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ORIGINAL ARTICLE

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Quantitative character variations of cambial derivatives in mangroves and their functional significance

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Abstract Quantitative character variations of xylem cambial derivatives during secondary growth of the trunk are described for five representative mangrove species: *Rhizophora stylosa* (Rhizophoraceae), *Bruguiera gymnorrhiza* (Rhizophoraceae), *Kandelia candel* (Rhizophoraceae), *Sonneratia alba* (Sonneratiaceae) and *Avicennia marina* (Avicenniaceae). Two variation patterns in tracheary element length were revealed among these species. For *R. stylosa*, *A. marina* and *S. alba*, both vessel elements and fibers showed an increase in length during the early stages of secondary growth, then tended to be constant in later growth. In the other two species, little change occurred in the length of either vessel elements or fibers throughout the thickening growth period. Variation patterns in tracheary element length appeared to correspond with the different mangrove species' adaptations to their habitats. In addition, these five species exhibited diverse variation patterns in quantitative characters of the rays as well as in other quantitative characters of the vessels and fibers during secondary growth of their trunk.

Keywords Quantitative character variations · Xylem cambial derivatives · Secondary growth of trunk · Mechanical and conductive adaptations · Mangroves

Introduction

Mangroves are communities of woody plants growing naturally in littoral habitats. Tidal forces, strong winds, frequent inundation and high soil salinity are among the major features of mangrove habitats. Most mangrove species have sturdy trunk wood, which plays an important role in supporting the plant against tidal forces and strong winds, and thus is a key factor for mangrove establishment in intertidal habitats. Because of its importance, there have been many investigations of mangrove trunk wood in an attempt to clarify the relationships between its structural characteristics and its functions (water conduction and mechanical support). Research on mangrove wood structure has always been a major topic including not only general comparative or systematic investigations on diverse mangrove genera or families (e.g., Panshin 1932; Marco 1935; Janssonius 1950; van Vliet 1976; Sun and Suzuki 2000) but also more detailed studies on selected species or genera (e.g., Zamski 1979; van Vliet and Baas 1984; Krishnamurthy and Sigamani 1987; Rao et al. 1987; Sun and Lin 1997). Many of the adaptive characters of mangrove wood structure have thus been revealed after the analyses and comparisons of the relationships between wood structure and habitat (e.g., Janssonius 1950; van Vliet 1976; Tomlinson 1994; Sun and Suzuki 2000).

However, the above-mentioned research has been restricted mainly to the general wood structure of mangrove species and the ecological adaptations of their trunk wood as a whole. As with terrestrial woody species, the trunk wood of mangroves is formed by the gradual accumulation of secondary xylem. Therefore, with regard to an adult tree, the different parts of its trunk wood, from the central part of the wood outwards, represent the structure formed at different developmental stages of growth. However, the presence and extent of any change in the anatomical characters of trunk wood at different growth stages of mangroves remain unknown.

Five representative mangrove species were selected for this research purpose, i.e., *Rhizophora stylosa* Griff., *Bruguiera gymnorrhiza* (L.) Lamk., *Kandelia candel* (L.) Druce, *Sonneratia alba* J. Smith and *Avicennia marina* (Frosk.) Vierh. In a previous paper (Sun and Suzuki 2000), we examined their wood structure with respect to

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differences in qualitative characters in different regions of trunk wood. The present work is a detailed investigation of quantitative character variations of their xylem cambial derivatives (i.e., vessel element length, tangential diameter, density, solitary vessel ratio and bar number per perforation plate of vessels; height, width and density of rays; length, diameter and wall thickness of fibers) during trunk thickening. On this basis, a comparison of the variation patterns of these quantitative characters was made among the five species to reveal any interspecific difference and its functional significance. The functions of trunk wood depend fundamentally on the anatomical characters of individual cambial derivatives. Therefore, the present work is relevant to analyzing how, throughout their life, individual mangrove plants have gradually modified their stem structure to adapt to their habitat.

Materials and methods

Wood samples were taken from trunk wood of adult trees of five mangrove species, i.e., *R. stylosa*, *B. gymnorrhiza*, *K. candel*, *S. alba* and *A. marina*, which grow naturally in Iriomote Island, Yaeyama, Okinawa Prefecture, Japan. The sampled trees for *R. stylosa*, *S. alba* and *A. marina* were sparsely established in seaward outer fringes of mangrove forests, flooded by all high tides and strongly influenced by strong winds and tidal forces, while those for *B. gymnorrhiza* and *K. candel* grow in more landward parts of the forests, were inundated only at spring high tides and much less influenced by strong winds and tidal forces. Although these sampled trees are different in height and trunk diameter, they have almost reached maximum trunk thickening for these species in this latitudinal region and in the investigated forests. Also since there are no distinct annual ring boundaries in the trunk wood, their exact age is unknown, so quantitative characters of cambial derivatives were investigated from the central wood outwards, attempting to elucidate their patterns of variation during secondary growth of the trunk. One sample disc of about 5 cm in thickness for each species was cut from a trunk 20 cm above the surface of the ground and preserved in 50% ethanol. The related details for research samples and their habitats are summarized in Table 1.

The samples were prepared using methods of both sectioning and maceration. For sectioning, a rectangular block, with radius length in the radial direction and 20 mm in both tangential and longitudinal directions, was cut from the center to the seaward region of each sample disc. From this, a series of cubic blocks with about 20 mm in radial direction were cut consecutively from the inner face outwards. Each block was softened in boiling water, then sectioned in transverse and radial directions with a sliding microtome. Tangential sections were also made at 4 to 10 mm intervals radially from the central wood outwards. All the sections were cut at a thickness of 15–20 μm, stained with safranin and fast green, dehydrated through an ethanol series, then permanently mounted on slides for microscopic observations and measurements.

For maceration studies, another rectangular radial block, the same size as for sectioning except only 4–5 mm wide in a tangential direction, was cut from the same sample disc next to the material for sectioning. Several sections 4–5 mm wide in radial direction were then removed for maceration at intervals of 4–10 mm along the radius of block from the innermost parts of secondary xylem outwards. These materials were trimmed into slivers thinner than a toothpick and macerated at 60°C for 36 h in an aqueous solution containing equal parts of glacial acetic acid and 6% hydrogen peroxide. They were then washed in distilled water, stained in safranin and prepared as temporary mounts for observation and quantitative character measurement under a light microscope.

In order to analyze the quantitative character variations of xylem cambial derivatives during thickening growth of the trunk, vessels, fibers and rays were all included in the investigation. Their quantitative characters were measured or calculated from several regions along the radius. The related values for the tangential diameter, vessel element length, bar number of vessels, for the length, diameter and wall thickness of fibers, and for the width and height of rays were based on 30 random measurements, while those for vessel density, solitary vessel ratio (proportion of solitary vessel number to total vessel number) and ray density were measured and calculated on 10 fields of view selected at random. All the values were represented as means with standard deviation and graphs were drawn with a computer program (DeltaGraph Pro 3). Fisher's test was also performed by statistical software (StatView 4.5) to test for any significant difference in quantitative characters of their cambial derivatives among different regions from the central wood outwards.

Results

Variation patterns of quantitative characters of xylem cambial derivatives for these five mangrove species during thickening growth of the trunk are illustrated. Micrographs of secondary xylem and macerated vessel elements show wood structure and changes in some quantitative characters in different regions of wood. The detailed description of their wood structure can be found in Sun and Suzuki (2000).

Table 1 Sizes of sampled trees and their habitats in Iriomote Island, Yaeyama, Okinawa Prefecture

Item	*Rhizophora stylosa*	*Bruguiera gymnorrhiza*	*Kandelia candel*	*Sonneratia alba*	*Avicennia marina*
Height of plant body (m)	5	5.5	3	5	4.5
Diameter of trunk at the height of 20 cm above the ground level (cm)	9	13	10	20	8
Habitat	Outer fringe, frequently inundated	Inward part, less inundated	Inward part, less inundated	Outer fringe, frequently inundated	Outer fringe, frequently inundated
Location	Funaura estuary (24°24′N; 123°49′E)			Shiiragawa estuary (24°19′N; 123°55′E)	

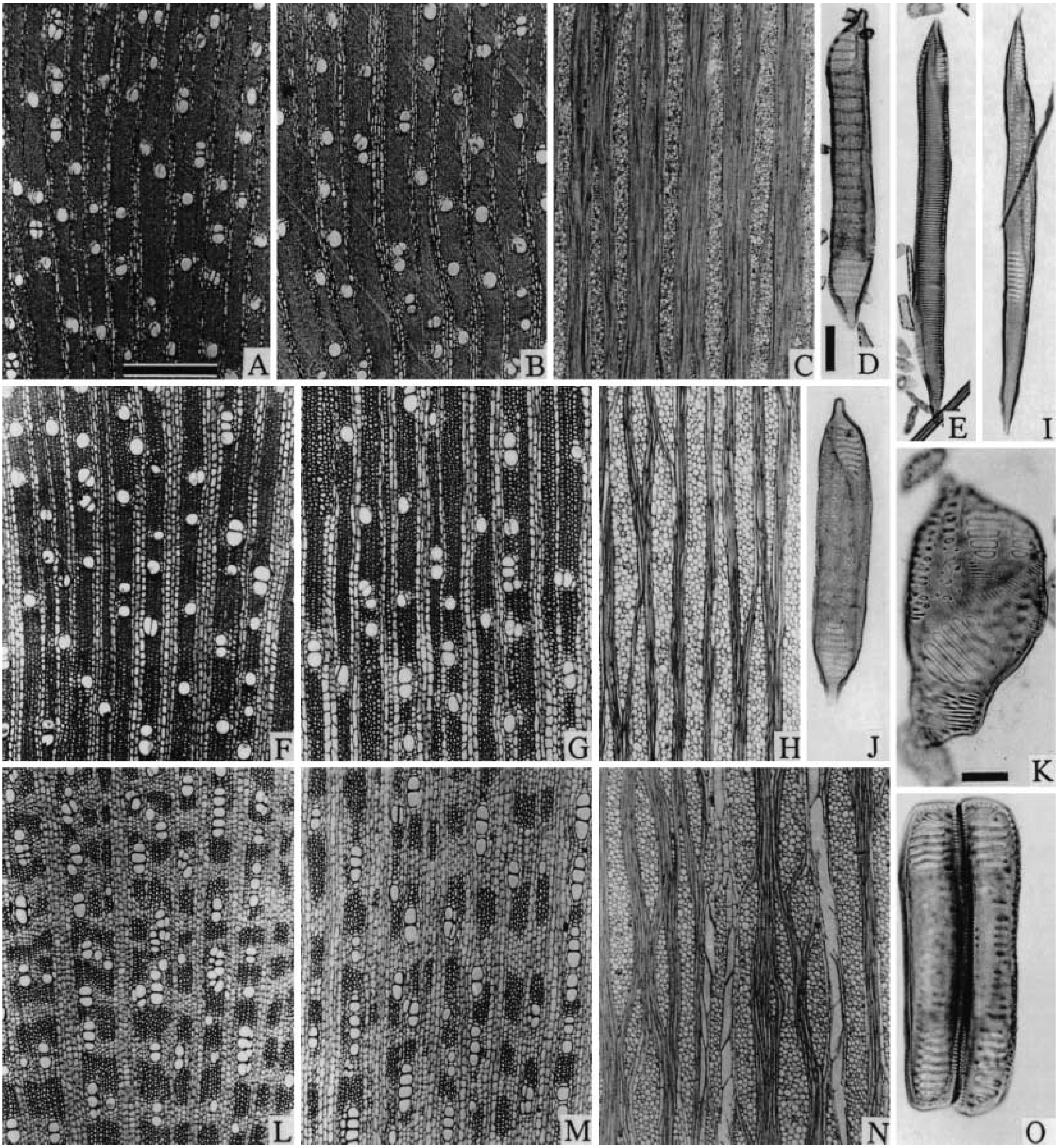

Fig. 1A–O Light micrographs of wood structure and macerated vessel elements in three mangrove species. **A–E** *Rhizophora stylosa*, showing higher vessel density in inner wood (**A**) than in outer wood (**B**); rays (**C**) and vessel elements common in inner (**D**) and outer wood (**E**). **F–K** *Bruguiera gymnorrhiza*, showing higher vessel density and solitary vessel ratio in inner wood (**F**) than in outer wood (**G**); rays (**H**) and vessel elements of three dimensions (**I–K**). **L–O** *Kandelia candel*, showing higher vessel density in inner wood (**L**) than in outer wood (**M**); rays (**N**) and vessel elements (**O**). Scale bar in **A** is 500 μm and also for **B, C, F–H** and **L–N**; scale bar in **D** is 100 μm and also for **E, I** and **J**; and scale bar in **K** is 50 μm, also for **O**

Rhizophora stylosa

This species exhibited diverse patterns in quantitative character variation of cambial derivatives during secondary growth (Fig. 2). Tangential vessel diameter (Fig. 2A) and bar number per perforation plate (Fig. 2C) increased only during the early accumulation of secondary xylem, and remained constant in later growth, although the increase in bar number was slight. Vessel element length (Figs. 1D, E, 2A) first increased gradually for a long period and then became constant in the outer wood. Vessel

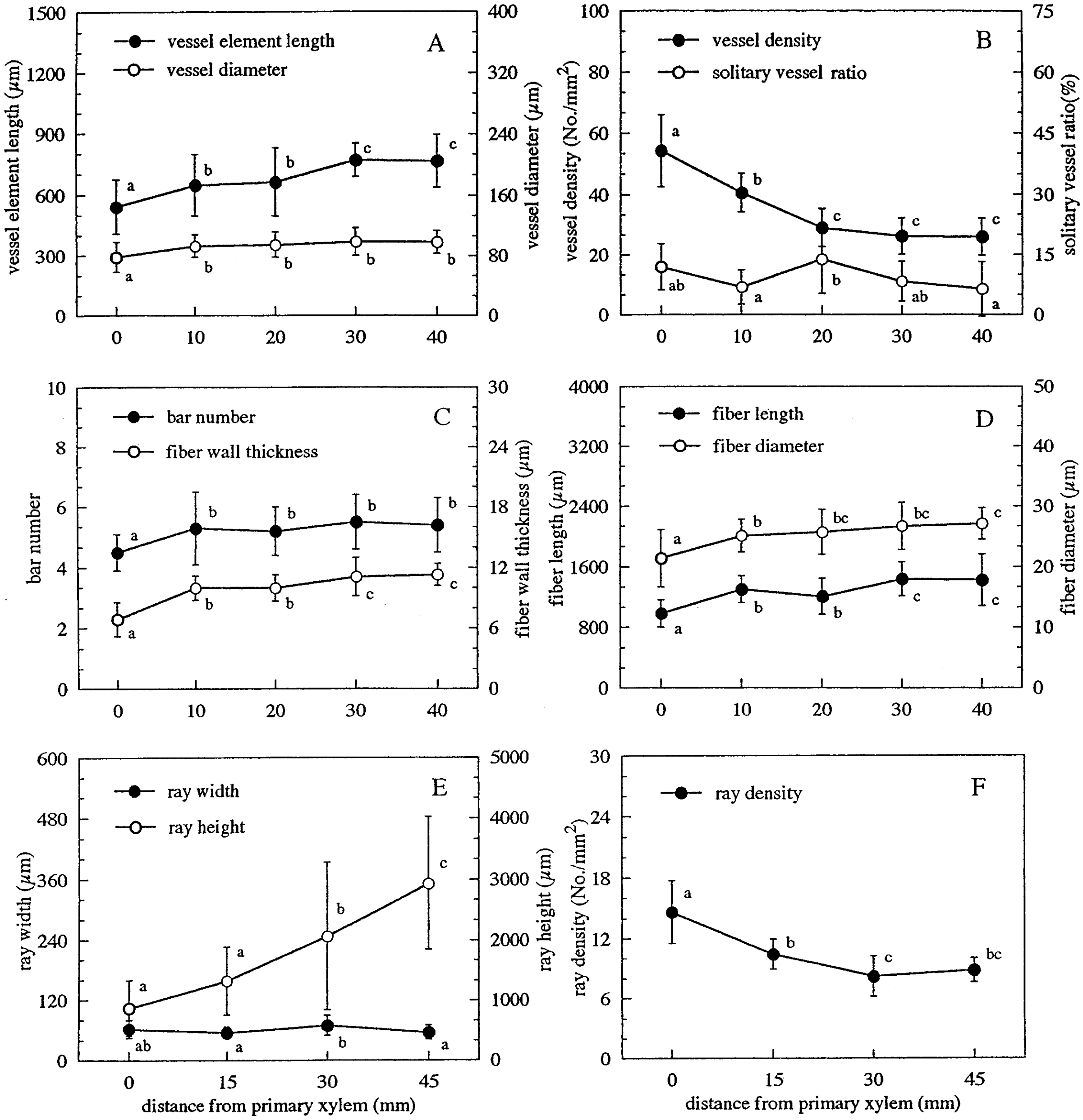

Fig. 2A–F Quantitative character variations of cambial derivatives in *Rhizophora stylosa*. **A, B** Vessels. **C** Vessels and fibers. **D** Fibers. **E, F** Rays. Results are means ± SD. Different letters within the same character indicate significant difference at 5% level (Fisher's test)

density (Figs. 1A, B, 2B) decreased sharply after the initiation of secondary growth, down to a minimum value in the middle wood, which was maintained in the outer wood. Solitary vessel ratio was more or less constant throughout growth (Fig. 2B). Fiber length (Fig. 2D), diameter (Fig. 2D) and wall thickness (Fig. 2C) all showed an obvious increase during the early accumulation of secondary xylem and then a slow increase in the middle wood. They finally became relatively constant in the outer wood. In rays (Fig. 1C), their height (Fig. 2E) increased almost linearly with trunk thickness, but their density (Fig. 2F) decreased in the early stages, then tended to be constant in later growth. Ray width remained more or less constant throughout the whole growth period (Fig. 2E).

Bruguiera gymnorrhiza

This species differed from *R. stylosa* in variation patterns of many quantitative characters of xylem cambial derivatives (Fig. 3). Vessel diameter (Fig. 3A), vessel element length (Figs. 1I–K) and bar number (Fig. 3C) were more or less constant during secondary growth of the trunk despite a little fluctuation in all cases. Vessel density and solitary vessel ratio first decreased, then tended to be constant in later growth (Figs. 1F, G, 3B). Fiber length (Fig. 3D), diameter (Fig. 3D) and wall thickness (Fig. 3E) all remained unchanged or relatively constant in the process of secondary xylem accumulation. In rays

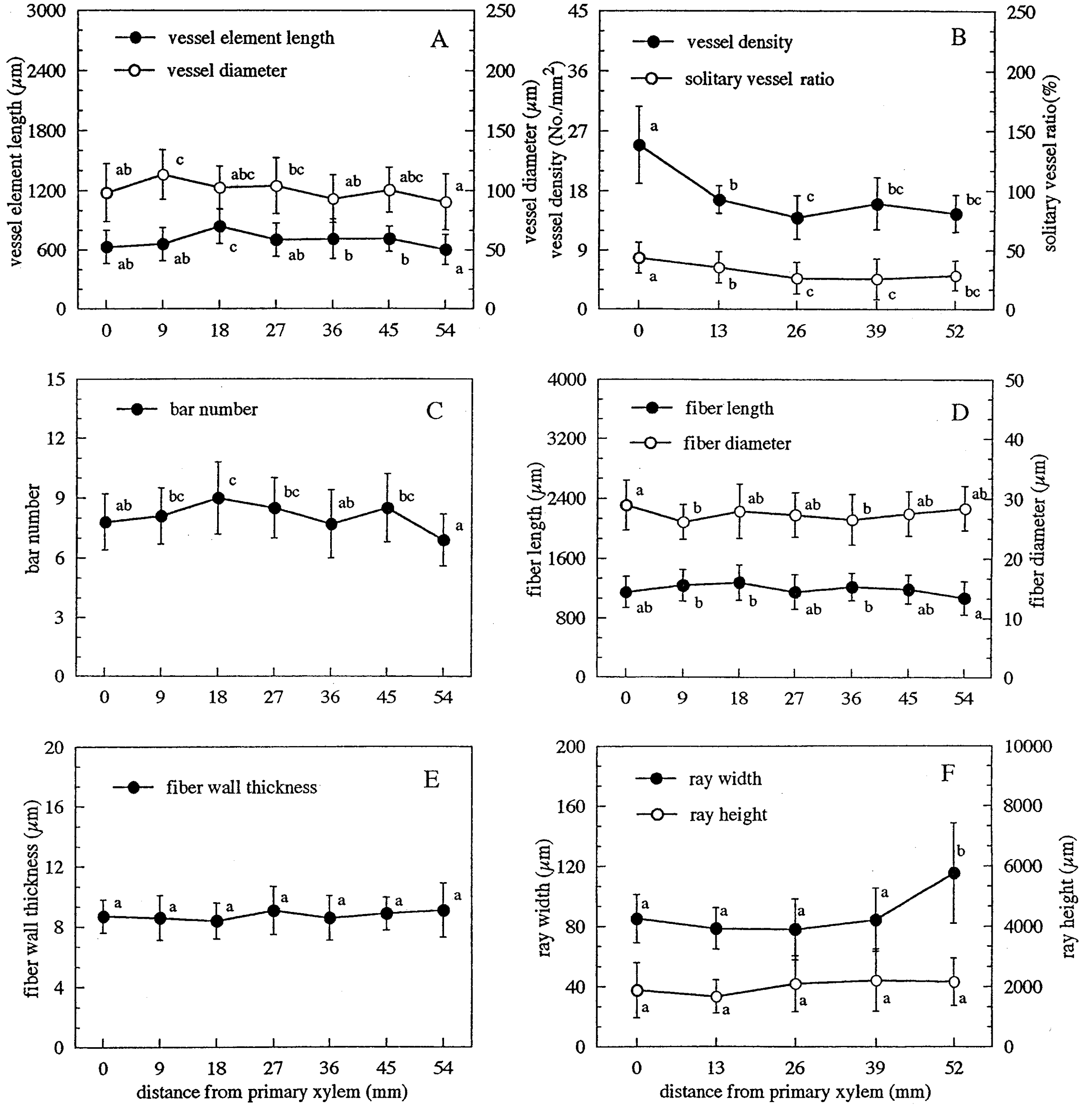

Fig. 3A–F Quantitative character variations of cambial derivatives in *Bruguiera gymnorrhiza*. **A–C** Vessels. **D, E** Fibers. **F** Rays. Results are means ± SD. Different letters within the same character indicate significant difference at 5% level (Fisher's test)

(Fig. 1H), both their height and width were constant throughout the growth period, but there was a sudden increase in ray width in the outermost wood (Fig. 3F).

Kandelia candel

This species showed similarities to *B. gymnorrhiza* in many quantitative characters of cambial derivatives (Fig. 4). Vessel element length (Fig. 4A) and bar number (Fig. 4C) remained constant throughout secondary growth of the trunk. Vessel diameter (Fig. 4A) was also constant throughout the growth period except for an increase at the beginning. Both vessel density (Fig. 1L, M) and solitary vessel ratio first decreased sharply, and then remained constant for solitary vessel ratio but increased to a small extent for vessel density in later growth (Fig. 4B). Fiber length (Fig. 4D) was more or less constant during growth despite slight fluctuations. Fiber diameter (Fig. 4D) increased in the early stages, and became constant afterwards, whereas fiber wall thickness (Fig. 4C) was relatively constant throughout the thickening growth period. Ray width (Fig. 4E) increased in the early stages, then tended to be more or less constant in later growth, whereas ray height (Fig. 4E) changed little

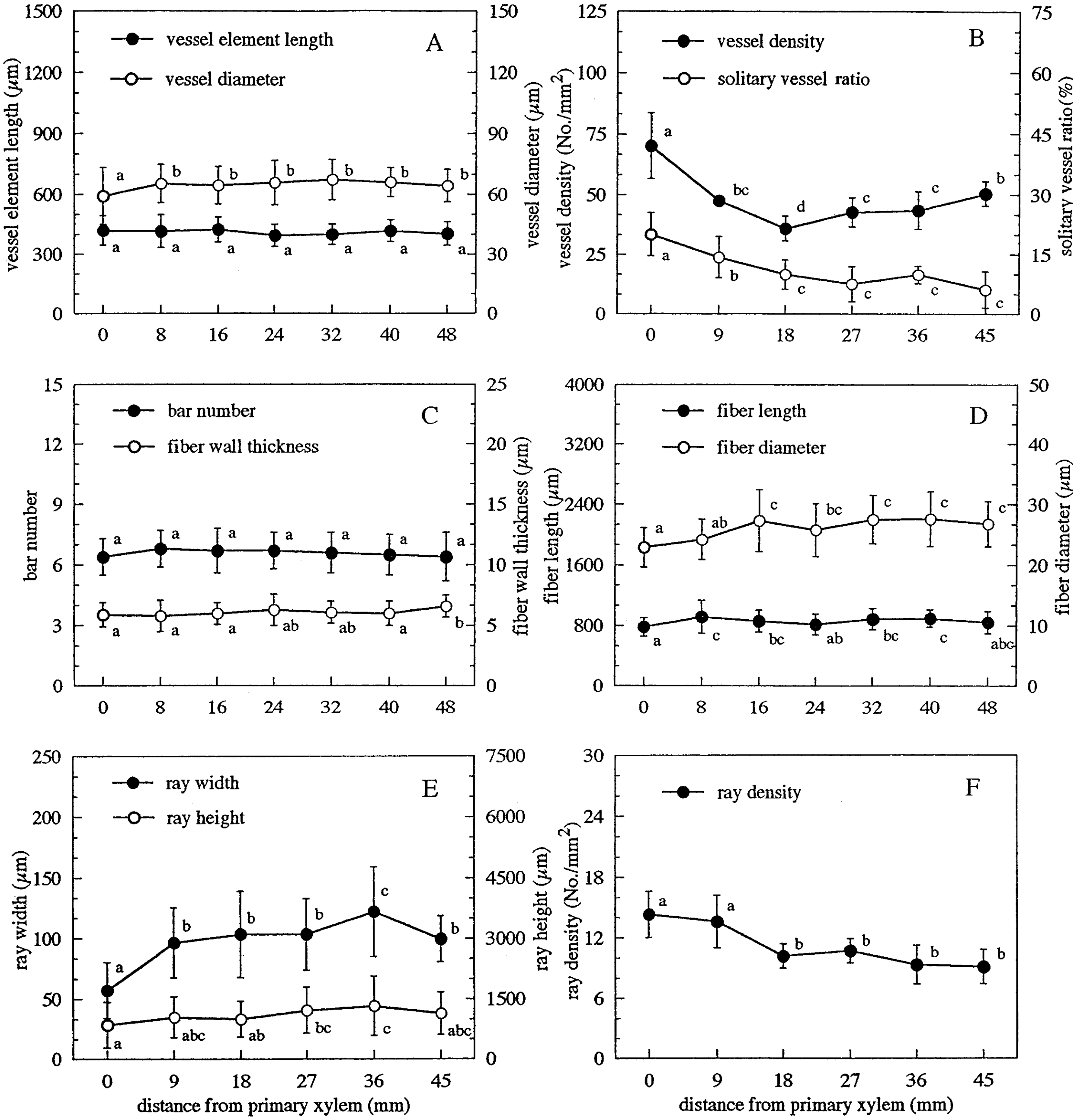

Fig. 4A–F Quantitative character variations of cambial derivatives in *Kandelia candel*. **A, B** Vessels. **C** Vessels and fibers. **D** Fibers. **E, F** Rays. Results are means ± SD. Different letters within the same character indicate significant difference at 5% level (Fisher's test)

during secondary growth despite a slight increase in the outer wood. Ray density (Fig. 4F) first decreased from a higher initial value, and then remained constant.

Sonneratia alba

Figure 5 illustrates the variation patterns of quantitative characters of cambial derivatives in this species. Both vessel element length and vessel diameter first increased for a relatively long period, and reached their maximum values in the outer wood despite a final drop towards the outermost wood (Figs. 5A, 6A, B). Solitary vessel ratio (Figs. 5B, 6A, B), in contrast, decreased sharply to a minimum in the middle wood, then increased again towards the outer wood. Vessel density (Figs. 5B, 6A, B) showed a steady decrease at first, then reached a constant value in later growth. Fiber length (Fig. 5C) gradually increased during early accumulation of secondary xylem, then remained constant in the outer wood despite a small decline in the region near the bark. Fiber diameter remained constant during the whole of secondary growth (Fig. 5C). Fiber wall thickness (Fig. 5D) was also constant in the inner wood, but then increased steadily in the outer wood. Rays of this species were predominantly

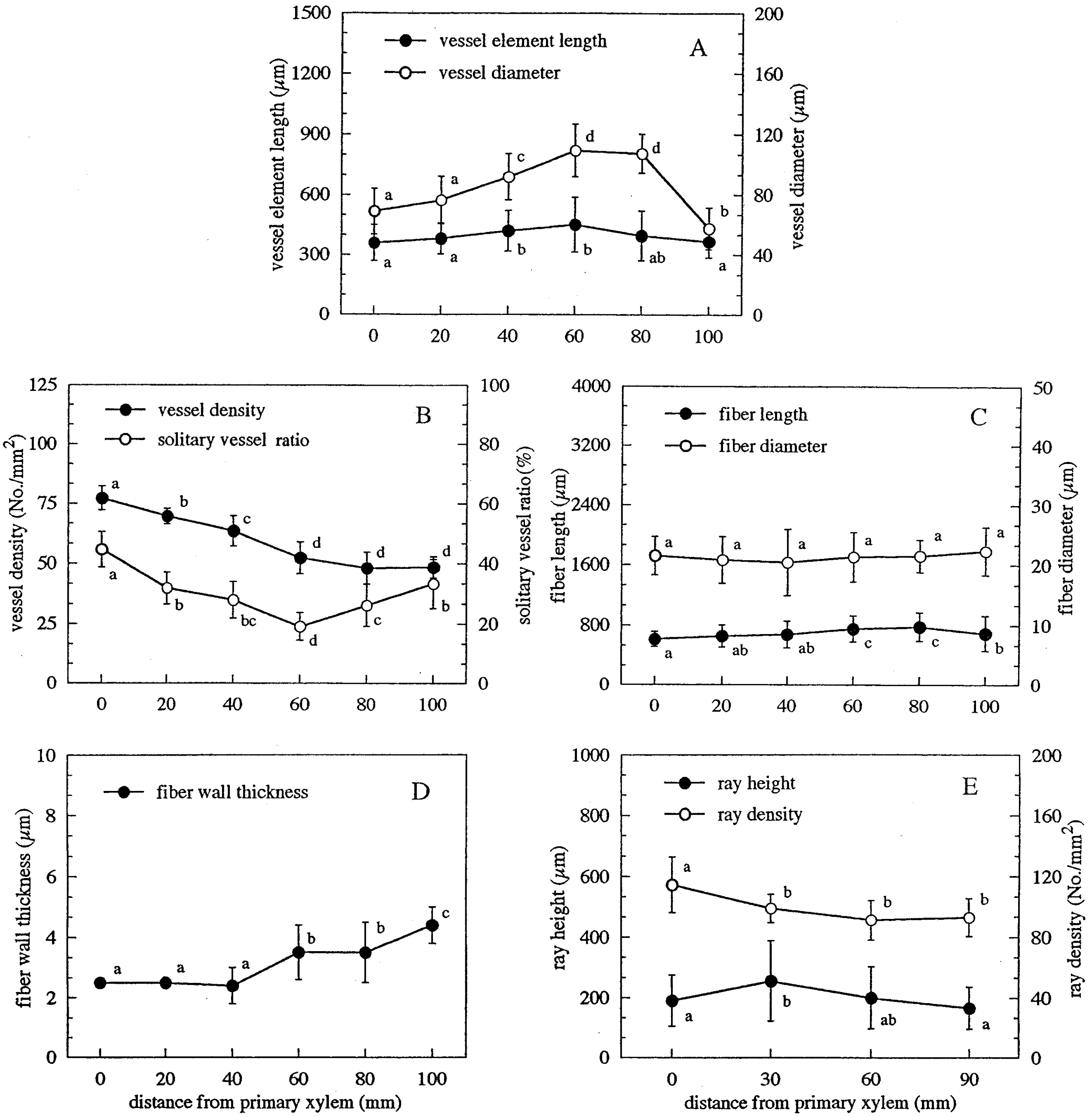

Fig. 5A–E Quantitative character variations of cambial derivatives in *Sonneratia alba*. **A, B** Vessels. **C, D** Fibers. **E** Rays. Results are means ± SD. Different letters within the same character indicate significant difference at 5% level (Fisher's test)

uniseriate (Fig. 6 C). Their density (Fig. 5E) decreased during the early accumulation of secondary xylem, then remained constant in later growth; whereas their height (Fig. 5E) was more or less constant during secondary growth of the trunk despite some fluctuation.

Avicennia marina

The thickening trunk growth in *Avicennia* results from the activity of several successive cambia (Zamski 1979; Tomlinson 1994; Sun and Suzuki 2000). Although individual concentric xylem bands were derived from different cambia (Fig. 6E, F), the quantitative character variations of their cambial derivatives also showed diverse patterns from the central part of trunk outwards (Fig. 7). In vessels, both vessel element length and vessel diameter gradually increased from the central wood outwards and then became constant in the outer secondary xylem (Fig. 7A), whereas vessel density (Figs. 6E, F, 7B) decreased sharply in the inner secondary xylem, and tended to be constant in the outer xylem tracts. Solitary vessel ratio (Fig. 7B) was generally inconstant at the different stages of secondary growth. Fiber length increased sharply from the central region of the trunk outwards, then tended to be constant in the outer secondary xylem

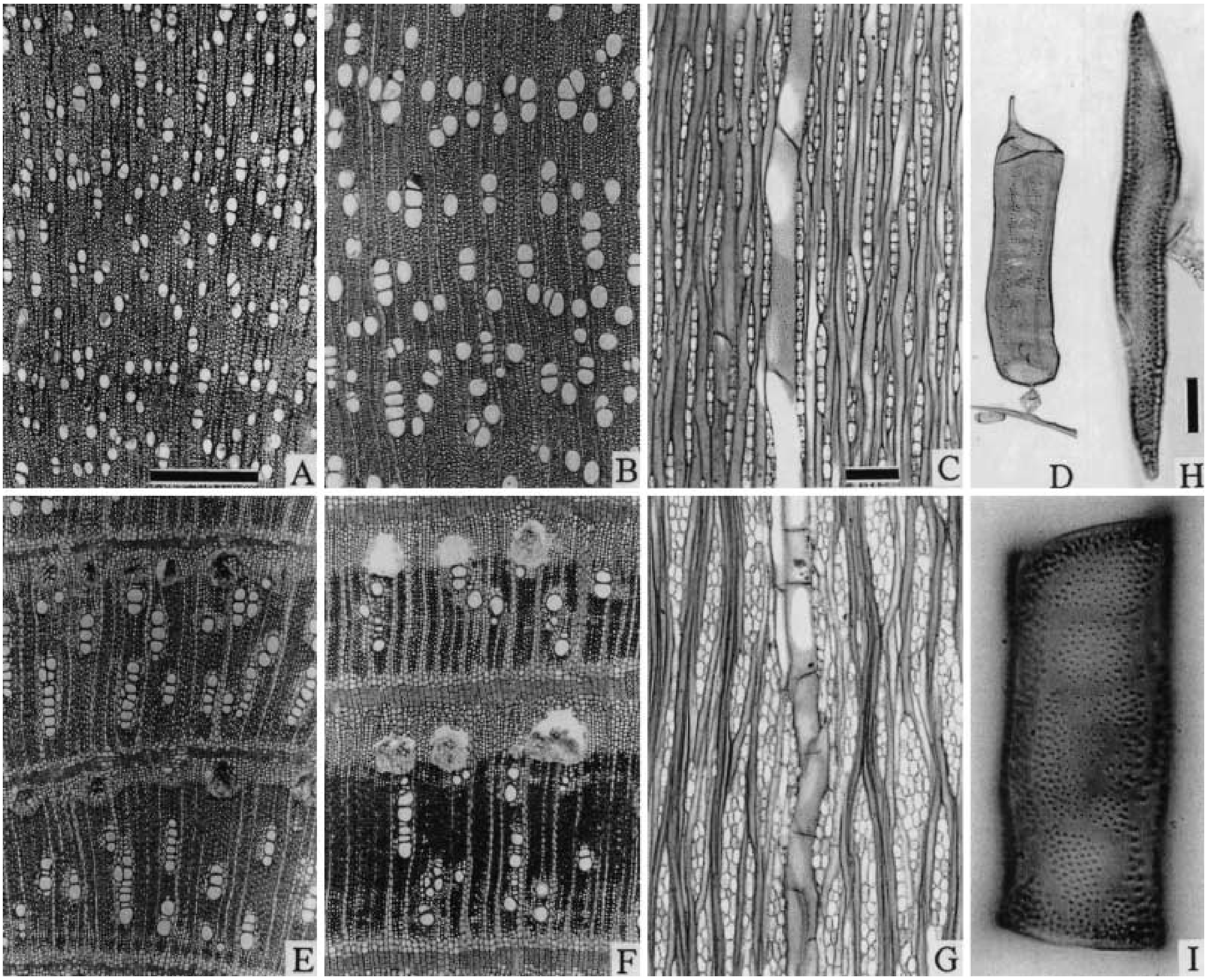

Fig. 6A–I Light micrographs of wood structure and macerated vessel elements in the other two species. **A–D** *Sonneratia alba*, showing higher vessel density, higher solitary vessel ratio and smaller vessels in inner wood (**A**) than in middle wood (**B**); predominantly uniseriate rays (**C**) and vessel element (**D**). **E–I** *Avicennia marina*, showing higher vessel density in inner wood (**E**) than in outer wood (**F**), rays (**G**) and vessel elements of two dimensions (**H–I**). Scale bar in **A** is 500 µm and also for **B** and **E, F**; scale bar in **C** is 100 µm and also for **D** and **G**; and scale bar in **H** is 25 µm, also for **I**

(Fig. 7C). Both fiber diameter (Fig. 7C) and wall thickness (Fig. 7D) showed an obvious increase in the first-formed secondary xylem tracts, then remained constant afterwards. Both ray width and height remained more or less constant throughout trunk growth despite a slight fluctuation at some stages (Fig. 7E). Ray density (Fig. 7F) decreased rapidly in the inner secondary xylem but then became constant in the outer secondary xylem.

Discussion

Significance of length variation in tracheary elements during secondary growth of the trunk in mangrove species

The tracheary elements of the five mangrove species were investigated in the present paper to reveal variations in their length during trunk thickening. We found that there were two patterns of size variation of tracheary elements. In *R. stylosa*, *A. marina* and *S. alba*, both vessel elements and fibers increased in length during early accumulation of secondary xylem, remaining constant after a maximum value was reached (although a drop occurred in the outermost wood of *S. alba*). In *B. gymnorrhiza* and *K. candel*, however, both vessel element and fiber lengths remained relatively constant throughout the whole period of secondary growth.

Regarding length variation of tracheary elements during secondary trunk growth, there have been few studies in terrestrial woody plants. The earliest was Sanio's investigation (cited in Spurr and Hyvarinen 1954) into the length variation of tracheids in *Pinus sylvestris*. The

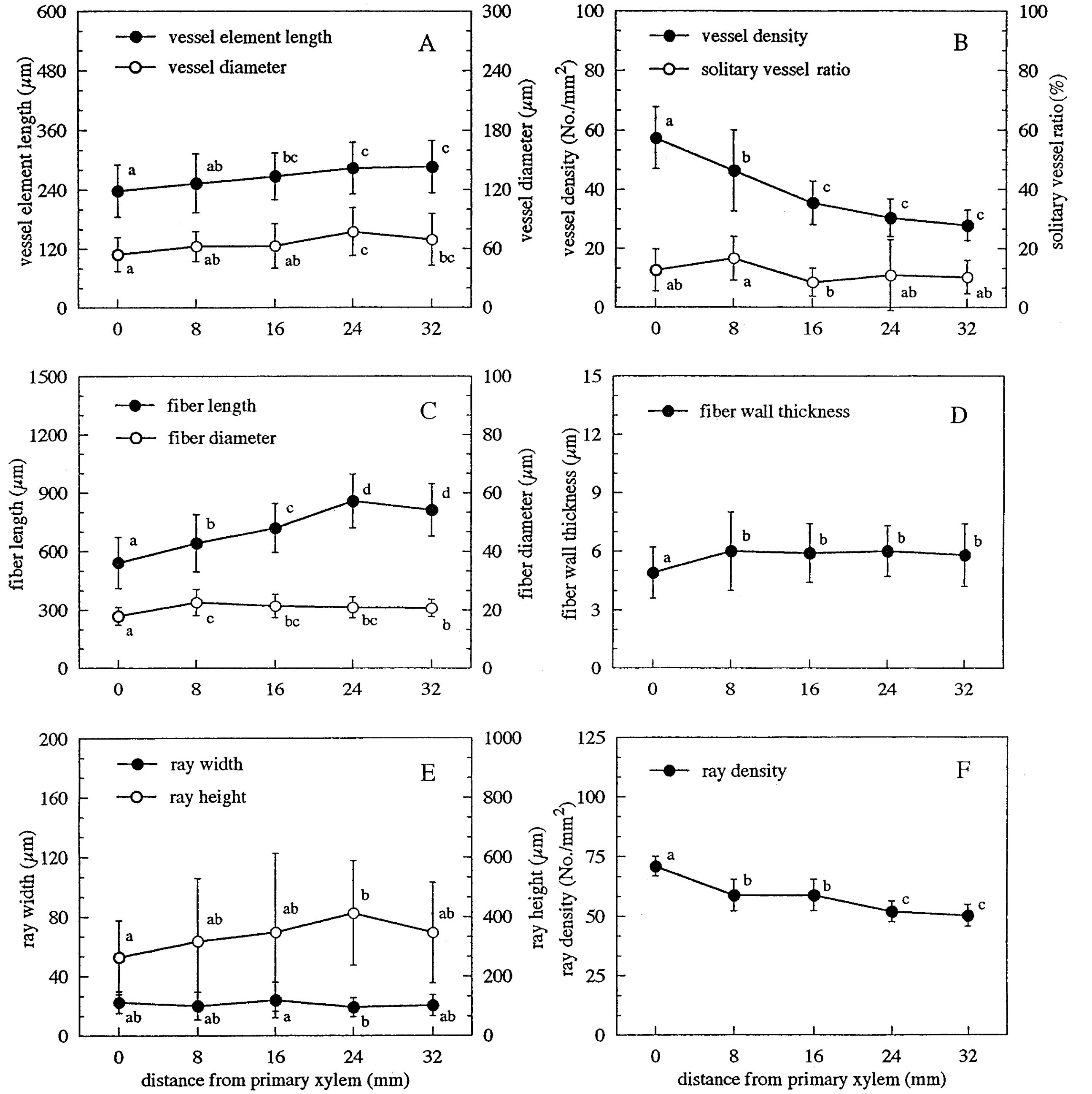

Fig. 7A–F Quantitative character variations of cambial derivatives in *Avicennia marina*. **A, B** Vessels. **C, D** Fibers. **E, F** Rays. Results are means ± SD. Different letters within the same character indicate significant difference at 5% level (Fisher's test)

famous length-on-age curve (Sanio curve) was then established, which indicated that tracheids generally increase in length from the central wood outwards, until a certain size is reached, after which they remain constant in the later stages of secondary growth. Later, the Sanio curve was also confirmed in many other terrestrial species (e.g., Bailey 1920, 1923; Bisset et al. 1951; Spurr and Hyvarinen 1954; Bannan and Bayly 1956; Dinwoodie 1961; Carlquist 1975, 1988; Baas 1976; Gartner 1995) and widely accepted as a common size variation pattern for tracheary elements in gymnosperms and typical woody dicotyledons with nonstoried wood, although some investigations on succulent plants and dicotyledon rosette shrubs showed deviations from the classic Sanio curve (Carlquist 1962, 1975, 1988; Mabberley 1974). However, in the present investigation of the five mangrove species, only the size variation pattern of tracheary elements in *R. stylosa*, *A. marina* and *S. alba* conformed to the Sanio curve, and that occurring in the other two species was clearly different from the Sanio curve.

The cause of the size variation pattern of tracheary elements during secondary growth of the trunk still remains unclear. Two well-known hypotheses have been proposed to provide an explanation. Philipson and Butterfield (1967) claimed that the size variation in tracheary elements should result from that occurring in cambial fusiform initials. They believed that frequency of pseudotransverse division of fusiform initials at the earlier stages of secondary growth, was fairly low and could not keep up with the need for an enlargement of cambium cylinder girth at a higher ratio. Thus, the daughter initial cells produced by pseudotransverse divisions elongated to overtake the mother initials in length. In this way, this increase in size of fusiform initials would lead to the increase in tracheary element length, as appeared in the Sanio curve. After some thickening growth had proceeded, pseudotransverse divisions in the cambial cylinder proceeded at a higher frequency compared to the need for the increase of cylinder girth during thickening growth. At this time, fusiform initials remained constant in length through the preferential loss of short initials. As a result, tracheary element length tended to be constant in the outer wood. This hypothesis provides a good explanation of the classical Sanio curve. However, it cannot explain the exceptions, in rosette plants for example, where the tracheary elements do not follow the above trend of size variation (Carlquist 1962). Also, this hypothesis cannot provide a plausible explanation for the deviation from the Sanio curve in *B. gymnorrhiza* and *K. candel*.

Carlquist (1962, 1975, 1988) also interpreted the cause of size variation of tracheary elements from the viewpoint of their functional significance during secondary trunk growth. He pointed out that any increase in the length of tracheary elements was related to the need for mechanical strength in plant body growth, and that if mechanical strength were of no selective value for plant growth, no increase in length or sometimes even a decrease might occur as secondary xylem accumulated. Thus, because of the need for mechanical support for growth of a young plant, the rapid increase of tracheary elements is an adaptive expression in wood structure; once enough mechanical strength is achieved from the accumulation of secondary xylem, tracheary element length is uniform in the later stages of plant growth. This hypothesis can also well explain the deviating curves of tracheary elements that occur in rosette trees and trees with phylogenetically secondary woodiness. Carlquist's interpretation still seems reasonable to explain diverse size variation patterns in different plant groups, although there are some different opinions (Mabberley 1974, 1982; Baas 1976).

We believe that the above-mentioned general principle of mechanical strength significance should also apply to mangrove species if we understand this principle in a broader sense. As we know, mangrove species grow in an intertidal zone whose major features include high temperature, high soil salinity, frequent inundation, and tidal forces and winds with wide fluctuations in strength. They are very different from common terrestrial plants in their habitat and adaptations. As there are interspecific differences along tidally maintained environmental gradients in the littoral zone, growth of the five species is influenced by different habitat factors (Tomlinson 1994; Field 1995). Therefore, it seems that satisfactory explanations of the size variation patterns of their tracheary elements must take account of the influences of habitat factors.

The five mangrove species investigated in this present study grow generally under two different habitat conditions. *R. stylosa*, *A. marina* and *S. alba* grow in habitats of high salinities, tidal forces and frequent inundation, and the samples for these species were collected from trees in the seaward outer fringe of the mangrove forest under the above habitat conditions. The characteristics of the trunk, as a major organ of mechanical support, determine whether or not a plant can become established and grow in this habitat. Tidal force, frequent inundation and strong winds on the fringe of the forest should be of selective value for developing mechanical strength in the trunk, especially for juvenile trees which have the weaker mechanical strength. Therefore, rapid elongation of cambial fusiform initials is necessary during the early stages of plant growth. This produces the observed increase in length of the tracheary elements during the early accumulation of secondary xylem, so as to meet the need for strengthening the mechanical support. After experiencing some thickening growth, mechanical support becomes sufficient due to adequate accumulation of xylem tissue, especially thick-walled fibers. Meanwhile, during this period, a number of stilt roots (*R. stylosa*) or cable roots (*S. alba* and *A. marina*) are formed to provide the trunk with additional mechanical strength while functioning to aerate the root system in the frequently inundated substrate. Thus, there seems to be no selective pressure for further increases in tracheary element length, so they remain constant during later thickening growth of the trunk.

The other two species, *B. gymnorrhiza* and *K. candel*, in the present study were collected from the inward part of the mangrove forest, where inundation was infrequent and the influences of tidal forces and strong winds were much weaker. Tracheary elements formed in the xylem had thick, lignified walls. It therefore seems that there is no selective pressure for improving mechanical strength throughout the whole growth process. This may be the major reason why tracheary elements remain relatively constant in size for these two species during the thickening growth of the trunk.

The above explanation for two size variation patterns of tracheary elements in the five mangrove species appears plausible. However, the real reasons for these variations in plant growth have not been clarified at present; further investigations are still required.

Significance of other quantitative character variations of xylem cambial derivatives

Apart from studies of the length variation of tracheary elements, there have been few investigations of other quantitative character variations of cambial derivatives, although some research on forestry has been conducted into such quantitative characters as vessel density, vessel diameter and axial parenchyma proportion, for analyzing the wood properties of commercial timbers (e.g., Lei et al. 1996; Hudson et al. 1998).

Up to now some research on other quantitative characters of vessels has shown that they generally increase in diameter during the thickening growth of the trunk until a maximum is reached (Metcalfe and Chalk 1983; Carlquist 1988). However, the variation pattern of vessel density requires verification, although it would be expected that a decrease in vessel density occurs as vessel diameter increases; but even here there are also some converse reports (Carlquist 1988). More information is also required concerning differences in vessel arrangement in different regions of the wood.

The diameters, densities and arrangement of vessels in the five mangrove species were also investigated in the present study. Concerning vessel diameter, the five species increased to different extents after the initiation of secondary growth, then became constant in later growth, although there was a decrease in the later stages in *S. alba*. Therefore, it is reasonable to assert that the variation pattern in vessel diameter for these mangrove species conforms to the above-mentioned trend. Vessel density in the five species all showed a sharp drop during early growth. Then, after a minimum value was reached, it tended to be constant in later growth, except for *K. candel* in which vessel density slightly increased again in the outer wood.

Thus, for these mangrove species, an increase in vessel diameter was accompanied by an overall decrease in vessel density. Increase in vessel diameter can improve the efficiency of water conduction to meet the increasing need for water in the developing crown. Decrease in vessel density also means that a greater proportion of fibers will be formed in later growth, augmenting mechanical strength. These variations in vessel diameter and density during plant growth are therefore well reconciled with the functions of mangrove trunks in terms of water conduction and mechanical strength. Regarding vessel arrangement, the results presented here revealed that solitary vessels remained a more or less constant ratio for *R. stylosa* and *A. marina* at every stage of trunk growth, but had higher proportions at early stages than in later growth for the other three species.

Regarding fibers, some researchers have indicated that both fiber diameter and wall thickness generally tend to increase from the central wood outwards (Metcalfe and Chalk 1983). However, the mangrove species investigated in the present study departed from this pattern. Fiber diameter showed no obvious changes in *B. gymnorrhiza* and *S. alba* during the whole thickening growth period, but in *K. candel* and *A. marina* fibers had a smaller diameter initially, increasing to a constant value in later growth. In *R. stylosa*, fiber diameter increased steadily as the trunk thickened. Fiber wall thickness remained constant at every stage of secondary growth for *B. gymnorrhiza* and *K. candel*, but increased steadily in *R. stylosa*. In *S. alba*, the fiber wall thickness was at first constant, but increased in the outer wood; whereas in *A. marina* it increased in the inner wood, then remained constant in the outer wood. Fiber dimensions have an important influence on mechanical support. An increase in fiber diameter with constant wall thickness means reduction in mechanical strength, while an increase in fiber wall thickness is believed to improve its mechanical strength. Although there were different variation patterns in the diameter and wall thickness of fibers in the five mangrove species of this study, changes in diameter during the thickening growth of trunk were generally accompanied by a change in the wall thickness. That is, fiber wall thickness increased as its diameter increased in *R. stylosa*, but fiber wall thickness remained fairly constant, as did its diameter in *B. gymnorrhiza*. This corresponding variation pattern for both the diameter and wall thickness generally occurred in the fibers of the other three species too.

Thus, for individual fibers, the five mangrove species could all remain relatively constant in mechanical strength despite differences in the variation patterns of their quantitative characters. Therefore, in addition to the variation patterns of fiber length described in the preceding paragraphs, these patterns in the diameter and wall thickness of individual fibers also suggest some significance for improving or maintaining mechanical strength of the trunk during its thickening growth.

There are also few previous data regarding variation in rays during the thickening growth. It is generally believed that there is little or no change in ray density (Metcalfe and Chalk 1983), but an increase in ray width, and an increase or decrease in ray height from the central wood outwards (Carlquist 1988). In the present study, the results indicate different variation patterns in the five mangrove species investigated. All five species showed an identical variation pattern in ray density, that is, ray density decreased at first, then became constant in the later stages of growth. Also, all the species maintained a more or less constant ray width as the trunk thickened, except for *K. candel* in which ray width increased at first and then tended to be constant. Ray height varied according to the species: *S. alba*, *A. marina* and *B. gymnorrhiza* maintained a more or less constant ray height throughout the thickening growth period; *K. candel* was a little lower initially, increasing slightly to remain relatively constant in later growth; and *R. stylosa* maintained a steady increase in ray height as the trunk thickened. Therefore, these mangrove species also exhibited very different variation patterns in both ray width and height.

Finally, we should point out that only parts of the stem radius, which represent some of the stages of thickening growth, were used in the investigation of the quantitative characters of cambial derivatives. These data allow us to analyze their variation during the whole thickening growth period. These points were joined together with straight lines (Figs. 2, 3, 4, 5, 7), but it does not mean that we can exactly know their value at any specific stage of growth based only on these straight lines.

In conclusion, five representative mangrove species were investigated to analyze quantitative character variations of vessels, fibers and rays during secondary growth of the trunk and their functional significance.

Length variation of tracheary elements (vessel elements and fibers) during the thickening growth of the trunk indicated two different patterns: for *R. stylosa*, *A. marina* and *S. alba* which grew in the outer seaward fringe of the mangrove forest, the tracheary element length increased at an early stage of secondary growth, and then tended to be constant after a maximum value was reached; while for *B. gymnorrhiza* and *K. candel* which grew in the inward part of the forest, it remained constant during the whole thickening growth of trunk wood. We considered that the increase in tracheary element length at an early stage of growth should improve mechanical strength for the seaward species, and that the constancy in tracheary element length during the whole growth of the trunk should be an indication of no selective pressure for the inward species improving their mechanical strength. Concerning vessel diameter and density, all these species showed an increase to different extents in vessel diameter but a decrease in vessel density during early secondary growth, and then tended to be constant in both vessel diameter and density in later growth, though there was a slight increase in vessel density again in outer wood of *K. candel* and a final decrease in vessel diameter of *S. alba*.

In addition to fiber length, fiber diameter and wall thickness also showed different variation patterns in the different species. In *R. stylosa*, fiber wall thickness increased as fiber diameter increased at first, but they all became constant in later growth. In *B. gymnorrhiza* both of them remained relatively constant, while in *A. marina* they initially showed an increase then became constant in later trunk growth. In *S. alba*, fiber wall thickness was constant at early stage and increased in later growth, but fiber diameter remained unchanged throughout the whole growth period. In *K. candel*, fiber diameter increased at first and then tended to be constant in later growth, but fiber wall thickness was relatively constant during thickening growth of the trunk. Fiber dimensions largely influence fiber mechanical strength. Despite diverse variation patterns in fiber dimensions of the different species, they suggest some significance in improving or maintaining the mechanical strength of the trunk during its thickening growth.

As for rays, all the five mangrove species first showed a decrease in ray density and then remained constant in later growth. Ray width also remained more or less constant during the whole of thickening growth in the five species except *K. candel* in which ray height increased at first and then became constant later. Ray height in the five species did not show any identical variation pattern. It remained more or less constant throughout thickening growth in *S. alba*, *A. marina* and *B. gymnorrhiza*, but showed a slight increase for a long period before a constant value was reached in *K. candel*, while in *R.stylosa* it showed a steady increase as the trunk thickened.

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