55～60

宇　大　演　報
第53号（2017）論　文

Bull. Utsunomiya Univ. For.
No. 53（2017）Article

Effects of different inclination angle of stems on anatomical and chemical characteristics of tension wood in *Cercidiphyllum japonicum* Sieb. et Zucc.

幹の傾斜角度の違いがカツラ引張あて材の組織学的・化学的特徴に及ぼす影響

Haruna Aiso, Saori Kezuka, Tokiko Hiraiwa, Futoshi Ishiguri, and Shinso Yokota
相蘇 春菜・毛塚 沙織・平岩 季子・石栗 太・横田 信三

Faculty of Agriculture, Utsunomiya University, Utsunomiya 321-8505, Japan
宇都宮大学農学部　〒 321-8505　宇都宮市峰町 350

ABSTRACT

Objectives of this study are to clarify the effects of different inclination angle of stems on surface-released strain, and anatomical and chemical characteristics of tension wood in *Cercidiphyllum japonicum* Sieb. et Zucc. Stems of seedlings were inclined at 0, 30, 50, and 70 degree from the vertical to promote the tension wood formation. Surface-released strain in inclined stems at all angles showed larger negative values compared to normal wood. Radial growth promotion on upper side was confirmed in all inclined stems, and eccentric growth ratio increased with increase of stem inclination angle. In the all inclined stems, formation of gelatinous (G)-layer and lack of S_3 layer were observed in wood fiber. Significant decrease in number and diameter of vessel, and pit aperture angle of wood fiber were observed on the all tension wood samples compared with those in normal wood, except for vessel diameter in the tension wood sample at 30 degree of inclination angle. Compared to normal wood, tension wood samples showed lower lignin and xylose contents, whereas higher glucose, arabinose, and galactose contents. Almost all anatomical and chemical characteristics were gradually altered with increase in stem inclination angle. However, vessel frequency, MFA, and lignin and galactose contents started to change at 30 degree of stem inclination angle, and these values were almost the same at other inclination angles. It is considered that rapid alteration in these four characteristics might be important for supporting inclined stems in *C. japonicum*.

Keywords: reaction wood, vessel morphology, microfibril angle, cell wall layer structure, chemical components

要　旨

本研究では、幹の傾斜角度の違いが引張あて材の表面解放ひずみ、組織学的・化学的特徴に及ぼす影響を明らかにするために、カツラ（*Cercidiphyllum japonicum* Sieb. et Zucc.）苗木の幹を異なる傾斜角度（0、30、50 および 70°）で固定して生育し、あて材形成を促した。表面解放ひずみは、いずれの傾斜角度の個体においても、0° に固定して生育した個体（正常材）と比較して、大きい負の値を示した。また、いずれの角度で傾斜した個体においても、傾斜上側への偏心成長が認められ、偏心率は、傾斜角度が増加するにつれて大きい値を示した。傾斜して生育したすべての個体の木繊維において、ゼラチン（G）層の形成と S_3 層の欠如が引張あて材部で認められた。また、引張あて材部では、傾斜角度 30° における道管直径を除いて、道管直径と数の減少および木繊維壁孔孔口の角度の減少が認められた。さらに、正常材と比較すると、引張あて材において、リグニンおよびキシロース量が減少し、反対にグルコース、アラビノースおよびガラクトース量が増加する傾向が認められた。これらの組織学的・化学的特徴のほとんどは、幹の傾斜角度の増加とともに変化する傾向が認められた。一方、道管数、ミクロフィブリル傾角、リグニン量およびガラクトース量は、傾斜角度 30° で変化し、その後、傾斜角度が増加しても値はほとんど同じであった。このことから、これら 4 つの形質は、カツラの傾斜した幹や枝を支持する際に重要な形質であると考えられる。

キーワード：あて材、道管形態、ミクロフィブリル傾角、壁層構造、化学成分量

1. Introduction

Woody plants develop specific tissue against gravitational and/or inclination stimulus (Onaka 1949; Scurfield and Wardrop 1962; Timell 1969; Yoshizawa 1987; Evert 2006; Groover 2016). This specific tissue is called as reaction wood. The reaction wood forms to return the axis of a leaning tree to the normal or vertical position, or maintain the original equilibrium position with regard to branch (Onaka 1949; Timell 1969; Yoshizawa 1987; Evert 2006; Groover 2016). In general, reaction wood in gymnosperms is called as compression wood, because excessive compressive growth stress occurrs on the lower side of inclined stems or branches (Onaka 1949; Yoshizawa 1987; Evert 2006; Groover 2016). Conversely, many angiosperms form reaction wood, generally referred to tension wood, on the upper side of inclined stems or branches (Onaka 1949; Timell 1969; Evert 2006; Hiraiwa *et al*. 2013; Aiso *et al*. 2016b; Groover 2016). Tension wood is characterized by the presence of gelatinous (G-) layer in the secondary wall of wood fiber (Onaka 1949; Scurfield and Wardrop 1962; Evert 2006; Groover 2016). Formation of G-layer, which has almost parallel microfibril orientation to the longitudinal direction of wood fiber, generates the greater tensile growth stress on the upper side of leaning stem or branches (Araki *et al*. 1983; Okuyama *et al*. 1994; Yoshida *et al*. 2000; Yamamoto 2004; Aiso *et al*. 2016b; Hung *et al*. 2016).

In both gymnosperms and angiosperms, the degree in development of reaction wood has been evaluated by growth eccentricity, growth stress, anatomical characteristics, and gene expression (Onaka 1949; Yumoto *et al*. 1983; Okuyama *et al*. 1994; Yamamoto and Okuyama 1994; Yoshida *et al*. 2000; Donaldson *et al*. 2004; Yamashita *et al*. 2009; Hiraiwa *et al*. 2007, 2013, 2014; Hung *et al*. 2016). The degree of development in compression wood is classified into “mild” to “severe” according to microscopic features, such as lignification of S_2 layer, circularity, intercellular space, and helical cavity in the secondary wall of tracheid (Yumoto *et al*. 1983). Recently, degree of expression in certain genes related to compression wood formation was also altered with increase in stem inclination angle of *Chamaecyparis obtusa* (Yamashita *et al*. 2009). Thus, many researchers have been concluded on the relationship between different stem inclination angle and degree in development of compression wood. On the other hand, in the development of tension wood, it has been pointed out that longitudinal tensile growth stress is related to increase in the transverse sectional area of the G-layer: the larger the growth stress, the greater the degree of tension wood development (Okuyama *et al*. 1994; Yamamoto and Okuyama 1994; Yoshida *et al*. 2000; Hung *et al*. 2016). The relationship between growth stress and degree of tension wood development was also clarified in some angiosperms which do not form G-layer in reaction wood on the upper side of inclined stems or branches (Yoshida *et al*. 2000; Hiraiwa *et al*. 2014). However, available information is still limited about effects of the difference in stem inclination angle or stimulus on the changes in anatomical and chemical characteristics of tension wood (Yoshida *et al*. 2000; Hiraiwa *et al*. 2007, 2013, 2014).

Cercidiphyllum japonicum Sieb. et Zucc. (katsura in Japanese) is known as a temperate angiosperm (Itoh 1996). *C. japonicum* forms ‘typical’ tension wood with G-layer in wood fiber: the secondary wall is consisted of S_1 + G-layer and S_1 + S_2 + G-layer (Onaka 1949; Saiki and Ono 1971; Araki *et al*. 1983). Objective of this study is to clarify the effects of the different inclination angle of stems on the intensity of growth stress, and anatomical and chemical characteristics in *C. japonicum*.

2. Materials and methods

Four 5-year-old katsura (*Cercidiphyllum japonicum* Sieb. et Zucc.) trees were used in this study. Mean height in these trees was approximately 2.0 m, and these trees were planted and grown in a nursery of Utsunomiya University, Japan (139° 55' E, 36° 33' N). In the beginning of November 2008, one tree were fixed 0 degree from the vertical as normal wood. Three trees were inclined and fixed in each angle (30, 50, or 70 degree) from the vertical by using poles, respectively.

After 17 months, surface-released strains were measured on the surface of xylem on random positions of normal wood and on the upper sides of all inclined samples by using strain gauge method (Sasaki *et al*. 1978). After measuring the surface-released strain, all trees were cut, and then 1-cm thick disks were prepared from the position nearby that for measuring surface-released strain. The disks were subsequently treated with 0.8 M sucrose aqueous solution for plasmolysis, and then fixed in 3% glutaraldehyde in phosphate buffer (pH 7.0). All the disks were stored in 50% ethanol aqueous solution.

To determine eccentricity, some disks were polished on their transverse sections by using sandpaper. The transverse sectional images of the disks were taken by using a digital camera, and then length of radius on the upper and the lower sides of the disk was measured by ImageJ software (National Institute of Health). In the present study, length of radius was defined as the distance from the initial position in the previous annual ring to cambium. Eccentricity was calculated by dividing length of radius on the upper side by that on the lower side. In the case of normal wood, eccentricity was calculated by using length of radius at random positions and that on its opposite side. In this study, all the following experiments were carried out on the upper sides of inclined samples and at random positions of normal wood.

Small wood blocks (10 (L) × 10 (R) × 5 (T) mm) including previous and current annual rings were prepared from the disks of each sample. Transverse sections (15 µm in thickness) were prepared by using a sliding microtome (ROM-380, Yamatokohki) from these small blocks.

The presence of G-layer was detected by microscopic observation of the transverse section after zinc chloride-iodine color reaction. Transverse sectional images were also taken with a digital camera (E-330, Olympus) equipped to a light microscope (BX51, Olympus). The images were trimmed into square image (35 × 35 µm) including only wood fibers by using Adobe Photoshop7.0 software (Adobe). Area percentage of G-layer was defined as the value obtained by dividing total area of G-layer in the image by the area of square images (1225 µm^2). In addition, non-stained and safranin-stained sections were prepared, and diameter and frequency of vessel were measured by the methods described in our previous reports (Aiso *et al*. 2016a, b).

Small wood sticks were also collected from the disks and macerated with Schulze's solution. Length of 80 wood fibers and 30 vessel elements was measured according to the method described by Aiso *et al*. (2013).

The radial blocks in 1-mm thickness were collected to measure pit aperture angle of wood fiber using a scanning electron microscope (SEM, JCM-5000, JEOL). Pit aperture angle of wood fiber is regarded as microfibril angle of S$_2$ layer in wood fiber, because the value of pit aperture angle of wood fiber is almost the same value as microfibril angle (MFA) of its S$_2$ layer (Donaldson 1991).

Mäule and phloroglucinol-HCl color reactions were applied to observe the lignin distribution according to the methods described in previous report (Yoshizawa *et al*. 1999).

To determine chemical composition, wood meal (42 to 80 mesh) was prepared from small wood blocks obtained for each sample using a Wiley mill. Lignin content was determined by acetyl bromide method according to Iiyama and Wallis (1988). Monosaccharide (glucose, xylose, arabinose, and galactose) contents were quantified by the method described in previous report (Hiraiwa *et al*. 2013).

3. Results

Higher values of surface-released strains were obtained in the all inclined samples compared to the normal wood (Table 1). Of three different inclination angles, the stems inclined at 50 and 70 degrees showed larger negative values (*ca*. -1,200 µε).

The tension wood samples exhibited a radial growth promotion on the upper side (Table 1). The stems inclined at 70 degrees showed the greatest eccentric growth ratio (5.3) among three inclination angles of stem.

G-layer was formed in all tension wood samples (Figure 1). Among these samples, tension wood samples at inclination angles of 50 and 70 degrees gave the larger area of G-layer (69.9% and 67.7%, respectively) compared to that at 30 degrees (62.8%) (Table 1). These wood fibers with G-layer lacked S$_3$ layer, whereas S$_3$ layer was present in the wood fiber of normal wood (Figure 2).

As shown in Table 2, significant decrease in number and diameter of vessels, and pit aperture angle of wood fiber were observed on the all tension wood samples compared with those in normal wood, except for vessel diameter in tension wood samples at 30 degree of inclination angle. The length of wood fiber significantly increased in almost all tension wood samples compared to that in normal wood, whereas significant difference in vessel element length was found only in the tension wood samples at 50 degree of inclination angle (Table 2). Values of wood fiber increment in all tension wood samples showed larger values compared to that in normal wood

Table 1. Surface-released strain, length of radius, and area percentage of G-layer in the normal and tension woods of *C. japonicum*.

IA (degree)	Surface-released strain (µε)	Length of radius (mm)			Area percentage of G-layer (%)
		US	LS	Ratio (US/LS)	
0 (NW)	-145	2.0	1.5	1.3	-
30	-745	5.1	1.8	2.8	62.8
50	-1204	5.0	1.5	3.3	69.9
70	-1211	4.2	0.8	5.3	67.7

IA, inclination angle; NW, normal wood; US, upper side; LS, lower side; '-' indicates no G-layer formation in area percentage of G-layer.

Table 2. Vessel morphology and cell length on the normal and tension woods of *C. japonicum*.

IA (degree)	Vessel frequency (No./mm^2)	Vessel diameter (µm)	Cell length (mm)			Pit aperture angle of wood fiber (degree)
			Wood fiber	Vessel element	Wood fiber increment	
0 (NW)	256 ± 40	36.8 ± 10.3	1.06 ± 0.20	0.87 ± 0.14	0.19	30.0 ± 3.0
30	$137 \pm 33^{**}$	38.5 ± 11.7^{ns}	$1.17 \pm 0.17^{**}$	0.93 ± 0.17^{ns}	0.24	$2.0 \pm 1.2^{**}$
50	$135 \pm 18^{**}$	$31.1 \pm 8.5^{**}$	1.08 ± 0.16^{ns}	$0.78 \pm 0.11^{*}$	0.30	$2.3 \pm 1.0^{**}$
70	$175 \pm 40^{*}$	$30.6 \pm 9.0^{**}$	$1.13 \pm 0.21^{*}$	0.83 ± 0.13^{ns}	0.30	$2.4 \pm 1.3^{**}$

IA, inclination angle; NW, normal wood; *, significance at 5% level by student's t-test; **, significance at 1% level by student's t-test; ^{ns}, no significance.

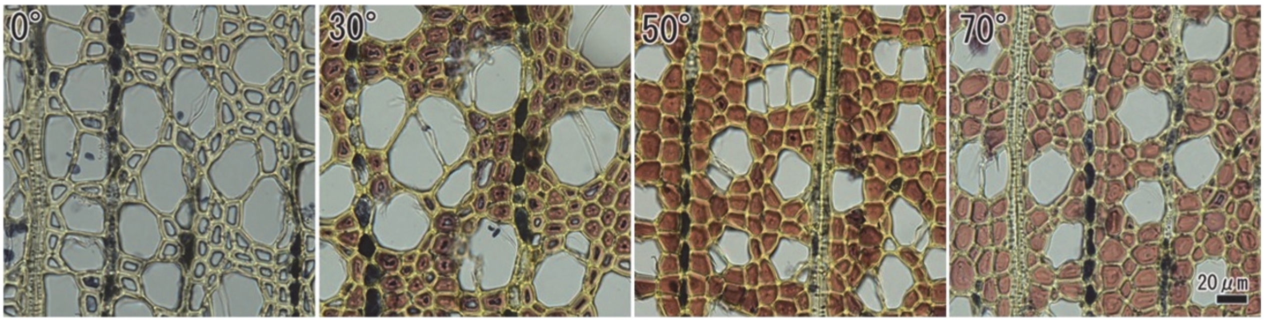

Figure 1. Photomicrographs of transverse sections of *C. japonicum* after zinc iodine-chloride color reaction.

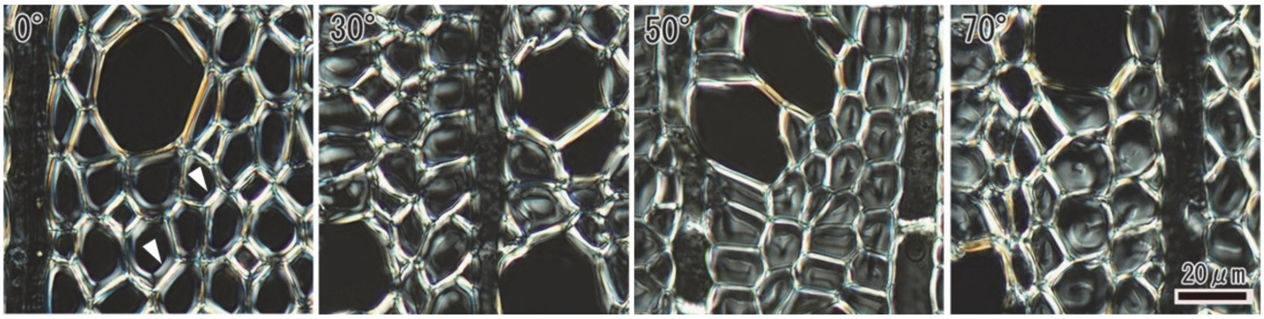

Figure 2. Polarizing photomicrographs of transverse sections without staining in *C. japonicum*. Arrowheads indicate the presence of S_3 layer.

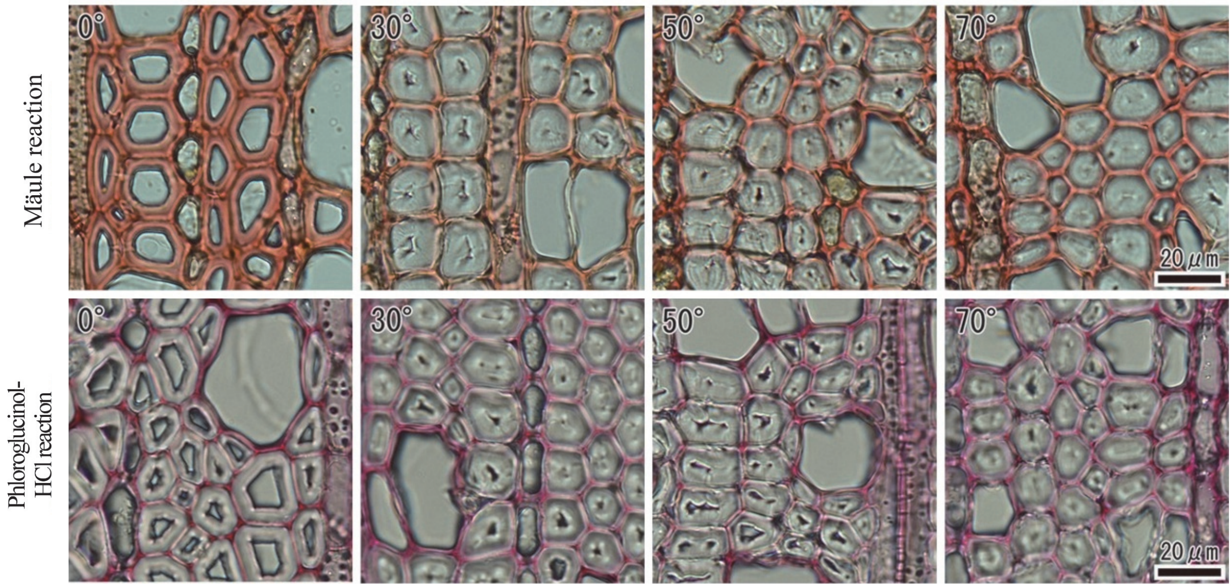

Figure 3. Photomicrographs of transverse sections of *C. japonicum* after Mäule and phloroglucinol-HCl color reactions.

Table 3. Chemical composition on the normal and tension woods of *C. japonicum*.

IA (degree)	Lignin (%)	Glucose (%)	Xylose (%)	Arabinose (%)	Galactose (%)
0 (NW)	24.9	64.9	33.9	0.4	0.8
30	20.9	78.3	17.5	0.8	3.4
50	20.3	83.6	11.3	1.3	3.7
70	20.5	81.8	13.0	1.3	3.9

IA, inclination angle; NW, normal wood.

(Table 2).

After Mäule reaction in normal wood, the compound middle lamellae of cell corner and the secondary wall of vessel showed orange brown, whereas the secondary wall of wood fiber showed pink (Figure 3). The compound middle lamellae of cell corner and vessel wall in normal wood were stained strongly in violet red color after phloroglucinol-HCl reaction compared to the secondary wall of wood fiber (Figure 3). These colorations in compound middle lamellae of cell corner and vessel wall in normal wood were similar to those in tension wood samples, although the G-layer of tension wood fiber was not stained by both reagents (Figure 3).

Table 3 shows chemical composition on the normal and tension woods of *C. japonicum*. Compared to normal wood, tension wood samples contained lower lignin and xylose contents, whereas higher glucose, arabinose, and galactose contents.

4. Discussion

It has been reported that *C. japonicum* forms 'typical' tension wood (Onaka 1949; Saiki and Ono 1971; Araki *et al*. 1983). Eccentric growth, decrease in diameter and frequency of vessels, and changes in wood fiber wall structure to S_1+G and S_1+S_2+G were observed in tension wood of this species (Onaka 1949; Saiki and Ono 1971; Araki *et al*. 1983). Similar characteristics were also observed in the present study.

In chemical composition, Timell (1969) reported that tension wood in several angiosperms with G-layer (*Acer pensylvanicum, A. rubrum, A. saccharum, Betula alleghaniensis, B. papyrifera, Fagus grandifolia, Populus tremuloides, Prunus pensylvanica, Robinia pseudoacacia, and Ulmus americana*) showed lower lignin and xylose contents, slightly higher arabinose and galactose contents, and higher glucose content accompanied with the increase of cellulose content. Changes in lignin and monosaccharides contents due to tension wood formation in *C. japonicum* in the present study were also similar to those obtained by Timell (1969).

Many researchers have been trying to clarify the effect of the difference in inclination stimulus for stem on reaction wood development in angiosperms (Yamamoto and Okuyama 1994; Yoshida *et al*. 2000; Hiraiwa *et al*. 2007, 2013, 2014; Hung *et al*. 2016). Most of these studies clarified the relationship between magnitude of tensile growth stress and degree of tension wood development in angiosperms. On the other hand, Yoshida *et al*. (2000) focused on the effect of inclination angle of stem on the development of reaction woods in *Prunus spachiana* f. *ascendens* and *Liriodendron tulipifera*. They fixed the stems of the seedlings at 0, 10, 20, 30, 40, 50, and 60 degree from the vertical. As the results, they found that surface-released strain and MFA proportionally decreased up to 20 degree, and the stems showed almost constant values for these characteristics from 20 to 60 degree. It is considered that degree of alteration in some anatomical characteristics due to reaction wood formation in angiosperms might correspond to the magnitude of inclination stimulus. Recently, the relationship between difference of stem inclination angle and degree of alteration in chemical composition by reaction wood formation was demonstrated in some angiosperms (Yoshida *et al*. 2000; Hiraiwa *et al*. 2007, 2013, 2014). For example, reaction wood of *L. tulipifera* showed gradual decrease in xylose and lignin contents with increase of inclination angle (Hiraiwa *et al*. 2013). In the present study, almost all anatomical and chemical characteristics were gradually altered with increase in stem inclination angle (Tables 1 to 3). However, vessel frequency, MFA, and lignin and galactose contents changed, and showed almost the same values at all inclination angles (Tables 2 and 3), suggesting that these characteristics are dramatically altered even by smaller inclination stimulus. Decrease in vessel frequency might be related to the increase in the percentage of wood fiber in secondary xylem. In addition, decreases in MFA and lignin content by tension wood formation are contributed to increase in longitudinal Young's modulus of stem (Okuyama *et al*. 1994; Yamamoto 2004). On the other hand, it has been pointed out that (1,4)-*β*-galactan might function for cross-linking between G-layer and secondary cell wall adjacent to G-layer (Arend 2008). Thus, increase in galactose content might be related to increase in cross linking between those two layers in wood fiber. Therefore, it is considered that rapid alteration in these three characteristics might be important factors for restoring inclined stems in *C. japonicum*.

5. Conclusion

Surface-released strain, and anatomical and chemical characteristics were investigated for artificially inclined stems of *Cercidiphyllum japonicum* trees to clarify the effects of inclination stimulus on severity of tension wood. Anatomical and chemical characteristics of inclined stems showed typical tension wood characteristics: larger tensile surface-released strain, eccentric growth on the upper side, decrease in diameter and frequency of vessel, formation of G-layer, lacking the S_3 layer, lower lignin and xylose contents, and higher glucose, arabinose, and galactose contents. Almost all anatomical and chemical characteristics were gradually altered with increase in inclination stimulus. However, vessel frequency, MFA, and lignin and galactose contents altered at all stem inclination angle, and showed almost constant values even at larger inclination angles. It is considered that these four characteristics might be important for restoring inclined stems in *C. japonicum*.

Acknowledgement

The authors express our thanks to late Emeritus Professor Dr. Nobuo Yoshizawa, Faculty of Agriculture, Utsunomiya University, for supporting accomplishment of this study.

References

Aiso H, Hiraiwa T, Ishiguri F, Iizuka K, Yokota S, Yoshizawa N (2013) Anatomy and lignin distribution of "compression-wood-like reaction wood" in *Gardenia jasminoides*. IAWA Journal 34: 263-272

Aiso H, Ishiguri F, Ohkubo T and Yokota S (2016a) Tension wood-like reaction wood in vessel-less *Tetracentron sinense*. IAWA Journal 37: 372-382

Aiso H, Ishiguri F, Toyoizumi T, Ohshima J, Iizuka K, Priadi D, Yokota S (2016b) Anatomical, chemical, and physical characteristics of tension wood in two tropical fast-growing species, *Falcataria moluccana* and *Acacia auriculiformis*. Tropics 25: 33-41

Araki N, Fujita M, Saiki H, Harada H (1983) Transition of fiber wall structure from normal wood to tension wood in certain species having gelatinous fibers of $S_1 + G$ and $S_1 + S_2 + S_3 + G$ types. Mokuzai Gakkaishi 29: 491-499

Arend M (2008) Immunolocalization of (1,4)-β-galactan in tension wood fibers of poplar. Tree Physiology 28: 1263-1267

Donaldson LA (1991) The use of pit apertures as windows to measure microfibril angle in chemical pulp fibers. Wood and Fiber Science 23: 290-295

Donaldson LA, Grace J, Downes GM (2004) Within-tree variation in anatomical properties of compression wood in radiata pine. IAWA Journal 25: 253-271

Evert RF (2006) Xylem: cell types and developmental aspects. In: Esau's plant anatomy. Wiley, New Jersey, pp 291-322

Groover A (2016) Gravitropisms and reaction woods of forest trees - evolution, functions and mechanisms. New Phytologist 211: 790-802

Hiraiwa T, Yamamoto Y, Ishiguri G, Iizuka K, Yokota S, Yoshizawa N (2007) Cell wall structure and lignin distribution in the reaction wood fiber of *Osmanthus fragrans* var. *aurantiacus* Makino. Cellulose Chemistry and Technology 41: 537-543

Hiraiwa T, Toyoizumi T, Ishiguri F, Iizula K, Yokota S, Yoshizawa N (2013) Characteristics of *Trochodendron aralioides* tension wood formed at different inclination angles. IAWA Journal 34: 273-284

Hiraiwa T, Aiso H, Ishiguri F, Takashima Y, Iizuka K, Yokota S (2014) Anatomy and chemical composition of *Liriodendron tulipifera* stems inclined at different angles. IAWA Journal 35: 463-475

Hung LF, Tsai CC, Tsai CC, Chen SJ, Huang YS, Kuo-Huang LL (2016) Study of tension wood in the artificially inclined seedlings of *Koelreuteria henryi* Dummer and its biomechanical function of negative gravitropism. Trees 30: 609-625

Iiyama K, Wallis ALA (1988) An improved acetyl bromide procedure for determining lignin in woods and wood pulps. Wood Science and Technology 22: 271-280

Itoh T (1996) Anatomical description of Japanese hardwoods II. Wood Research and Technical Note 32: 66-176

Okuyama T, Yamamoto H, Yoshida M, Hattori Y, Archer RR (1994) Growth stresses in tension wood: Role of microfibrils and lignification. Annals of Forest Science 51: 291-300

Onaka F (1949) Studies on compression-wood and tension-wood. Wood Research 1: 1-88

Saiki H, Ono K (1971) Cell wall organization of gelatinous fibers in tension wood. Bulletin of the Kyoto University Forests 42: 210-217

Sasaki Y, Okuyama T, Kikata Y (1978) The evolution process of the growth stress in the tree: The surface stresses on the tree. Mokuzai Gakkaishi. 24: 149-157

Scurfield G, Wardrop AB (1962) The nature of reaction wood: VI. The reaction anatomy of seedlings of woody perennials. Australian Journal of Botany 10: 93-105

Timell TE (1969) The chemical composition of tension wood. Swedish Paper Journal 72: 173-181

Yamamoto H (2004) Role of the gelatinous layer on the origin of the physical properties of the tension wood. Journal of Wood Science 50: 197-208

Yamamoto H, Okuyama T (1994) Determining method of degree of reaction wood by released strain of the growth stress (II): Tension wood in hardwood. Wood Industry 49: 20-23

Yamashita S, Yoshida M, Yamamoto H (2009) Relationship between development of compression wood and gene expression. Plant Science 176: 729-735

Yoshida M, Okuda T, Okuyama T (2000) Tension wood and growth stress induced by artificial inclination in *Liriodendron tulipifera* Linn. and *Prunus spachiana* Kitamura f. *ascendens* Kitamura. Annals of Forest Science 57: 739-746

Yoshizawa N (1987) Cambial responses to the stimulus of inclination and structural variations of compression wood tracheids in gymnosperms. Bulletin of the Utsunomiya University Forests 23: 23-141

Yoshizawa N, Ohba H, Uchiyama J, Yokota S (1999) Deposition of lignin in differentiating xylem cell walls of normal and compression wood of *Buxus microphylla* var. *insularis* Nakai. Holzforschung 53: 156-160

Yumoto M, Ishida S, Fukazawa K (1983) Studies on the formation and structure of the compression wood cells induced by artificial inclination in young trees of *Picea glauca*: IV. Gradation of the severity of compression wood tracheids. Research Bulletins of the College Experiment Forests, Hokkaido University 40: 409-454