に基づいた記載と比較して高緯度への適応形態を明らかにすることを試みた。材料は沖縄県西表島産のオヒルギ *Bruguiera gymnorrhiza*（ヒルギ科），ヤエヤマヒルギ *Rhizophora stylosa*（ヒルギ科），メヒルギ *Kandelia candel*（ヒルギ科），マヤプシキ *Sonneratia alba*（ハマザクロ科），ヒルギダマシ *Avicennia marina*（ヒルギダマシ科）の5種で，いずれも自生地で幹の部分の円盤を切り取り，切片を作成するとともに組織を解離して光学顕微鏡で観察，計測した。その結果，我々の試料は熱帯域の標本で記載された木材構造とは，次の3つの点で異なっていた。第1に，オヒルギの太くて極端に短い道管要素，ヤエヤマヒルギの道管状仮道管，メヒルギの隔壁木繊維，マヤプシキの異形放射組織，ヒルギダマシの厚壁組織の微細構造など，これまでの報告には記載されていない構造が明らかになった。第2に，オヒルギの道管–柔細胞間壁孔，ヤエヤマヒルギの道管配列，メヒルギのゼラチン繊維，マヤプシキの道管穿孔，ヒルギダマシの隔壁木繊維などについての我々の観察結果はこれまでに記載されたものとは異なっていた。第3に，西表島の試料では既報告に比べて総体的に道管要素及び繊維が短く，道管直径が大きくなるなど，形質に数量的な違いが認められた。

このような定性的及び定量的な形質の違いの原因は，ひとつにはこれまでの報告の記載内容が不十分であることに基づくものであり，他方には日本のマングローブ樹木が緯度の高い地域へ適応した形態を持っていることによる考えられた.

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