J Wood Sci (2002) 48:99–105

ORIGINAL ARTICLE

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Tensile growth stress and lignin distribution in the cell walls of black locust (*Robinia pseudoacacia*)

Received: December 15, 2000 / Accepted: March 9, 2001

Abstract Seven specimens that contained a continuous gradient of wood from normal to tension wood were collected from an inclined black locust (*Robinia pseudoacacia*), and the released strain of growth stress was quantified. Lignin distribution in the cell wall was investigated using ultraviolet (UV) microspectrophotometry to examine its relation to the intensity of growth stress. The UV absorption at cell corner middle lamella and in the compound middle lamella remained virtually constant, irrespective of the contractive released strain (i.e., tensile growth stress). The gelatinous (G)-layer began to differentiate, and the UV absorption decreased there in accordance with increases in the contractive released strain. The absorption maximum (λmax) remained virtually constant at the cell corner middle lamella and in the compound middle lamella at 277–280 nm, irrespective of the released strain. The λmax for the secondary wall of normal wood was 272 nm and shifted to 268 nm in the G-layer of tension wood as the contractive released strain increased. The percentage of the cross-sectional area, consisting of the G-layer, with respect to the whole cross-sectional area increased with the contractive released strain.

Key words Gelatinous layer · Lignin distribution · Microspectrophotometry · Tensile growth stress · Tension wood

Introduction

The microfibrillar angle, cellulose crystallinity, and lignin content in cell walls are important factors in the generation of growth stress.[1] Cell wall model analysis incorporating these factors indicates that growth stress is a combination of tensile stress induced in microfibrils in an axial direction and isotropic compressive stress evolved in the matrix.[2] This result was based on elucidating the relations between growth stress, cell wall structures, and the amounts of the chemical components. However, the experimental result, especially the relation between growth stress and lignin content, lacked accuracy. The distribution of lignin in cell walls was not considered because sawdust was used for the analysis. Therefore, our study included measurements of lignin in both cell walls and the middle lamellas.

Growth stress is the stress generated in cell walls. A previous investigation of the relation between the lignin content in the cell wall and compressive growth stress used ultraviolet (UV) microspectrophotometry to examine compression wood in *Cryptomeria japonica*.[3] It was found that more compressive growth stress was associated with a higher lignin content, especially in the outer portion of the secondary wall.

This study investigated lignin distribution in the cell wall in tension wood of *Robinia pseudoacacia*, which has gelatinous fibers. We used UV microspectrophotometry to examine its relation to tensile growth stress.

Materials and methods

An inclined 23-year-old black locust (*Robinia pseudoacacia* L.), 7 m tall and 43 cm in diameter at breast height, growing in West Virginia was studied. This species has gelatinous fibers arranged in layers P + S1 + S2 + G in the upper side of inclined stems.[4]

Measuring growth stress

Nine and eight measuring points were established around the circumference of the trunk 94 and 145 cm from the ground, respectively, where the stem was bent severely. As described in previous reports,[5,6] a strain-gauge method was used on the standing tree. The bark, phloem, and thin cambial zone at each measuring point were carefully removed

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with a knife so as not to scratch the outer surface of the secondary xylem. Strain gauges 8 mm long and connected to a strain meter were glued lengthwise on the outer surface of the secondary xylem. After initial measurements were made in the standing position, a groove was cut to the depth of the current growth layer (1 cm) close to the two longitudinal edges of the strain gauge with a thin saw to release the growth stress. The distance from the edge of the gauge to the groove was 5 mm.

After measuring the released strain of the growth stress, wood block specimens were obtained from a point directly above each measuring position to determine elastic moduli and density. The elastic moduli were determined with a tensile test using small 10 × 20 × 1 mm test specimens of green wood. Elastic moduli in the longitudinal and tangential directions and Poisson's ratios were measured to convert the released strains to growth stresses.

The densities of air-dried specimens were measured using a gravimetric mercury method. Cross sections 12–20 μm thick were sliced from each specimen using a sliding microtome. The percentage of cross-sectional area consisting of the gelatinous (G)-layer with respect to the whole cross-sectional area was determined from the sections using an image analyzer (Zeiss, IBAS-II).[1,7]

UV microspectrophotometry

Small blocks of xylem tissue containing the current growth layer were obtained from the measuring positions and fixed with 3% glutaraldehyde. After dehydration through a graded ethanol series, the blocks were embedded in epoxy resin. Cross sections 0.5 μm thick were cut with a diamond knife and mounted on quartz slides with glycerin. The thickness of the thin sections was measured with an accuracy of 0.01 μm by a universal surface shape profiler (Kosaka, SE-3E) to select sections with uniform thickness and to correct the UV absorption spectra.[3] The thin sections were observed at wavelengths of 270–280 nm under a microspectrophotometer (Zeiss, MPM800). UV absorption spectra were obtained of the cell corner middle lamella, the compound middle lamella, the secondary wall, and the G-layer for wavelengths of 250–300 nm using the smallest measuring spot available with the microspectrophotometer (0.5 μm diameter). The spot diameter, was larger than the width of the middle lamella; therefore, the measurements of the middle lamella were affected by the secondary wall. To reduce this error, the measuring spot was centered on the middle lamella and peculiar spectra were omitted. As in previous studies,[3,8,9] the measuring method was as follows. Measurements were taken at 15–20 positions and averaged to determine the UV absorption spectra. The microspectrophotometer settings were an objective lens magnification of ×100, program of λ-scan, bandwidth of 1 nm, scan step of 1 nm, and number of scans 45. Seven specimens were selected for UV spectral analysis so the growth stress measurements of the specimens covered the range from normal wood to tension wood.

Results

Released strain of growth stress

Eccentric growth was found in both measuring disks on the upper side of the trunk, where the largest tensile growth stresses were measured and gelatinous fibers existed. The smallest tensile growth stresses were measured on the opposite, lower side (Table 1). Tensile growth stress, indicated as a negative (contractive) released strain, increased with development of the G-layer. The contractive released strain was proportional to the percentage of cross-sectional area of the G-layer to the whole sight (Fig. 1). A previous paper provides a detailed description of these data.[1] The specimens selected for UV spectral analysis and observation are indicated by asterisks and labeled in Table 1.

UV micrography

Figure 2 shows micrographs and absorption profiles across the cell walls of fibers at a wavelength of 278 nm. Results similar to the following were obtained for wavelengths of 270–280 nm. In normal wood specimens with a −0.0143% released strain (Fig. 2a), the UV absorbance was high at the cell corner middle lamella and in the compound middle lamella, and it was low and constant in the secondary wall. In the specimen with a released strain of −0.1188% (Fig. 2b), fibers were sometimes found whose UV absorbance was not constant across the secondary wall. In these fibers the inner layer of the secondary wall had a slightly higher absorbance than the outer layer. In the specimen with a released strain of −0.2056% (Fig. 2c), fibers with this property were frequently observed, and no definite gelatinous fibers were found. In the specimen with a released strain of −0.2510% (Fig. 2d), many gelatinous fibers were observed.

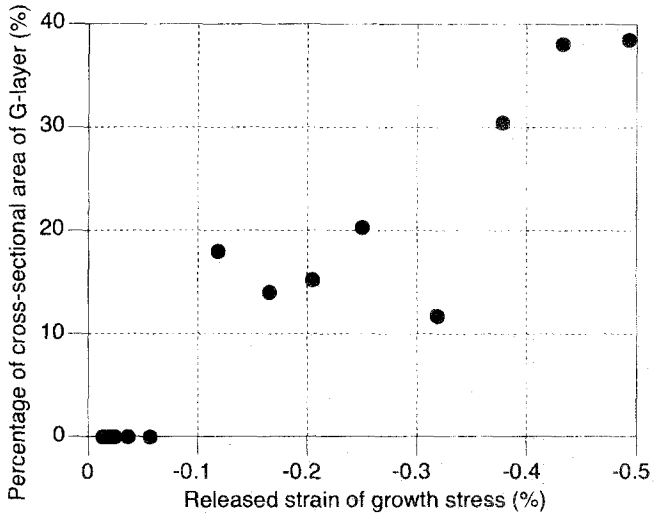


Fig. 1. Percentage of the cross-sectional area of the gelatinous layer (*G-layer*) with respect to the whole cross-sectional area in samples graded according to the released strain of growth stress. A contractive (negative) released strain indicates tensile growth stress

Table 1. Growth stress and other selected properties measured around an inclined trunk

Peripheral position (degrees)	Released strain (%)	Young's modulus (Gpa)	Density in air-dried condition (g/cm^3)	Growth stress (MPa)	Radius vector (cm)	Percent of cross-sectional area of G-layer (%)	Specimen label
Disk 1 (94 cm from ground)							
0*	−0.4931	14.56	0.97	68.76	8.0	38.5	g
30*	−0.4332	9.91	0.80	42.81	7.5	38.1	f
53	−0.3195	20.75	0.70	66.09	7.5	11.8	
80	−0.0146	22.97	0.75	3.36	7.0	0	
120	−0.0227	21.76	0.77	4.97	4.5	0	
190	−0.0371	16.75	0.76	6.41	4.0	0	
260	−0.0251	17.79	0.85	4.47	6.0	0	
290*	−0.2056	17.81	0.84	36.41	6.5	15.3	c
330*	−0.1188	6.64	0.65	7.88	7.0	18.0	b
Disk 2 (145 cm from ground)							
0*	−0.3785	14.43	0.77	54.61	7.0	30.5	e
28	−0.1661	13.63	0.90	22.56	7.5	14.1	
65	−0.0200	14.83	0.81	2.94	7.0	0	
110*	−0.0143	20.15	0.72	2.78	5.5	0	a
180	−0.0151	10.40	0.77	1.60	5.0	0	
256	−0.0240	17.68	0.76	4.19	6.0	0	
292	−0.0573	13.69	0.71	7.81	6.0	0	
330*	−0.2510	14.00	0.79	35.15	6.0	20.3	d

Position 0 is the uppermost position on the trunk
Samples marked with an asterisk were used for microspectrophotometry and labeled a to g

The G-layer had a lower UV absorption than the secondary wall. In the specimens with released strains of −0.3785% (Fig. 2e), −0.4332% (Fig. 2f), and −0.4931% (Fig. 2g), the G-layer was thick and the lumen narrow. In these specimens, abnormal gelatinous fibers with a thinner G-layer and high UV absorbance in the inner part of the G-layer and low UV absorbance in the outer part of the G-layer were sometimes observed (Fig. 2h).

UV absorption spectra

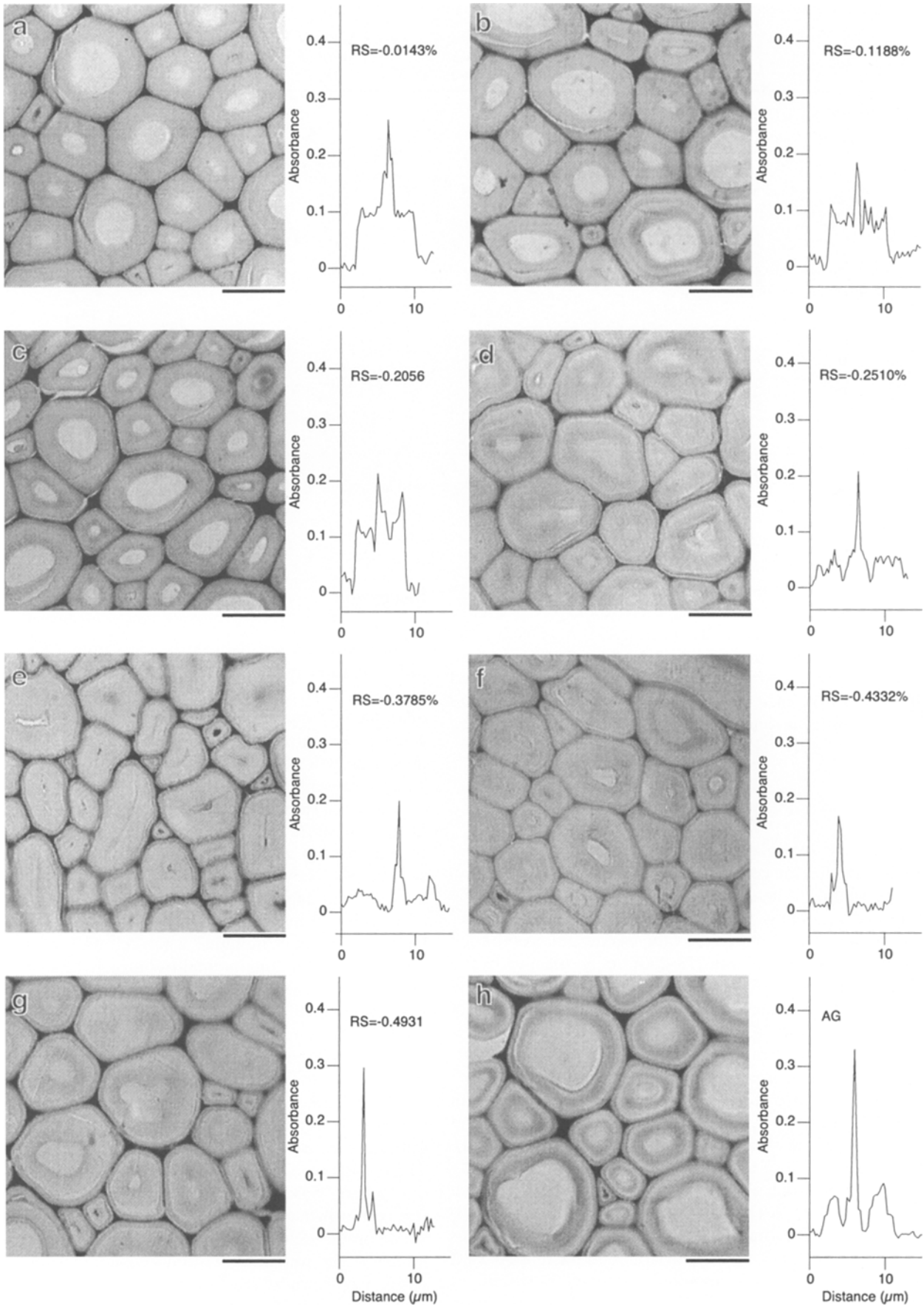
The average UV absorption spectra for the cell corner middle lamella, the compound middle lamella, and the secondary wall or G-layer are shown in Fig. 3. Spectra of the abnormal gelatinous fibers mentioned above were not included when determining the averages. The λmax of the cell corner middle lamella was 278–280 nm, irrespective of the released strain of growth stress. The UV absorption of the cell corner middle lamella remained constant, the λmax of the compound middle lamella was 277–280 nm, and the UV absorption of the compound middle lamella remained constant, in all cases irrespective of the released strain. The λmax was 272 nm in the secondary wall of normal wood with a small contractive released strain (Figs. 2a,b, 3a,b) and shifted to 268 nm in the indefinite G-layer (Figs. 2d, 3d). In specimens with a contractive released strain exceeding −0.3785% and the absolute value of the released strain exceeding 0.3785% (Figs. 2e–g, 3e–g), the λmax was obscure and the absorbance low. In the abnormal gelatinous fibers with a high UV absorbance found in the inner part of the G-layer, which were sometimes observed in specimens with a larger contractive released strain, the UV absorption of the cell corner middle lamella was high (Figs. 2h, 3h).

Discussion

Growth stresses are induced in the cambial layer during differentiation and maturation of new cells and are impeded by the mass of the whole trunk.[10,11] The growth stress is quantified by measuring the strain released when the xylem is cut. A negative (contractive) released strain represents tensile growth stress, and a positive (expansive) released strain represents compressive growth stress.

There is a strong correlation between the released strain of growth stress and the intensity of reaction wood.[1,12,13] In compression wood, the longitudinal expansive released strain is positively correlated with the Klason lignin content, microfibrillar angle, darkness of color, and transverse areas of the cell wall and intercellular space. It is negatively correlated with Young's modulus in the cell wall substance.[12] In tension wood the longitudinally contractive released strain increases with the α-cellulose content and crystallinity. It is negatively correlated with the Klason lignin content and microfibrillar angle. These relations apply to species that lack gelatinous fibers on the upper side of an inclined stem.[1,13]

The released strain of growth stress has been used to obtain a continuous, quantitative classification of wood samples because of the above significant correlations.[6,14–16] The tension wood of *Eucalyptus* species, which lack gelatinous fibers, was characterized by measuring the released strain of growth stress at the outer surface of the secondary xylem on the stem.[14] The released strain was used to determine a grade from normal wood to reaction wood in *Buxus sempervirens*, whose reaction wood resembles gymnosperm compression wood, and a clear correlation between the released strain and the lignin structure was found.[15] The


a
RS=-0.0143%
b
RS=-0.1188%
c
RS=-0.2056
d
RS=-0.2510%
e
RS=-0.3785%
f
RS=-0.4332%
g
RS=-0.4931
h
AG
Absorbance
0.4
0.3
0.2
0.1
0
0
10
Distance (μm)

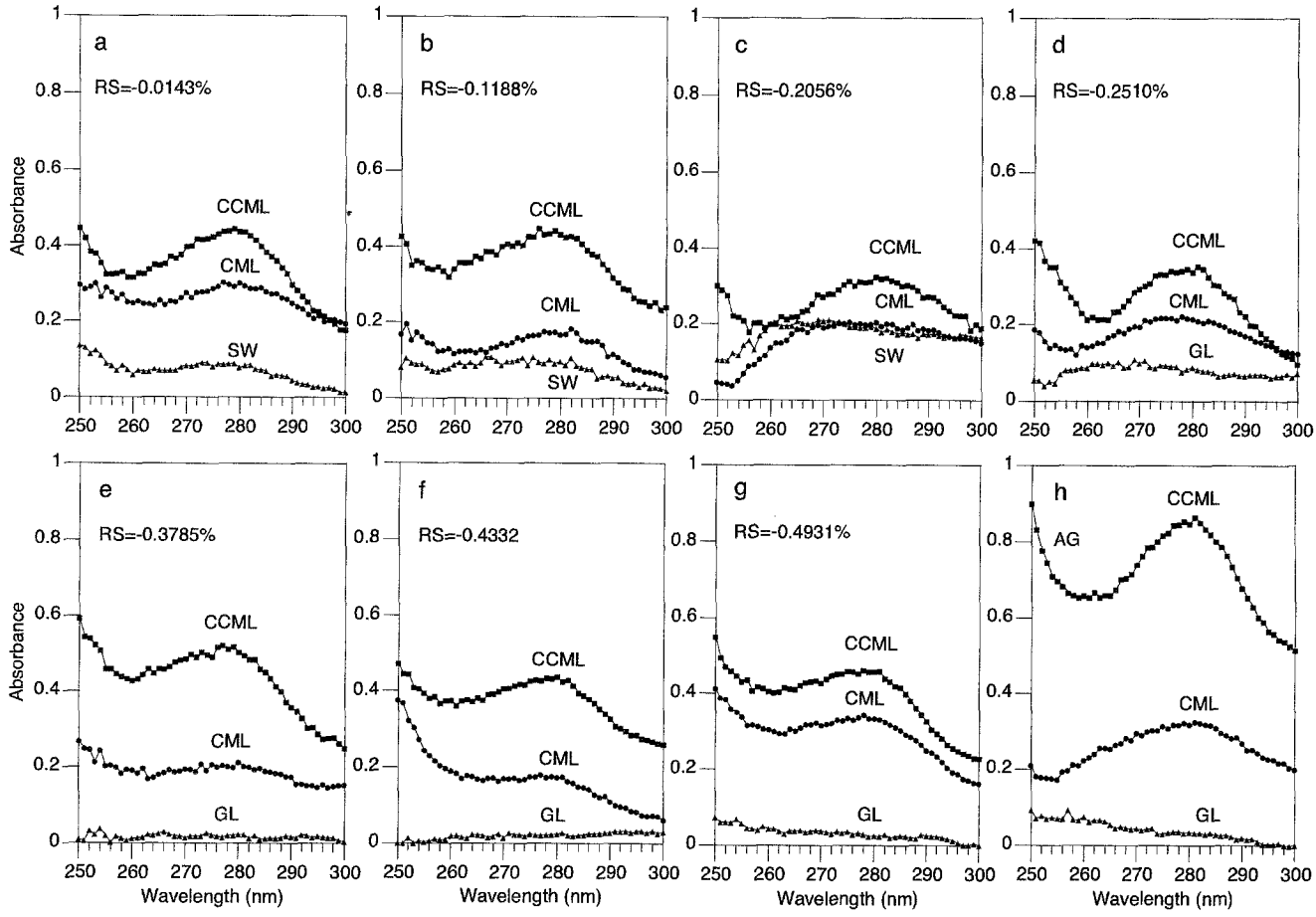


Fig. 3. UV absorption spectra of a cell corner middle lamella (*CCML*), the compound middle lamella (*CML*), the secondary wall (*SW*), and the gelatinous layer (*GL*) of fibers in samples graded according to the released strain (*RS*) of growth stress (**a–g**). Abnormal gelatinous fibers (*AG*) are observed in intense tension wood (**h**)

equilibrium position of a weeping branch of *Prunus spachiana* was estimated by measuring the released strain because the intensity of reaction wood could not be determined with an anatomical method.[6] Compression wood-responsive proteins were investigated in *Pinus pinaster* samples classified by growth stress.[16]

Measuring the released strain of growth stress is a useful way to estimate the intensity of reaction wood, as mentioned above. Growth stress measurements allow xylem samples to be classified quantitatively from normal wood to reaction wood. The larger the contractive released strain, the larger the tensile growth stress and the higher the intensity of the tension wood.

The seven specimens measured using microspectrophotometry in this study ranged from normal wood (Fig. 2a) to intense tension wood (Fig. 2g). In the specimens cells were likely to have lignin deposited in the G-layer. Some studies indicate that there is a lignified layer in the G-layer.[4,17–20] Jutte[17] found a lignified layer in the G-layer of *Ocotea rubra* and showed that an unlignified cell wall might be the first phase of tension wood. He also urged that "tension wood" be redefined. UV micrographs of some hardwood species show that lignin often penetrates the G-layer, and that cells in transitional regions between normal and reaction wood are more likely to have lignin deposited in the G-layer than cells in the center of an area of reaction wood.[18] Araki et al.[4] examined the cell wall structure of transitional fibers between normal and tension wood in *Robinia pseudoacacia* L. and *Populus euramericana* Guinier and found that concentric rings stained with $KMnO_4$ did not exist in the definitive G-layers but were present in the transitional G-layers. In a leguminous woody xerophyte, G-like layers classified as unlignified, partially lignified, and completely lignified types were observed at the innermost portion of the secondary wall of wood fibers.[20] Scurfield[19] attributed reduced lignification of the G-layer to retardation of lignin precursor pen-

Fig. 2. Ultraviolet (UV) photomicrographs of cross-sectional and absorption profiles across the cell walls of fibers at a wavelength of 278 nm in samples graded according to the released strain (*RS*) of growth stress (**a–g**). *AG*, abnormal gelatinous fibers observed in intense tension wood (**h**). Bar 10 μm

Table 2. Absorbance at wavelength 278 nm and λmax in various regions of cell walls of fibers in samples graded according to the released strain of growth stress

Specimen label	Released strain (%)	Absorbance, by region of cell wall				λmax (nm), by region of cell wall			
		CCML	CML	SW	GL	CCML	CML	SW	GL
a	−0.0143	0.46 (0.11)	0.27 (0.10)	0.09 (0.04)	–	279 (0.9)	279 (3.5)	273 (3.1)	–
b	−0.1188	0.44 (0.08)	0.15 (0.07)	0.09 (0.03)	–	279 (0.5)	280 (2.6)	272 (0.9)	–
c	−0.2056	0.37 (0.09)	0.20 (0.11)	0.18 (0.07)	–	278 (1.8)	277 (5.1)	268 (4.0)	–
d	−0.2510	0.35 (0.06)	0.25 (0.12)	–	0.06 (0.01)	279 (1.2)	279 (1.8)	–	268 (2.0)
e	−0.3785	0.51 (0.07)	0.17 (0.06)	–	0.04 (0.02)	279 (1.0)	279 (1.6)	–	–
f	−0.4332	0.43 (0.05)	0.16 (0.07)	–	0.03 (0.04)	278 (1.4)	274 (2.5)	–	–
g	−0.4931	0.45 (0.11)	0.32 (0.04)	–	0.04 (0.02)	279 (0.9)	277 (1.5)	–	–
h	AG	0.78 (0.12)	0.35 (0.14)	–	0.05 (0.01)	280 (1.9)	277 (5.1)	–	–

CCML, cell corner middle lamella; CML, compound middle lamella; SW, secondary wall; GL, gelatinous layer; AG, abnormal gelatinous layer observed in intense tension wood
Standard deviation is given in parentheses

etration of the G-layer, rather than to a lack of precursor availability.

Judging from the examples cited above and our UV micrographs, the transition process of cell wall from normal wood to tension wood with increasing intensity seems to be as follows. The degree of lignification of the secondary wall gradually decreases. Consequently, the unlignified layers develop into G-layers. The thickness of the G-layers increases with the intensity of the tension wood.

Gelatinous fibers with partly lignified G-layers are thought to be found in the transitional region between normal and tension wood. However, abnormal gelatinous fibers with partly lignified G-layers were observed in the intense tension wood regions. The abnormal gelatinous fibers observed in the intense tension wood differed from the gelatinous fibers observed in the transitional region. The former had more lignin at the cell corners than do normal gelatinous fibers.

As seen by microspectrophotometry of transverse sections of thin cell walls, there are problems in that the adjacent cell walls are often measured by nonparallel illumination. Thus, in this study many measurements were conducted and peculiar spectra were omitted to obtain average UV absorption spectra. However, the standard deviations were large (Table 2) because spectra seemed to have some errors due to the fact that the measuring spot, 0.5 μm, diameter, was larger than the width of the compound middle lamella.

This study investigated the relation between the released strain of growth stress and UV absorbance at a wavelength of 278 nm. As the contractive released strain increased, the UV absorbance of the secondary wall and indefinite G-layer decreased ($r = 0.36$, $P = 0.004$), and the UV absorbance at cell corner middle lamella and in the compound middle lamella remained virtually constant (Table 2). The indefinite G-layers observed during the first phase from normal to tension wood seem to be partly lignified. The increased UV absorbance of secondary wall of the specimens with a released strain of −0.2056% (Fig. 3c, Table 2, specimen c) might be due to the lignified G-layers.

The abnormal gelatinous fibers with a higher lignin content at the cell corner middle lamella occurred in tension wood, especially in intense tension wood, in which a larger contractive released strain of growth stress was measured and definite gelatinous fibers were differentiated. This is a new finding. In tension wood, the lignin of the secondary wall decreased, whereas that at the cell corner middle lamella and in the compound middle lamella did not. Large tensile growth stresses are generated in tension wood and help to reorient the tree to a more favorable position. The tensile growth stresses are produced as fibers tend to shrink.[21–24] The lignin at the cell corner middle lamella and in the compound middle lamella cements the fibers together. In intense tension wood, fibers are tied to each other strongly by the lignin at the cell corner middle lamella and in the compound middle lamella. Thus, transmission of large tensile growth stresses through the wood is ensured.

Ultraviolet microspectrophotometry has been used to determine the lignin distribution in various regions of the cell wall, but it is not effective for quantifying hardwood lignin.[25] To quantify hardwood lignin, the use of bromine uptake determined by transmission electron microscopy–energy-dispersive x-ray analysis (TEM-EDXA) and the UV absorbance of cell walls has been investigated.[26] Hardwood lignins consist mainly of syringyl (S) and guaiacyl (G) units. As seen by microspectrophotometry, there are some problems when evaluating lignin structures. The UV absorption of lignins generally gives a rather broad peak at about 280 nm. Consequently, accurate measurement of the S/G ratio by UV spectroscopy is difficult, because the λmax values of S- and G-units are similar: 270 and 280 nm, respectively.[27] In addition, S and G lignins have different absorption properties. The absorptivity of G lignin is three times as great as that of S lignin. The stronger peak of G lignin reduces the absorption peak of S lignin. Generally, the S/G ratio increases as the λmax in a spectrum shifts from 280 nm.[27,28]

The λmax at the secondary wall shifted to 268 nm as the contractive released strain increased, whereas it remained constant at the cell corner middle lamella and in the compound middle lamella (Table 2). Therefore, the S/G ratios

of lignins at the cell corner middle lamella and in the compound middle lamella were constant, regardless of the tensile growth stress or the intensity of tension wood; in contrast, the ratio in the secondary wall increased as it became more gelatinous. The lignin content of the secondary wall decreased during this conversion from secondary wall to G-layer. The results in this study agree with the results of chemical analyses of *Eucalyptus* tension wood obtained by Baillères et al.[14]

Large tensile growth stresses seem to be generated principally in the G-layer of tension wood.[29] The mechanism generating tensile growth stress has been studied, and it is suggested that the contraction of cellulose microfibrils parallel to the fiber axis produces large tensile growth stress.[30–32] This study revealed that the percentage of the cross-sectional area of the G-layer to the whole sight increases with the contractive released strain of growth stress. The result is consistent with those in previous studies. Abnormal gelatinous fibers whose thin G-layer was partly lignified were sometimes observed in intense tension wood. This finding will be examined in detail to investigate the process of generating tensile growth stress.

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