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ORIGINAL ARTICLE

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Asynchronous wood formation in young *Acacia mangium* planted in Malaysia

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Abstract In general, tropical trees have less-distinct growth rings. Even if the trees have some concentric structures, there is little information on the timing of their formation. The objective of this report is to show the asynchronous wood formation from the observation of indistinct, ring-like structures. Young *Acacia mangium* planted in Malaysia was investigated for asynchronous wood formation anatomically and macroscopically. Tree heights and girths at breast height for 28 trees were measured every other week. Wood disks from four trees were sampled at breast height for this research. The radial variation of vessel dimensions and the number of cambial cells in different radial directions and the wood anatomy of discontinuous bands were investigated using thin sectioning and soft radiographic methods. The vessel dimension was quite different in their radial variation even for four radial directions with a similar radius. There was a large variation in the number of cambial cells among radial directions in young *Acacia mangium*. Bands of low density included a layer of vessels aligned in a spiral rather than in a closed circle.

Key words *Acacia mangium* · Discontinuous band · Asynchronous wood formation · Spiral alignment of vessel

Introduction

Since the introduction of *Acacia mangium* into Sabah, Malaysia during the 1960s, it has been planted extensively in Southeast Asia because of its fast growth, good form, and the utilization potential of the wood.[1] The planting area, including hybrids with *Acacia auricuriformis*, is expected to increase.[2] Breeding, silviculture, and wood quality of *Acacia mangium* has been researched in many countries for timber utilization.[3–8] The growth increment has also been measured using a dendrometer.[3] There is a possibility that this species can be used in other research fields because of its widespread distribution. There are, however, few detailed reports on its anatomy.[1] Although discontinuous bands in the disk have been observed,[9] the distribution, anatomy, and formation of a concentric wood structure have not been described in detail. The present study investigated these characteristics using optical microscopy and soft X-ray methods to evaluate the asynchronous wood formation along the circumference and radius. Discontinuous bands seen during the present study have also been observed in other tropical species.[9–11] The results of the present study provide useful information on the formation of the discontinuous wood structure.

The objective of our research project was to investigate the characteristics of wood formation, such as ring formation, during the maturation process of *Acacia mangium*, a representative fast-growing species in tropical regions. The present report is included in the project and focuses on revealing the asynchronous wood formation in the young trees of this species. Wood anatomy during the maturation process, such as the appearance of interlocked grain, will be investigated in the future.

Materials and methods

Experimental site, selection of trees, and sampling of wood disk

Acacia mangium saplings in the experimental forest of Universiti Putra Malaysia (UPM), Peninsula Malaysia (3°N, 101°E), where the precipitation was about 2400 mm in 1997, were used to investigate the location and wood anatomy of

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discontinuous bands. The site has a slope of less than 20° that faces south. The 1-year-old saplings (approximately 1.8m high 1 year after germination) were planted on the slope in the beginning of November 1996; and 27 saplings had subsequent steady growth. Two healthy trees (trees A and B) and another two trees (trees C and D) were felled in September 1998 and September 1999, respectively, and wood disks from the trees were sampled at breast height to investigate the macroscopic and anatomical features of their stems. Tree C was healthy, and tree D showed slow radial growth for some months.

Observation of phenological features

The phenological features of 27 trees were observed every month from July 1997 to September 1998. In particular, the timing of defoliation and new foliage of shade leaves were investigated every 2 weeks from June to September 1998.

Measurement of tree growth

The height and girth at breast height (GBH) of 22 trees were measured biweekly or monthly from July 1997 to September 1999. A 10-m measuring pole and a fiberglass measuring tape were used for height and GBH measurements, respectively.

Measurement of vessel dimension

The vessel dimensions in tree C were measured from pith to cambium. Radial series of 30-μm cross sections were prepared from four radial directions with a similar radius. The sections were directly scanned at 4000 dots per inch (dpi) with a Polascan 4000 film scanner (Japan Poladigital, Tokyo, Japan), and then the vessel lumen area and radial diameter on scanned images were measured using Scion Image (Scion Corp., Frederick, MD, USA). The radial variation of the vessel area ratio in 250-μm radial widths was calculated for intervals of 50μm from the vessel lumen area data.

Wood anatomy of wood disks

Wood disks of felled trees were polished using an orbital sander and scanned with an ES8000 color image scanner (Seiko Epson, Japan). The radial direction at 12 o'clock (Fig. 1a) was set arbitrarily on the image of wood disks; then six radial directions (i.e., 1, 3, 5, 7, 9, and 11 o'clock) were determined clockwise from the 12 o'clock position.

To simplify comparisons of the location and characteristics of discontinuous bands between radial directions, the coordinates of the images were transformed from polar (Fig. 1a) to orthogonal (Fig. 1b) using the function of coordinate transformation in Adobe Photoshop 5.0J (Adobe Systems, Japan). With this process, the distance from pith to cell is maintained, although the cells close to the pith are distorted tangentially, and those close to the cambium are thinned tangentially. Therefore, the process is not useful for measuring cell dimension but is useful for investigating the location of discontinuous bands. In this orthogonalized image, some discontinuous bands are not traceable because they are divided at the edge of the image. Thus, the same orthogonalized images were apposed to make the bands traceable perfectly on the images (Fig. 1b). In Fig. 1b, the horizontal axis indicates the clockwise radial direction to the right, and the left edge indicates 12 o'clock. The vertical axis indicates the distance from the pith or the median point upward. Cell dimension is distorted tangentially but is maintained radially.

Thin slices (1 or 3mm thick) were cut from each wood disk at breast height from trees A, B, and C and from the four successive 5cm thick disks at around breast height of tree D with a motor band saw (Ryobi Power Tool Co., Japan). The soft X-ray images were obtained and scanned into images to investigate the distribution of structures with

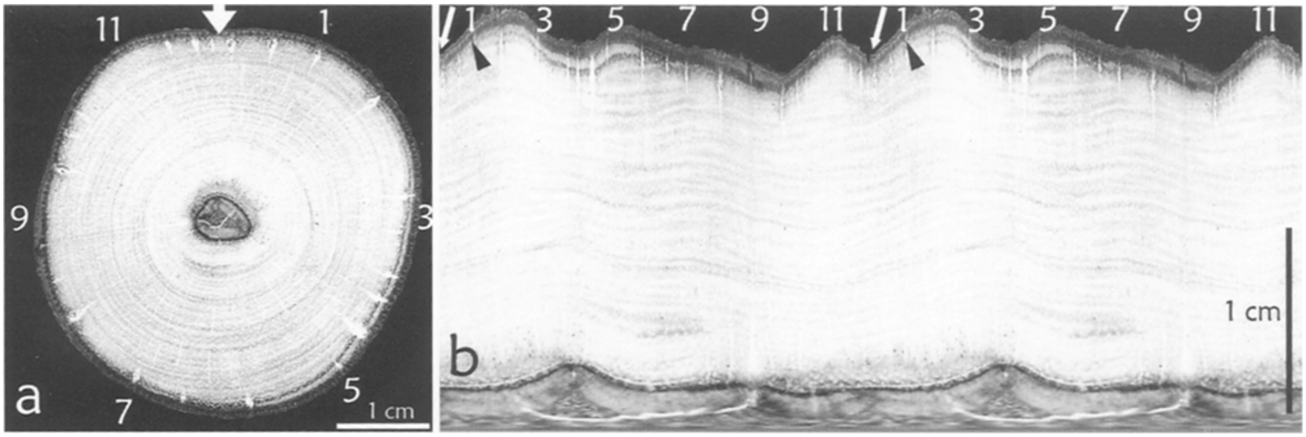

Fig. 1. Polar-coordinate (**a**) and two successive orthogonalized-coordinate (**b**) images of wood disks in tree A. *Arrows* indicate 12 o'clock, selected arbitrarily. The *numbers* indicate radial directions of 1, 3, 5, 7, 9, and 11 o'clock. *Arrowheads* indicate 1 o'clock, where the darker ring is adjacent to cambium

different densities, such as discontinuous darker bands, using type EMB, a soft X-ray generator (Softex Co., Japan).

Microscopic observation of cambial cells

Trees A and B were selected for a comparison of cambial activity in different radial directions. From wood disks fixed with 3% glutaraldehyde, samples in six radial directions, including the cambial zone, were embedded with epoxy resin. Thin sections of the embedded blocks (3μm) were sliced, and microphotographs were obtained. On the microphotographs, the number of cells in the cambial zone (*Nc*), the enlarging zone (*Ne*), and the zones including the S_1 layer but not the S_3 layer of the secondary wall (*Ns*) per radial file were counted using an ordinary and a polarized light microscopy. In general, elongation growth of cells precedes thickening growth; and so intrusive growth is observed not within cambium but within an enlarging zone. For this measurement the boundary between the cambial and enlarging zones was determined based on the existence of the tips of the cells, which grew intrusively, on a cross section including cambium. The S_1 and S_3 layers were observed because of their birefringence with a polarized light microscope.

Results and discussion

Phenological features of shade leaves, variation of tree growth, and ring formation

Almost all of the trees had continuous height and radial growth (Fig. 2a), although four trees showed no radial growth for some months. The average GBH of 22 four-year-old trees in July 1999 was approximately 24.1 cm. The value was lower than in other reports Tsai[7] reviewed. Most of the darker bands on the wood disks of felled trees were indistinct and discontinuous, as mentioned by Sahri et al.,[1] except rings had formed 1 year after germination. It was quite difficult to determine the exact location of the regions formed within a growing period or a year, because each indistinct band was formed while the trees grew continuously according to the tree growth data.

Twenty-five trees had defoliated before the intensive observation period, and nine trees foliated new shade leaves during the period. There was little difference, however, in radial growth between trees with and without foliation of new shade leaves. No distinct darker ring was observed on the wood disks of felled trees during the observation period.

Trees A, B, and C grew more or less continuously and formed no distinct darker rings in their xylem, although tree A had a distinct darker band adjacent to the cambium. On the other hand, tree D had little radial growth over a couple of months (arrowhead, Fig. 2), in which the girth increment was approximately 1.5 mm per month. After the slow radial growth, the tree reactivated until there was approximately 4.0 mm per month in girth growth. Based on the measurement of the ring length, the ring was possibly formed during the 2-month slow radial growth.

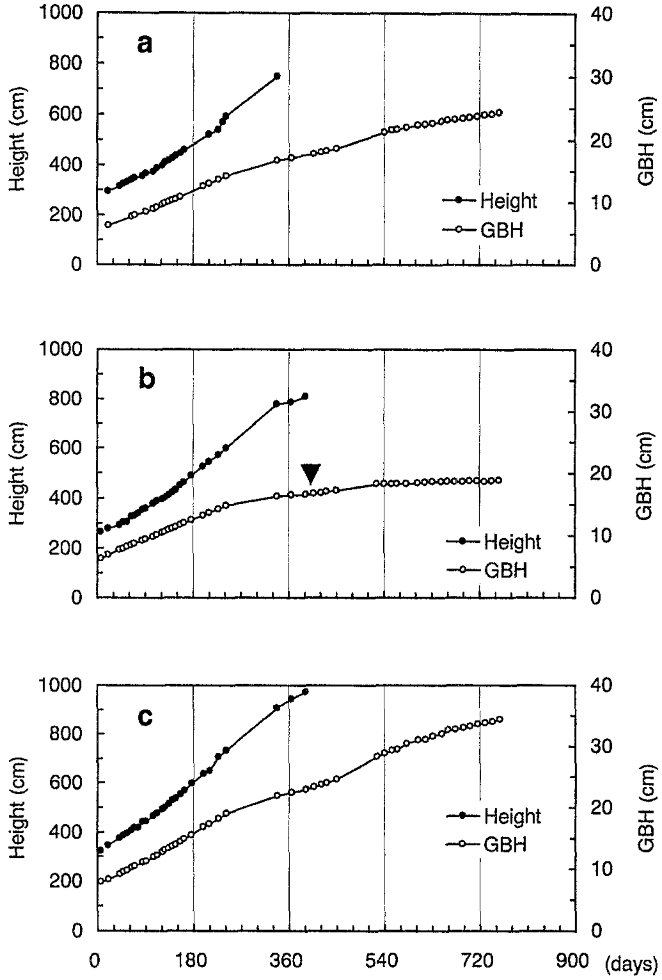

Fig. 2. Height and girth at breast height (GBH) growth for an average of 22 trees (**a**), tree D (**b**), and tree C (**c**). Horizontal axis indicates the number of days from the start of measurement. *Solid* and *open circles* indicate height and GBH, respectively. *Arrowhead* indicates 2-month inactive radial growth

Variety in radial variation of vessel dimension for radial directions

The radial variation in vessel lumen area and radial diameter had a similar tendency in tree C (Fig. 3). In Fig. 3 the relatively larger vessel elements existed around peaks in the radial variation. The positions of the peaks were different for the four radial directions with a similar radius, which suggests that the wood formation is variable in different radial directions.

Location of higher-density and lower-density bands

Higher-density bands including some darker rings and lower-density bands including more vessels were observed on the soft X-ray images from the wood disk of every tree

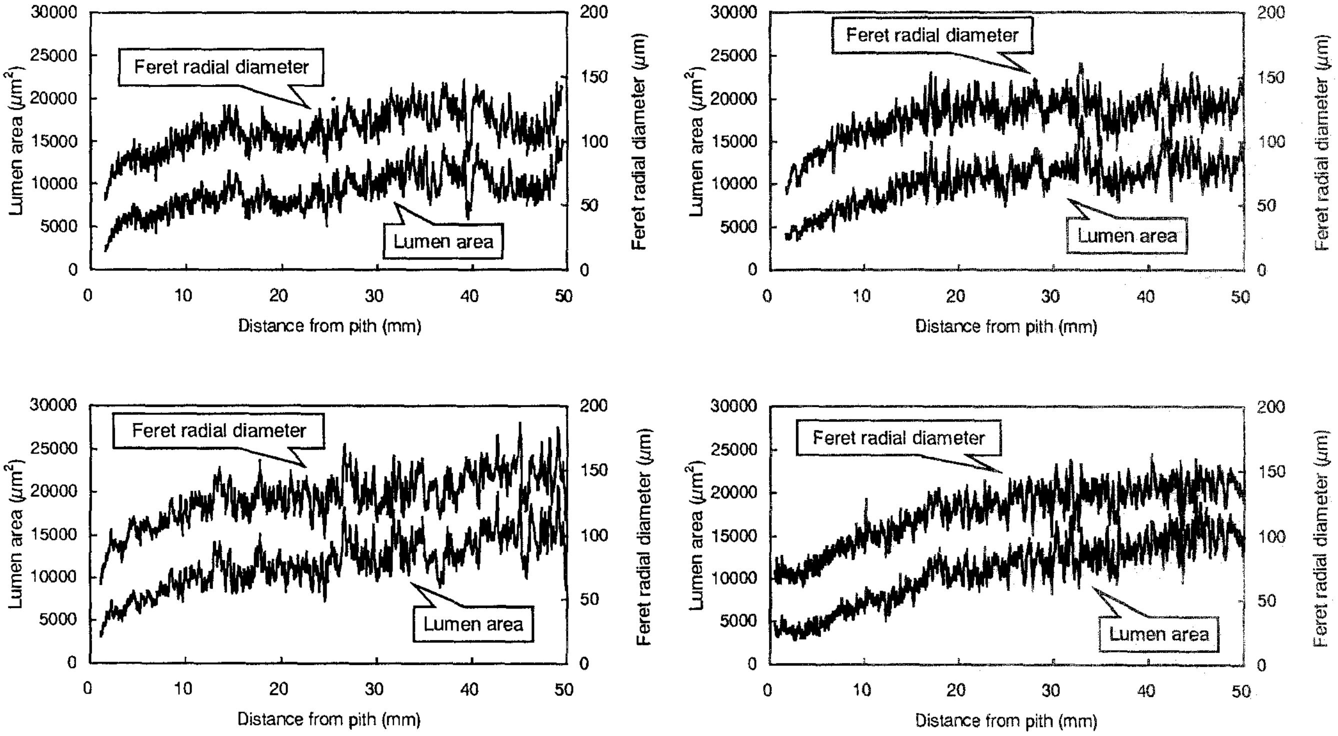

Fig. 3. Radial variation in Feret's diameter and area of each vessel element in various radial directions with a radius similar to that of tree C. *Upper and lower line charts* represent the variation in Feret's radial diameter and the lumen area of the vessel elements, respectively. The positions of some peaks varied among the radial directions

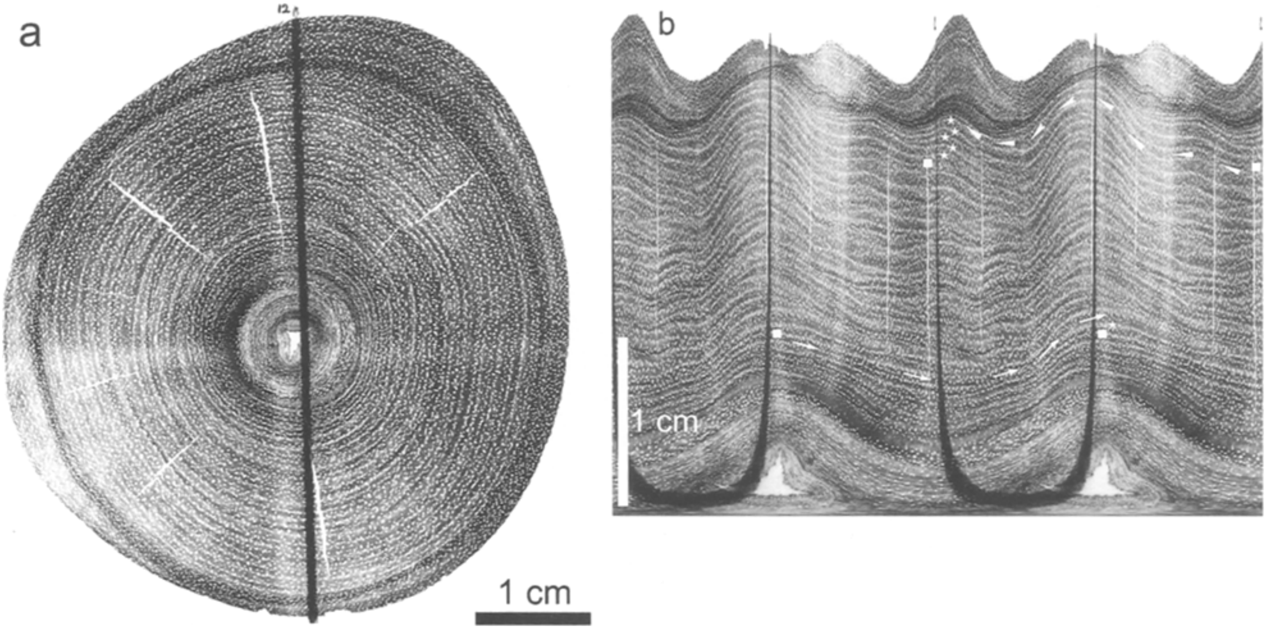

Fig. 4. Soft X-ray images of tree D. Polar (**a**) and two successive orthogonalized (**b**) images. *Squares* in the outer and inner parts of **b** indicate the same positions respectively. *Arrowheads* and *arrows* trace the lower-density spiral bands in the outer and inner part of the disk from the *square*, respectively. *Stars* indicate the lower-density bands between the *squares* and *arrowheads* or *arrows*

(Fig. 4). The higher-density bands consist of more wood fibers with less-thick walls, as in the latewood-like darker bands in tree D. Square marks in the outer and inner part of the disk in Fig. 4b indicate the same positions, respectively. Lower-density bands in the outer and inner parts of the disk are shown by the arrowheads and arrows in Fig. 4b, respectively. These bands aligned in a spiral, rather than in a closed circle, indicating that the vessel elements were formed not simultaneously but gradually toward the circumference. This point needs further research to reveal the circumferential transition of cambial activity and radial growth. There were also other spiral bands (stars in Fig. 4b), suggesting that some spiral bands were formed synchronously, rather than one by one. The spiral in the outer part of the disk (arrowheads in Fig. 4b) was clockwise from the outer toward the inner end of the spiral, in contrast to the anticlockwise spiral in the inner end (arrows in Fig. 4b). It suggests that the direction of the spiral formation reversed in the region between the inner and outer parts of the disk. The lower-density bands in tree C were characterized by radial variation in the vessel area ratio (star in Fig. 5).

Variety of cambial activity between radial directions

The number of *Nc*, *Ne*, and *Ns* of contemporary cambium in trees A and B varied in different radial directions (Fig. 6). The magnified pictures show the position of the cells, which had started at the S_3 layer. Particularly, the number of xylem cells, including the S_1 but not the S_3 layer (*Ns*), in tree A reasonably varied among radial directions; the *Ns* at 7 o'clock was 9.8 cells, whereas at 11 o'clock it was 0.2 (Fig. 7). Although the total number of cells of *Nc, Ne,* and *Ns* was approximately equivalent for 3, 5, and 7 o'clock, *Ns* at 7 o'clock and *Nc* at 3 o'clock were the highest among the areas from 3 o'clock to 7 o'clock. The value of each area at

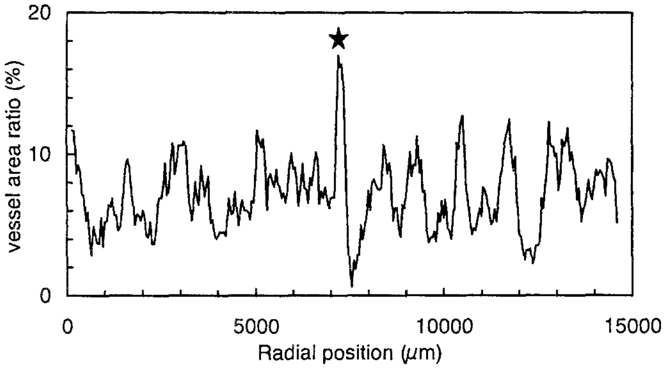

Fig. 5. Radial variation of the vessel area ratio in tree C. Sharp peak (*star*) shows the position of lower-density bands with aligned vessels

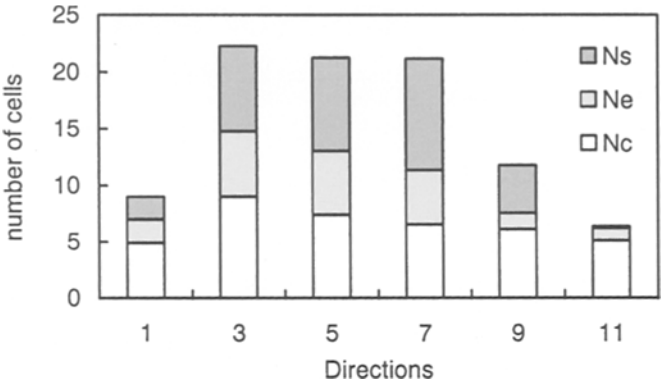

Fig. 7. Number of differentiating cells in six radial directions of tree A. The *white*, *light gray*, and *dark gray columns* indicate *Nc, Ne,* and *Ns*, respectively. Cambial cells at 3 to 7 o'clock were active, whereas the cells at 11 o'clock were inactive

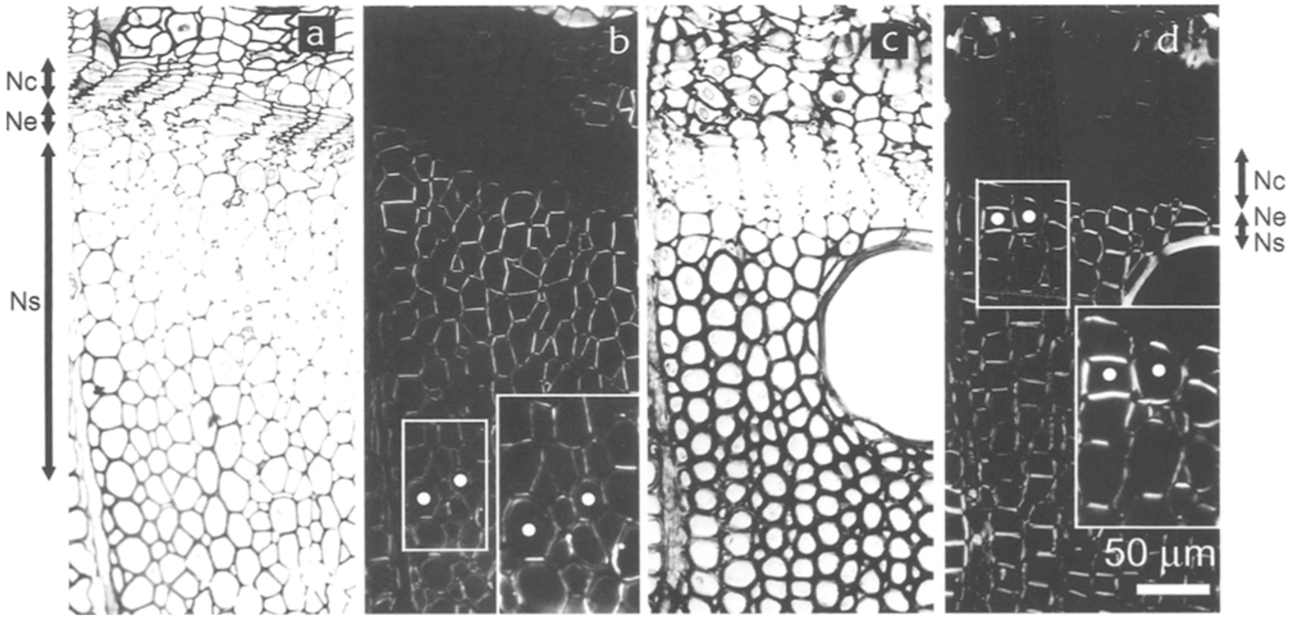

Fig. 6. Differentiating cells at 7 o'clock (**a, b**) and 11 o'clock (**c, d**) of tree A. These micrographs were obtained using ordinary (**a, c**) and polarized (**b, d**) light. *Nc, Ne,* and *Ns* represent the number of cells in the cambial zone, the enlarging zone, and the zones including the S_1 layer but not the S_3 layer. Zones within the *white frames* were magnified, and *circles* in the magnifications indicate the outermost cells with S_3 layer

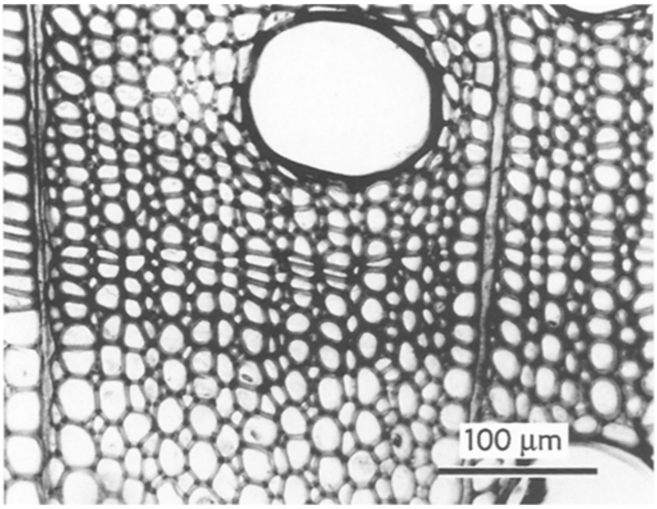

Fig. 8. Micrograph of the distinct darker band in tree A. *Arrows* indicate 12 o'clock, selected arbitrarily. Wood fibers in the center of the figure show latewood-like features (i.e., radially flattened and thick-walled)

5 o'clock was transitive. *Ne* and *Nc* at 1 and 11 o'clock were small (approximately zero).

Fujii et al.[12] considered the possibility that the rate of xylem formation in three *Shorea* may be different in the direction in the stem and evaluated the activity of xylem development using the ratio of the zone of developing secondary wall to the zone of the primary wall. The variety in cambial activity in different radial directions has not been investigated. The data in the present report show that cambial activity varied for the different radial directions in young *Acacia mangium*.

Location of a distinct darker band

In the orthogonalized image of the wood disk of tree A, a distinct but discontinuous darker band was found adjacent to the cambium. The band was farthest from the cambium at 7 o'clock, coming closer to it counterclockwise, and touched it at 1 o'clock (arrowhead in Fig. 1b). In general, darker bands in tree A were more or less discontinuous in any radial direction and had latewood-like characteristics, such as thicker-walled wood fibers and smaller vessels (Fig. 8). Therefore, it is possible that the cambium was more or less inactive during the formation of these bands. The location of the darker band indicates that the cambium reactivated after formation of the darker band at 7 o'clock, but it was still inactive at 11 o'clock.

Asynchronism of cambial reactivation between radial directions

The data for spiral bands, the circumferential variety of cambial activity, and the location of the distinct darker band suggest that cambial reactivation in young *Acacia mangium* occurs not symplastically, but asynchronously and directively along the circumference (i.e., clockwise or counterclockwise). It suggests that the cells at 7 o'clock, which had formed after cambial reactivation, began to deposit in the secondary wall, at 3 o'clock divided actively, at 1 o'clock had just resumed dividing, and at 11 o'clock remained inactive. In the present report, asynchronism of cambial reactivation is suggested from the data on spiral ring location and the variety of cambial activity between radial directions. However, it is still ambiguous whether cambial reactivation starts at a certain point, such as at 7 o'clock in tree A in the present research. Physiological research on ring formation is expected to reveal the asynchronism of cambial reactivation.

In general, mature *Acacia mangium* has a tendency for vessels to align in oblique lines on the cross section,[8] whereas young *Acacia mangium* in the present study had little tendency toward this alignment. The appearance of vessel alignment in oblique lines must be investigated through the maturation process.

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