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GROWTH STRAINS AND RELATED WOOD STRUCTURES IN THE LEANING TRUNKS AND BRANCHES OF *TROCHODENDRON ARALIOIDES* – A VESSEL-LESS DICOTYLEDON

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SUMMARY

Leaning trunks and branches of *Trochodendron aralioides* Sieb. & Zucc., a primitive vessel-less dicotyledon, show increased radial growth and gelatinous fibers on the upper side similar to the features found in dicotyledons with vessels. The patterns of peripheral longitudinal growth strain are variable among trees but similar at different heights within the same leaning trunk. Growth strains on the lower side of the trunks are very small but they are relatively large on the lower side of the branches. Growth stress in the branches is partly affected by the gravitational bending stress, which would be exerted mostly on the lower side. Large spring back strains of branches are associated with large surface strains. Both the microfibril angle (MFA) and the percentage area of gelatinous fiber show positive relationships with the measured strains. The MFA of the S_2 wall layer in tracheids in the opposite wood is 24.6 ± 2.2°, whereas the MFA of gelatinous layer in the tension wood is only 14.2 ± 2.7°. The difference of MFA between the gelatinous fibers and the opposite wood is one of the factors accounting for the large contracting force for reorientation.

Key words: *Trochodendron aralioides*, gelatinous fiber, microfibril angle, surface growth strain, vessel-less angiosperm.

INTRODUCTION

Secondary growth in coniferous and dicotyledonous trees is formed as a result of vascular cambial activity generating xylem cells inward and phloem cells outward. During the formation of secondary cell wall in the wood, growth stress accumulates (Boyd 1972; Yamamoto *et al.* 1991; Guitard *et al.* 1999) and sometimes simultaneously heterogeneous growth stress occurs on the periphery of stems. Growth stress tends to keep the leaning trunks and branches at an equilibrium position. Increased growth stresses are found at specific locations on the periphery of leaning trunks and the branches and

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are associated with the formation of reaction woods where eccentric stem swelling occurs (Watanabe 1967). Using a simulation of a mechanical model, Yamamoto *et al.* (2002) concluded that the growth stress generated in the reaction wood is sufficient to counteract gravitational self-loading of branches. The formation of reaction wood accompanied with the increased growth stresses enables the leaning trunk to exhibit the observed growth reorientation.

In conifers, compression wood is formed on the lower side of a leaning trunk where there is strong compressive stress (Timell 1986). There are different levels of severity of compression wood, and a typical compression wood has high specific gravity, higher lignin and galactan contents, and lower cellulose content than normal wood. The tracheids of severe compression wood are shorter than normal wood, their cross sections are usually round with intercellular space, and the S_3 layer is missing. The S_2 cell wall of compression wood may have helical checking with large microfibril angle (MFA) (Boyd 1980).

Angiosperms usually form tension wood on the upper side of leaning trunks or branches where strong tensile stress exists (Panshin *et al.* 1964; Okuyama *et al.* 1986, 1994). In the species with gelatinous fibers (*i.e. Prunus*, *Robinia*, *Acer*, *Quercus*, *Sassafras*), large longitudinal tensile stresses appear in the region where the cross-sectional area of gelatinous layers are large (Okuyama *et al.* 1994). In species that lack gelatinous fibers (*i.e. Magnolia* and *Liriodendron*), higher cellulose content, lower lignin content, and smaller MFA are observed in the tension wood than the normal wood (Okuyama *et al.* 1994). Like compression wood, there are different severities of tension wood with various values of MFA, cellulose / lignin ratio, G-layer thickness, and growth stress.

Höster and Liese (1966) reported that, whether they are gymnosperms or not, trees and shrubs with a xylem consisting mostly of axial tracheids tend to develop compression wood. Some species of the primitive dicotyledons are vessel-less and the axial tracheids are the main component of the xylem. The reaction wood of some primitive dicotyledons, such as *Drimys* and *Pseudowintera*, is mostly compression wood-like (Kučera & Philipson 1977, 1978; Timell 1986). The only significant anatomical characteristics of the so-called compression wood of *Pseudowintera colorata* is the large microfibril angle (Meylan 1981). It is possible that these vessel-less dicotyledons reorient themselves by producing cells with high MFA without developing a typical compression wood or tension wood cell. In *Magnolia*, no gelatinous fibers are found (Okuyama *et al.* 1994), but there are large tensile stresses in the regions with small MFAs. Okuyama *et al.* (1994) suggested that the high tensile longitudinal growth stress is mainly due to the tensile stresses of the cellulose microfibrils that run in the axial direction.

Trochodendron aralioides Sieb. & Zucc., the only species of the genus and of the family Trochodendraceae (Smith 1945; Cronquist 1981), is a primitive, vessel-less tree. Although the xylem contains no vessels, Jorgensen *et al.* (1974) reported that the phloem is the angiosperm type. In Taiwan, *T. aralioides* grows up to 10 m high and commonly is found on the slope of foggy mountain areas (Chaw 1992). In contrast to *Drimys* and *Pseudowintera*, the reaction wood of leaning trunks and branches of *Trochodendron* occurs on the upper (adaxial) side, which is similar to that found in angiosperms with vessels. In this study, we examined the anatomy and the peripheral distribution of released growth strains of leaning trunks and branches of *T. aralioides*. We then discussed the relationships between anatomical structures of tension wood and growth strains of the leaning trunks and branches in this species.

MATERIALS AND METHODS

Plant materials

Inclined trunks and branches from six 25–30-year-old trees of *Trochodendron aralioides* were studied. Two leaning trees (A and B) were selected from Yingzihling (121° 19' E, 24° 54' N, 942 m above sea level), and four trees (C–F) were from Chilanshan station (121° 15'–121° 30' E, 24° 15'–24° 45' N, 1100 m above sea level), Forest Conservation Institute, Taiwan. The diameter at breast height (DBH) of trees A, B, C, D, E and F were 14, 16.5, 7.5, 11, 9, and 11 cm, respectively.

Growth stress measurements

The trunk of *Trochodendron aralioides* is usually dichotomously branched at various heights. In tree A the first dichotomous branching was at 3 m above ground but tree B was already dichotomously branched at about 1 m (Fig. 1a, b). Measurements of the peripheral distributions of surface growth strains on the inclined trunks were made on the standing trees around the circumference (at 45° intervals) at 65 cm above ground for tree A. In tree B, measurements were made at both 35 and 62 cm above ground (Fig. 1a, b) to learn the effect of dichotomous branching. Given orderly distributed pattern of the peripheral stresses in the first two trees, the measurements for trees C and D were made only at the upper, lateral, and lower positions at about 60 cm above ground. The lower side of the trunk was designated as 0°, and the upper side as 180°. Immediately after removing the bark at the specified positions, electrical resistance strain gauges were glued with cyanoacrylate adhesive to the xylem in the longitudinal direction. A portable digital strain meter (Model UCAM–1A Kyowa Ltd., Tokyo, Japan) with a 40-channel scanner (USB–11A) was used for measurement. After calibrating the strain gauges to zero, the surface growth strain was released by the kerf method (Sasaki *et al.* 1978), *i.e.*, grooves 1–1.5 cm deep were made in the xylem around the strain gauge with a handsaw as well as a chain saw and the released strain was determined when the readings stabilized. The tested areas were cut into blocks for microscopical studies.

In order to have suitable branch locations for measurements on the standing trees, we selected one branch from tree E and two branches from tree F to measure the spring back strains and the longitudinal surface growth strains at different distances from the trunk (see Table 2). The measurements were made on standing trees. After removing the bark, strain gauges were glued in the longitudinal direction at the upper side and the lower side of the marked positions of the branches. After gauges were zeroed, the branch was cut off and its spring back strain due to the self-loading determined. Thereafter, the longitudinal surface growth strains were measured by cross-cutting the branch at a position 5 mm in front or behind the strain gauge.

Anatomical and structural study

A segment from each of the tested areas was collected for microstructural studies. Cross-sectional and tangential sections (0.5 × 1 cm) were prepared for microscopic examination. The relative amounts of the lignified wall, gelatinous wall, and lumen of the cells were measured on 0.015 mm^2 area from 50 cross sections for each segment. The microfibril angle (MFA) in the reaction and the opposite wood zones was determined on 25–35 μm thick tangential sections cut from the latewood of the outermost two rings of each wood block for which we had measured strain. The sections were stained with 2% iodine solution for 1 min. and observed after rinsing with 60% nitric acid (Huang *et al.* 1997). The MFAs were measured in 50 gelatinous fibers or the lignified tracheids at each point.

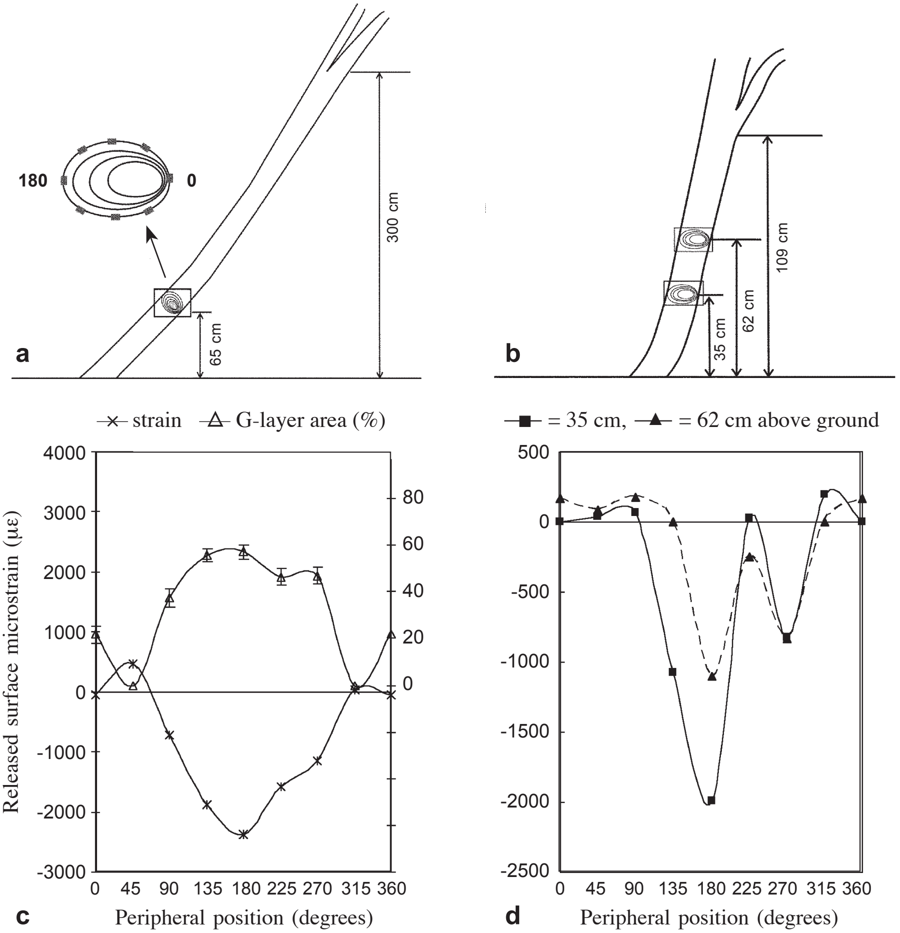

Figure 1. Measurements of released surface growth strains around the periphery of **a**: the trunk of tree A at 65 cm height and **b**: tree B at heights of 35 and 62 cm. **c**: Peripheral distribution of surface growth strains and G-layer area (%) in tree A. **d**: Peripheral distribution of surface growth strains at two heights in tree B.

Table 1. Tree number and the averages of growth strains, microfibril angles (n = 50) and cell wall area percentages (n = 50) at different positions of the leaning trunks.

Tree number	Growth strain (μm)			Cell wall area (%)			MFA (°)		
				G-fiber in tension wood		Tracheid in opposite wood	G-fiber in tension wood		Tracheid opposite wood
	Upper	Side	Lower	G-layer	S$_2$-layer	S$_2$-layer	G-layer	S$_2$-layer	S$_2$-layer
A	-2383	-933	-59	57.2 (3.1)	13.6 (3.1)	56.7 (2.4)	9.4 (1.9)	14.0 (2.2)	24.0 (2.6)
B$_1$	-1989	-827	191	56.5 (2.7)	11.2 (3.1)	55.6 (2.0)	11.4 (1.7)	23.8 (2.5)	29.0 (2.5)
B$_2$	-1100	-831	166	57.7 (2.4)	12.3 (2.6)	57.1 (1.8)	11.3 (2.4)	18.4 (2.4)	25.8 (2.6)
C	-1866	-211	-57	67.4 (3.4)	15.1 (2.9)	52.2 (2.1)	15.9 (2.2)	24.5 (2.6)	27.2 (2.3)
D	-863	-389	-60	58.7 (3.4)	9.8 (2.6)	56.0 (2.1)	10.9 (2.2)	14.2 (2.6)	17.9 (2.5)

B$_1$: at trunk height of 35 cm; B$_2$: at trunk height of 62 cm.
MFA: average of microfibril angle.
Number in brackets is standard deviation.

RESULTS AND DISCUSSION

Peripheral longitudinal growth strain of the leaning trunks

Large negative released growth strains in the longitudinal direction were detected on the upper side (180°) of the inclined trunks of trees A–D (Table 1, Fig. 1c, d), indicating these trees had large tensile stresses like most angiosperms when they are leaning. Normally tensile stress is found on the periphery of the erect trunks of both gymnosperms and angiosperms and the compressive stress occurs almost exclusively in the compression woods of the inclined trunks of gymnosperms (Huang *et al.* 1998, 2005). However, a small compressive strain was found on the lower side of the leaning trunk of the vessel-less *Trochodendron aralioides*.

Growth strains of the branches

Observation of branch cross sections showed that the pith was more eccentric in samples closest to the trunk (Table 2). The symmetry of the cross section may also be affected significantly by the direction of the winds. The increased adaxial radial growth of the tension wood is similar to that found in most hardwoods.

Spring back strains were contractile on the upper side, and extensive on the lower side of branches (Table 2). High contraction surface strains (-1453 με ± 343 με) existed longitudinally on the upper side of branches; however, high extension surface strain (1975 με ± 646 με) existed longitudinally on the lower side of branches. Note that the average magnitude of the spring back strain on the lower side of the branch is about

65% larger than the surface strain. There is also a positive relationship between the growth strain and the spring back strain. The relationships are stronger for the lower side ($R^2 = 0.83$) than for the upper side ($R^2 = 0.53$) of the branch (Fig. 2).

Yoshida *et al*. (1992a, b, 1999) reported that the relationships between growth stresses and physical properties were different in branches than in stems. They suggested that in addition to the growth stress, other factors such as the response to weeping (self-loading in axes that aren not close to vertical) contributes to the strains of branches. In this study, we observed a greater growth strain on the lower sides of the branch than in the

Table 2. Tree and branch number, growth strains, spring back strains, microfibril angles (n = 50) and cell wall area percentages (n = 50) at different distances from the trunk.

Branch number	L (cm)	R_1 (cm)	R_2 (cm)	Spring back strain (μm)		Surface growth strain (μm)		Cell wall area (%)			MFA (°)		
								G-fiber in tension wood opposite		Tracheid in opposite wood	G-fiber in tension wood opposite		Tracheid in opposite wood
				Upper	Lower	Upper	Lower	G-layer	S_2-layer	S_2-layer	G-layer	S_2-layer	S_2-layer
E	16.5	2.1	1.2	-1455	1748	-1562	977	57.4 (2.8)	13.7 (2.4)	56.0 (1.9)	13.1 (2.4)	20.1 (1.7)	24.1 (2.7)
	32.0	1.8	1.2	-1391	1868	-2185	882	67.8 (2.2)	13.8 (2.3)	58.3 (2.7)	12.0 (1.9)	17.7 (1.8)	24.1 (2.7)
	61.0	1.5	1.2	-1134	1327	-1500	225	70.4 (3.0)	14.1 (2.2)	59.0 (2.1)	12.9 (2.4)	19.1 (2.1)	25.3 (2.2)
F_1	16.5	2.8	1.2	-518	1074	-976	-83	70.8 (2.8)	13.8 (2.8)	59.8 (1.9)	11.8 (2.2)	18.2 (1.9)	21.7 (2.2)
	45.0	1.7	1.2	-1611	914	-1821	537	67.6 (2.7)	21.9 (3.1)	57.0 (2.1)	11.6 (1.6)	18.0 (1.8)	24.6 (2.8)
	79.5	1.4	1.2	-923	2187	-1003	469	72.8 (2.9)	19.8 (2.9)	58.8 (3.0)	11.7 (2.2)	18.1 (1.9)	22.5 (2.4)
	106.5	1.2	1.1	-1411	1366	-1962	320	69.3 (2.4)	21.1 (2.7)	60.0 (2.6)	11.0 (1.8)	17.8 (2.1)	25.3 (2.7)
F_2	23.4	0.9	0.8	-1802	2459	-1953	1813	64.2 (2.8)	17.1 (2.9)	63.1 (3.0)	10.6 (2.2)	18.0 (1.8)	22.2 (2.5)
	46.1	0.7	0.7	-1991	3633	-1843	3102	66.1 (2.7)	17.3 (3.1)	63.2 (2.4)	10.6 (2.3)	18.1 (2.0)	25.2 (2.7)
	56.4	0.7	0.7	-2008	2674	-1836	2397	66.8 (2.9)	15.9 (3.0)	61.6 (2.8)	11.0 (1.7)	17.9 (2.1)	24.6 (2.7)
	79.4	0.6	0.6	-1736	2474	-1536	2329	73.1 (2.8)	15.4 (3.1)	54.8 (3.0)	11.1 (1.9)	18.4 (2.2)	22.0 (2.6)

L: Distance from trunk.
R_1: Distance from the cambium to the pith on the upper side of a cross section.
R_2: Distance from the cambium to the pith on the lower side of a cross section.
Number in brackets is standard deviation.

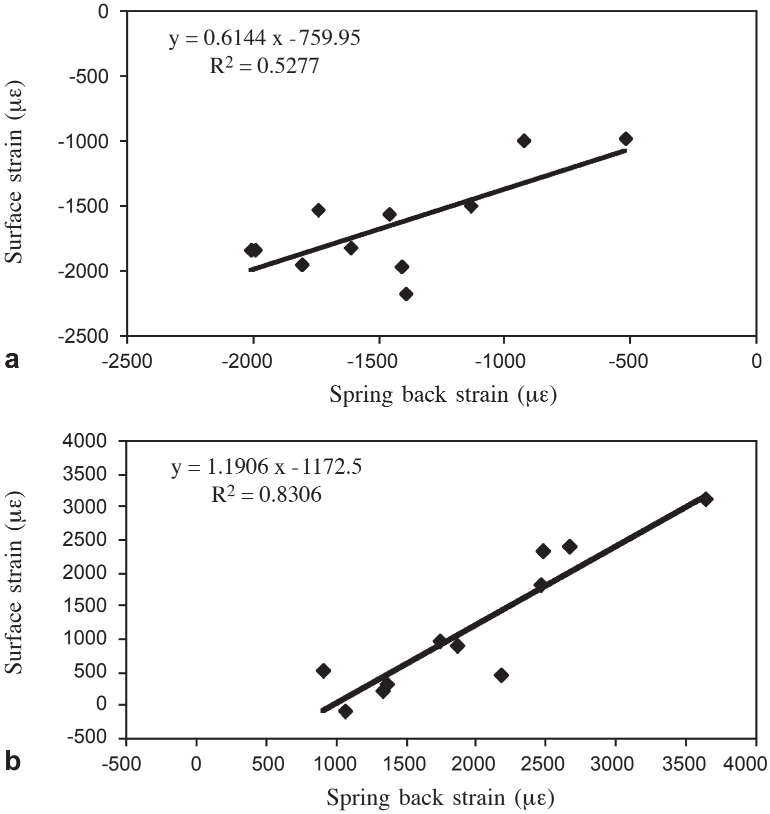

Figure 2. Relationships between spring back and surface strains of **a** upper side and **b** lower side of the branches.

trunk of *T. aralioides*. The average spring back strain on the lower side of branches is about 65 % larger than that of the surface strain. This may suggest that generation of growth stress in the branches is partly affected by the gravitational bending stress due to self-loading, which may be exerted mostly on the lower side of the branch.

Wood structures in relation to surface growth strains

The current study confirmed the observation of Onaka (1949) that the vessel-less angiosperm *Trochodendron* has tension wood and G-fibers. Figures 3a and 3c show the gelatinous fibers in the tension wood and figures 3b and 3d show the tracheids in the opposite wood of *T. aralioides*. Similar to the findings of Onaka (1949), the gelatinous fiber of *Trochodendron* had thick gelatinous layers in place of most of the S_2-layer of the normal tracheid.

The upper sides of both inclined trunks and branches contained tension wood tissue with gelatinous fibers and displayed high contractive strains. This result agrees with the study of Washusen and Waugh (2003) that the growth strain was found to be a good indicator of the presence of gelatinous fibers in wood tissue taken from the immediate

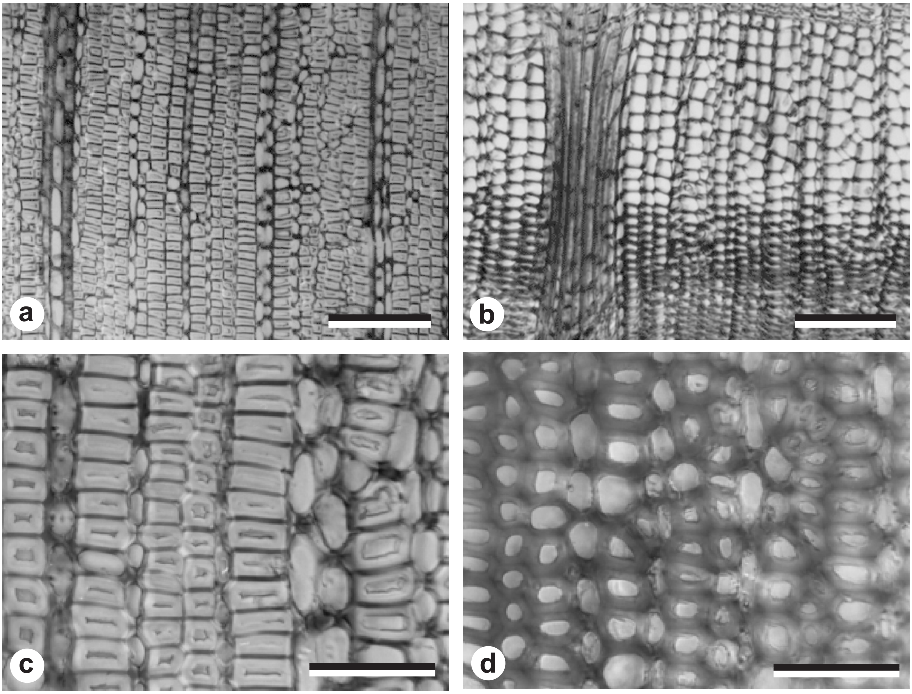

Figure 3. Cross-section images of **a** and **c** gelatinous fibers in the tension wood and **b** and **d** tracheids in the opposite wood. — Scale bars in a & b = 100 μm, in c & d = 40 μm.

position where growth strain was measured (Fig. 1c). We also found that the patterns of peripheral longitudinal growth strain are variable among trees (Fig. 1c versus 1d) but very similar at different heights along the segment of a leaning trunk (Fig. 1d). Gelatinous fibers can be found within old vertical trunks, but such reaction wood is associated with internal stresses or the residual stress from previous reorientation of axis displacement (Trénard & Guéneau 1975). In gymnosperms, compression wood occurs on the lower sides of the leaning trunks and branches which show large positive strain values. Although the lower side of branch-wood of *T. aralioides* exhibits high extension strains (positive values), no typical compression wood was found. It is well known that the gelatinous layer of tension wood fibers contributes to the mechanical function of the dicotyledonous trees (Archer 1986; Clair *et al.* 2003).

There was a positive relationship between the percentage of G-layer and the absolute values of the contractive strain in the trunk of tree A (Fig. 1c). Figures 4a and 4b compare the measured surface strains of gelatinous fibers in tension wood and non-gelatinous fibers in opposite wood of the trunk and branches. There was a higher percentage of gelatinous layer and lower cell lumen area in the tension wood of branches than trunks (Fig. 5). Opposite wood was very similar in terms of cell composition in branches and trunks, and had a much higher cell lumen area than the tension wood (Fig. 5).

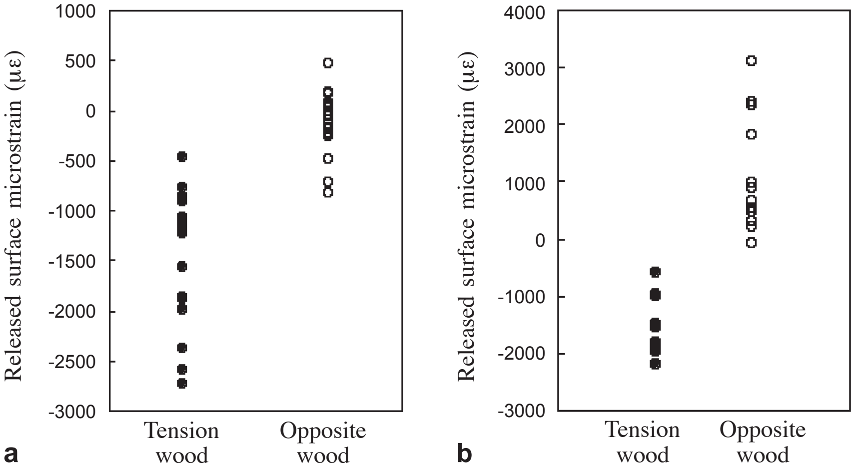

Figure 4. Measured surface strains of gelatinous fibers in the tension wood and tracheids in the opposite wood of **a** the trunks and **b** the branches.

In both gymnosperms and arboreal dicotyledons, stress is considered to arise from the cellulosic component of the wood according to the cellulose tension hypothesis (Bamber 2001). It is suggested that in dicotyledons the cellulose microfibrils are laid down as stretched and extended, longitudinally oriented springs and thus exert a tensile force tending to right or stabilize the tree. The low values of lignin/cellulose ratio

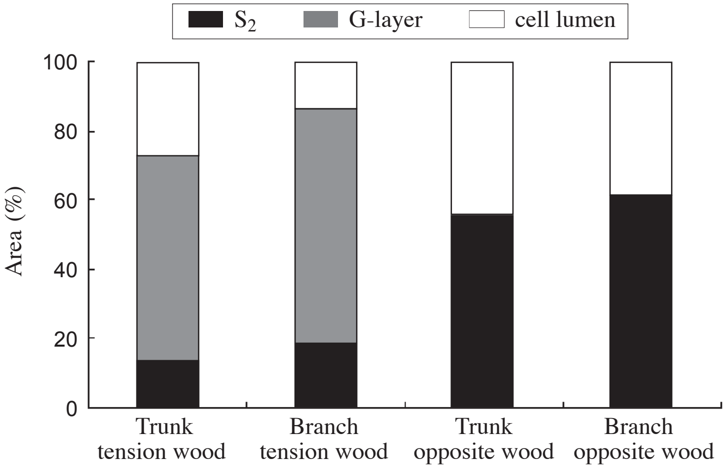

Figure 5. Averages of the area percentages of lignified wall, gelatinous wall, and lumen of the cells in the cross sections from trunks and branches.

and MFA often reported from tension wood and especially from gelatinous fibers are thought to facilitate the contraction of microfibrils, thus maximizing longitudinal tensile stress. There is a close relationship between growth stress and MFA (Okuyama *et al.* 1994, 1986; Yamamoto *et al.* 1995). Okuyama *et al.* (1994) suggested that microfibril angle is the important factor in the generation of force in tension wood. Based on the unified hypothesis, Guitard *et al.* (1999) applied the mechanical model to discuss the relationship between the growth strain and MFA. They calculated the critical MFA at which the longitudinal growth stress changed from tensile to compressive at about 20~30°. In *Chamaecyparis*, the MFAs have a transition angle at 20~25° (Yamamoto *et al.* 1991; Huang *et al.* 2005).

The large difference between the gelatinous fibers and the non-gelatinous fibers is one of the main factors that account for the large contractile force. Based on the difference in MFA, the contribution of the non-gelatinous fibers in the tension wood zone to the tensile stress may be small. Figure 6 shows the relationship between the MFA and the released longitudinal growth strain on the surface of the trunks and branches. All the MFAs of the gelatinous layer of G-fibers were below 20° and significantly smaller than the MFAs of the S_2-layer of the tracheids in opposite wood. The positive trends between MFA and the released surface strain can be seen, and the change from tension to compression stress at 20° MFA is clearer for the data collected from the branches.

As described in this paper and in other studies, reaction wood in angiosperms is more diverse than in gymnosperms. The processes of re-orientating the trunk and branches involve the generation of growth stresses which may or may not trigger the formation of tension wood in a vessel-less angiosperm. Necesaný and Oberländerová (1967) suggested that the wood of homoxylous species, such as most of the gymnosperms, has

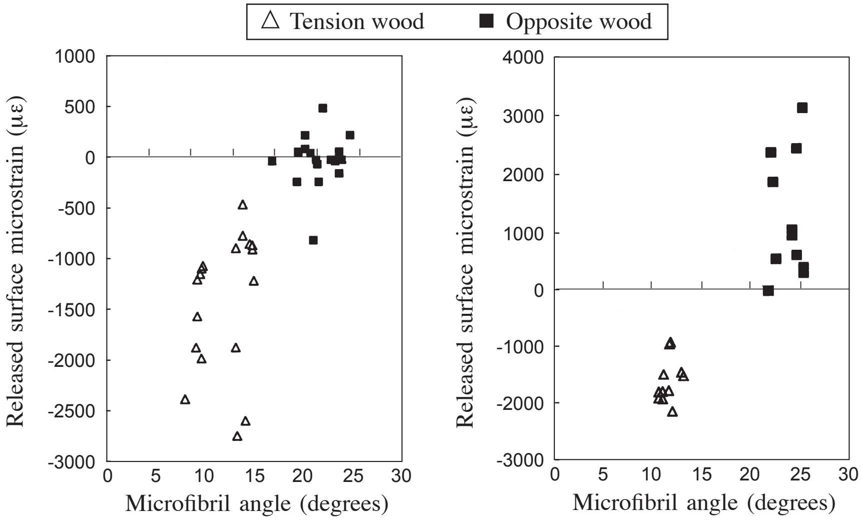

Figure 6. Microfibril angle and the measured surface strains on the tension and opposite wood sides of **a** the trunks and **b** the branches.

growth promotion in the abaxial part of leaning axes. This suggestion proved to be valid in the vessel-less dicotyledonous trees of *Pseudowintera colorata* which form wood with a high MFA wood on the lower side and lack typical tension wood on the upper side (Meylan 1981). Such features are consistent with *Pseudowintera*'s taxonomic position as one of the most primitive angiosperms (Kučera & Philipson 1978). However, the results presented here and the finding of Onaka (1949) that tension wood is formed on the upper side of a stem and branches of *Trochodendron* suggest that, unlike *Drimys* and *Pseudowintera*, *Trochodendron* may belong phylogenetically to the advanced group of angiosperms, the basal eudicotyledons (APG 2003). In addition to growth strain and wood anatomy reported in this paper, it would be interesting to investigate other aspects of the nature of reaction wood formation such as wood chemistry and the complex interactions between growth regulators and environment factors of vessel-less angiosperms.

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