Diurnal Periodicity in Cell Wall Formation in Conifer Wood Cells

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Summary: This paper has summarized studies on diurnal periodicity in wood cell wall formation. Diurnal differences can be observed in the innermost surface of developing secondary cell walls in differentiating conifer tracheids using field emission scanning electron microscopy (FE-SEM). Cellulose microfibrils are clearly evident during the day, while amorphous material is prevalent at night. Studies using immunogold labeling techniques and FE-SEM revealed that the amorphous material contained high levels of hemicelluloses. These findings suggest a diurnal periodicity in the supply of cell wall components to developing secondary walls during cell wall formation in conifer tracheids. Other studies have demonstrated that the diurnal differences in the innermost surface of developing secondary walls corresponded to the 24-h light-dark cycle and diurnal changes in the volume of differentiating cells. This diurnal periodicity seems to be associated with diurnal changes in light conditions and the water status, such as turgor pressure, of differentiating cells.

Key word: Cell wall, Diurnal periodicity, Immunogold labeling, Scanning electron microscopy, Tracheid

Introduction

Wood, or xylem, in the stem of trees is the most abundant terrestrial biomass. This huge biomass has major roles not only as raw material for industrial products, but also as a renewable source of energy, such as biofuels. Wood is formed as part of the radial growth of the stem by the activity of the vascular cambium, a lateral meristem located between the inner bark and wood[1]. The cambium cells produce new xylem cells toward the inside and new phloem cells toward the outside of the stem. Xylem is primarily composed of vessel elements and wood fibers in hardwood species, and tracheids in conifers.

The most fundamental constituent of wood is the highly developed cell wall of xylem cells. The main components of the wood cell wall are cellulose, hemicellulose, and lignin. Cellulose is a linear polysaccharide composed of β-1,4-linked glucose units, which associate to form the fibrous, crystalline microfibril[2]. Hemicelluloses are branched polysaccharides that consist of many different sugar monomers. There are various hemicelluloses found in plant cell walls, e.g., glucomannans, xylans, and xyloglucans. Lignin is a phenolic polymer composed of 3 types of monomeric precursors called monolignols: *p*-coumaryl alcohol, coniferyl alcohol, and sinapyl alcohol. In wood cell walls, cellulose microfibrils are embedded in an amorphous hemicellulose-lignin matrix. Wood cell walls consist of primary and secondary walls formed at different periods during cell differentiation. Primary walls are thin walls formed during or immediately following cell division. Secondary walls are thick walls formed inside the primary wall after cell growth (expansion) following cell division is completed. Secondary walls can be classified into 3 layers on the basis of the orientation of cellulose microfibrils: outer (S_1), middle (S_2), and inner (S_3) layers (Fig. 1). The S_2 layer occupies 75-85% of the total thickness of the cell wall. Various properties of wood are closely associated with the ultrastructure and properties of these cell walls.

Elucidating the mechanism of cell wall formation is important for a more detailed understand-

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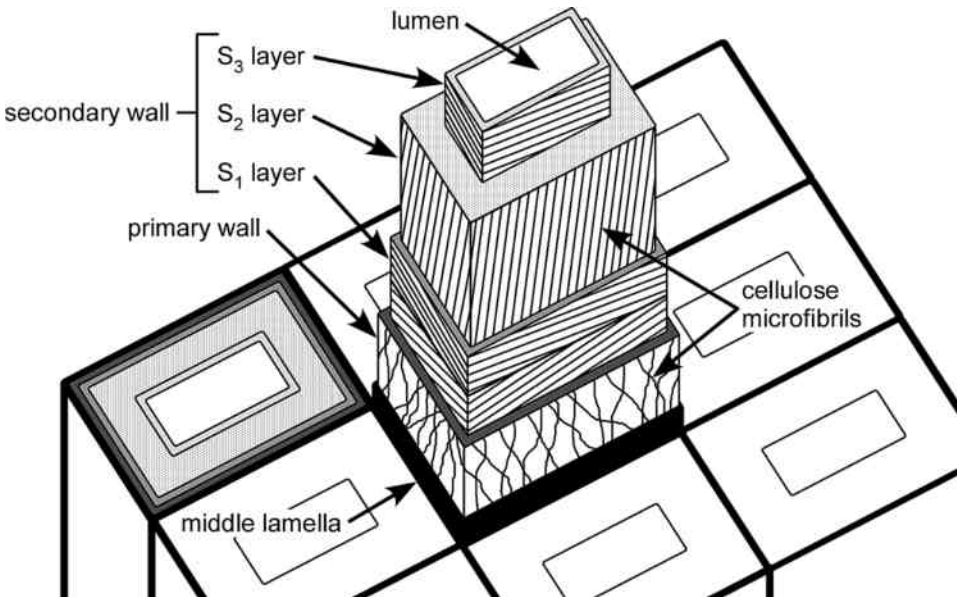

Fig. 1 A schematic model of the cell wall structure of a softwood tracheid.

ing of wood properties and advanced utilization of wood materials. Growth and development in plants, including wood formation in trees, are strongly influenced by external environmental factors, such as light, water, temperature, nutrients, and physical forces. In the natural environment, many environmental factors change diurnally. Recent studies have suggested that there is a diurnal periodicity in the supply of cell wall components used in the formation of wood secondary cell walls. In this review, studies on diurnal periodicity in wood cell wall formation have been summarized.

Biosynthesis of Wood Cell Wall Components

Cellulose is synthesized at the plasma membrane by the cellulose synthase complex (CSC), a rosette-shaped complex of enzymes consisting of at least 3 types of glycosyltransferases (GTs)[2–4]. CSCs synthesize cellulose (β-1,4-glucan) chains by polymerizing glucose residues from intracellular uridine diphosphate (UDP)-glucose substrates. CSC is believed to synthesize up to 36 individual cellulose chains that bind together to form the microfibril. Newly synthesized cellulose microfibrils are directly extruded into the cell wall. CSCs are thought to move in the plasma membrane, while elongating the microfibrils in a direction regulated by cortical microtubules, which serve as guiding tracks for active CSCs[5].

The biosynthesis of hemicelluloses, such as glucomannans, xylans, and xyloglucans, occurs in the Golgi apparatus[6–11]. Hemicelluloses are synthesized via the formation of their backbones by glycan synthases and the addition of side chain residues to the backbones by GTs[12]. Various sugar nucleotides, such as UDP-glucose, UDP-xylose, guanosine diphosphate (GDP)-glucose, and GDP-mannose, are used as the precursors for hemicellulose synthesis. Glycan synthases and GTs produce hemicelluloses by repeatedly transferring glycosyl residues from the precursors to acceptor molecules, namely, the elongating backbones or side chains. Synthesized hemicelluloses are packaged into Golgi vesicles and transported to the plasma membrane. They are then secreted to the cell wall by exocytosis resulting from the fusion of the Golgi vesicle membrane with the plasma membrane[6,11].

Lignin biosynthesis involves 2 major steps: monolignol biosynthesis inside the cell, followed by lignin polymerization in the cell wall. Monolignols are synthesized from phenylalanine derived from the shikimate biosynthetic pathway[13] through the general phenylpropanoid and monolignol-specific pathways[14–16]. Cinnamyl alcohol dehydrogenase that catalyzes the final

reaction to synthesize monolignols is localized in the cytosol, indicating that newly synthesized monolignols are present in the cytosol[17]. After their biosynthesis, monolignols are transported to the cell wall by a mechanism that remains unclear. Lignin polymerization occurs through dehydrogenative polymerization of monolignols that is catalyzed by peroxidases and laccases[18,19].

Diurnal Differences in the Innermost Surface of Developing Secondary Walls in Differentiating Tracheids

In conifers, over 90% of the wood is composed of tracheids, and the properties of wood are directly affected by the characteristics of tracheid cell walls. Hosoo et al.[20] collected samples of differentiating xylem during the day and at night from the trunk of *Cryptomeria japonica*. Then, they observed differences between day and night in the innermost surface of developing secondary walls in differentiating tracheids using field emission scanning electron microscopy (FE-SEM). The S_2 layer occupies a large part of the cell wall in tracheids, and most of the differentiating xylem cells were S_2-forming tracheids. Therefore, this study focused on the innermost surface of developing S_2 layers. Cellulose microfibrils were clearly observed during the day, while an amorphous material was observed and cellulose microfibrils were not evident at night (Fig. 2). The amorphous material observed at night was clearly different from cellulose microfibrils. In conifer tracheids, lignin deposition begins at the cell corners and in the middle lamella at approximately the same time as the start of S_1 layer formation. Lignin is then slowly deposited in the primary walls and S_1 layers during S_2 layer formation. Finally, it is most actively deposited throughout the secondary walls after the S_3 layer has formed[21-23]. Therefore, lignin is not likely to be observed in the innermost surface of developing secondary walls. Instead, one can infer that the amorphous material is likely to be a matrix containing hemicellulose.

The development of immunostaining methods enabled the labeling of each hemicellulose in the wood cell wall. Immunostaining is a technique used to detect a component (antigen) of interest within a tissue or cell via antibody-antigen interactions. The presence of a target antigen is detected under a microscope by labeling the antibody-antigen complex with a detector antibody conjugated to an indicator, such as a fluorescent dye, colloidal gold particle, radioactive marker, or enzyme. Studies using immunogold labeling, in which target antigens are labeled with colloidal gold particles, combined with transmission electron microscopy (TEM) have been able to determine the localization and deposition process of glucomannans, xylans, and xyloglucans in wood cell walls[24-28]. Awano et al.[29] investigated the distribution of xylans in wood fibers of *Fagus crenata* using immunogold labeling combined with

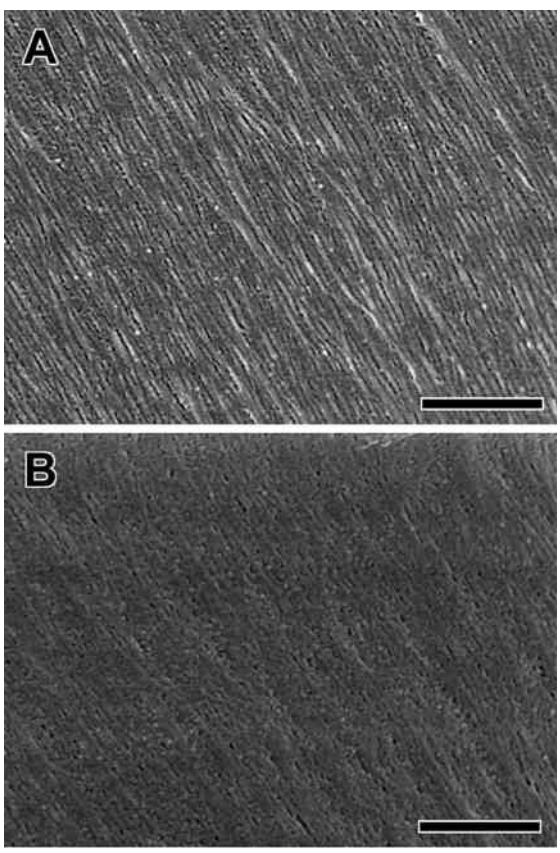

Fig. 2 Electron micrographs of the innermost surface of developing secondary walls (S_2 layers) in differentiating tracheids of field-grown *Cryptomeria japonica*. The longitudinal cell axes in the micrographs are vertical. A : A sample collected at 14 : 00. B : A sample collected at 05 : 00. Bars=500nm.

FE-SEM. Sandquist et al.[30] observed the immunolocalization of xyloglucans in tension wood fibers of the poplar using TEM and FE-SEM.

Glucomannans and xylans are the 2 major hemicellulose components in softwoods. Hosoo et al.[20] observed diurnal differences in the amount of glucomannans, immunogold-labeled with an anti-glucomannan antibody, in the innermost surface of developing secondary walls in differentiating *C. japonica* tracheids using FE-SEM. The amount of anti-glucomannan labeling was small during the day when cellulose microfibrils were clearly evident (Fig. 3A). Conversely, a large amount of anti-glucomannan labeling was observed in the amorphous material at night (Fig. 3B). These results indicate that the amorphous material contained abundant levels of glucomannans. Another immunogold-SEM study suggested that the amorphous material contained xylans in addition to glucomannans[31]. Thus, it was confirmed that the amorphous material present in the innermost surface of developing secondary walls at night was a matrix containing hemicellulose. The above findings indicate that there is a diurnal periodicity in the supply of cell wall components to developing secondary walls during cell wall formation in conifer tracheids.

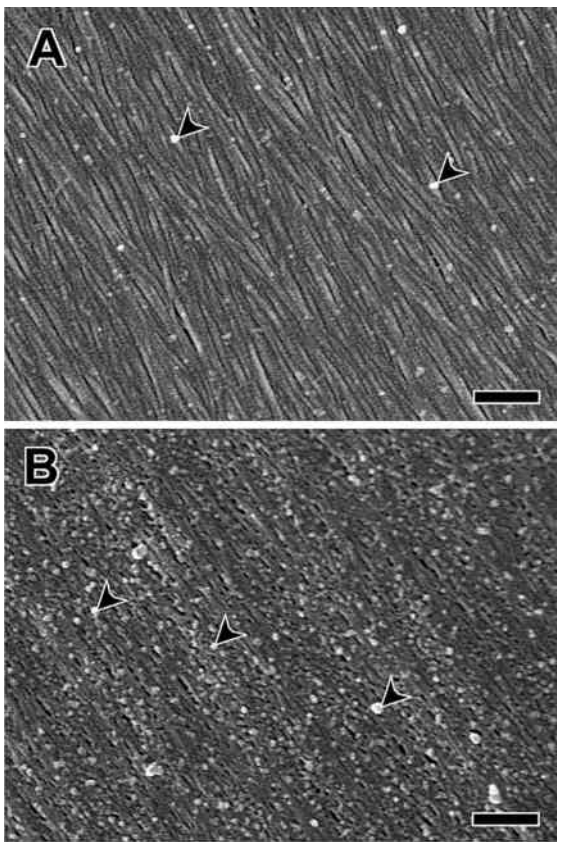

Fig. 3 Electron micrographs of the innermost surface of developing secondary walls (S_2 layers) immunogold-labeled with an anti-glucomannan antibody in differentiating tracheids of field-grown *C. japonica*. The longitudinal cell axes in the micrographs are vertical. Arrowheads show single or large aggregated gold particles representing anti-glucomannan labels. A : A sample collected at 14 : 00. B : A sample collected at 05 : 00. Bars＝200nm.

Effect of Light on Diurnal Differences in Secondary Wall Formation

Light is one of the most important environmental factors for plant growth and survival. It plays an important role in a number of plant developmental processes, including the initiation of cell differentiation in vegetative meristems, chloroplast development, hypocotyl elongation, leaf expansion, and flowering[32–34]. The contents of cell wall components change under different light intensities or qualities in herbaceous plants[35–37]. The expression of certain genes and the activities of certain enzymes involved in the biosynthesis of cell wall polysaccharides and lignin are affected by light exposure or light intensity in *Arabidopsis thaliana* and maize[38–40].

Hosoo et al.[41] studied the effect of a light-dark cycle on the diurnal differences observed in the innermost surface of developing secondary walls in differentiating tracheids. Saplings of *C. japonica* were grown in 2 growth chambers, in which temperature and relative humidity were kept constant and the light-dark phase of the photoperiodic cycle differed. In one chamber, the natural light-dark phase was reproduced, while in the other, it was reversed. Samples were collected during the light and dark periods, and the innermost surface of developing secondary walls (S_2 layers) was observed using FE-SEM. When the light and dark periods of the photoperiodic cycle were reversed, the diurnal differences in the inner-

most surface of developing secondary walls were also reversed. Regardless of the sampling time, cellulose microfibrils were clearly observed during the light period, while amorphous material containing hemicellulose was observed during the dark period. This study indicates that the diurnal periodicity in the supply of cell wall components to developing secondary walls during cell wall formation occurs, corresponding to the 24-h light-dark cycle.

Relationship between Water Status of Differentiating Cells and Diurnal Differences in Secondary Wall Formation

The water status within a tree is an important factor that affects xylem development. Many studies have investigated the relationship between the water status and xylem development in trees by anatomical analysis[42–47]. Plant cell growth (expansion) is driven by turgor pressure, which is the outward pressure of the protoplast that swells and pushes against the cell wall because of water uptake into the cell. During xylem cell development in trees, cell size (volume) is determined by the interaction between turgor pressure and cell wall properties of differentiating xylem cells[48,49].

The volumetric changes in differentiating cells in the stem of a tree can be estimated from the changes in the tangential strain on the inner bark surface[50]. The tangential strain is proportional to the volumetric changes in the cells. Diurnal changes in the tangential strain are observed in field-grown trees (Fig. 4)[20,50–52]. The strain reaches a maximum just before daybreak and gradually decreases to a minimum during the day. After reaching its minimum, the strain increases at night. Studies using *C. japonica* saplings grown in growth chambers, in which temperature and humidity were constant, demonstrated that the pattern of diurnal changes in the tangential strain corresponded to the light-dark phase during the 24-h photoperiodic cycle[41,43]. Regardless of the time, the strain became high during the dark period, while it became low during the light period (Fig. 5). These studies revealed that the volume of differentiating cells changes diurnally and corresponds to the 24-h light-dark cycle.

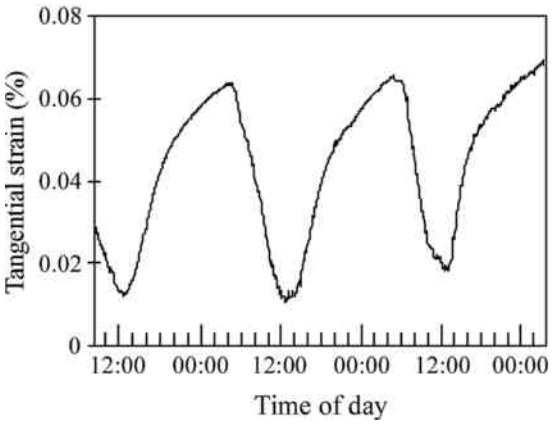

Fig. 4 Changes in tangential strain on the inner bark surface of a field-grown *C. japonica* tree at the end of July.

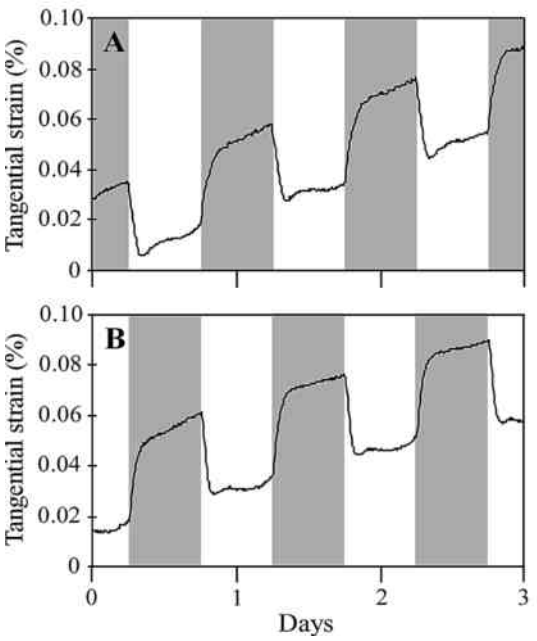

Fig. 5 Changes in tangential strain on the inner bark surface of *C. japonica* saplings in 2 growth chambers. Shaded areas indicate dark periods. A : A sapling grown in the natural light-dark cycle (lights on at 06 : 00 ; lights off at 18 : 00). B : A sapling grown under the reverse light-dark cycle to nature (lights on at 18 : 00 ; lights off at 06 : 00).

In the innermost surface of developing secondary walls in differentiating *C. japonica* tracheids, the time when amorphous material was observed corresponded to the time when the tangential

strain was high during the dark period, and, conversely, cellulose microfibrils were observed during the light period when the tangential strain was low[41]. This indicates that cellulose microfibrils are observed when the volume of differentiating cells is low as a result of water loss by transpiration and that the matrix containing hemicellulose is observed when differentiating cells are fully turgid as a result of cellular imbibition during periods of low transpiration. Hemicelluloses are synthesized in the Golgi apparatus and then secreted to the cell wall by exocytosis[6,11]. The exocytotic process in higher plants is associated with turgor pressure, and the secretion of new cell wall materials is enhanced by increasing turgor pressure[53,54]. It seems probable that the hemicellulose secretion becomes active at increased turgor pressure at night, or during the dark period, and that the amorphous material becomes visible on the innermost surface of developing secondary walls with the accumulation of hemicelluloses. The diurnal periodicity in the supply of cell wall components to developing secondary walls during cell wall formation is likely to be associated with changes in the water status (e.g., turgor pressure) of differentiating tracheids.

Conclusion

Diurnal differences in the innermost surface of developing secondary walls were found in the differentiating tracheids of conifers. This indicates that there is a diurnal periodicity in the supply of cell wall components to developing secondary walls during cell wall formation in conifer tracheids. In addition, the relation between the diurnal differences in the innermost surface of developing secondary walls and environmental factors is becoming clearer. However, many areas of the diurnal periodicity in cell wall formation remain unclear. For example, it has not yet been determined if the diurnal periodicity is primarily triggered by changes in the water status, such as turgor pressure, or the light conditions. Analyses of gene expression and enzyme activity involved in the biosynthesis and secretion of cell wall components such as cellulose and hemicellulose will be important in future studies. Detailed knowledge of the mechanism of diurnal periodicity in cell wall formation would lead to a better understanding of wood properties and advanced utilization of wood materials.

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針葉樹木材細胞の細胞壁形成における日周性

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要　約

本論文では，木材細胞壁形成の日周性に関する研究動向について概説する。針葉樹仮道管の二次壁新生面を電解放出形走査電子顕微鏡（FE-SEM）で観察すると，日周的な差異が見られる。昼はセルロースミクロフィブリルが明瞭に観察され，夜は無定形物質が観察される。免疫金標識法とFE-SEM観察を用いた研究により，無定形物質がヘミセルロースを多く含むことが明らかになった。これらの知見は，針葉樹仮道管の細胞壁形成において分化中二次壁への細胞壁成分の供給に日周性が存在することを示唆している。他の研究により，二次壁新生面における様相の日変動は，24時間の明暗周期や分化中細胞の体積の日変動に伴って起こることが分かってきた。分化中二次壁への成分供給の日周性は，光条件や分化中細胞の水分状態（膨圧）の日変動と関連があると予想される。