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A review on structures of secondary wall in reaction wood fiber of hardwood species

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Abstract: Due to a non-vertical orientation of the stem or branch, which may begin as responses of prevailing winds, snow, slope, or asymmetric crown shape, a specialized wood tissue forms, is called “reaction wood”. In hardwood species, the reaction wood tends to form on the upper side of a leaning stem or branch, is known to as “tension wood”. It is usually related with eccentric growth and changes in structure and chemistry of wood. During the formation of tension wood many changes found in wood cells, especially in wood fibers. The changes of wood properties in tension portion result different shrinkage characteristics during drying, creates a serious problem at adjacent portion of normal wood. However, tension wood is problematic in the hardwood industries and this wood is economically less valued. However, the studies on tension wood are necessary for beneficial applications in the wood industries sectors as well as research sectors. The knowledge on tension wood anatomy is still a matter for tree growers and timber processors, especially who are often involved in the furniture making. Besides, the understanding of tension wood formation provides a unique opportunity to obtain information on the molecular and biochemical mechanisms in the expression patterns of genes/proteins. The studies on reaction wood anatomy are not enough that we concluded any model. This review describes the features of fibers in tension wood todate, including secondary wall layers structure. Until date, six types structure of secondary cell wall layers for tension wood fibers such as, $S_1 + S_2 + S_3 + G$, $S_1 + S_2 + G$, $S_1 + G$, $S_1 + \acute{G}$, $S_1 + S_2$, and $S_1 + S_2 + S_3$ have been reported, which considered being involved in plant evolution.

Keywords: Angiosperm, Cell Wall Layers, Microfibril Angle, Tension Wood, Wood Fiber

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1. Introduction

Wood is a renewable natural resource, providing 1) timber for house building, furniture, packaging, 2) fibers for pulp, paper, plywood industries, and 3) firewood for energy. Furthermore, wood is a potential source of lignocellulose-based biofuels. Wood consists of different types of cell. Cell number and their arrangement differ depending on species [1-4]. Cells show two major functions in living trees: to provide a channel for water and minerals from the roots to the crown and to provide mechanical support for controlling the increasing mass of the tree. Besides, they contribute to tree growth over more than one year by storing temporary reserves. In most angiosperms, the roles have been separated with water travelling through specialized vessels, and support being provided by fibers, while parenchyma cells, organized in rays, are involved in the radial transfer of assimilates between phloem and xylem.

A modification of wood at a portion in the leaning stem or branch can occur to withstand the pressure from the mass of the tree. Modifications of this structure enable branches to maintain their direction of growth against the force of gravity, or to enable stems forced nonvertical alignment to regain a vertical orientation. These latter occur variations in the wood properties, which are of benefit to the tree may also have negative economic consequences for the forestry and timber industries. By the cambium reactions in the response to a gravitational stimulus, leaning stems or branches formed modified wood with its special anatomical and chemical properties, is called “reaction wood” [5-13]. In angiosperm, reaction wood is generally formed on the upper side, and this wood is denoted as “tension wood” [14]. A mechanical stress of a large magnitude, known as “maturation stress” or “growth stress” [15, 16], occurs in the cell walls during the formation of wood cells. This stress provides the tree with a motor system [17], necessary to maintain the stem at a constant angle during growth [18] or to achieve adaptive reorientations. In angiosperms, growth stress known as tensile stress [19], which also involved in the formation of tension wood. The involvement of plant hormones found in tension wood formation, is mainly regulated by auxins and gibberellic acid (GA). Joint effects of different classes of plant hormones or interactions among them may play crucial roles in the regulation mechanisms for tension wood [20].

The main problem of tension wood associated with the quality and utilization of wood and timber containing tension tissues is that their shrinkage characteristics are different from those of adjacent normal wood. Since tension wood is typically localized on one side (upper side) of the trunk, is often found only in the proportion of the total number of annual rings and it causes differential shrinkage effects during drying, which leads to warping, twisting, bending, and cracking of logs, planks, machined parts, and veneers. Warping and twisting of lumber containing tension wood is a serious problem of the hardwood industrial, particularly when the tension wood exists extensively at log. Collapse is another problem in wood industries associated with the seasoning of tension wood from the green condition [21]. Although some species have a greater tendency for collapse than others, the presence of tension wood aggravates this trend. For facilitated industrial utilization, it is very important to understand anatomical characteristics and wood properties in reaction wood. The presence of different characteristics in tension wood differs from the normal wood, especially tension characteristics in fiber. The secondary cell wall structure of tension fiber is one of the major characteristics. A large variations show within secondary cell wall structure of tension wood fibers, which will be a tool for establishment of evolutionary development of secondary wall structure in tension wood fiber for dicotyledons, and also be a source for studding origin and evolution of species.

Much effort has been put into reaction wood anatomy, wood properties, and wood chemistry considered to the commercial point of view. The purpose of this review is to introduce about features of fiber in reaction wood with respect to secondary wall structure which has recently taken on major importance in the minds of tree growers, timber users, and researchers involve in tension wood characterization and in evolutionary study on plant.

2. Tension Wood Characteristics

Tension wood is an abnormal wood formed typically on the upper side of branches and leaning or crooked stems of dicotyledonous trees. Tension wood differs from normal wood with the following main characteristics: i) Radial growth increment at upper side of leaning stem or branch is found in stem cross section [6, 18, 22, 23], ii) Green-sawn boards of tension wood are woolly surface [6], iii) Wider rings are found in tension wood zone [24], iv) The size and number of vessels decrease with the formation of tension wood in generally [5, 25, 26], v) An internal gelatinous layer (G-layer) is present in tension wood fibers [5, 21, 27], which contains extensive α-cellulose, is unlignified or less lignified and microfibrils in G-layer are oriented nearly parallel or parallel along the axis of the fiber [28, 29], vi) Particularly, tensile strength in tension wood is high, is found on upper side at either presence of G-layer [22, 30] or absence of G-layer [31] in tension fiber, vii) The microfibril angles in S_2 layer of tension wood fiber are smaller than that of normal wood [25] and they are oriented nearly parallel or parallel in G-layer of the fiber [28, 29], and viii) Lignification of tension wood is lesser that normal wood [6,32-35].

3. Mechanisms for Tension Wood Formation

A mechanical stress of a large magnitude in tree known as “Maturation stress” or “growth stress” [15], which occurs in the cell walls during the formation of wood cells and provides the tree a motor system [17]. It is necessary to maintain the stem at a constant angle during growth [18] or to achieve adaptive reorientations. In angiosperms, a large tensile maturation stress (Maturation stress) is generated in the tension wood.

It is well known that the mechanism of tensile maturation stress has not been fully understood until date although the studies on the ultrastructure, chemical composition, molecular activity, mechanical state, and behavior of tension wood have been greatly stated. Different models have been proposed and discussed to explain the origin of the maturation stress [36-38]. During the maturation process, the specific organization of the G-layer suggests a tensile force induced in the microfibrils. this mechanism have been explained with different hypotheses, such as amorphous zones contract within the cellulosic microfibrils [39], microfibril aggregates form by the action of xyloglucans [37,40], and the effect of changes in moisture content was stimulated by pectin-like substances [36]. Goswami *et al.* [41] proposed an alternative model, who revealed that the maturation stress originates during cell maturation in the swelling of the G-layer and it transmits to the adjoining secondary layers, as a result the larger MFAs convert efficiently from lateral stress into axial tensile stress. The proposed model is not steady when the hygroscopic behavior of tension wood is discovered, which shrinks when it dries and not when it takes up water [22, 42, 43], this hypothesis focused attention on the possible role of cell wall layers other than the G-layer. Many types of wood fibers lacking a G-layer are known to produce axial tensile stress, such as normal wood [15] and the tension wood of many tropical species [5, 44, 45], so that mechanisms strictly depends on an action of the G-layer cannot provide a general explanation for the origin of tensile maturation stress in wood.

4. Structure of Secondary Cell Wall Layer in Tension Wood Fiber

The plant cell wall in wood tissue has a multicomposite structure, consisting of several layers formed at different periods during cell differentiation. After the cell wall reaches its final size, the mechanically crucial secondary cell wall, consisting of three different layers such as S_1, S_2, and S_3 (Fig. 1, Fig. 2A) is formed [46]. The cellulose microfibril orientation and chemical composition varies among three layers of secondary cell wall. The S_2 layer is the thickest (75%–85% of the total thickness of the cell wall) and most important for mechanical stability [47]. Between adjacent cells, a middle lamella layer attached to the primary cell wall ensures the adhesion of a cell to its neighbors (Fig. 1, Fig. 2A).

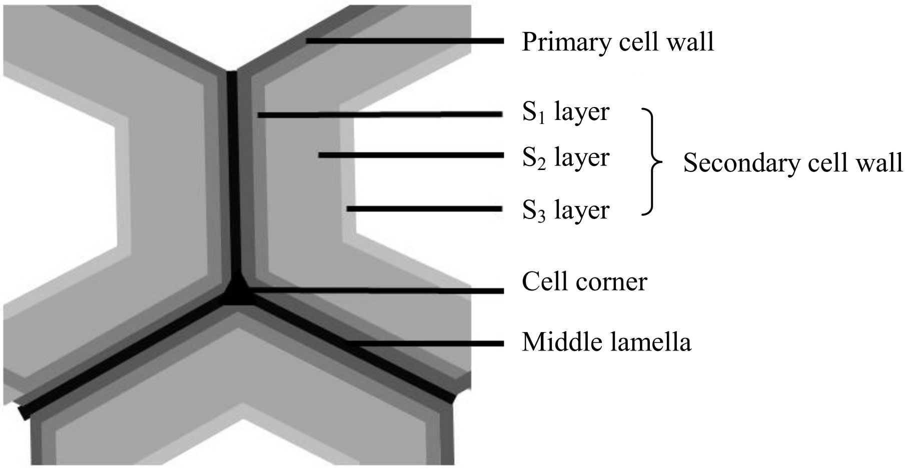

Fig 1. *Diagrammatic figure of cell wall layers in normal wood fibers showing middle lamella, primary cell wall, secondary cell wall (S_1, S_2, S_3 layers).*

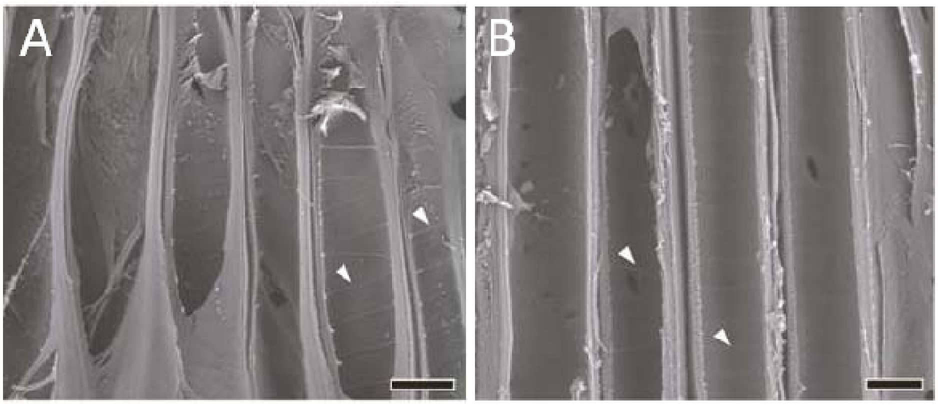

Fig 2. *Scanning electron microphotographs of inner most layer of wood fibers. A) normal wood, B) tension wood. Both normal and tension woods fiber walls consist of S_3 layers but lacks of G-layer; arrow heads, helical thickenings deposited on the S_3 layer, bar = 10 µm.*

The chemical composition and the alignment of the cellulose microfibrils in fiber walls show significant different within interspecies and intraspecies variability [6, 48]. Similarly, structures of secondary cell wall in fibers are also significantly differed between normal and tension wood [49]. The differences with respect to thickness in the secondary cell wall of tension fibers are remarkable although investigations are limited. Gierlinger and Schwanninger [49] reported that thickness of cell middle lamella (CML) and primary cell wall in tension fibers decrease. In contrast, no alteration in thickness of primary cell wall in tension fibers has been investigated by Côté and Day [6].

In tension wood fibers, secondary wall is characterized by a thick cell wall and a special cell wall layer, usually referred to as G-layer, which is not found in normal wood fibers [6, 50-52]. During tension wood formation, usually the S_3 layer replaced by the so-called G-layer [29]. In contrast, lacking of G-layer in tension wood fibers of some hardwood species is also observed which similar to secondary wall structure of normal wood fiber [23, 25, 26, 53]. Until date, six types of wall layer structures in secondary wall of tension wood fiber are found in different hardwood species, as shown in Fig. 3. In the species which are formed G-fiber or Ǵ- fiber, the structures of the secondary cell wall have been classified as, i) $S_1 + S_2 + S_3 + G$ structured secondary wall: after formation of S_1, S_2, S_3 layers, additionally G-layer is formed as a innermost layer where S_3 layer is partially altered with G-layer [6, 21], ii) $S_1 + S_2 + G$ structured secondary wall: G-layer is formed after development of S_1 and S_2 layers, where S_3 layer entirely replaced with G-layer [5, 6, 21, 22, 27, 30], iii) S_1 + G structured secondary wall: G-layer is developed after formation of S_1 layer and it develops rapidly instead of S_2 and S_3 layers during high growth stress condition [21, 6], iv) S_1 + Ǵ structured secondary wall: Ǵ-layer is formed after generation of S_1 layer and S_2 or S_3 layers are entirely lacking. It is characterized by unlignified, porous, and microfibrils in Ǵ-layer is oriented parallel to fiber axis. The presence of Ǵ-layer has first reported by Araki *et al.*, [54] in tension wood of *Cercidiphyllum japonicum*, *Cornus controversa*, and *Alnus pendula* (Fig. 3). In the species which are lacked G-fiber or Ǵ- fiber, the structure of the cell wall layer of tension wood fiber has been classified as, v) S_1 + S_2 structured secondary wall: without formation of G-layer or S_3 layer was observed during complete maturation of wood fiber. The lack of S_3 layer in reaction wood fiber without G-layer has been demonstrated by earlier studies in some species: *Magnolia obovata* and *M. kobus* [25], *Liriodendron tulipifera* [53], and *Osmanthus fragrans* [26]. This type of secondary wall structure usually is found in primitive angiosperms [25]. In these species, the microfibrils were oriented in a Z helix at the innermost part of the S_2 layers, vi) S_1 + S_2 + S_3 structured secondary wall: this three-layered secondary wall structure is similar to the wall structure of normal wood fiber. Usually, S_1 layer is formed first and following S_2 and S_3 layers are deposited in the inner side of fiber cell lumen. Recently, we [23] reported this structure in reaction wood fiber without a G-layer for the first time (Fig. 2, Fig. 2B).

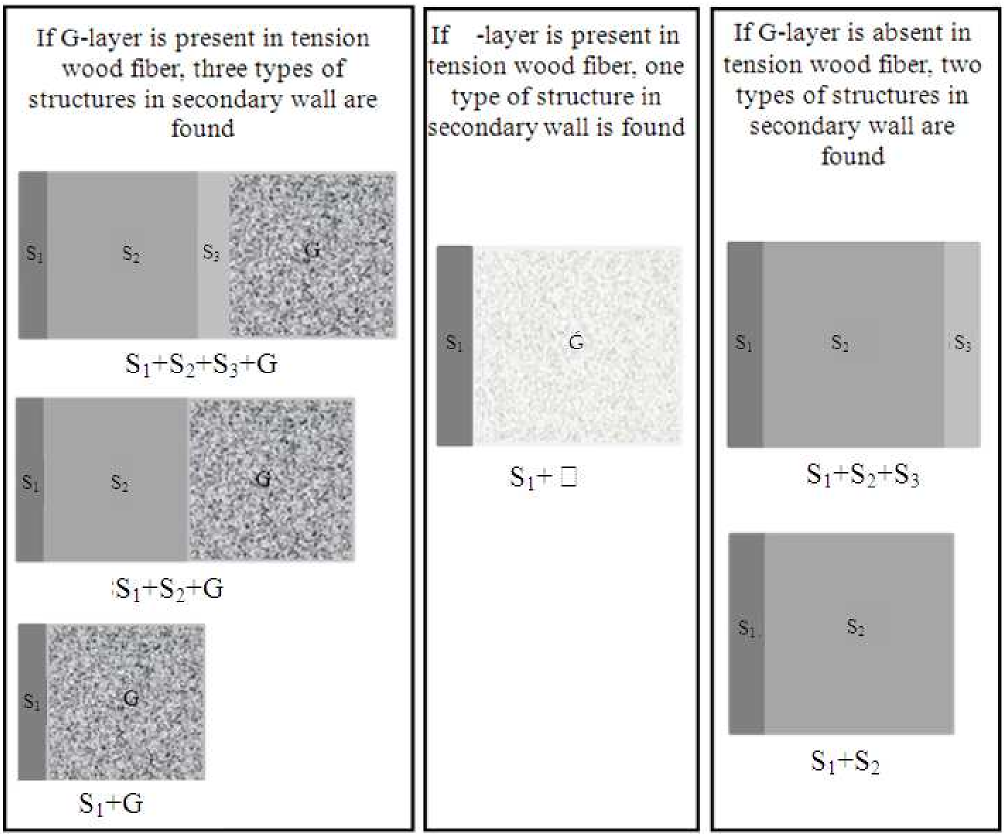

Fig 3. *Diagrammatic figure shows different six types of secondary wall structure in tension fiber either with G-, Ǵ-layer or without G-layer. Secondary wall of normal wood fiber generally composed of S_1, S_2, S_3 layers, but due to formation of reaction wood, secondary wall composes with the different types of structure.*

5. Conclusions

Accompanying the formation of tension wood, there are several alterations found in the wood cells, especially in wood fiber. The changes in secondary wall structure of tension wood fiber are noticeable among all changes. The alterations in the secondary cell wall structure of tension wood fiber are often classified into six types, $S_1 + S_2 + S_3 + G$, $S_1 + S_2 + G$, $S_1 + G$, S_1 + Ǵ, $S_1 + S_2$, and $S_1 + S_2 + S_3$. One type of secondary cell wall structure among six types is formed in one species during tension wood formation. Therefore, one type of secondary cell wall structure is an identified character for one species. The variations in secondary cell wall structure in tension wood fiber is an potential tool to establish an evolutionary development of secondary wall structure of tension wood fiber for dicotyledons, and to illustrate origin and evolution of species, as described previously in the evolutionary development of vessel elements [55] and wood rays [56] of dicotyledons. The review stated here will helpful for researcher involved studies on tension wood as well as evolution of plant.

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