IAWA Journal, Vol. 24 (1), 2003: 13–26

MACROSCOPIC AND ANATOMICAL INVESTIGATION OF INTERLOCKED GRAIN IN ACACIA MANGIUM

by

Y. Ogata[1], M. Fujita[1], T. Nobuchi[1] & M.H. Sahri[2]

SUMMARY

Interlocked grains record change in the orientation of axial elements. In this report, vessel and fiber orientations in *Acacia mangium* Willd. were compared macroscopically and microscopically to analyze the interlocked grain. A method to print the cylindrical surface of a dry wood disk after bark exfoliation was devised to evaluate the stem axis and circumferential grain fluctuation and revealed circumferential heterogeneity in the vessel orientation. Fiber orientation manifested on some radial splits also was heterogeneous. A 3 mm-thick transverse plate was used to estimate vessel orientation with soft X-ray photography, which enables a wider-ranging evaluation than microscopy. Serial tangential thin plates and sections were used to measure fiber orientation angle with reflecting and polarized light microscopy, respectively, and fast Fourier transform. Both vessel and fiber orientations had a similar radial tendency and distinct inversion of the grain. However, the vessel orientation had a larger amplitude of change than fiber orientation.

Key words: *Acacia mangium*, interlocked grain, vessel and fiber orientation, disk cylindrical printing, soft X-ray, polarized microscopy, fast Fourier transform.

INTRODUCTION

Wood grain represents the orientation of all axial elements rather than that of individual cells, and is an important factor for timber utilization. There are straight, spiral, interlocked, and wavy grains (Harris 1988). Grain is controlled by orientation of fusiform initials in the cambial cylinder. In some regions, cambial domains with various orientations to the stem axis move basipetally and serve to gradually alter the cambial domain orientation in the lower location (Hejnowicz & Zagórska-Marek 1974). The time series of domain orientation is recorded in axial xylem elements derived from the fusiform initials. Traversing growth layers radially, changes in the orientation are detectable with time (Krawczyszyn & Romberger 1980). Circumferential fluctuation in grain orientation has been reported (Ozawa 1972; Harris 1988), indicating that heterogeneous cambial domains coexist at the same time and at the same stem level.

---

1) Laboratory of Plant Cell Structure, Division of Forest and Biomaterials Science, Graduate School of Agriculture, Kyoto University, Kitashirakawa-Oiwake-cho, Sakyo-ku, Kyoto 606-8502, Japan [E-mail of Y. Ogata: zennoske@kais.kyoto-u.ac.jp].

2) Faculty of Forestry, Universiti Putra Malaysia, 43400 UPM, Serdang, Selangor, Malaysia.

Interlocked grain includes undulatory inversion of grain orientation and there are some cases of several alternating Z helices (+) and S helices (–). The grains in many temperate trees show periodicity over some annual rings (Ohkura 1958; Harris 1988). Therefore, grain inversion is likely influenced by an endogenous rhythm. In contrast, Détienne (1979) reported that *Daniellia* had grain inversion approximately coincident to the annual rings, possibly restricted by environmental factors. Although in many reports grain orientation has been measured in every growth layer, it is essential to evaluate seasonal change of grain to determine whether grain inversion is influenced by endogenous or exogenous factors (Wobst et al. 1994). Moreover, interlocked grain is frequent in tropical trees that grow in essentially constant environments, which renders it difficult to determine the period and the increment of their growth. To identify causal factors for grain change in tropical trees, precise investigation of the radial growth rhythm is required.

Many methods to evaluate grain orientation have been devised (Harris 1988). Macroscopic evaluation of fiber orientation at the stem level includes observation of inner bark by exfoliating the outer bark from a living tree and splitting a wood disk radially with a hatchet or a knife (Ohkura 1958; Ozawa 1972; Pape 1999). Vessel orientation has been examined using an ink test (Harris 1988; Kanai et al. 1996). These methods are efficient and convenient for macroscopic observation of grain orientation. Analysis of abrupt change (Bhat & Bhat 1983) or seasonal change (Wobst et al. 1994) of grain, however, requires evaluation at the tissue or cell level.

Serial tangential sectioning (Hejnowicz & Zagórska-Marek 1974; Détienne 1979; Krawczyszyn & Romberger 1980; Bhat & Bhat 1983; Wloch 1985, 1987) and wire insertion (Knigge & Schulz 1959; Kanai et al. 1996) have been applied for wood fiber and vessel orientation, respectively. Although these methods provide more exact orientation data, they are time-consuming and the size of the region that can be evaluated is restricted. If the vessel diameter is 100 μm or more, X-ray irradiation parallel to vessels enables discrimination of each vessel (Ogata et al. 2002a). In the present report, this method, termed "inclinable soft X-ray photography" was developed to evaluate individual vessel orientation.

The present report focuses on *Acacia mangium*, which has been extensively planted in tropical regions. The species is fast growing. *Acacia mangium* has straight or slightly interlocked grain (Atipanumpai 1989; Abdul-Kader & Sahri 1993; Sahri et al. 1993), but the timing and radial pattern of the grain change is not known. Moreover, the growth rings of this species are indistinct and its radial growth rate fluctuates circumferentially (Ogata et al. 2002b). At present, it is difficult to analyze radial growth over time in tropical trees that do not have distinct growth rings. In contrast, analysis of the grain is expected to reveal the growth properties of tropical trees. To examine the heterogeneity of the grain orientation, the cylindrical surface of a wood disk was viewed as a cambial cylinder, which provided information on grain at the time of sampling. Macroscopic and microscopic methods have been applied for grain analysis. To compare the data of both methods, the same datum axis (stem axis) is required. Most studies have been made on either vessel or fiber orientation; there are few reports comparing vessel and fiber orientation. In the present report, several new methods were used to measure grain orientation and the relationship between the vessel and fiber orientation angle was measured in adjacent regions.

MATERIALS AND METHODS

Materials and disk sampling

Wood disks (5 cm thick) were sampled at breast height from two 3- and two 4-year-old and one 5- and one 14-year-old *Acacia mangium* and dried at room temperature. An arbitrary radial direction on each disk was defined as the datum radial direction (0 o'clock) and every direction was named clockwise on the upper surface of the disk. Upper and lower cutting surfaces of the disk were polished using an orbital sander and the upper surface was selected as the datum plane (I in Fig. 1).

Printing the cylindrical surface of disks to detect tree axis and vessel orientation

To determine the inclination angle of the upper surface to the tree axis, the cylindrical surface of a wood disk was dipped in black ink and surrounded with a paper to print the outline of the cylinder (II in Fig. 1). The print of the cylinder was expanded into a plane and scanned using an image scanner to obtain a two-dimensional image of the print (disk cylindrical printing).

A similar print was softly transcribed on tracing paper to print the grain pattern on the disk cylinder. In this report, the angle inclination of the upper surface of a disk from the 14-year-old tree to the tree axis was evaluated using this method. Vessel orientation angles in six directions on the cylindrical surface of wood disks from all trees studied were also measured.

Radial splitting of disks to reveal interlocked grain

Each wood disk of the 3-, 4-, 5-, and 14-year-old trees was split into four or eight directions from the upper surface using a hatchet (III in Fig. 1) to macroscopically examine the radial splitting pattern on the lower surface which shows the wood fiber orientation (radial splitting). On the cylindrical surface of the disks, fiber orientation manifested by radial splitting and vessel orientation on the print of the disk cylinder were compared in each split direction.

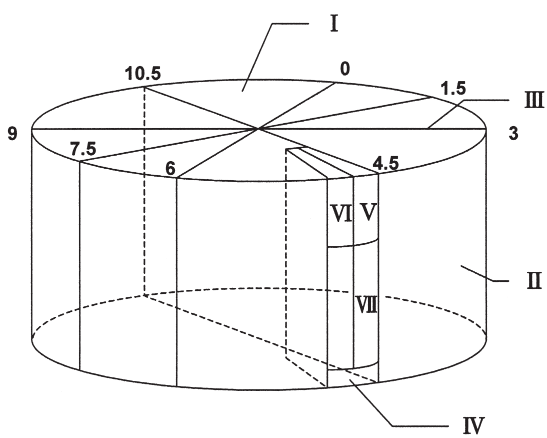


Fig. 1. Scheme of experimental processes in a wood disk of a 14-year-old tree. Arabic numerals show directions on the disk split radially, determined clockwise from an arbitrary direction (0 o'clock) on the upper surface of a disk. Roman numerals represent the position of sampling wood portions in each process.

Transverse plate cutting for examination of individual vessel orientation with inclinable soft X-ray photography

In a thin plate, the outline of a vessel image oriented parallel to the soft X-ray is clear (Ogata et al. 2002a). Therefore, when the plate is inclined to the irradiation axis at various degrees and then photographed, vessel orientation in the whole plate can be evaluated and three-dimensional information of vessel orientation can be expressed on a two-dimensional image. In this report, the measurements were restricted to a direction of 4.5 o'clock in the 14-year-old tree to compare vessel and fiber orientation macroscopically and anatomically (IV to VII in Fig. 1). A thin transverse plate (c. 3 mm in thickness, 30 mm radially, and 10 mm tangentially) was sliced from a wood portion including the radial splitting surface (IV in Fig. 1). An inclinable stand for an experimental plate was prepared (Ogata et al. 2002a) and equipped with a Type EMB soft X-ray generator (SOFTEX, Yokohama, Japan). The thin plate in close contact with FG or Minicopy, a super-fine grained film (Fuji Photo Film, Tokyo, Japan), was attached on the stand with various inclination angles, and a soft X-ray photograph was taken. A radial pivot was used to change the inclination of the stand from -10 degrees (S-helix) to +10 degrees (Z-helix) at a precision of 1 or 2.5 degrees (inclinable soft X-ray photography).

This inclinable soft X-ray photography was applied to 3-, 4-, and 5-year-old trees and radial changes in vessel orientation in young *Acacia mangium* were investigated.

Serial tangential dividing and sectioning for evaluation of fiber orientation

A wood block of c. 5 mm (L), 30 mm (R), and 3 mm (T) was sampled from region V in Figure 1, marked with a pencil at 1-mm radial intervals, and then divided into tan-gential plates 1 mm thick. After coating the tangential surfaces with gold, the plates were illuminated almost horizontally and from an approximate vertical direction to the fibers on the plate (lateral illumination), a reflected image was taken, including the upper surface as a datum plane. The image was scanned at 4000 dpi (dots per inch) using a film scanner and fast Fourier transform (FFT) was applied to the image using NIH Image, an image analyzing software (Scion Image beta 4.0.1; Scion Corporation, Frederick, Maryland), to obtain its power spectral pattern (PSP).

A tangential series of 200 sections, 50 μm thick (total radial extent = 10 mm), was sliced from region VI (Fig. 1). When fiber orientation in these sections is placed parallel to either crossed polar direction under a polarized microscope, the wood fiber walls are totally extinguished. Wood fiber orientation to the tree axis was reckoned from the datum plane and extinction direction.

Maceration of tangentially separated wood plates for measurement of fiber length

A wood block of c. 10 mm (L), 30 mm (R), and 3 mm (T) was sampled from region VII in Figure 1, and marked at 0.5-mm radial intervals. Thin tangential plates 0.5 mm thick were taken centripetally from the cambium across a radial extent of 28 mm. Every thin plate was macerated using Franklin's method and mounted with gum arabic on a slide. Macerated fibers on the slide were magnified 100 times using an image projector and their central lines were traced on tracing paper with a black marker (Japan Wood

Research Society 2000). The lines were scanned at 300 dpi to obtain their images and 50 fiber lengths per thin plate were measured using NIH Image.

RESULTS AND DISCUSSION

Evaluation of inclination angle of disk surfaces to tree axis

A print of the cylindrical surface from the disk in a 14-year-old tree is shown in Figure 2. When a disk is completely vertical to the tree axis, the disk cylindrical print is a rectangle composed of the perimeter and thickness of the disk (Fig. 3a). In contrast, when a disk is inclined to the tree axis, this print reveals a sinuous curve (Fig. 3b). The highest (H) and lowest (L) points in this curve correspond with respective actual points of the disk and segment HL provides the inclination angle and direction of the disk to the tree axis (Fig. 3c). Based on the print shown in Figure 2, the upper surface of this disk from the 14-year-old tree was inclined by c. 2.1 degrees to the tree axis and the directions showing the highest (H) and lowest (L) points were 7.5 and 1.5 o'clock, respectively.

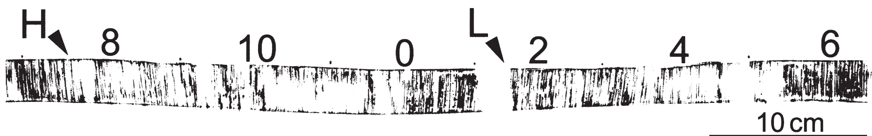


Fig. 2. Print of the cylindrical surface of a wood disk in a 14-year-old tree. Numerals represent directions in the same way as in Figure 1. – H & L: The highest (7.5 o'clock) and lowest (1.5 o'clock) point of the upper surface of a disk, respectively. Lines within a print show vessel orientation in each direction.

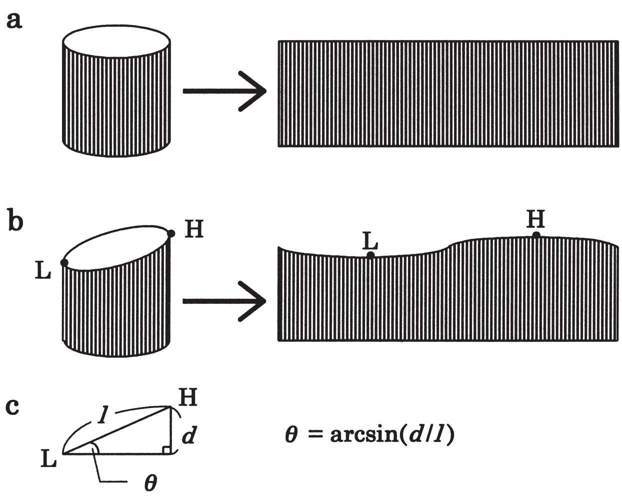


Fig. 3. How to determine the inclination angle of the disk surface to a tree axis using disk cylindrical printing. – a & b: Upper surface of a disk is vertical and inclined to a tree axis, respectively. – c: Calculation of inclination angle. H & L: The highest and the lowest point of the upper surface of a disk and a cylindrical print. – d: Difference in height between H and L (mm). – l: Length of segment HL (mm). – θ: Inclination angle of the upper surface of a disk to a tree axis (degree).

Disk cylindrical printing is very useful to evaluate the inclination angle of the cutting surface of a disk relative to the tree axis even after processing, e.g., polishing. Moreover, cut and polished surfaces are available as the datum plane for macroscopic and anatomical research on vessel and fiber orientation.

Detailed observation of the grain pattern printed on a paper revealed a large number of discernible lines. Vessels were more convex than wood fibers on the cylindrical surface. In general, when bark is removed from the stem during a growing period, xylem cells in the enlarging zone are torn so that the cambium stays with the bark. Vessel elements complete their differentiation earlier than fibers and thus vessel elements and wood fibers are convex and concave, respectively, following bark exfoliation and drying. Fresh vessel orientation was visualized circumferentially by disk cylindrical printing. Furthermore, the vessel orientation pattern on cylindrical coordinates was transformed into an image on orthogonal coordinates, serving to greatly increase the efficiency of image analysis.

Indistinct growth ring structure in tropical trees renders it impossible to decide when every tissue is formed, even if a serial change of grain can be detected on a radial split of each wood disk. Moreover, radial growth is not circumferentially synchronized (Ogata et al. 2002b). Thus, it is difficult to compare the growth between different radial directions, particularly in tropical trees with indistinct growth rings. Precise analysis of the radial splitting pattern over time is not yet possible. The cylindrical surface left after bark removal possesses information on vessel orientation in the whole circumference and this orientation can be detected using an extremely easy method to print the cylindrical surface of a wood disk. This method is applicable to logs of several meters in length or to a branch and is expected to reveal longitudinal grain pattern. In the present report, these circumferential analyses were applied only to the restricted wood disks, mentioned below.

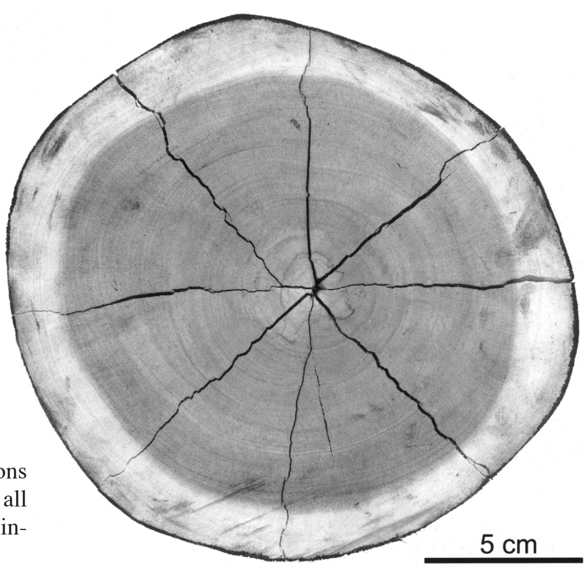


Fig. 4. Radial split in eight directions in a disk of a 14-year-old tree. In all directions there are distinct grain inversions.

Macroscopic characteristics of interlocked grain pattern

Characteristic radial splitting patterns showing grain inversion were observed on all radial splits in the 14-year-old tree macroscopically, except for the central part of the disk (Fig. 4). Usually, radial splitting corresponded to the fiber orientation. Therefore, these radial splitting patterns are deduced to represent fiber orientation along the radial direction and would represent the orientation of the fusiform initials.

Although radial splitting is a convenient method for checking the grain pattern, it should be applied for estimation of the long-term tendency of grain change from the splitting curve. There can be experimental errors, such as fiber breakage by splitting, and an abrupt change in grain orientation might be undetectable using this method (discussed below). Split orientation at the outermost region of a disk directly indicates fiber orientation in each direction at the time of felling the tree, discussed in the next section.

On radial splits in the 3- and 4-year-old trees, radial changes in fiber orientation were indistinct (Fig. 5a, b). In contrast, the split in the 5-year-old tree revealed inversion of the fiber orientation adjacent to the cambium (Fig. 5c).

a

b

c

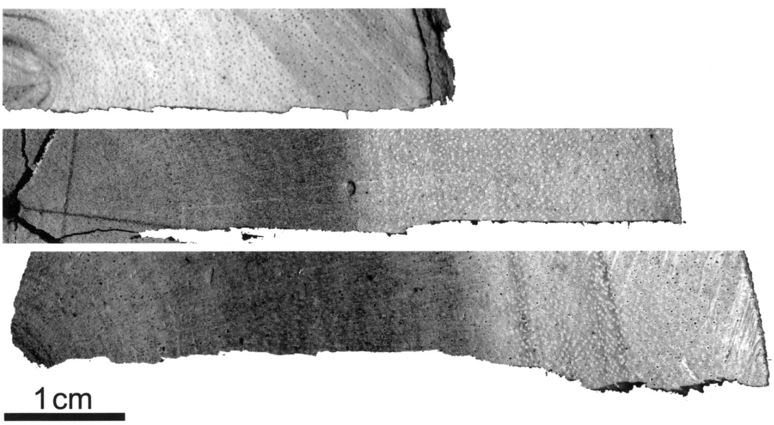


Fig. 5. Radial splits in wood disks in young trees. – a, b & c: Wood disks of a 3-, 4-, and 5-year-old tree, respectively. – a & b show no distinct inversion of grain; c shows some grain inversion adjacent to the cambium (right edge).

Circumferential fluctuation of grain orientation on wood disks

Vessel and fiber orientation determined from disk cylindrical printing and radial splitting, respectively, had similar tendencies, although inclinable soft X-ray photography revealed that both orientations differed greatly in a specific region (next section). These findings indicate that both orientations are basically similar but in a narrow region possibly show different patterns. Both orientations fluctuated circumferentially on the same disk. For example, in the 14-year-old tree, both orientations were straight between 10 and 0 o'clock, an S-helix adjacent to 3 o'clock, and a Z-helix between 7 and 9 o'clock (Fig. 2). Table 1 shows vessel orientation angles in six directions on the cylindrical surface of disks in all trees studied. Circumferential difference of the orientation was approximately 5 degrees in 3- and 4-year-old and 10 degrees in 5- and 14-year-old trees, suggesting that grain orientation becomes more heterogeneous with maturation of the tree and that the orientation fluctuates circumferentially even in young trees. As mentioned above, the cylindrical surface of a wood disk includes information on the cambial cylinder at the time of felling the tree. Therefore, circumferential fluctuation in grain orientation at the same level suggests heterogeneity in xylem radial growth between different directions. An analysis of domain orientation in the cambial cylinder throughout a longer stem is necessary to clarify the characteristics of xylem radial growth in tropical trees.

Table 1. Vessel orientation angle (degree) on removed surface in six directions split radially in every tree. First line and column show every direction and every tree age, respectively. Positive and negative values represent Z-helix and S-helix orientation, respectively. Differences in orientation angle in 3- and 4-year-old trees are approximately 5 degrees and that in 5- and 14-year-old trees are approximately 10 degrees.

	0	2	4	6	8	10
3-year-old	-0.8	+1.8	+3.7	+2.9	+2.9	-0.8
	+2.5	+4.3	-2.3	-1.1	0.0	+2.9
4-year-old	-1.8	-3.8	-3.3	-4.3	-2.2	-1.3
	+2.5	+0.9	-0.6	+2.9	+2.1	+1.2
5-year-old	+3.6	+4.3	+0.5	+7.5	+10.7	+0.9
14-year-old	-3.0	-3.9	-2.7	-1.0	+8.1	+0.6

Characterization of vessel orientation using inclinable soft X-ray photography

Serial inclinable soft X-ray photographs of a thin transverse plate of a disk cut from sapwood of the 14-year-old tree are shown in Figure 6. A tangential group of vessels is outlined by irradiation from a specific angle; i.e. orienting to the angle (region C in Fig. 6a) and outlines of another group of vessels shift tangentially (region U in Fig. 6a). Radial tracking of vessel groups from the pith side to the cambium side shows distinct inversion of the orientation angle (Fig. 6b–d); i.e., centrifugally from the pith side, straight (zone 1 in Fig. 6c), Z-helix (zone 2 in Fig. 6b), straight (zone 3 in Fig. 6c), S-helix (zone 4 in Fig. 6d), straight (zone 5 in Fig. 6c), S-helix (zone 6 in Fig. 6d), and finally straight vessels (zone 7 in Fig. 6c). Adjacent to the high-density band (arrowheads in Fig. 6d) within zone 5, S-helix vessels distributed in a narrow tangential line are surrounded by Z-helix vessels. Amplitude of vessel orientation angle in the whole experimental region was approximately 10 degrees. Although vessel orientation was similar to fiber orientation when evaluated using radial splitting (Fig. 4), inclinable soft X-ray photography detected a abrupt radial change in the grain. Bhat and Bhat (1983) found a sharp change in grain orientation in *Anacardium occidentale* using serial tangential sectioning, whereas we were able to detect this sharp change using inclinable soft X-ray photography in the present study.

Soft X-ray photography enables examination of vessel orientation in an area of approximately 5 cm^2 and eliminates the influences of tyloses, and rough surfaces. More-

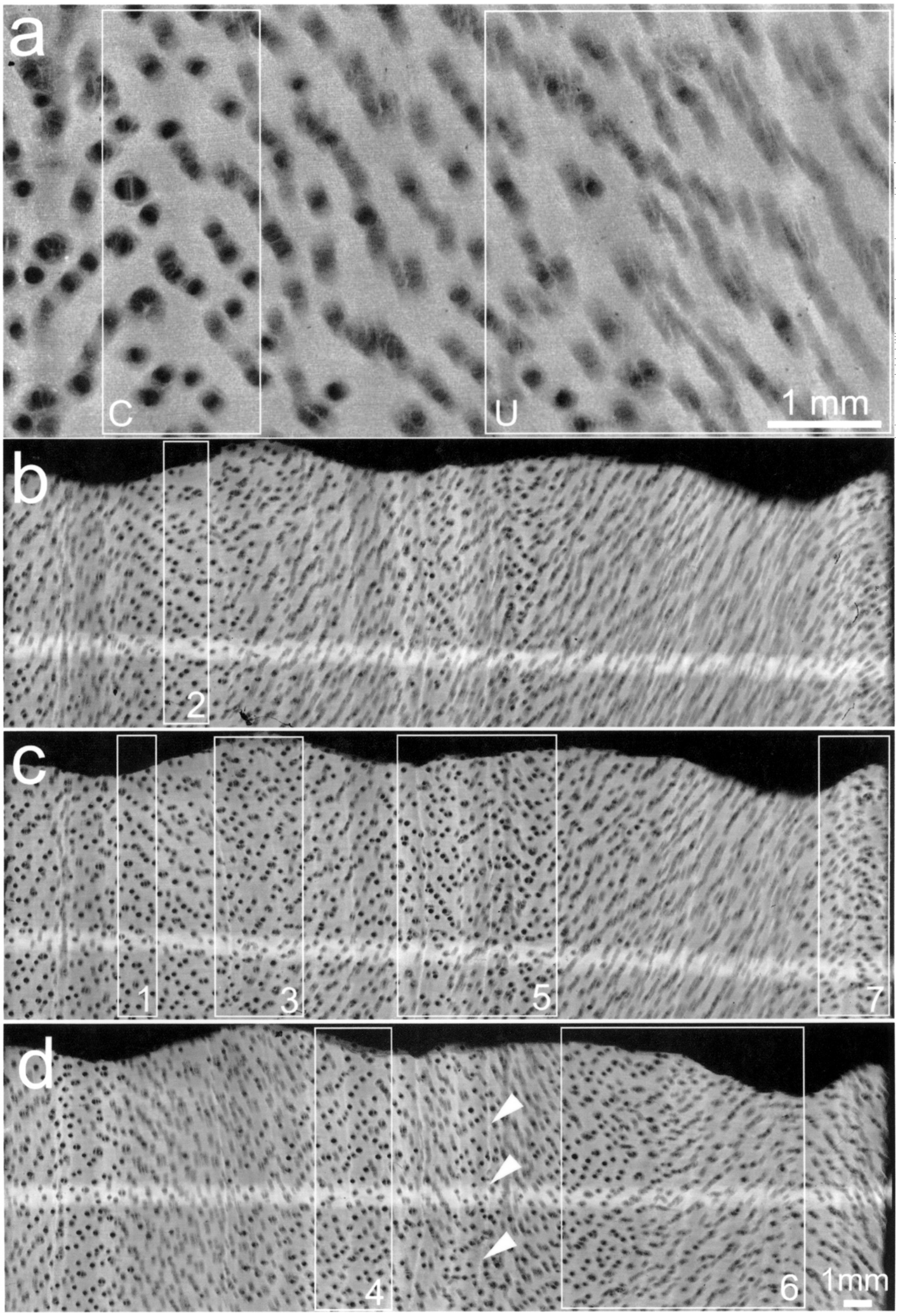


Fig. 6. Inclinable soft X-ray photographs in a 14-year-old tree. – a: Enlargement of photograph with no inclination of wood sample (c). – b–d: Vessels of 5 degrees in Z-helix, straight, and of 5 degrees in S-helix, respectively, are clearly observed. There are regions mainly including straight-oriented vessels (zones 1, 3, 5 & 7), Z-helix (zone 2), and S-helix (zones 4 & 6).

over, it provides a two-dimensional expression of the orientation of each vessel (Ogata et al. 2002a). Therefore, this method is convenient and precise for examining vessel orientation, i.e., grain orientation, particularly in diffuse-porous hardwoods.

In a soft X-ray photograph of a 5-year-old tree, there was inversion of vessel orientation adjacent to its cambium. In contrast, the inner xylem in a 5-year-old disk and whole disks of 3- and 4-year-old trees had relatively random distributions of vessels orienting to a specific angle. This result and the data shown in Table 1 suggest that grain orientation fluctuates circumferentially and radially as a tree matures.

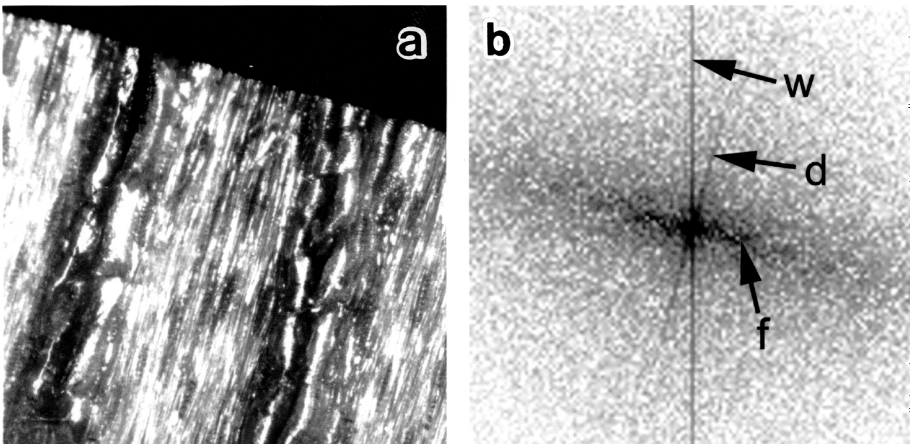


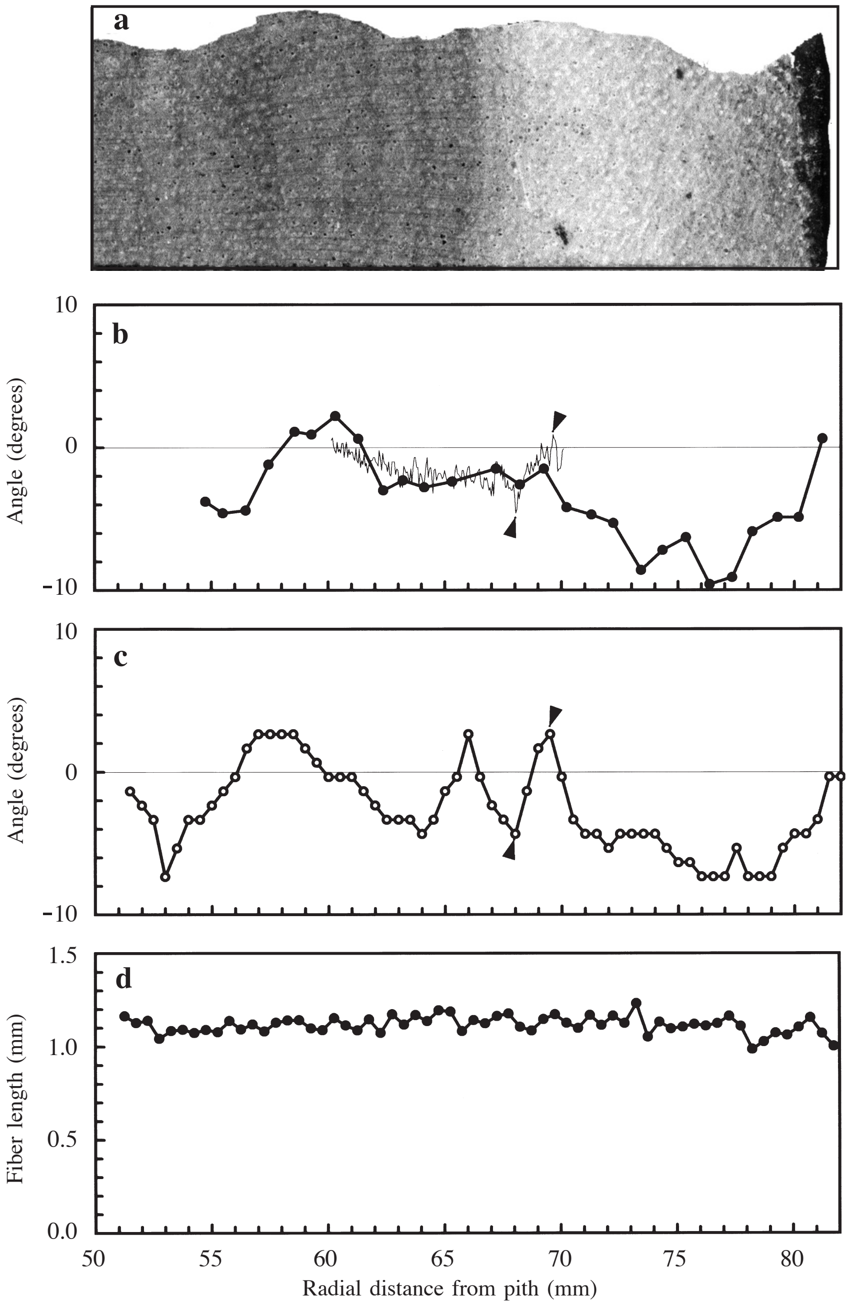
Fig. 7. Estimation of wood fiber orientation using lateral illumination and fast Fourier transform (FFT). – a: Micrograph using lateral illumination. – b: Low frequency region of power spectral pattern (PSP) obtained by applying FFT to the micrograph (a). w = vertical pattern originated from the peripheral edge, called 'window'; d = pattern from upper surface as a datum plane; f: pattern from fiber orientation.

Radial change of fiber orientation and its relationship to vessel orientation

In PSP computed from reflected images of thin tangential plates (Fig. 7a) using FFT, three distinct patterns were detectable (Fig. 7b). There was a vertical pattern that originated from the peripheral edge, called a 'window' of an image (w in Fig. 7b), a pattern from the upper surface of a disk as a datum plane (d in Fig. 7b), and a pattern from wood fiber orientation (f in Fig. 7b). Fiber orientation was somewhat dispersive and thus polar coordinate analysis was applied in the low frequency area of PSP (Maekawa et al. 1993; Fujita et al. 1995). The fiber orientation angle to the datum plane was calculated and modified into the angle to the tree axis using the data from disk cylindrical printing (Fig. 8).

→

Fig. 8. Radial changes in fiber and vessel orientation and fiber length in a 14-year-old tree. Horizontal and vertical axes represent radial distance from the pith and orientation angle to a tree axis, respectively; the right edge is coincident with removed surface. – a: Radial split. – b: Line chart with and without markers represents fiber orientation angle applying FFT to serial thin



tangential plates, and applying polarized light microscopy to serial tangential sections, respectively. – c: Vessel orientation angle using inclinable soft X-ray photography. – d: Wood fiber length using Franklin's method for maceration. In a–c, tendencies of orientation angle are similar to each other. Arrowheads show a trough and a peak in a region showing a sharp change in grain orientation.

The macroscopic pattern of fiber orientation on a radial split is shown in Figure 8a. In this figure, the peak and the trough on the radial split shows Z- and S-helix fiber orientation, respectively, corresponding to line charts showing radial changes in fiber and vessel orientation investigated anatomically (Fig. 8b & c). A line chart with markers in Figure 8b shows radial changes in wood fiber orientation determined using PSP, in which the horizontal axis represents radial distance from the pith and right edge is coincident with the surface following bark exfoliation. These radial changes in fiber orientation were similar to those viewed using radial splitting. Examination by FFT measures a more exact fiber orientation angle than does radial splitting and without laborious work such as serial sectioning.

The line chart with no marker in Figure 8b indicates radial changes in wood fiber orientation seen in serial tangential sections using polarized light microscopy. Although the tendency was similar to that examined using FFT, a sharp radial change was demonstrated more clearly using this method (arrowheads in Fig. 8b).

Figure 8c shows the mode angle of vessel orientation in each 0.5-mm radial division using inclinable soft X-ray photography. Radial changes in vessel orientation were similar to radial changes in fiber orientation and the amplitude in radial changes in their orientations was approximately 10 degrees. In a region including sharp radial change in vessel orientation (arrowheads in Fig. 8c), however, amplitude in vessel orientation was larger than amplitude in fiber orientation. Particularly, at 66-mm radial distance from the pith, vessel orientation showed a distinct peak, whereas fiber orientation had only a slight radial change. It is interesting that wood fibers and vessels derived from the same cambial domain had quite different orientations. It is possible that vessel elements can adapt to sudden changes in their orientation by different methods to connect to adjacent elements. On the other hand, wood fibers possibly represent the original orientation of the cambial domain. Fusiform initials can possibly modify their orientation by pseudo-transverse division and intrusive growth; nevertheless, it is possible that abrupt changes in the orientation of fusiform initials are restricted.

In the present report, heterogeneity in wood fiber and vessel orientation was determined quantitatively and, significantly, vessel orientation shows greater amplitude than fiber orientation. Observation of morphogenetic events in the cambium during induction of sudden changes in vessel orientation as well as radial changes in the orientation of fusiform initials is necessary.

Fluctuation of fiber length along radial direction

Figure 8d shows radial changes in the wood fiber length along the same direction mentioned above. Although there was some variation adjacent to the cambium, its relationship to fiber and vessel orientation is not known. Bhat and Bhat (1993) reported that wood fiber length was shorter in the region with radial changes in the grain. If the cambium has frequent pseudo-transverse divisions in such regions, the length of fusiform initials would be expected to be temporarily shorter immediately after the division. Wood fiber length, however, is affected by elongation so that the shortening of fusiform initials due to division possibly does not influence fiber length. To compare the fiber length with grain orientation showing abrupt change, it is necessary to measure the orientation and the length in the same section. Determining cambial cell length at the time when it formed each wood fiber will reveal the relationship between interlocked grain and cambial cell length.

ACKNOWLEDGEMENTS

The authors are grateful to the Faculty of Forestry, Universiti Putra Malaysia, for preparation and maintenance of the site. Part of this study was financially supported by a Kajima Foundation research grant and the Tanabe Southeast Asia Nations Friendship Foundation.

REFERENCES

Abdul-Kader, R. & M.H. Sahri. 1993. Properties and Utilization. In: K. Awang & D. Taylor (eds.), Acacia mangium: Growing and utilization: 225–241. Winrock International and FAO, Bangkok, Thailand.

Atipanumpai, L. 1989. Acacia mangium: Studies on the genetic variation in ecological and physiological characteristics of a fast-growing plantation tree species. Acta For. Fenn. 206: 1–92.

Bhat, K.V. & K.M. Bhat. 1983. Anatomical changes associated with interlocked grain in Anacardium occidentale L. IAWA Bull. n.s. 4: 179–182.

Détienne, P. 1979. Contrefil à rythme annuel dans les faro, Daniellia sp. pl. Rev. Bois For. Trop. 183: 67–71.

Fujita, M., H. Kajita, T. Maekawa & H. Saiki. 1995. Evaluation of particle orientation by the Fourier transform image analysis. J. Soc. Mat. Sci., Japan 44: 267–272.

Harris, J.M. 1988. Spiral grain and wave phenomena in wood formation. Springer-Verlag, Berlin, etc.

Hejnowicz, Z. & B. Zagórska-Marek. 1974. Mechanism of changes in grain inclination in wood produced by storeyed cambium. Acta Soc. Bot. Pol. 43: 381–398.

Kanai, Y., M. Fujita & K. Takabe. 1996. Vessel network tracing by wire insertion and pigment injection. Bull. Kyoto Univ. For. 68: 127–136.

Knigge, W. & H. Schulz. 1959. Methodische Untersuchungen über die Möglichkeit der Drehwuchsfeststellung in verschiedenen Alterszonen von Laubhölzern. Holz Roh- u. Werkstoff 17: 341–351.

Krawczyszyn, J. & J.A. Romberger. 1980. Interlocked grain, cambial domains, endogenous rhythms, and time relations, with emphasis on Nyssa sylvatica. Am. J. Bot. 67: 228–236.

Maekawa, T., M. Fujita & H. Saiki. 1993. Characterization of cell arrangement by polar coordinate analysis of power spectral patterns. J. Soc. Mat. Sci., Japan 42: 126–131.

Ogata, Y., T. Kadokawa & M. Fujita. 2002a. Experimental conditions for quantitative image analysis of wood cell structure (II): Non-microscopic image sampling over a very wide area using a film scanner. J. Jap. Wood Res. Soc. 48: 341–347.

Ogata, Y., T. Nobuchi, M. Fujita & M.H. Sahri. 2002b. Asynchronous wood formation in young Acacia mangium planted in Malaysia. J. Wood Sci. 48: 89–94.

Ohkano, T. 1984. Estimate of spiral grain in the stem of a standing tree by the branches. Proc. Pacific Regional Wood Anat. Conf. Tsukuba, Japan: 43–45.

Ohkura, S. 1958. On the macroscopic features of twisted fibre in trees. J. Fac. Agri. Shinshu Univ. 8: 59–100 [in Japanese].

Ozawa, K. 1972. Features in spiral grain of Karamatsu (Larix kaempferi Sarg.) from a stand in Tohoku District. J. Jap. For. Soc. 54: 269–274.

Pape, R. 1999. Influence of thinning on spiral grain in Norway spruce grown on highly productive sites in southern Sweden. Silva Fennica 33: 3–12.

Sahri, M.H., F.H. Ibrahim & N.A.A. Shukor. 1993. Anatomy of Acacia mangium grown in Malaysia. IAWA J. 14: 245–251.

Wloch, W. 1985. Time-variable frequency of events in domains of Tilia cambium. Acta Soc. Bot. Pol. 54: 29–40.

Wloch, W. 1987. Transition areas in the domain patterns of storeyed cambium of Tilia cordata Mill. Acta Soc. Bot. Pol. 56: 645–665.

Wobst, J., J.V. Oliver-Villanueva & R. Doebel. 1994. Variabilität der Faserneigung im Holz der Esche (Fraxinus excelsior L.) und Douglasie (Pseudotsuga menziesii (Mirb.) Franco). Holz Roh- u. Werkstoff 52: 342–346.