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An overview of microfibril angle in fiber of tension wood

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Abstract: The angle between helical windings of microfibrils in the secondary cell wall of fibers and the long axis is called microfibril angle (MFA). Stiffness of wood depends on variations in the MFA. The large MFA shows low stiffness, which is found in juvenile wood and this character make threes vulnerable to high winds breaking. Timber containing a high proportion of juvenile wood is unsuitable for use as high-grade structural timber. On the other hand, the small MFA in wood shows high stiffness, which has importance in a good view of the trend in forestry. The timber with high stiffness is commonly high economic value. They are grown mainly for construction, timber and furniture. Until date, it is under pressure for increased timber production means that ways will be sought to improve the quality of timber by reducing MFA. Commonly, MFA decrease during the formation of tension wood therefore study on tension wood related to MFA formation is important for MFA reduction in normal wood. The study on tension wood formation could predict expression patterns of genes/proteins for reduction of MFA. Herein, the orientation of microfibril and MFA in cell wall layers of normal and tension wood fiber are discussed.

Keywords: Angiosperm, Microfibril Angle, Tension Wood, Wood Anatomy, Wood Fiber

1. Introduction

Wood is one of the most important natural product, is a renewable source of energy. Therefore, it has a major role as an environmentally cost-effective alternative to burning fossils fuels in future. The wood also plays a major role in the provision of energy-sufficient material for our buildings and many other daily products. During wood cells formation, trees sink huge atmospheric CO_2 as a result tree growth occurrence, thereby reducing CO_2 which one of the major contributors to decline global warming. When a tree grows vertically, redial growth showed similar in the all sides of stems, in which normal wood is formed. In contrast, a non-vertical orientated stems or branches showed dissimilar redial growth in upper and lower side and showed defective wood growth incremented portion. This type of wood is formed for tree bending, which is caused by prevailing winds, snow, slope, or asymmetric crown shape, is known as reaction wood. The combined result of reaction wood cells is to “push” the tree upright in the case of conifers, and to “pull” the tree to a vertical position in hardwoods [1,2], which aims to re-orient a leaning stem or branch, so as to enable the tree find a more favorable position [2].

In hardwood species, reaction wood is called tension wood as it tends to form in zones of the tree held in tension e.g. the upper side of a leaning stem. In tension wood, the overall lignin content is lower, the cellulose content is higher and microfibril angle (MFA) is lower than corresponding normal wood. An extra layer exists in the innermost position, called the gelatinous, or G-layer. The G-layer is almost entirely made up of cellulose, with an almost vertical MF angle. During maturation, G-layer shrinks strongly in the longitudinal direction, thereby creating a very strong state of tensile stress in the cell. The variation of tensile stress in wood properties is reflected by the coexistence of these several different types of wood within a single tree. The wood variation by normal and tension provides a unique opportunity to dissect the molecular and biochemical mechanisms in hardwood underlying such differences.

The term MFA in wood science refers to the angle between the direction of the helical windings of microfibrils in the secondary cell wall of fibers and tracheids, and the long axis of cell. Differences in MFA have a profound effect on the properties of wood, in particular its stiffness. The large MFA in juvenile wood confers low stiffness and gives the sapling the flexibility, it needs to survive high winds without breaking. It also means, however, that timber containing a high quantity of juvenile

wood is unsuitable for use as high-grade structural timber. This fact has taken on increasing importance in view of the trend in forestry towards short rotation cropping of fast grown species. These trees at harvest may contain 50% or more of timber with low stiffness and therefore, low economic value. Although they are presently grown mainly for pulp, pressure for increased timber production means that ways will be sought to improve the quality of their timber by reducing juvenile wood MFA. In general, MFA decrease during the formation of tension wood therefore it is stated that tension wood has a high stiffness. But low content lignin and shorter length of fiber exist in tension portion and occur different growth stress between normal wood and tension wood, which results low economic valued wood production. The study on tension wood formation could provide the understanding process of reduction of MFA in normal wood formation and predictable natural variations in the expression patterns of genes/proteins.

The mechanism by which the orientation of microfibril deposition is still a matter of advanced research on wood and the application of molecular techniques is likely to enable modification in the orientation of microfibril deposition. In this review, we discus about the orientation of microfibril and MFA in cell wall layers of normal and tension wood fiber. The purpose of this review is to examine what is known about an aspect of fiber cell wall structure for tension wood which has recently taken on major importance in the minds of tree improvers and timber users.

2. Cell Wall Layers, Microfibril Angle and Microfibril Orientation in Fiber Cells of Normal Wood

The plant cell wall is composed of several layers that are fabricated at different periods during cell differentiation. The first layer to be developed after cell division is called the middle lamella, which is found between the wood cells, and ensures the adhesion of a cell with its neighbors. The middle lamella is only 0.5 to 1.5 μm thick and is made up of pectic substances to which lignin may be added during the differentiation period (Fig. 1). At the beginning of cell differentiation, the primary cell wall forms. This primary wall is highly elastic layer, is attached to the middle lamella and is approximately 0.1 μm thick (Fig. 1). The primary cell wall is made up of several layers of microfibrils, which are arranged randomly within this wall. Pectic substances, lignin, and hemicelluloses can be found between these microfibrils. As the developing cell reaches its definitive size, a new layer is formed inside the primary cell wall, which is the most important layer for the cell, in terms of mechanical strength. This new secondary cell wall is divided into three different layers, S1, S2, and S3 (Fig. 1) [2]. Each of these layers is composed of cellulose microfibrils, aligned in an ordered, parallel arrangement, which differs from S layer to S layer. Hemicelluloses and lignin are also present in each of these layers. These three S layers can be modified during cell maturation, which lasts for several days after the birth of the wood cell, e.g. the amount of lignin and cellulose laid down in the secondary cell wall may be influenced by abiotic factors such as mechanical stress, i.e. wind and stem lean. The S1 layer is the thinnest of the S layers, being only 0.1 to 0.35 μm thick, and representing just 5% to 10% of the total thickness of the cell wall. This layer is considered as an intermediate between the primary cell wall and the S2 layers. The MFA in S2 layer with regard to the cell axis is 60° to 80°. The S2 layer is the thickest layer in the secondary cell wall, and is the most important, with regard to mechanical support. The thickness of the S2 layer varies between 1 and 10 μm, and accounts for 75% to 85% of the total thickness of the cell wall. The MFA in this layer is 5° to 30° to the cell axis, and can be even higher, depending on external mechanical stress. The angle of the cellulose microfibrils in the S2 layer can influence greatly the physical and mechanical properties of the cell and even stem wood as a whole (Fig. 2A, 3A). As the MFA increases, with regard to the cell axis, wood becomes less rigid, and the longitudinal modulus of elasticity decreases, as in the case of juvenile and compression wood. The innermost layer of the secondary cell wall, the S3 layer, is relatively thin, being only 0.5 to 1.10 μm thick. The microfibrils are ordered in a parallel arrangement, but less strictly than in the S2 layer, and the MFA is 60° to 90° with regard to the cell axis.

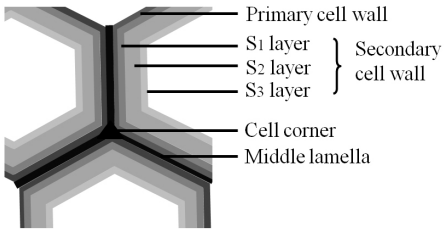

Fig. 1. *Diagrammatic figure of cell wall layers in normal wood fibers.*

The microfibrils in the S1, S2 and S3 layers of fibre walls are organised into lamellae in which their predominant orientations are as predicted by [3], although there is slight variation from lamella to lamella within a layer [4]. Both the S1 [4,5] and the S3 [6] have occasionally been demonstrated to have lamellae in which the microfibrils may be oriented in helices of opposite sign (so-called S and Z helices) (Fig. 2A, 3A). The S2 layer, however, has microfibrils in a right-handed or Z helix only.

3. Mechanism of Orientation of Microfibrils Deposition in Tension Wood Fiber

Wood cells are differentiated with the cambial activities at the periphery of the stem. The formation of the secondary wall occurs at the end of cell elongation by the deposition of

successive layers made of cellulose microfibrils bounded by an amorphous polymeric matrix. A specific chemical composition and a particular orientation of the microfibrils relative to the cell axis have found in each layer [7]. Microfibrils are made of crystalline cellulose and are by far the stiffest constituent of the cell wall. The MFA in each layer is determinant for cell wall architecture and wood mechanical properties.

A mechanical stress of a large magnitude, known as "growth stress" [1,8], occurs in the cell walls during the formation of wood cells. This stress fulfills essential biomechanical functions for the tree. It compensates for the comparatively low compressive strength of wood and thus improves the stem resistance against bending loads. It also provides the tree with a motor system [9], necessary to maintain the stem at a constant angle during growth [10] or to achieve adaptive reorientations. In angiosperms, a large tensile growth stress is generated by a specialized tissue called "tension wood". This type of reaction cell is common in plant organs whose function involves the bending or contraction of axes, such as tendrils, twining vines [11].

The mechanism at the origin of tensile growth stress has not been fully understood. However, several reports have greatly improved the knowledge about the ultrastructure, chemical composition, molecular activity, mechanical state, and behavior of tension wood. Different models have been proposed and discussed to explain the origin of maturation stress [12-23]. The specific organization of the G-layer suggests a tensile force induced in the microfibrils during the maturation process. Different hypotheses have been proposed to explain this mechanism, such as the contraction of amorphous zones within the cellulose microfibrils [18], the action of xyloglucans during the formation of microfibril aggregates [23,24], and the effect of changes in moisture content stimulated by pectin-like substances [21,22] argued an alternative model, initially proposed by [25], which proposed that the maturation stress originates in the swelling of the G-layer during cell maturation and is transmitted to the adjacent secondary layers, where the larger MFAs allow an efficient conversion of lateral stress into axial tensile stress. Although the proposed mechanism is not consistent with the known hygroscopic behavior of tension wood, which shrinks when it dries and not when it takes up water [26-28], this hypothesis focused attention on the possible role of cell wall layers other than the G-layer. As a matter of fact, many types of wood fibers lacking a G-layer are known to produce axial tensile stress, such as normal wood of angiosperms and conifers [1] and the tension wood of many tropical species [29-31], so that mechanisms strictly based on an action of the G-layer cannot provide a general explanation for the origin of tensile maturation stress in wood.

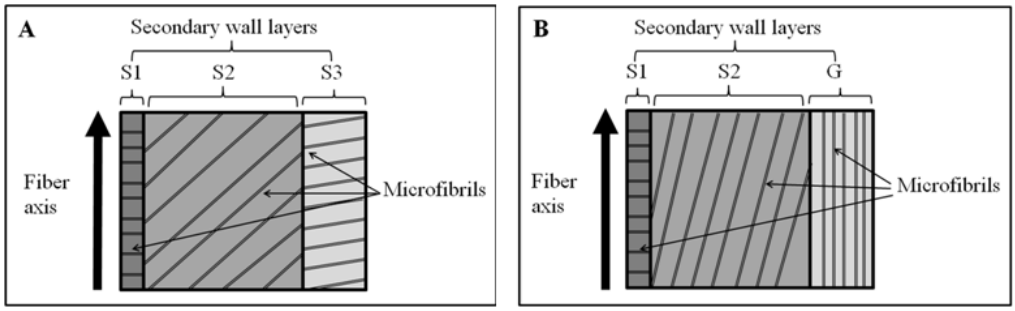

Fig. 2. *Diagrammatic figure of secondary cell wall layer of wood fiber showing microfibrils arrangements in S1, S2 and S3 layers. A) Normal wood fiber: microfibril angles with fiber axis in S1, S2 and S3 layers. B) Tension wood fiber: microfibril angles with fiber axis in S1, S2 and G layers. Microfibril angles in S2 layer reduce and microfibril arranged parallel with fiber axis.*

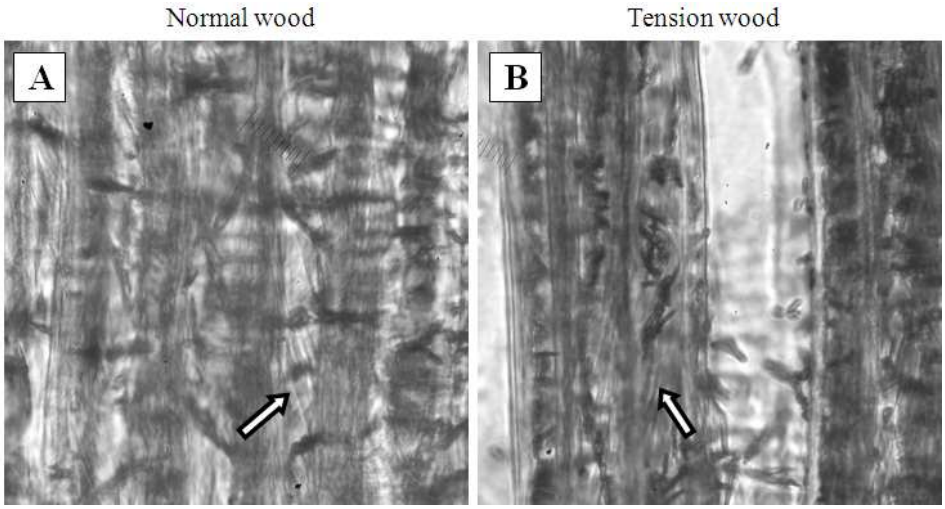

Fig. 3. *Radial section of normal and tension woods showing microfibril angle with fiber axis in the S2 layer of fiber. Redial section of normal wood (A) and tension wood (B). Arrows indicate the microfibrils in S2 layer.*

4. Microfibril Angle in Tension Wood Fiber

The microfibril angle (MFA) is the angle between the direction of the helical windings of cellulose microfibrils in the secondary cell wall of fibers and tracheids and the long axis of cell. Technologically, it is usually applied to the orientation of cellulose microfibrils in the S2 layer that makes up the greatest proportion of the wall thickness, since it is this which most affects the physical properties of wood. Both the S1 [4,5] and the S3 [6] have occasionally been demonstrated to have lamellae in which the microfibrils may be oriented in helices of opposite sign (so-called S and Z helices). The S2 layer, however, has microfibrils in a right-handed or Z helix only [32]. Usually, MFA of S2 layer in wood fiber can decrease or no change accompanying with the differentiation of reaction wood fibers.

It is widely known that microfibrils of G-layers orient nearly parallel to the longitudinal axis of cells (Fig. 2B, 3B) [33-38]. In some species having no G-layer in reaction wood, it has been reported that microfibril angle of S2 layer decreased [15, 39-42] reported that the microfibril angle of S2 layer was very small (5 to 10 degrees) in reaction wood of *Magnolia acuminat*e and *Liriodendron tulipifera*. In *Magnolia obovata* and *M. kobus*, the innermost surface of S2 layer of fiber tracheid wall also showed a small microfibril angle [41]. Microfibril angle of S2 layer in wood fiber may not always decrease by the reaction wood formation in some species having S3 layer and lacking G-layer, or efficient tensile stress so as to make the microfibril angle small in other sample trees used here may have not been generated. More detailed investigation is still needed to clarify the changes of microfibril angle in the S2 layer for many other species with three-layered secondary wall without G-layer. It is well known that microfibril angle in wood fiber gradually changes from secondary wall to G-layers [34,36,37]. In *Fraxinus mandshurica*, the microfibril changed its orientation angle progressively, with clockwise rotation, from the S-helix until it was oriented approximately parallel to the fiber axis [37]. Araki *et al.* [36] reported that the microfibril orientation in transition layer gradually changed to a parallel orientation to the cell axis in some species of tension wood fibers forming S1 + S2 + G or S1 + G. On the other hand, in reaction wood fiber without G-layer and S3 layer as in *Osmanthus fragrans*, microfibril angle of S2 layer gradually decreased from about 30 to about 15 degrees from the early stage toward the later stage of S2 layer formation [43].

To maintain or recover the position of stems or branches to appropriate orientation, high tensile stress in longitudinal direction was often generated on the upper sides of inclined stems or branches [29,44-49]. A relationship between growth stress and microfibril angle of secondary wall in wood fibers has been reported in reaction wood in angiosperms: the microfibril angle was smaller in the S2 layers of reaction wood fibers compared to that of opposite wood fibers ([15, 40-42,50]. Okuyama *et al*. [15] suggested that microfibril angle is an important factor in the generation of growth stress in tension wood. In addition, it was reported that tensile growth stress significantly increased in reaction wood of two *Magnolia* species, resulting in decrease of the microfibril angle of S2 layer and increase of the α-cellulose content [15]. Sultana *et al*. [51] reported that only two species showed the smaller microfibril angles in the S2 layers of reaction wood fibers compared to the opposite wood fibers. However, no significant, but relatively high negative correlation was found between decrease rate of microfibril angle and growth eccentricity rate. It is considered that tensile stress generated on the upper side of leaning branches makes the microfibril angle small. Thus, in some angiosperm trees having neither S3 layers nor G-layers in reaction wood fibers, the lower microfibril angle of S2 layer in wood fiber may be related to the high tensile growth stress generated on the upper side of inclined stems or branches. These high tensile growth stresses may contribute to in maintaining the appropriate angle of stems or branches.

5. Conclusions

Stiffness carries wood quality and it depends on variations of the microfibril angle (MFA). The low MFA shows high stiffness and it is suitable for using as high-grade structural timber. It is current view for timber researchers that reducing MFA in juvenile wood of short rotation cropping of fast grown species to reduce pressure for increased timber production. In general, MFA decrease during the formation of tension wood therefore strategies on MFA reducing possible to discover by studying tension wood. The present overview is illustrated the MFA orientation in tension wood fiber and changes in respective to cell wall layers of normal are discussed.

References

[1] Archer RR (1986) Growth Stresses and Strains in Trees. Springer Verlag, Berlin.

[2] Timell TE (1986) Compression wood in gymnosperms I. Springer-Verlag, Berlin New York.

[3] Bailey IW, Kerr T (1935). The visible structure of the secondary wall and its significance in physical and chemical investigations of tracheary cells and fibres. J Arnold Arboretum, 16: 273–300.

[4] Frei E, Preston RD, Ripley GW (1957) The fine structure of the walls of conifer tracheids VI. Electron microscopy of sections. J Exp Bot, 8: 139–146.

[5] Wardrop AB (1954) The mechanism of surface growth involved in the differentiation of fibres and tracheids. Australian J Bot, 2: 165–175.

[6] Wardrop AB (1964) The structure and formation of the cell wall in xylem. In The Formation of Wood In Forest Trees (ed. M. H. Zimmermann). Academic Press, New York.

[7] Mellerowicz EJ, Sundberg B (2008) Wood cell walls: biosynthesis, developmental dynamics and their implications for wood properties. Curr Opin Plant Biol, 11: 293–300.

[8] Fournier M, Chanson B, Thibaut B, Guitard D (1991) Mechanics of standing trees: modelling a growing structure submitted to continuous and fluctuating loads. 2. Tridimensional analysis of maturation stresses. Case of standard hardwood. Ann Sci For, 48: 527–546 (in French).

[9] Moulia B, Coutand C, Lenne C (2006) Posture control and skeletal mechanical acclimation in terrestrial plants: implications for mechanical modeling of plant architecture. Am J Bot, 93: 1477–1489.

[10] Alme´ras T, Fournier M (2009) Biomechanical design and long-term stability of trees: morphological and wood traits involved in the balance between weight increase and the gravitropic reaction. J Theor Biol, 256: 370–381.

[11] Bowling AJ, Vaughn KC (2009) Gelatinous fibers are widespread in coiling tendrils and twining vines. Am J Bot, 96: 719–727.

[12] Boyd JD (1972) Tree growth stresses. Part V. Evidence of an origin in differentiation and lignification. Wood Sci Technol, 6: 251–262.

[13] Bamber RK (1987) The origin of growth stresses: a rebuttal. IAWA Bull, 8: 80–84

[14] Bamber RK (2001) A general theory for the origin of growth stresses in reaction wood: how trees stay upright. IAWA J, 22: 205–212.

[15] Okuyama T, Yamamoto H, Yoshida M, Hattori Y, Archer RR (1994) Growth stresses in tension wood: role of microfibrils and lignification. Ann Sci For, 51: 291–300.

[16] Okuyama T, Yoshida M, Yamamoto H (1995) An estimation of the turgor pressure change as one of the factors of growth stress generation in cell walls: diurnal change of tangential strain of inner bark. Mokuzai Gakkaishi, 41: 1070–1078.

[17] Yamamoto H (1998) Generation mechanism of growth stresses in wood cell walls: roles of lignin deposition and cellulose microfibril during cell wall maturation. Wood Sci Technol, 32: 171–182.

[18] Yamamoto H (2004) Role of the gelatinous layer on the origin of the physical properties of the tension wood. J Wood Sci, 50: 197–208.

[19] Alme´ras T, Gril J, Yamamoto H (2005) Modelling anisotropic maturation strains in wood in relation to fibre boundary conditions, microstructure and maturation kinetics. Holzforschung, 59: 347–353.

[20] Alme´ras T, Yoshida M, Okuyama T (2006) The generation of longitudinal maturation stress in wood is not dependent on diurnal changes in diameter of trunk. J Wood Sci, 52: 452–455.

[21] Bowling AJ, Vaughn KC (2008) Immunocytochemical characterization of tension wood: gelatinous fibers contain more than just cellulose. Am J Bot, 95: 655–663.

[22] Goswami L, Dunlop JWC, Jungnikl K, Eder M, Gierlinger N, Coutand C, Jeronimidis G, Fratzl P, Burgert I (2008) Stress generation in the tension wood of poplar is based on the lateral swelling power of the G-layer. Plant J, 56: 531–538.

[23] Mellerowicz EJ, Immerzeel P, Hayashi T (2008) Xyloglucan: the molecular muscle of trees. Ann Bot (Lond), 102: 659–665.

[24] Nishikubo N, Awano T, Banasiak A, Bourquin V, Ibatullin F, Funada R, Brumer H, Teeri TT, Hayashi T, Sundberg B (2007) Xyloglucan endo-transglycosylase (XET) functions in gelatinous layers of tension wood fibers in poplar: a glimpse into the mechanism of the balancing act of trees. Plant Cell Physiol, 48: 843–855.

[25] Mu¨nch E (1938) Statik und Dynamik des Schraubigen Baus der Zwellwand, besonders der Druck- and Zugholzes. Flora, 32: 357–424.

[26] Clair B, Thibaut B (2001) Shrinkage of the gelatinous layer of poplar and beech tension wood. IAWA J, 22: 121–131.

[27] Fang CH, Clair B, Gril J, Alme´ras T (2007) Transverse shrinkage in G-fibers as a function of cell wall layering and growth strain. Wood Sci Technol, 41: 659–671.

[28] Clair B, Gril J, Di Renzo F, Yamamoto H, Quignard F (2008) Characterization of a gel in the cell wall to elucidate the paradoxical shrinkage of tension wood. Biomacromolecules, 9: 494–498.

[29] Onaka F (1949) Studies on compression and tension wood. Wood Res, 1: 1–88 (translation from Japanese).

[30] Clair B, Ruelle J, Beauche^ne J, Pre´vost MF, Fournier Djimbi M (2006) Tension wood and opposite wood in 21 tropical rain forest species. 1. Occurrence and efficiency of the G-layer. IAWA J, 27: 329–338.

[31] Ruelle J, Yamamoto H, Thibaut B (2007) Growth stresses and cellulose structural parameters in tension and normal wood from three tropical rainforest angiosperm species. BioResources, 2: 235–251.

[32] Barnett JR, Bonham VA (2004) Cellulose microfibril angle in the cell wall of wood fibers. Biol Rev Camb Philos Soc, 79: 461–472.

[33] Wardrop AB, Dadswell HE (1955) The nature of reaction wood: IV. Variations in cell wall organization of tension wood fibres. Australian J Bot, 3: 177-189.

[34] Saiki H, Ono K (1971) Cell wall organization of gelatinous fibers in tension wood. Bull Kyoto Univ Forests, 43: 210-217.

[35] Araki N, Fujita M, Saiki H, Harada H (1982) Transition of fiber wall structure from normal wood to tension wood in *Robinia pseudoacacia* L. and *Populus euramericana* Guinier. Mokuzai Gakkaishi, 28: 267-273.

[36] Araki N, Fujita M, Saiki H, Harada H (1983) Transition of fiber wall structure from normal wood to tension wood in certain species having gelationous fibers of S1 + G and S1 + S2 + S3 + G types. Mokuzai Gakkaishi, 29: 491-499.

[37] Prodhan AKMA, Funada R, Ohtani J, Abe H, Fukazawa K (1995a) Orientation of microfibrils and microtubules in developing tension-wood fibres of Japanese ash (*Fraxinus mandshurica* var. *japonica*). Planta, 196: 577-585.

[38] Prodhan AKMA, Ohtani J, Funada R, Abe H, Fukazawa K (1995b) Ultrastructural investigation of tension wood fibre in *Fraxinus mandshurica* Rupr. var. *japonica* Maxim. Ann Bot, 75: 311- 317.

[39] Okuyama T, Yamamoto H, Iguchi M, Yoshida M (1990) Generation process of growth stresses in cell walls II: Growth stresses in tension wood. Mokuzai Gakkaishi, 36: 797-803.

[40] Sugiyama K, Okuyama T, Yamamoto H, Yoshida M (1993) Generation process of growth stresses in cell walls: Relation between longitudinal released strain and chemical composition. Wood Sci Technol, 27: 257- 262.

[41] Yoshizawa N, Inami A, Miyake S, Ishiguri F, Yokota S (2000) Anatomy and lignin distribution of reaction wood in two *Magnolia* species. Wood Sci Technol, 34: 183-196.

[42] Yoshida M, Ohta H, Yamamoto H, Okuyama T (2002) Tensile growth stress and lignin distribution in the cell walls of yellow poplar, *Liriodendron tulipifera* Linn. Trees, 16: 457-464.

[43] Hiraiwa T, Yamamoto Y, Ishiguri F, 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 Chem Technol 41: 537-543.

[44] Côté WA Jr, Day AC (1965) Anatomy and ultrastructure of reaction wood. In: Côté WA Jr (ed), Cellular ultrastructure of woody plants, Syracuse University Press, New York, pp391-418.

[45] Wardrop AB (1965) The formation and function of reaction wood. In: Côté WA Jr (ed), Cellular ultrastructure of woody plants, Syracuse University Press, New York, pp, 371-390.

[46] Côté WA Jr, Day AC, Timell TE (1969) A contribution of the ultrastructure of tension wood fibres. Wood Sci Technol, 3: 257–271.

[47] Scurfield G (1973) Reaction wood: Its structure and function. Science 179: 647-655.

[48] Wilson BF, Archer RR (1977) Reaction wood: Induction and mechanical action. Annual Rev Plant Physiol, 28: 23-43.

[49] Fisher JB (1985) Induction of reaction wood in *Terminalia* (Combretaceae): Roles of gravity and stress. Ann Bot, 55: 237-248.

[50] Yamamoto H, Okuyama T, Sugiyama K, Yoshida M (1992) Generation process of growth stresses in cell walls IV: Action of the cellulose microfibril upon the generation of the tensile stresses. Mokuzai Gakkaishi, 38: 107-113.

[51] Sultana RS, F Ishiguri, S Yokota, K Iizuka, T Hiraiwa, N Yoshizawa (2010) Wood anatomy of nine Japanese hardwood species forming reaction wood without gelatinous fibers. IAWA J, 31(2): 191-202.