J Wood Sci (2011) 57:345–351
DOI 10.1007/s10086-011-1196-8

ORIGINAL ARTICLE

Yoshihiro Hosoo · Masato Yoshida · Hiroyuki Yamamoto

Effect of light intensity on diurnal differences in the supply of cell wall components to the innermost surface of developing S_2 layers of tracheids in *Cryptomeria japonica*

Received: January 10, 2011 / Accepted: April 13, 2011 / Published online: July 16, 2011

Abstract We investigated the effect of light intensity on diurnal differences in secondary wall formation of tracheids. Saplings of *Cryptomeria japonica* were grown in growth chambers with light intensity cycles set for 12-h high light : 12-h low light by combining two of four light intensity levels: 1.5, 2.8, 4.3, and 10.0 klx. Volumetric changes of differentiating cells were monitored by measuring the tangential strain on the inner bark surface, and the innermost surface of developing secondary walls of differentiating tracheids during the high-light and low-light periods was observed by field-emission scanning electron microscopy. Changes in the aspects of the innermost surface of developing secondary walls and the tangential strain corresponded to changes in the light intensity level. Cellulose microfibrils were clearly observed when the light intensity was high (10.0 or 4.3 klx) and the volume of differentiating cells was low, while abundant amorphous material was observed when the light intensity was lowest (1.5 klx) and the cells were turgid, regardless of the light intensity cycle. These results suggest that the diurnal periodicity in the supply of cell wall components to developing secondary walls is associated with changes in light intensity during the photoperiodic cycle.

Key words *Cryptomeria japonica* · Diurnal periodicity · Photoperiodicity · Secondary wall formation · Tracheid

Introduction

The most fundamental constituent of wood in the stem of trees is the highly developed cell wall of xylem cells. The differentiation of xylem cells involves four major steps: cell expansion, the deposition of a thick secondary cell wall, lignification, and cell death.[1,2] Wood cell walls consist of crystalline cellulose microfibrils embedded in an amorphous hemicellulose–lignin matrix. In secondary walls, three layers can be distinguished based on the orientation of the cellulose microfibrils: the outer, middle, and inner layers (S_1, S_2, and S_3 layers, respectively).

Diurnal differences in the innermost surface of developing secondary walls of differentiating tracheids in *Cryptomeria japonica* can be observed by field-emission scanning electron microscopy (FE-SEM). Cellulose microfibrils are clearly evident during the day, and an amorphous material is prevalent at night.[3,4] We demonstrated that the amorphous material was a matrix containing hemicellulose.[4,5] The diurnal differences in the innermost surface of developing secondary walls were also seen in *C. japonica* saplings grown in growth chambers in which all conditions were constant except the photoperiodic cycle.[5,6] Our previous studies showed that the diurnal differences corresponded to the diurnal changes in the volume of differentiating cells.[3,4,6]

Light directly affects plant growth by its intensity, quality, and duration. Photosynthesis, respiration, and transpiration in trees are affected by light intensity.[7,8] The contents of cell wall components change under different light intensities or qualities in herbaceous plants.[9–11] The expression of some genes and the activities of some enzymes involved in the biosynthesis of cell wall polysaccharides and lignin are regulated by light exposure or light intensity in *Arabidopsis thaliana* and maize.[12–15] We demonstrated that diurnal differences in the innermost surface of developing secondary walls were affected by light; cellulose microfibrils were observed during the light period and amorphous material was observed during the dark period, regardless of the light–dark phase or day length during the 24-h light–dark cycle.[6,16] These studies suggest that the diurnal periodicity in the supply of cell wall components to developing secondary walls may occur in response to the changes in light intensity.

This study investigated the effect of light intensity on diurnal differences in the innermost surface of developing

Y. Hosoo (✉)
International Young Researchers Empowerment Center, Shinshu University, Minamiminowa, Kamiina, Nagano 399-4598, Japan
Tel. +81-265-77-1528; Fax +81-265-77-1528
e-mail: hosoo@shinshu-u.ac.jp

M. Yoshida · H. Yamamoto
Laboratory of Bio-material Physics, Graduate School of Bioagricultural Sciences, Nagoya University, Nagoya 464-8601, Japan

secondary walls. We analyzed *C. japonica* saplings grown in growth chambers in which two light intensities alternated every 12 h during the 24-h photoperiod. Volumetric changes of differentiating cells were monitored by measuring the tangential strain on the inner bark surface, and the innermost surface of developing secondary walls of differentiating tracheids was observed by FE-SEM. Observations made under different light intensities were compared, and the relation between light intensity and the diurnal periodicity in secondary wall formation was examined.

Materials and methods

Plant materials

Cloned saplings of 3-year-old *C. japonica* (mean height, 107 cm; mean basal diameter, 1.3 cm) planted in pots were placed in growth chambers (MLR-350; Sanyo, Tokyo, Japan) at a controlled temperature (25° ± 2.5°C) and a relative humidity of 70%–90% at the beginning of June. Five levels of light intensity (L0, L1, L2, L3, and L4) were automatically controlled in the chambers. Level L0 was equivalent to total darkness. Illuminance was measured for levels L1, L2, L3, and L4 at the center of the chamber using a digital light meter (DX-100, Takemura, Tokyo, Japan) and was 1.5, 2.8, 4.3, and 10.0 klx, respectively. Level L1 was equivalent to the brightness of a shopping arcade at night, level L2 was equivalent to a field at twilight on a sunny day, level L3 was equivalent to a field during daytime on a dark rainy day, and level L4 was equivalent to shade during the daytime under clear skies. The saplings were first grown under a 12-h light (L4):12-h dark (L0) cycle (L4L0; lights on at 10:00 and lights off at 22:00). After about 1 week, the L4L0 cycle was changed to a light intensity cycle with a 12-h high-light period and a 12-h low-light period (light intensity changed at 10:00 and 22:00). Six kinds of light intensity cycles were used by combining two of four (L1, L2, L3 and L4) light intensity levels: L4L1, L4L2, L4L3, L3L1, L3L2, and L2L1. The light conditions during each cycle are shown in Table 1. The saplings were irrigated with 200 ml of water at 10:00 every day. To estimate the volumetric changes in differentiating cells, one of the saplings was subjected to a tangential strain measurement on the inner bark surface.

Table 1. Light conditions during the different light intensity cycles (12-h high light:12-h low light) in growth chambers

Light-intensity cycle	High-light period		Low-light period	
	Level[a]	Illuminance[b] (klx)	Level	Illuminance (klx)
L4L1	L4	10.0	L1	1.5
L4L2	L4	10.0	L2	2.8
L4L3	L4	10.0	L3	4.3
L3L1	L3	4.3	L1	1.5
L3L2	L3	4.3	L2	2.8
L2L1	L2	2.8	L1	1.5

[a] Cycles were set using four light intensity levels, denoted L1, L2, L3, and L4

[b] Illuminance was measured at the center of the growth chamber

After about 2 weeks, samples for FE-SEM observations were collected from each chamber during the high-light and low-light periods (about 1 h before the light intensity changed). The stems were cut into segments about 5 cm long and then divided into small pieces containing differentiating xylem. The samples were fixed with 3% glutaraldehyde in 0.07 M phosphate buffer (pH 7.0) overnight at 4°C. The samples were degassed occasionally during fixation until the samples were totally immersed in fixing solution.

Measurement of tangential strain (estimation of volumetric changes in differentiating cells)

A knife was used to remove 15-mm squares of outer bark from the stem 10 cm above the ground. A 5-mm strain gauge (KFG-5-120-C-11; Kyowa, Tokyo, Japan) was glued tangentially to the surface of the inner bark using a cyanoacrylate adhesive (CC-33A; Kyowa). The strain gauge was connected to a strain meter (UCAM-20PC, Kyowa) by a three-wire connection. To prevent dehydration of the inner bark and to shield it from light, the strain gauge and inner bark were covered with layers of lanolin, vinyl, and aluminum foil. Measurements were made at 10-min intervals. Differences in the pattern of changes in tangential strain between the L4L0 cycle and each of the six light intensity cycles were examined. The environmental conditions in the growth chambers were uniform throughout the study, and all saplings in the same chamber grew under the same conditions. Hence, tangential strain measured for one sapling in each chamber was applied to all saplings grown under the same light conditions, including those used for FE-SEM observations.

Scanning electron microscopy

Radial sections were investigated because they are useful for detecting specific developmental stages of differentiating tracheids. Radial sections approximately 200 µm thick were prepared from fixed segments using a freezing/sliding microtome at –20°C. The sections were treated with 50% sodium hypochlorite for 10 min to remove the protoplasm. After washing with distilled water, the sections were conductive-stained with 1% OsO_4 in distilled water for 2 h. They were washed with distilled water, dehydrated through a graded ethanol series, and then dried using the *t*-butyl alcohol freeze-drying method.[17] The dried sections were coated with approximately 3.5-nm-thick platinum–palladium using an ion sputter coater (E-1030; Hitachi, Tokyo, Japan). Subsequently, the innermost surface of the developing secondary walls in differentiating tracheids was observed by FE-SEM (S-4500; Hitachi) at an accelerating voltage of 1.5 kV and a working distance of 5 mm. Several sections were prepared from each sample and approximately ten different cells in each individual section were observed.

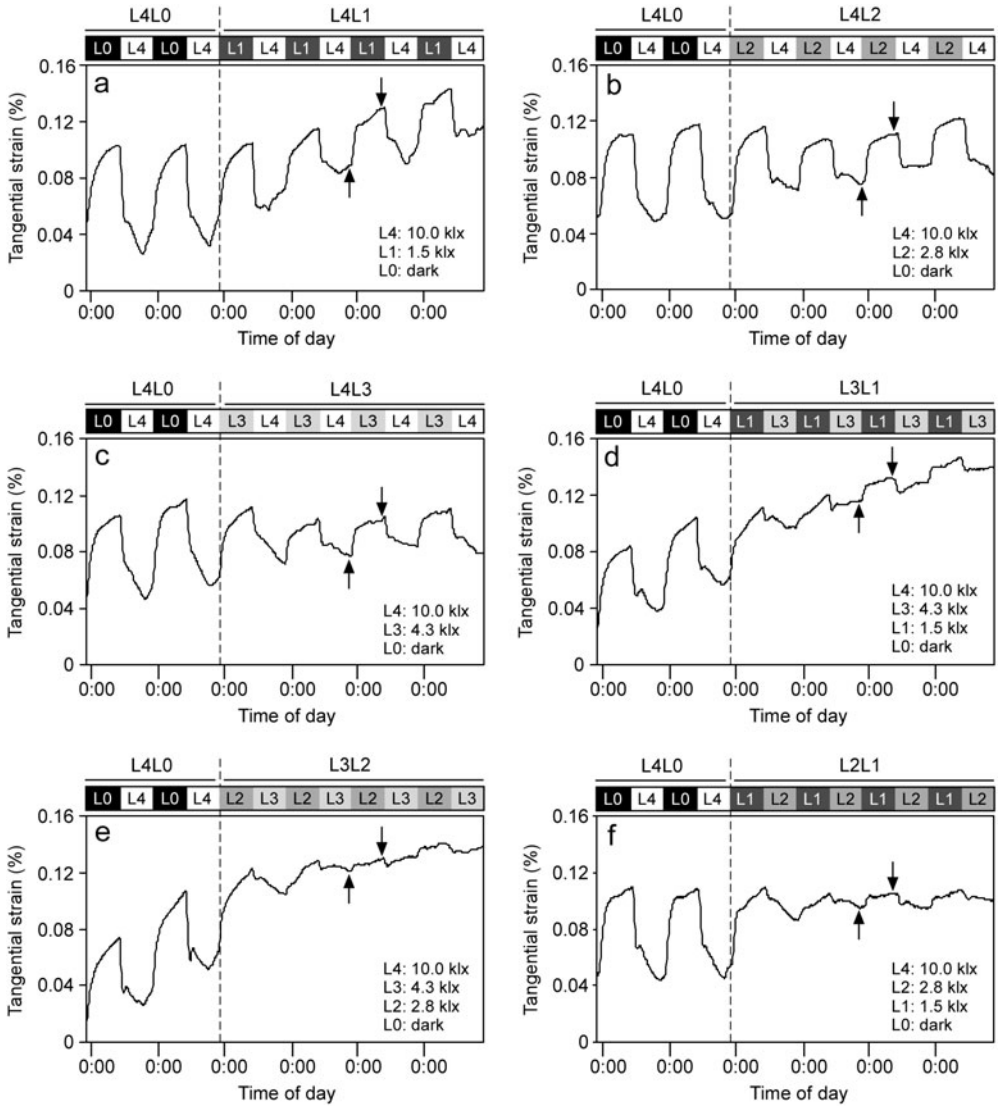

Fig. 1. Changes in tangential strain on the inner bark surface of saplings grown in growth chambers. **a** A sapling grown under the 12-h L4:12-h L1 (L4L1) cycle. **b** A sapling grown under the 12-h L4:12-h L2 (L4L2) cycle. **c** A sapling grown under the 12-h L4:12-h L3 (L4L3) cycle. **d** A sapling grown under the 12-h L3:12-h L1 (L3L1) cycle. **e** A sapling grown under the 12-h L3:12-h L2 (L3L2) cycle. **f** A sapling grown under the 12-h L2:12-h L1 (L2L1) cycle. The saplings were first grown under 12-h L4 and 12-h L0 (L4L0) and then under each of the light intensity cycles shown in panels **a**–**f**. *Arrows* show the sampling times. *Horizontal bars* at the top indicate the light intensity levels during each light cycle

Results

Tangential strain on the inner bark surface

Figure 1 shows the changes in tangential strain on the inner bark surface. Diurnal changes in tangential strain were observed in saplings grown under L4L1, L4L2, and L4L3 cycles (Fig. 1a–c). The tangential strain increased sharply immediately after the change from the high-light (L4) to the low-light (L1, L2, or L3) period, and then continued to increase more slowly. The strain decreased rapidly immediately after the change from the low-light period to the high-light period. Under these cycles, daily fluctuations in the strain were smaller than those under the L4L0 cycle, and the increase in the strain during the low-light period was smaller than that during the dark (L0) period. The increase in the strain during the low-light period after the L4 period was largest during the L1 period and smallest during the L3 period. Diurnal changes in tangential strain were also observed in saplings grown under the L3L1, L3L2, and L2L1 cycles. Periodic fluctuations in the strain under these cycles were less clear (Fig. 1d–f) compared with those under the L4L0 cycle or other light intensity cycles containing the L4 high-light period.

FE-SEM observation of the innermost surface of developing secondary walls

The S_2 layer occupies a large part of the cell wall in conifer tracheids, and most differentiating xylem cells are S_2-forming tracheids in coniferous species, including *C. japonica*. Therefore, we investigated the innermost surface of developing S_2 layers in this study.

In the specimens collected from the L4L1 chamber during the L4 period, cellulose microfibrils were clearly observed and amorphous material was rarely found on the innermost surface of developing secondary walls (Fig. 2a). In specimens collected during the L1 period, amorphous material was observed on the innermost surface (Fig. 2b), and the appearance of the material was similar to that observed at night or during the dark period in a growth chamber.[4,6] In the specimens collected from the L4L2

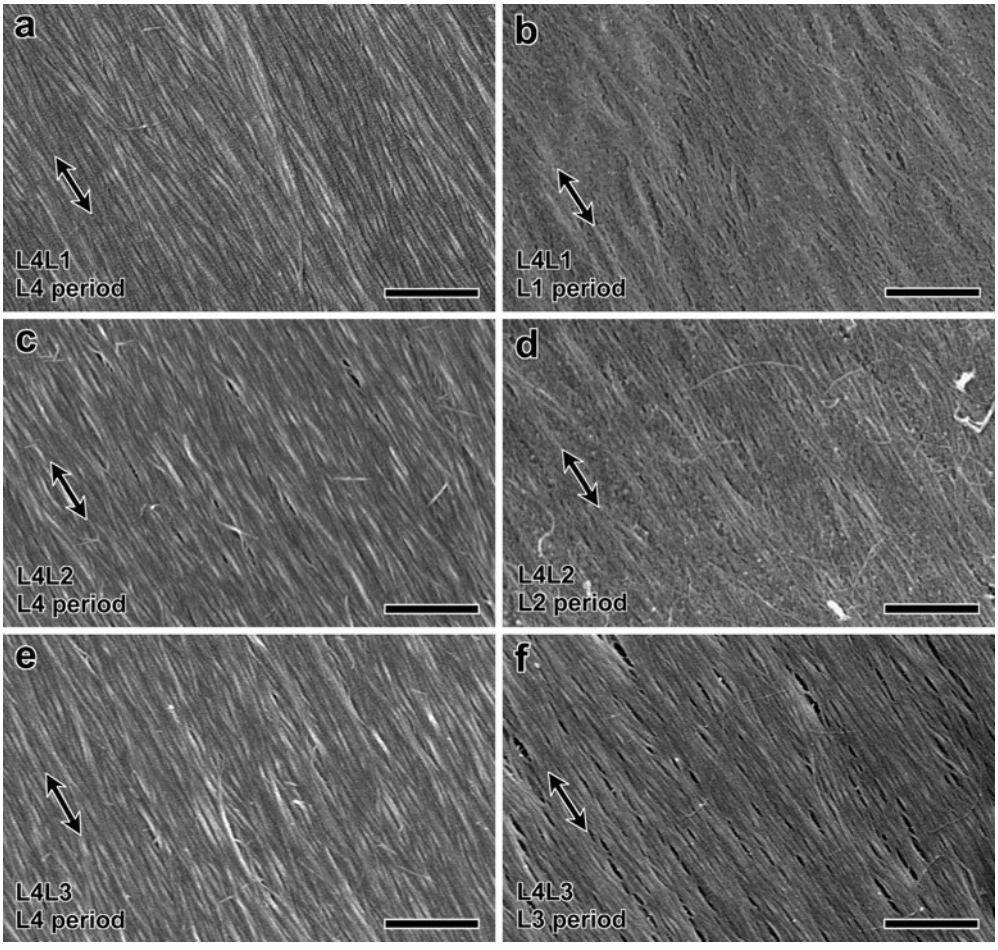

Fig. 2. Electron micrographs of the innermost surface of developing secondary walls in specimens collected from saplings grown under light intensity cycles that included the L4 high-light period, i.e., the L4L1 (**a**, **b**), L4L2 (**c**, **d**), and L4L3 (**e**, **f**) cycles. The longitudinal cell axes in the micrographs are vertical. *Double-headed arrows* show the orientation of cellulose microfibrils. **a**, **c**, **e** Specimens collected during the high-light (L4) period. **b**, **d**, **f** Specimens collected during the low-light (L1, L2, or L3) period. *Bars* 500 nm

chamber during the L4 period, cellulose microfibrils were clearly observed (Fig. 2c). In the specimens collected during the L2 period, cellulose microfibrils were visible and amorphous material was less clearly visible than in those collected during the L1 period of the L4L1 cycle (Fig. 2d). In the specimens collected from the L4L3 chamber, cellulose microfibrils were clearly observed during both the L3 and L4 periods (Fig. 2e, f). In the specimens collected from the L3L1 and L2L1 chambers, the aspects of the innermost surface of developing secondary walls were similar to those in the L4L1 specimens. Cellulose microfibrils were evident during the high-light period, while amorphous material was prevalent during the low-light period (Fig. 3a, b, e, f). In the specimens collected from the L3L2 chamber, cellulose microfibrils were observed during both the L2 and L3 periods (Fig. 3c, d). Although amorphous material was observed during the L2 period, the amount of this material was small.

Discussion

Diurnal differences in the innermost surface of developing secondary walls were observed under light intensity cycles containing the L1 low-light period (L4L1, L3L1, and L2L1 cycles). In contrast, diurnal differences were not clearly observed under cycles consisting of high light intensities, i.e., the L4L3 and L4L2 cycles, although the difference in light intensity between the high-light and low-light periods during these cycles was larger than that during the L3L1 and L2L1 cycles. Cellulose microfibrils were clearly observed when the light intensity was high, especially during the L3 and L4 periods, whereas abundant amorphous material was observed when the light intensity was lowest, i.e., during the L1 period, regardless of the combination of light intensities in the light intensity cycle. These results indicate that changes in the aspects of the innermost surface of developing secondary walls corresponded to changes in the light intensity level. Diurnal differences in the innermost surface appear to be associated with the change in light intensity itself rather than the difference in light intensity between the high-light and low-light periods or day and night.

Amorphous material similar to that observed at night or during the dark period[4,6] was prevalent on the innermost surface of developing secondary walls during the L1 period. This result suggests that abundant amorphous material was present on the innermost surface not only under the condition of darkness but also under low light intensity (1.5 klx). We previously demonstrated that the amorphous material contained glucomannans and xylans, which are major hemi-

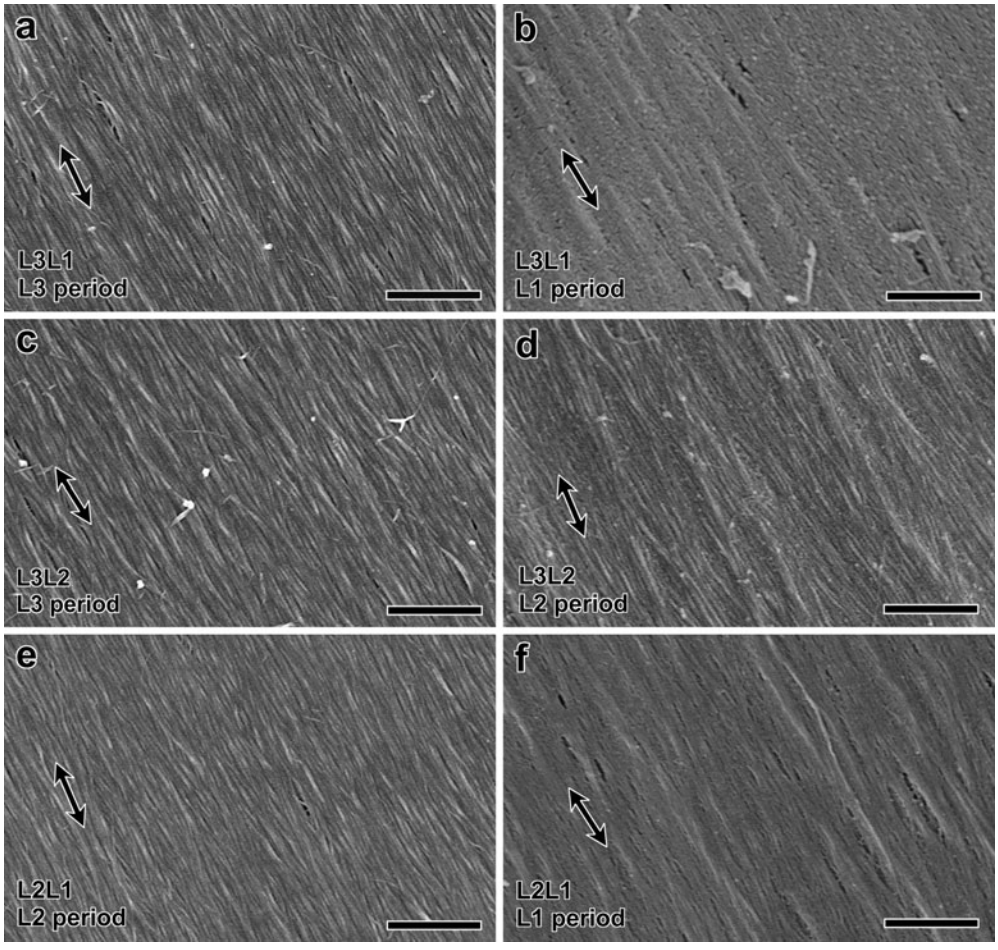

Fig. 3. Electron micrographs of the innermost surface of developing secondary walls in specimens collected from saplings grown under the L3L1 (**a**, **b**), L3L2 (**c**, **d**), and L2L1 (**e**, **f**) light intensity cycles. The longitudinal cell axes in the micrographs are vertical. *Double-headed arrows* show the orientation of cellulose microfibrils. **a**, **c**, **e** Specimens collected during the high-light (L2 or L3) period. **b**, **d**, **f** Specimens collected during the low-light (L1 or L2) period. *Bars* 500 nm

celluloses in softwoods.[4,5] It is likely that abundant matrix containing hemicellulose is present in the innermost surface when the light intensity is sufficiently low (equivalent to L1 or darker).

The changes in tangential strain are induced by changes in the water content and the volume of differentiating cells.[18–20] The strain is proportional to the volume of differentiating cells. Diurnal fluctuations in the strain became smaller as the difference in light intensity between the high-light and low-light periods decreased. The increase in the strain after the L4 high-light period became larger as the light intensity of the low-light period became lower. These results suggest that the volume of differentiating cells changes in correspondence with the changes in light intensity. The volume of differentiating cells was lowest in the specimens collected during the L4 period because of water loss by transpiration. Cell volume in the specimens collected during the L2 and L3 periods was larger than that in the specimens collected during the L4 period because of reduced transpiration. Differentiating cells were most turgid in the specimens collected during the L1 period as a result of water absorption.

Hemicelluloses are synthesized in the Golgi apparatus and then secreted into the cell walls across the plasma membrane by exocytosis.[21,22] The exocytosis process in higher plants is controlled by turgor pressure, and the secretion of new cell wall materials is enhanced by increasing turgor pressure.[23,24] Our results showed that abundant amorphous material was observed on the innermost surface of developing secondary walls during the L1 period when differentiating cells were most turgid. The changes in turgor pressure of differentiating cells that result from changes in light intensity may be involved in the supply of amorphous material to the innermost surface. It seems probable that increased turgor pressure of differentiating cells enhanced secretion of hemicelluloses to the innermost surface and that amorphous material became evident with the accumulation of the matrix containing hemicellulose during the L1 period. Conversely, it is inferred that hemicellulose secretion is low during the L2, L3, and L4 periods because turgor pressure of differentiating cells is low.

Cellulose microfibrils were clearly observed, and amorphous material was rarely observed on the innermost surface of developing secondary walls during the high-light periods, including the L2 period during the L2L1 cycle. Thus, cellulose microfibrils were clearly seen on the innermost surface when the light intensity was relatively high and the turgor pressure of differentiating cells was relatively low during periodic changes in light intensity and turgor

pressure. A small amount of amorphous material in addition to cellulose microfibrils was observed during the L2 low-light period, which was equivalent to relatively low light and relatively high turgor pressure conditions during the L3L2 and L4L2 cycles. It is possible that diurnal differences in the supply of cell wall components to the innermost surface were affected by diurnal rhythms of light intensity and turgor pressure. Differences in the innermost surface during the L2 period between different light intensity cycles may depend on whether the L2 period was equivalent to the high-light or the low-light period.

The *cellulose synthase-like* (*Csl*) genes have been proposed to encode enzymes that synthesize the backbones of hemicelluloses.[25,26] Studies of *Csl A* subfamily (*CslA*) genes from bryophytes, conifers, and angiosperms have demonstrated that they encode enzymes with mannan and glucomannan synthase activities.[27–29] In maize, mannan synthase activity and the transcript level of a *CslA* gene closely related to a rice *CslA* gene encoding glucomannan synthase were reduced by exposure to high light intensity after the dark period.[15] Glucomannans are the most abundant hemicelluloses in softwoods.[30] Amorphous material was rarely observed on the innermost surface of developing secondary walls when light intensity was high, especially during the L3 or L4 period, possibly because both synthesis and secretion of hemicelluloses was inactive.

Cellulose microfibrils are synthesized at the plasma membrane by cellulose synthase complexes and are directly secreted into the cell wall.[31,32] Uridine diphosphate (UDP)-glucose is the direct substrate for cellulose synthesis, and UDP-glucose pyrophosphorylase (UGP) and sucrose synthase are key enzymes providing the UDP-glucose substrate.[33,34] In *Populus* spp., a *UGP* gene is coordinately up-regulated with cellulose synthase during late cell expansion and secondary wall formation of xylem cells,[35] and the overexpression of bacterial UGP in this species increases the cellulose content of the wood.[36] A *UGP* gene was up-regulated by exposure to high light intensity in *A. thaliana*.[13] It seems possible that cellulose synthesis is enhanced with increasing production of UDP-glucose substrate and that cellulose microfibrils are abundantly supplied to the innermost surface of developing secondary walls under high light conditions.

Changes in the aspects of the innermost surface of developing secondary walls and volumetric changes of differentiating cells were affected by changes in the light intensity level during the 24-h photoperiod. Cellulose microfibrils were clearly evident when the light intensity was high and the volume of differentiating cells was low, while abundant amorphous material was observed when the light intensity was lowest and the cells were fully turgid, regardless of the light intensity cycle. These findings suggest that the diurnal periodicity in the supply of cell wall components to developing secondary walls is associated with the changes in light intensity during the photoperiodic cycle.

Acknowledgments This study was performed through Special Coordination Funds for Promoting Science and Technology of the Ministry of Education, Culture, Sports, Science and Technology of Japan.

References

1. Savidge RA (1996) Xylogenesis. Int Assoc Wood Anat J 17:269–310
2. Plomion C, Le Provost G., Stokes A (2001) Wood formation in trees. Plant Physiol 127:1513–1523
3. Yoshida M, Hosoo Y, Okuyama T (2000) Periodicity as a factor in the generation of isotropic compressive growth stress between microfibrils in cell wall formation during a twenty-four hour period. Holzforschung 54:469–473
4. Hosoo Y, Yoshida M, Imai T, Okuyama T (2002) Diurnal differences in the amount of immunogold-labeled glucomannans detected with field emission scanning electron microscopy at the innermost surface of developing secondary walls of differentiating conifer tracheids. Planta 215:1006–1012
5. Hosoo Y, Imai T, Yoshida M (2006) Diurnal differences in the supply of glucomannans and xylans to the innermost surface of cell walls at various developmental stages from cambium to mature xylem in *Cryptomeria japonica*. Protoplasma 229:11–19
6. Hosoo Y, Yoshida M, Imai T, Okuyama T (2003) Diurnal differences in the innermost surface of the S_2 layer in differentiating tracheids of *Cryptomeria japonica* corresponding to a light-dark cycle. Holzforschung 57:567–573
7. Alexander JD, Donnelly JR, Shane JB (1995) Photosynthetic and transpirational responses of red spruce understory trees to light and temperature. Tree Physiol 15:393–398
8. O'Grady AP, Worledge D, Wilkinson A, Battaglia M (2008) Photosynthesis and respiration decline with light intensity in dominant and suppressed *Eucalyptus globulus* canopies. Func Plant Biol 35:439–447
9. Miyamoto K, Ueda J, Takeda S, Ida K, Hoson T, Masuda Y, Kamisaka S (1994) Light-induced increase in the contents of ferulic and diferulic acids in cell walls of *Avena* coleoptiles: its relationship to growth inhibition by light. Physiol Plant 92:350–355
10. Casal JJ, Sánchez RA, Paganelli-Blau AR, Izaguirre M (1995) Phytochrome effects on stem carbon gain in light-grown mustard seedlings are not simply the result of stem extension-growth responses. Physiol Plant 94:187–196
11. Senanayake SGJN (1995) The effects of different light levels on the nutritive quality of four natural tropical grasses. Trop Grassl 29:111–114
12. Walton JD, Ray PM (1982) Inhibition by light of growth and Golgi-localized glucan synthase in the maize mesocotyl. Planta 156:302–308
13. Ciereszko I, Johansson H, Kleczkwski LA (2001) Sucrose and light regulation of a cold-inducible UDP-glucose pyrophosphorylase gene via a hexokinase-independent and abscisic acid-insensitive pathway in *Arabidopsis*. Biochem J 354:67–72
14. Cona A, Cenci F, Cervelli M, Federico R, Mariottini P, Moreno S, Angelini R (2003) Polyamine oxidase, a hydrogen peroxide-producing enzyme, is up-regulated by light and down-regulated by auxin in the outer tissues of the maize mesocotyl. Plant Physiol 131:803–813
15. van Erp H, Walton JD (2009) Regulation of the *cellulose synthase-like* gene family by light in the maize mesocotyl. Planta 229: 885–897
16. Hosoo Y, Yoshida M, Imai T, Okuyama T (2005) The effect of day length on diurnal differences in the innermost surface of the S_2 layer in differentiating tracheids. J Wood Sci 51:323–327
17. Inoue T, Osatake H (1988) A new drying method of biological specimens of scanning electron microscopy: The *t*-butyl alcohol freeze-drying method. Arch Histol Cytol 51:53–59
18. 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. Mokuzai Gakkaishi 41:1070–1078
19. Yoshida M, Yamamoto O, Okuyama T (2000) Strain change on the inner bark surface of an inclined coniferous sapling producing compression wood. Holzforschung 54:664–668
20. Yoshida M, Ikawa M, Kaneda K, Okuyama T (2003) Stem tangential strain on the tension wood side of *Fagus crenata* saplings. J Wood Sci 49:475–478
21. Northcote, DH, Davey R, Lay J (1989) Use of antisera to localize callose, xylan and arabinogalactan in the cell-plate, primary and secondary walls of plant cells. Planta 178:353–366

22. Samuels AL, Rensing KH, Douglas CJ, Mansfield SD, Dharmawardhana DP, Ellis BE (2002) Cellular machinery of wood production: differentiation of secondary xylem in *Pinus contorta* var. *latifolia*. Planta 216:72–82
23. Fricke W, Jarvis MC, Brett CT (2000) Turgor pressure, membrane tension and the control of exocytosis in higher plants. Plant Cell Environ 23:999–1003
24. Proseus TE, Boyer JS (2005) Turgor pressure moves polysaccharides into growing cell walls of *Chara corallina*. Ann Bot 95: 967–979
25. Richmond TA, Somerville CR (2001) Integrative approaches to determining Csl function. Plant Mol Biol 47:131–143
26. Hazen SP, Scott-Craig JS, Walton JD (2002) Cellulose synthase-like genes of rice. Plant Physiol 128:336–340
27. Liepman AH, Wilkerson CG, Keegstra K (2005) Expression of cellulose synthase-like (*Csl*) genes in insect cells reveals that *CslA* family members encode mannan synthases. Proc Natl Acad Sci USA 102:2221–2226
28. Suzuki S, Li L, Sun YH, Chiang VL (2006) The cellulose synthase gene superfamily and biochemical functions of xylem-specific cellulose synthase-like genes in *Populus trichocarpa*. Plant Physiol 142:1233–1245
29. Liepman AH, Nairn CJ, Willats WGT, Sørensen I, Roberts AW, Keegstra K (2007) Functional genomic analysis supports conservation of function among cellulose synthase-like A gene family members and suggests diverse roles of mannans in plants. Plant Physiol 143:1881–1893
30. Timell TE (1967) Recent progress in the chemistry of wood hemicelluloses. Wood Sci Technol 1:45–70
31. Carpita N, McCann M (2000) The cell wall. In: Buchanan BB, Gruissem W, Jones RL (eds) Biochemistry and molecular biology of plants. American Society of Plant Physiologists, Rockville, MD, pp 52–108
32. Doblin MS, Kurek I, Jacob-Wilk D, Delmer DP (2002) Cellulose biosynthesis in plants: from genes to rosettes. Plant Cell Physiol 43:407–1420
33. Kleczkowski LA (1994) Glucose activation and metabolism through UDP-glucose pyrophosphorylase in plants. Phytochemistry 37:1507–1515
34. Amor Y, Haigler CH, Johnson S, Wainscott M, Delmer DP (1995) A membrane-associated form of sucrose synthase and its potential role in synthesis of cellulose and callose in plants. Proc Natl Acad Sci USA 92:9353–9357
35. Hertzberg M, Aspeborg H, Schrader J, Andersson A, Erlandsson R, Blomqvist K, Bhalerao R, Uhlén M, Teeri TT, Lundeberg J, Sundberg B, Nilsson P, Sandberg G (2001) A transcriptional roadmap to wood formation. Proc Natl Acad Sci USA 98:14732– 4737
36. Coleman HD, Canam T, Kang KY, Ellis DD, Mansfield SD (2007) Over-expression of UDP-glucose pyrophosphorylase in hybrid poplar affects carbon allocation. J Exp Bot 58:4257–4268