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ORIGINAL ARTICLE

Anatomical, chemical, and physical characteristics of tension wood in two tropical fast-growing species, *Falcataria moluccana* and *Acacia auriculiformis*

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ABSTRACT The anatomical, chemical, and physical characteristics of tension wood were investigated in the commercially important tropical fast-growing plantation species *Falcataria moluccana* and *Acacia auriculiformis*. In both cases, pots containing seedlings of the two species were tilted at 50° from a vertical position to promote tension wood formation. During this period, upward bending occurred in the seedlings of both the species. Samples were collected from three different stem positions (lower position, middle position, and upper position). A distinct gelatinous (G-) layer was observed at the lower position in *F. moluccana*, and lower and middle positions in *A. auriculiformis*. Compared to normal wood, the anatomical and chemical characteristics, except for the vessel frequency, were significantly different at the lower position in *F. moluccana*, and at the lower and middle positions in *A. auriculiformis*, pointing to "typical" tension wood in the inclined stems of both species. Compared to normal wood, the basic density significantly increased at the lower position in *F. moluccana*, but not in *A. auriculiformis*. Although a common inclination method was used, the position of the G-layer differed between the two species, suggesting that the degree of response to the inclination stimulus varies among species.

Key words: tension wood, basic density, lignin content, polysaccharide content

INTRODUCTION

Reaction wood is known as a specialized tissue which is formed in leaned or crooked stems or branches in woody plants. In gymnosperms, reaction wood is termed compression wood, which is formed on the lower side of inclined stems or branches (Onaka 1949, Panshin and de Zeeuw 1980, Yumoto et al. 1983, Yoshizawa 1987). On the other hand, in angiosperms, this specialized tissue is formed on the upper side of inclined stems or branches and is known as tension wood (Onaka 1949, Panshin and de Zeeuw 1980).

Tension wood is generally characterized by the presence of a gelatinous (G)-layer, which is mostly composed of cellulose with the small microfibril angle in wood fibers (Onaka 1949, Panshin and de Zeeuw 1980, Baba et al. 1996, Clair et al. 2006, Ruelle et al. 2006, Mukogawa et al. 2008, Yoshinaga et al. 2012, Nugroho et al. 2013). However, some angiosperms such as *Magnolia* spp. and *Liriodendron tulipifera* do not form the typical G-layer, although other anatomical and chemical characteristics are similar to those of "typical" tension wood (i.e., with a G-layer in the wood fibers) on the upper side of inclined stems or branches (Onaka 1949, Yoshida et al. 2000, Yoshizawa et al. 2000, Hiraiwa et al. 2014). Furthermore, in *Gardenia jasminoides*, reaction wood is formed on the lower side of inclined stems or branches. Because the nature of reaction wood in angiosperms is very similar to that of compression wood in gymnosperms (Onaka 1949, Aiso et al. 2013), it is termed "compression-wood-like reaction wood" in angiosperms (Aiso et al. 2013). Although most studies on the formation of reaction wood in angiosperms have been focused on temperate angiosperms, several studies have investigated tropical angiosperms (Shiokura and Lantican 1987, Baba et al. 1996, Clair et al. 2006, Ruelle et al. 2006, 2007, Mukogawa et al. 2008, Nugroho et al. 2013). In studies of the anatomical characteristics of reaction wood in 21 tropical angiosperm species of French Guiana (Clair et al. 2006, Ruelle et al. 2006), 7 species formed "typical" tension wood, 13 formed "tension-wood-like reaction wood", and one species did not form any of the above. Thus, in the tropical angiosperms, the anatomical and chemical characteristics of reaction wood differ among species.

The formation of tension wood also changes the wood density (Panshin and de Zeeuw 1980, Jourez et al. 2001, Ishiguri et al. 2012). Panshin and de Zeeuw (1980) pointed out that the thick-walled G-layer increases the density of tension wood. In a study of three Japanese angiosperms, Ishiguri et al. (2012) reported that the basic density (i.e., the ratio of oven-dry weight/green volume) of "typical" tension wood significantly increased in two of the species (*Castanea crenata* and *Acer crataegifolium*) and decreased in one of the species (*Cerasus jamasakura*). Thus, the tendency toward changes in wood density due to reaction wood formation appears to vary among species.

It has been reported that the degree of inclination stimulus influenced the extent of reaction wood formation (Yumoto et al. 1983, Yoshida et al. 2000, Hiraiwa et al. 2014). Hiraiwa et al. (2014) showed that inclining the stems of *L. tulipifera* by 0, 30, 50, and 70° from the vertical position resulted in a gradual decrease in the lignin content. The decrease in lignin corresponded with the inclination angle up to 50°, whereas the lignin content produced was almost the same as in normal wood at an inclination angle of 70°.

Although the formation of reaction wood has physiological implications for the survival of the trees, the presence of tension wood results in some challenges during wood processing (Panshin and de Zeeuw 1980, Ruelle et al. 2007). Panshin and de Zeeuw (1980) pointed out that when veneers contain tension wood, the wood is sometimes buckled and their surface is rough. Therefore, the nature of reaction wood requires clarification for optimal utilization of wood resources. *Falcataria moluccana* and *Acacia auriculiformis* are important tropical fast-growing plantation species in Southeast Asian countries. The harvested woods from plantations of these species have been utilized for various purposes, including the manufacture of pulpwood and plywood (Soerianegara and Lemmens 1994). However, only limited reports are available for the anatomy of tension wood in tropical fast-growing species (Shiokura and Lantican 1987, Nugroho et al. 2013). In the present study, we investigated the anatomical, chemical, and physical characteristics of tension wood formation in *F. moluccana* and *A. auriculiformis*.

MATERIALS AND METHODS

Materials

Two 3-year-old seedlings of *F. moluccana* (1.1 m in height and 1.5 cm in diameter at the base) and two 2-year-old seedlings of *A. auriculiformis* (1.3 m in height and 2.0 cm in diameter at the base) were used for the experiments. The seeds were provided by the Indonesian Institute of Sciences and the seedlings were grown under tropical conditions (range from 19 to 25℃ in temperature and from 84 to 97% in relative humidity) in a greenhouse at Utsunomiya University, Japan.

From the middle of April to the middle of September, 2008, pots containing the seedlings of both species were tilted at 50° from a vertical position to induce the formation of tension wood (Fig. 1). The main stems of the remaining seedlings of both the species were maintained in a vertical position to allow normal wood formation. During this period, upward bending occurred in the seedlings of both the species (Fig. 1). Due to the obscure color of reaction wood in hardwood species, each stem was pinned with a small nail to identify the area of secondary xylem after inclination. After 5 months, all the seedlings were cut. Then, 1-cm thick disks were sectioned from three positions of the main stems: (1) lower position, (2) middle position, and (3) upper

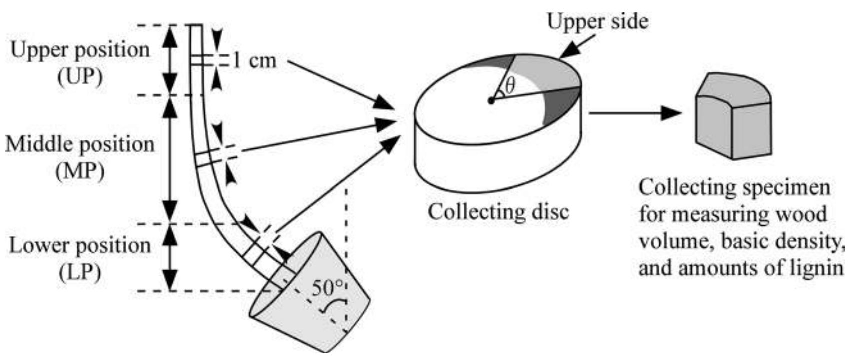

Fig. 1. Diagram showing tension wood formation and sampling methods. The sample disks were collected at three different positions [lower (LP), middle (MP), and upper (UP) positions, respectively]. In both the species, the upper position was approximately 0° from the vertical position. After identifying the tension wood position, small specimens in the central angle at 45° (θ) were prepared for measuring the basic density, wood volume, and lignin content. The shadow area is the tension wood area identified by the pinning method.

position (Fig. 1). In the normal wood, disks were collected from the stem at 20–70 cm from the base. Stems in the upper position were maintained at almost 0° from a vertical position. All the stems were fixed with 3% glutaraldehyde in phosphate buffer (pH = 7.0) for a day and then washed under running tap water for a day.

Anatomical characteristics

Small wood specimens were collected from the upper side of the inclined stems and normal wood. Transverse sections (15 μm in thickness) were obtained by using a sliding microtome (ROM-380, Yamatokohki). Some sections were double stained with safranine and fast green, whereas others were stained with a zinc chloride-iodine solution to detect the G-layer and with phloroglucinol-HCl and Mäule reagents to observe the lignin distribution. To determine the area percentage of the G-layer, digital images of the transverse sections stained with zinc chloride-iodine solution were obtained by an optical microscope (BX51, Olympus) equipped with a digital camera (E-P3, Olympus). Three digital images (40 × 40 μm in actual size), including only wood fibers with a G-layer, were processed using the Photoshop software ver. 7.0 (Adobe Systems Incorporated). The area of the G-layer was measured with image analysis software (ImageJ, National Institute of Health). The area percentage of the G-layer was calculated by dividing the measured area of the G-layer by the total area of the digital images (160 μm^2). The average of the three measurements made at each position was used to calculate the mean area percentage of the G-layer. The double stained sections were dehydrated with a graded ethanol series. The dehydrated sections were then dipped into xylene and mounted with biolite. Digital images of the transverse sections were also obtained with an optical microscope, which was equipped with a digital camera. The diameter of the vessels were measured using ImageJ software. In each sample, the diameters of 30 vessels were measured in radial and tangential directions, and the mean diameter was calculated based on the average of the values in the radial and tangential directions. To determine vessel frequency (number of vessels in each digital image), four transverse digital images were taken from each position, and number of vessels were then counted. The average values from four images were used to calculate the mean vessel frequency value. To estimate the microfibril angle of the S_2 or G- layer, 30 pit aperture angles of wood fiber were measured using a scanning electron microscope (JCM-5000, JEOL).

Lignin distribution and content

Lignin distribution in the secondary wall of wood fiber was observed using phloroglucinol-HCl and Mäule reactions. Subsequently, the absorption spectra of the sections were obtained at 450–650 nm using a microspectrophotometer (UMSP50, Carl Zeiss) according to a method previously reported (Aiso et al. 2013). Due to the temporary nature of the color reactions, measurements were made within 15 minutes.

The lignin content in each sample was determined three times by the acetyl bromide method (Iiyama and Wallis 1988).

Basic density

To determine the basic density, six small wood specimens [ca. 3 (R) × 5 (T) × 10 (L) mm] were collected from each position on the upper side of the inclined samples and the normal wood (Fig. 1). The green volume of the specimens was measured by the water displacement method, and the weight was measured after oven-drying at 105 ± 3℃. The basic density was calculated by dividing the oven-dried weight by the green volume, and the mean values were then calculated based on the average basic density measurements in each wood specimen.

Estimation of biosynthesized lignin and polysaccharides contents

Biosynthesized lignin and polysaccharides contents per unit volume were estimated at each position in normal wood and tension wood. The normal wood and tension wood positions in the disks were estimated by the pinning method (Fig. 1). The area of tension wood was determined by photomicrographs using ImageJ software, followed by the calculation of the wood volume of tension wood position in 1 cm thickness. The wood weight was calculated by multiplying basic density by the estimated volume. Biosynthesized lignin (BL) and biosynthesized polysaccharides (BP) per unit volume were calculated by the following equations:

$$BL\ (g\ cm^{-3}) = W \times (L/100)/V$$

$$BP\ (g\ cm^{-3}) = W/V - BL$$

, where W is substantial wood weight (g) calculated by multiplying the area by 1 cm (thickness of disk), L (%) is the lignin content determined by the acetyl bromide method, and V is estimated wood volume (cm^3).

Table 1. Anatomical and chemical characteristics, and basic density of normal and upper side of inclined stem in *Falcataria moluccana*, *Acacia auriculiformis*, and other fast-growing tree species.

Species	Position	Area percentage of G-layer (%)	Vessel diameter (μm)	Vessel frequency (No. mm^{-2})	Pit aperture angle of wood fiber (degree)	Lignin (%)	Basic density (g cm^{-3})
Falcataria moluccana	NW	*	113.6 ± 22.4 ab	4.0 ± 0.3 ab	28.8 ± 1.2 a	24.1 ± 0.6 a	0.30 ± 0.01 b
	LP	39.4	84.4 ± 10.5 c	3.1 ± 0.5 b	1.1 ± 0.6 d	10.9 ± 0.7 c	0.52 ± 0.07 a
	MP	*	111.3 ± 20.0 b	3.6 ± 0.5 b	22.0 ± 2.3 c	20.8 ± 1.1 b	0.32 ± 0.03 b
	UP	*	125 ± 18.3 a	4.5 ± 0.5 a	27.3 ± 2.4 b	23.4 ± 1.0 a	0.30 ± 0.02 b
Acacia auriculiformis	NW	*	104.3 ± 15.6 a	12.5 ± 1.7 a	27.6 ± 1.1 a	20.8 ± 0.6 a	0.58 ± 0.02 ab
	LP	46.0	70.6 ± 11.5 c	10.4 ± 0.8 a	1.1 ± 0.4 b	15.9 ± 1.5 b	0.62 ± 0.02 a
	MP	37.5	73.5 ± 14.3 bc	10.4 ± 0.6 a	1.0 ± 0.3 b	17.7 ± 0.3 b	0.54 ± 0.04 b
	UP	*	80.8 ± 16.8 b	11.0 ± 0.7 a	27.2 ± 1.4 a	21.0 ± 1.3 a	0.51 ± 0.09 b
Falcataria moluccana[1)]	OW	−	230 − 300	−	−	−	0.26 − 0.30**
	TW	−	180 − 200	−	−	−	0.31 − 0.41**
Eucalyptus camaldulensis[2)]	NW	−	−	22.5 ± 0.7	22.3 ± 1.7	21.1	−
	TW	−	−	9.6 ± 1.3	3.5 ± 1.0	6.5	−
Acacia mangium[3)]	NW	−	44.7 ± 1.0	51.8 ± 2.6	−	−	−
	TW	−	35.8 ± 0.8	33.4 ± 1.5	−	−	−

NW, LP, MP, and UP, refer to Fig. 2. OW, opposite wood; TW, tension wood; 1), Shiokura and Lantican (1987); 2), Baba et al. (1996); 3), Nugroho et al. (2013). Asterisks indicate no G-layer formation. Values with double asterisks are oven-dry density. The same alphabets followed by means and standard deviations indicate no significant difference by TukeyHSD test ($p < 0.05$). Lignin (%) indicates lignin content per extracted oven-dried wood weight.

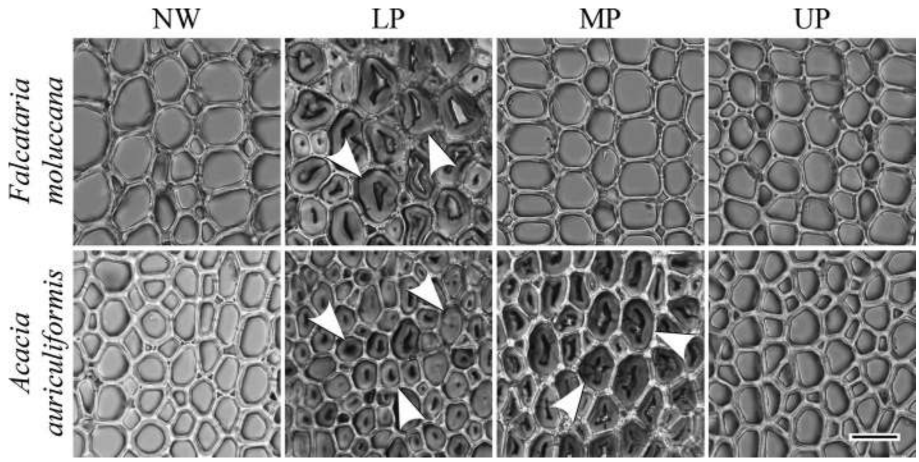

Fig. 2. Photomicrographs of transverse sections stained with a zinc chloride-iodine solution. Arrowheads indicate the G-layer. Scale bar = 20 μm. NW, normal wood; LP, lower position; MP, middle position; UP, upper position.

RESULTS

Anatomical characteristics

A distinct G-layer was observed at the lower position in *F. moluccana* and at the lower and middle positions in *A. auriculiformis*, whereas it was not observed at the other positions in either of the species (Fig. 2). The area percentage of the G-layer was 39.4% at the lower position in *F. moluccana*, and 46.0% and 37.5% at the lower and middle positions, respectively, in *A. auriculiformis* (Table 1).

In both species, significant differences were observed in the vessel morphologies of the normal wood and tension wood (Table 1 and Fig. 3). In *F. moluccana*, the vessel diameter greatly decreased at the lower position in tension wood compared with that in the normal wood and at the other positions. In contrast, similar values of vessel diameter were noted in the normal wood and at the middle and upper positions. However, there were no significant changes in the vessel frequency between normal wood and various positions (i.e., lower, middle, and upper). On the other hand, in *A. auriculiformis*, the vessel diameters were significantly decreased in at all positions of tension wood compared with that of the normal wood, whereas no significant changes were found in the vessel frequency among the normal wood and respective positions.

The pit aperture angles of wood fibers in normal wood were 28.8 ± 1.2° and 27.6 ± 1.1° for *F. moluccana* and *A. auriculiformis*, respectively (Table 1 and Fig. 4). Similar values were observed at the upper position in both the species. In *F. moluccana*, the smallest pit aperture angle of wood fiber was observed at the lower position, although it slightly decreased at the middle position. In *A. auriculiformis*, the pit aperture angle of the wood fiber significantly decreased at the lower and middle positions.

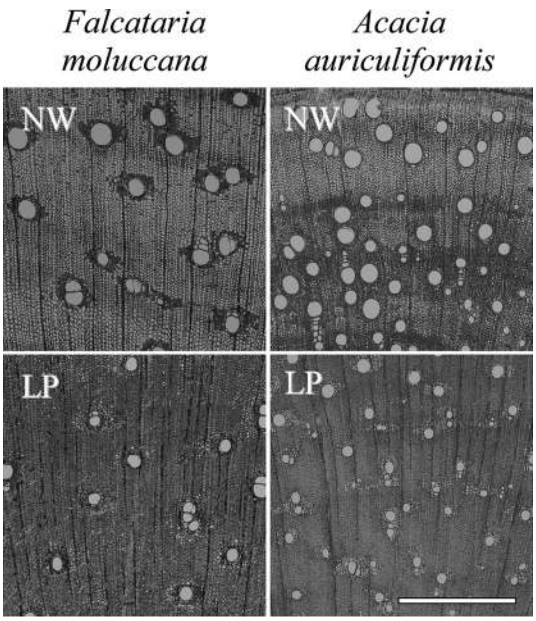

Fig. 3. Photomicrographs of transverse sections stained with safranine and fast green. Scale bar = 300 μm. NW, normal wood; LP, lower position.

Lignin distribution and content

In *F. moluccana*, the lowest absorbances were observed in the lower position at 550 nm after phloroglucinol-HCl color reaction and at 520 nm after Mäule color reaction (Fig. 5). On the other hand, in *A. auriculiformis*, the lowest absorbance at 550 nm after the phloroglucinol-HCl color reaction was obtained in the middle position, whereas the lowest absorbance at 520 nm after Mäule color reaction was observed in the lower position. There was a significant decrease in the lignin content in the lower and middle positions of both the species (Table 1).

Basic density

In *F. moluccana*, the basic density of the normal wood and that of the lower position significantly differed, whereas no such difference was observed between the basic density of the normal wood and that of the middle and upper positions (Table 1). In *A. auriculiformis*, the basic density of the wood at the three positions was not significantly different from that of the normal wood.

Estimated biosynthesized lignin and polysaccharide content

Compared to that of normal wood, the biosynthesized polysaccharide increased at the lower position in both the species. However, the biosynthesized lignin was not significantly different at any of the three sampling positions in either of the species. In *F. moluccana*, the lignin to polysac-

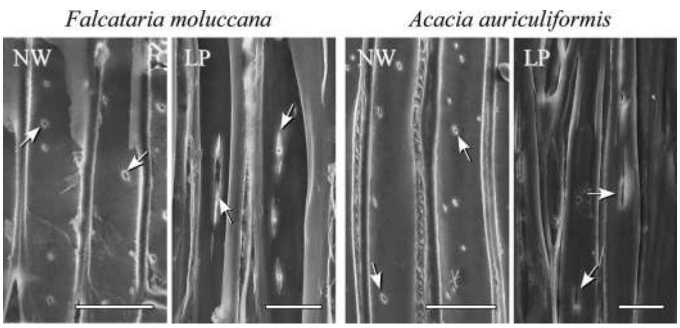

Fig. 4. Scanning electron microphotographs of radial specimens. Arrows indicate the pit aperture. Scale bar = 20 μm. NW, normal wood; LP, lower position.

charide ratio in normal wood was lower (1.00 : 3.29) than that of *A. auriculiformis* (1.00 : 3.75) (Table 2). At the lower position in *F. moluccana*, the lignin to polysaccharide ratio was remarkably different (1.00 : 7.67) (Table 2). The ratio also increased in the lower and middle positions of *A. auriculiformis*. However, in *F. moluccana*, the ratio at the middle and upper positions was almost the same as that in the normal wood.

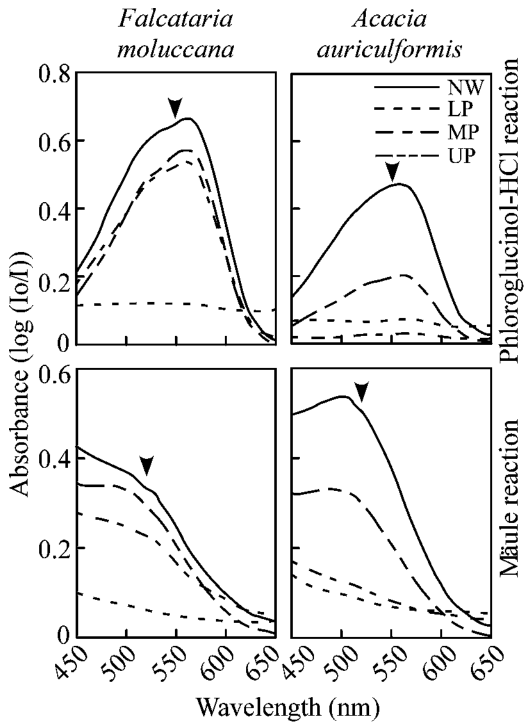

Fig. 5. Visible-light absorption spectra of the wood fibers after phloroglucinol-HCl and Mäule stainings. NW, normal wood; LP, lower position; MP, middle position; UP, upper position. Arrowheads indicate absorbance at 550 nm and 520 nm with phloroglucinol-HCl and Mäule stainings, respectively.

DISCUSSION

Anatomical, chemical, and physical characteristics

In temperate angiosperms, several studies have reported that reaction wood is characterized by the presence of the G-layer with small microfibril angle, lower lignin and higher cellulose contents and fewer and a smaller diameter of vessel (Onaka 1949, Panshin and de Zeeuw 1980, Joseleau et al. 2004, Daniel et al. 2006, Yoshinaga et al. 2012). Some angiosperms, such as genera of *Magnolia* and *Liriodendron*, are known to form "tension-wood-like reaction wood" because they do not form a typical G-layer by reaction wood formation. These exhibit similar anatomical and chemical characteristics to those of "typical" tension wood (Onaka 1949, Yoshida et al. 2000, Yoshizawa et al. 2000, Hiraiwa et al. 2014). A similar tendency has also been reported in tropical angiosperms (Shiokura and Lantican 1987, Baba et al. 1996, Clair et al. 2006, Ruelle et al. 2006, Mukogawa et al. 2008, Nugroho et al. 2013). Nugroho et al. (2013) reported a decrease in vessel diameter and frequency in tension wood of *Acacia mangium*, which forms a typical G-layer in wood fibers. Another study reported that in tension wood of *Eucalyptus camaldulensis*, the microfibril angle of the wood fiber G-layer showed almost 0° from a vertical and lignin content was lower than that of normal wood (Baba et al. 1996). In angiosperms, reaction wood with these characteristics is regarded as "typical" tension wood. Clair et al. (2006) investigated the presence of the G-layer in the reaction wood of 21 tropical angiosperms. They found that 14 of the species did not form the "typical" tension wood by reaction wood formation. Among these 14 species, the microfibril angle of the S_2 layer decreased in 13 of the species that did not form a G-layer (Ruelle et al. 2006), suggesting that the reaction woods in these species

Table 2. Estimated amounts of lignin and polysaccharides per unit volume of normal and upper side of inclined stem in *Falcataria moluccana* and *Acacia auriculiformis*.

Species	Position	Estimated biosynthesized lignin (BL, g cm^{-3})	Estimated biosynthesized polysaccharide (BP, g cm^{-3})	Ratio (BL : BP)
Falcataria moluccana	NW	0.07	0.23	1.00 : 3.29
	LP	0.06	0.46	1.00 : 7.67
	MP	0.07	0.24	1.00 : 3.43
	UP	0.07	0.23	1.00 : 3.29
Acacia auriculiformis	NW	0.12	0.45	1.00 : 3.75
	LP	0.10	0.52	1.00 : 5.20
	MP	0.10	0.46	1.00 : 4.60
	UP	0.11	0.39	1.00 : 3.55

NW, LP, MP, and UP, refer to Fig. 2.

can be considered "tension-wood-like reaction wood". On the other hand, lignin in angiosperms is mainly composed of syringyl and guaiacyl units (Lin and Dence 1992). It has been reported that phloroglucinol-HCl reagents stain coniferyl and sinapyl aldehyde units in lignin, and an absorption maximum in the visible-light absorption spectra is observed at approximately 550 nm; the spectra obtained by Mäule reaction showed an absorption maximum at approximately 520 nm, indicating the presence of syringyl units (Lin and Dence 1992, Yoshizawa et al. 2000). Apparent peaks are generally not found in the G-layer after staining with phloroglucinol-HCl and Mäule reactions because the G-layer is mostly composed of cellulose (Joseleau et al. 2004, Daniel et al. 2006). In the present study, no apparent peaks were found at approximately 550 nm and 520 nm after phloroglucinol-HCl and Mäule color reactions, respectively, in the lower position in *F. moluccana* and lower and middle positions in *A. auriculiformis* (Fig. 5). These results suggest that both the syringyl and guaiacyl lignin remarkably decreased by the reaction wood formation. In addition to the formation of the distinct G-layer, significant decreases in the vessel diameter, microfibril angle of the wood fiber G-layer, and lignin content were observed at the lower position in *F. moluccana*, and lower and middle positions in *A. auriculiformis* (Table 1, and Figs. 2, 3, and 4). These changes in the anatomical and chemical characteristics by tension wood formation were similar to those reported in earlier studies in tropical angiosperms (Shiokura and Lantican 1987, Baba et al. 1996, Nugroho et al. 2013, Table 1). Based on these results, it can be said that *F. moluccana* and *A. auriculiformis* form "typical" tension wood in xylem when their stems are inclined.

Panshin and de Zeeuw (1980) pointed out that the thick-walled G-layer increases the density of tension wood. However, Ishiguri et al. (2012) reported a significant increase in the basic density of "typical" tension wood in two species (*Castanea crenata* and *Acer crataegifolium*) and a decrease in one species (*Cerasus jamasakura*) out of three temperate Japanese angiosperms investigated. Ruelle et al. (2007) investigated air-dry density in opposite and tension wood of 10 tropical angiosperms grown in French Guiana. Among the 10 species studied, the air-dry density significantly increased in three species (*Ocotea guyanensis*, *Carapa procera*, and *Qualea rosea*), and decreased in two species (*Miconia fragilis* and *Virola surinamensis*). No significant changes in air-dry density were found in five species (*Cecropia sciadophylla*, *Eperua falcate*, *Laetia procera*, *Eschweilera decolorens*, and *Simarouba amara*). In the present study, the basic density in the lower position of *F. moluccana* significantly increased in response to tension wood formation (Table 1). However, there were no significant changes in the basic density in the lower and middle positions of *A. auriculiformis* (Table 1). If the G-layer thickness was related to the basic density, changes in the basic density due to tension wood formation would be related to result in changes in the cellulose content. As shown in Table 2, the biosynthesized lignin content (per unit volume) did not differ among the positions in either of the species. However, secondary xylem at the lower position of *F. moluccana* showed the G-layer formation (Fig. 2), a remarkable increase in biosynthesized polysaccharide content, and a significant increase in basic density (Tables 1 and 2). These results suggest that changes in the basic density due to tension wood formation in *F. moluccana* may result only in an increase in biosynthesized polysaccharide content. On the other hand, the biosynthesized polysaccharide content was slightly different in the lower and middle positions of *A. auriculiformis*, and the ratio of biosynthesized lignin to biosynthesized polysaccharide was lower than that in the lower position of *F. moluccana*. These differences may be related to slight or no changes in basic density in the lower and middle positions of *A. auricullformis* (Table 1).

Differences in the degree of reaction wood development at the three positions

It has been reported that the degree of reaction wood formation differs by the magnitude of the inclination stimulus (Yumoto et al. 1983, Yoshizawa 1987, Yoshida et al. 2000, Hiraiwa et al. 2014). Yoshida et al. (2000) reported that the value of surface-released strain, which is closely related to the degree of reaction wood, gradually decreased toward the tip side in inclined *Liriodendron tulipifera* stems. They concluded that once the orientation of the stems was restored, large growth stress was not required anymore. In the present study, compared to normal wood, the G-layer formation and significant changes in all anatomical and chemical characteristics, except for vessel frequency, were observed in the lower position of *F. moluccana* and in the lower and middle positions of *A. auriculiformis*. Although the inclination method was common for both the species, the position of the G-layer formation differed between the two species, suggesting that the degree of response to an inclination stimulus varies among species.

Yumoto et al. (1983) investigated the effect of differences in the inclination angle of stems in *Picea glauca* seedlings on the degree of reaction wood formation. They reported that the degree of reaction wood development was classified by the degree of development of helical cavity and the degree of excessive lignification. On the other hand, the effect of inclination angle of stems on the degree of reaction wood formation was also evaluated in temperate broad-leave tree species, *L. tulipifera*, which does not form typical G-layer in their reaction wood (Hiraiwa et al. 2014). They found that the degree of reaction wood formation could be evaluated by the microfibril angle of wood fiber and the lignin content. In the present study, a distinct G-layer was not formed in the middle position of *F. moluccana*, although the pit aperture angle of wood fiber and the lignin content (particularly that of the secondary wall of the wood fiber) significantly decreased. However, the peak at 550 nm after the phloroglucinol-HCl reaction was observed in the middle position of *F. moluccana*, in which the lignin content significantly decreased (Fig. 5). Thus, it is considered that a low degree of tension wood was formed in the middle position of *F. moluccana*. Therefore, the degree of reaction wood development in the tropical fast-growing tree species used in the present study may also be evaluated by the degree of decrease in the microfibril angle of wood fiber and lignin content.

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