行政院國家科學委員會專題研究計畫　成果報告

# 昆蘭樹反應材及其相關性質之研究(2/2)

計畫類別：個別型計畫
計畫編號：NSC92-2313-B-002-045-
執行期間：92年08月01日至93年07月31日
執行單位：國立臺灣大學生命科學系

計畫主持人：黃玲瓏

報告類型：完整報告

處理方式：本計畫可公開查詢

中　華　民　國 93年11月18日

# 昆蘭樹反應材及其相關性質之研究
# Studies on the reaction wood and related properties of *Trochodendron aralioides*

## Abstract

The inclined trunks and branches frequently display eccentric growth and show specific structural changes in the cell layers, cell morphology and cell wall constitution during the formation of secondary tissues. In conifers, compression wood forms in the lower side, while in dicotyledons, tension wood forms in the upper side. *Trochodendron aralioides* Sieb. Et Zucc. is a primitive, vessel-less dicotyledonous native tree to Taiwan. In this study, the surface growth strains at the upper and lower sides of different positions of branches were measured by kerf method and the related structures were investigated. We found that high tensile strains ($-1652 \times 10^{-6} \pm 386 \times 10^{-6}$) existed longitudinally on the surface of upper side of branches. The absolute value of strains decreased obviously from the upper to the lower sides. On the lower surface, longitudinal compressive strains ($1179 \times 10^{-6} \pm 1058 \times 10^{-6}$) occurred. The basal part of branches exhibited generally pronounced radial secondary growth promotion to the upper side and formed reaction wood eccentrically. The observation of wood structure of the surface strain measured wood blocks showed that tension wood (with gelatinous fiber-tracheids) located mostly on the upper side and displayed higher tensile strain than the opposite wood (without gelatinous fiber-tracheids). The microfibril angles of S2 wall layer in fiber-tracheids on the opposite wood were $23.78 \pm 1.42^{\circ}$, while the microfibril angles of gelatinous layer in gelatinous fiber-tracheids in the tension wood were $14.40 \pm 2.32^{\circ}$. By the ANOVA analysis, longitudinal surface strains varied significantly with the microfibril angles of the fiber-tracheid cells.

**Keywords:** *Trochodendron aralioides*; tension wood; released surface growth strain; spring back strain, fiber-tracheid; gelatinous fiber-tracheid; gelatinous layer; microfibril angle.

## 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. It has been shown that during the formation of secondary wall of xylem cells, growth stress accumulates (Boyd 1972, Yamamoto et al. 1991, Guitard et al. 1999). Simultaneously with secondary growth, heterogeneous growth stress occurs on the surface of the trunk. Tree trunks and branches accumulate growth stresses during each year of growth. The accumulation of growth stress is the unavoidable result of physiological adjustments to environmental stress (Niklas 1992, Mattheck and Kubler 1995).

Increased growth stress is found at specific locations in the leaning trunk where eccentric swelling growth occurs and forms reaction wood (Watanabe 1967). Growth stress forces the trunk and branch to grow in a vertical orientation to maximize exposure to sunlight. In conifers, compression wood is formed on the lower side of a leaning trunk where there is strong compressive stress (Timell 1986). However in the dicotyledonous trees tension wood is formed on the upper side where strong tensile stress exists (Okuyama et al. 1986; 1994). Compression wood is characterized by thick-walled, heavily lignified, rounded tracheids, whereas tension wood is characterized anatomically by the presence of an inner unlignified gelatinous layer in the secondary wall of wood fibers. Some other less obvious variations in wood anatomy may also be associated with dicotyledonous reaction wood. Even in an upright growing trunk, growth stress forms inside the trunk. In response to environmental stress, such as wind, the sapwood is in the danger of compression damage. So that, in both coniferous and dicotyledonous trees, longitudinal tensile stress develops on the peripheral portion of the trunk, whereas compression stress accumulates inside the trunk (Archer and Bynes, 1974; Archer 1986).

*Trochodendron aralioides* Sieb. Et Zucc., the single species of the family Trochodendraceae, has been regarded as one of the most primitive angiosperm families (Cronquist, 1981). It is native to Taiwan, Japan, South Korea, and the Ryukyu Islands (Smith 1945). The primary basis for viewing *Trochodendron* as archaic is their lack of xylem vessels. Xylem vessels are only lacking in a few other extant woody angiosperms, which include *Tetracentron* of Trochodendrales, the 5 genera of Winteraceae, and one species of *Amborella*. In the preliminary study of the inclined trunks or branches of *Trochodendron aralioides*, it is of particular interest because the pronounced growth promotion occurs on the upper (adaxial) side that is similar to those found in angiosperms with vessels, not as the gymnosperms without vessels. Most of the previous studies dealt in the growth stress of trunk and log, and only a few investigations have been made regarding the problem in branch (Ohsak et al. 1968; Yoshida et al. 1992 a, b and 2000; Dietrich and Mattheck 1995; Yamamoto et al. 2002). In this work, the peripheral distribution of surface growth strains of the leaning trunks of *Trochodendron aralioides* was measured by kerf method and the anatomy of reaction wood was investigated.

## Materials and Methods

Three branches from two trees of *Trochodendron aralioides* Sieb. Et Zucc. at chilanshan station (121°15′–121°30′E, 24°15′–24°45′N, altitude 1100m), Forest Conservation Institute, Taiwan, were used for investigations. The trees A and B have 9 and 11 cm diameter at breast height respectively. In measuring the surface growth strain of the branches, longitudinal strains were measured. To determine the effect of branch length on growth strain, three points of the branches at different distances away from the trunk were examined. After removing the bark, electrical resistance strain gauges were glued with cyanoacrylate adhesive in the longitudinal direction at the upper side and the lower side of the specified position of the branches. A portable digital strain meter (Model UCAM – 1A Kyowa Ltd., Tokyo, Japan) with a 40- channel scanner (USB – 11A) was used for measurement. After zeroing the gauges, branch was cut down and spring back strain owing to the self-weigh could be read. Thereafter calibrating the strain gauges to zero, the surface growth strain was released by the kerf method (Sasaki et al. 1978), i.e., cross – cutting the branch at a position 5 mm in the front and behind the strain gauge and the released strain was determined immediately.

The anatomical structures in the cross and radial sections from all the strain examined wood blocks were observed microscopically. Several samples were also cut from side wood. The existence of tension wood structure was confirmed by the presence of gelatinous fibers. The percentage of the gelatinous wall areas was measured in the sections at each point. Several tangential – sliced samples, 20 μm in thickness, were cut from the outer two annual ring of each strain measuring position. The mean microfibril angles (MFAs) in the gelatinous wall and lignified S2 wall layer of each slab were determined by the method of iodine staining and polarized light microscopy. The MFAs were measured in 50 fiber-tracheids from the late wood at each point, and the average value was calculated. Each average was compared with the magnitude of the released surface growth strain.

## Results and Discussion

### *Longitudinal growth strain distribution in branches*

Angiosperms usually form tension wood on the upper side of leaning trunks or branches

(Panshin et al. 1964). The stress generated from this specialized tissue differs from that of normal wood (Okuyama et al., 1994). Tension wood produces tensile stress in the longitudinal direction that extends the constraint of the wood and forces the leaning trunks or branches of angiosperms to grow upward or to maintain a definite angle between main trunk and branch. The branches suffer bending stress due to its self-weight. This stress is then superposed on the growth stress. In the study on growth stress of the branches, Yoshida et al. (1992 a and b) reported that the relationships between growth stresses and physical properties were different from those of stems. They suggested that something other than growth stress, which is different from the normal wood and the reaction wood in a stem, was induced into the branch.

*Trochodendron aralioides* Sieb. Et Zucc. is a small tree growing up to 10 m high which is endemic to Taiwan and singly belongs to the primitive vessel-less angiosperm family Trochodendraceae. The vessel-less dicotyledonous tree *Pseudowintera* forms compression wood. However, Gnetales, Gymnosperms with vessels, forms tension wood as response wood. The cross-sections of the branches of *Trochodendron aralioides* Sieb. are more or less oval in shape (Fig. 3a). Growth eccentricity exhibit to the upper (adaxial) side similar to that found in the most of hardwoods. Table 1 shows the spring back strain and surface growth strain of three branches at different distances from trunks. It can be seen that the spring back strains are contractive on the upper side, and extensive on the lower side of branch. High tensile strains ($-$ 1989 x $10^{-6}$ and $-$ 2383 x $10^{-6}$) existed longitudinally on the surface of upper side of trunks. From the upper to the lower side of leaning trunks, the absolute value of strains decreased obviously. Growth strains on the lower side were slightly above zero. The growth strain increases with the increase of spring back strain on the lower side, and the former is obviously smaller than the latter. These two strains have a linear relationship ($R^2$=0.6311) (Fig. 1).

*Gelatinous fiber-tracheid and microfibril angle (MFA) in relation to surface growth strains*

Histological the distinguishing feature of tension wood is the presence of gelatinous fibers with G-layer in the inner of the cell wall. MFA is smaller angle. Eccentric growth in some dicotyledons may be on the lower side, as in conifers.

The observation of wood structure of the surface strain measured wood blocks showed that tension wood (tissue with gelatinous fiber-tracheids) displayed higher tensile strain than opposite wood (tissue without gelatinous fiber-tracheids) (Fig. 2). Figures of 3b, d, and f show the gelatinous fiber-tracheids with thick gelatinous layer inside the lignified S2 layer of cell wall while figures of 3c, e, and g show that only the lignified S2 layer of cell wall were found. On the fiber-tracheids of the opposite wood, there were some slant simple pits (Fig. 3g).

Figure 3 h shows the arrangement of microfibrile in the gelatinous layer of the iodine stained gelatinous fiber-tracheids in tension wood, whereas figure 3i shows the arrangement of microfibrile in lignified S2 layer of the iodine stained fiber-tracheids in opposite wood. The average of MFAs of the gelatinous layer and the lignified S2 layer of the gelatinous fiber-tracheids in the tension wood was 11.86 ± 0.72°and 17.96 ± 0.38°respectively, while the average MFAs of the lignified S2 layer of the fiber-tracheids in the opposite wood was 23.78 ± 1.40° (Fig. 4a).

Figure 5a shows the relationships between the MFA in gelatinous layer and lignified S2 layer of cell wall of the gelatinous fiber-tracheids in the tension wood as well as the MFA in the lignified S2 layer of cell wall of the fiber-tracheids in the opposite wood and the released longitudinal growth strain on the surface of branches. The released strains tend to increase with the increase of MFAs. By the ANOVA analysis, longitudinal surface strains varied significantly with the MFAs of the fiber-tracheids. It is interesting to find that both of the MFAs in the gelatinous layer and the lignified S2 layer of the cell wall of the gelatinous fibers in the tension wood varied significantly with the MFAs in the lignified S2 layer of the cell wall of the fiber-tracheids in the opposite wood. The MFAs on the upper side of branch are apparently smaller than those on the lower side because of the existence of extension wood. There is a close relationship between growth stress and MFA (Okuyama et al. 1994, 1986, Yamamoto et al. 1995). The released strain changed from extension to contraction at 15° ~ 20°, and the contractive strain increased dramatically in the tension wood region. This relationship is different to the result of Yamamoto et al. (1991) in *Chamaecyparis obutusa* Endl., which has a transition angle at 20~25°. 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 tension to compression at about 20~30°. This compressive stress is entirely associated with the specialized tissue of compression wood. This suggests that lignin swelling takes part in the generation of compressive stress in the compression wood. Compression wood usually has a higher lignin content and greater MFA than normal wood. The magnitude of the compressive stress can be used to evaluate the extent of the development of compression wood. However to evaluate the extent of the occurrence of tension wood need to be work out. Besides, in the *Trochodendron*, the MFAs of branch are larger than those of trunk (data not shown).

Observation of branch cross sections showed that the pith became somewhat more eccentric as its distance from the trunk is decreased, indicating intensive development of tension wood which can induce a large tensile stress. However it might be affected significantly by the direction of the winds. These results support the hypothesis (Boyd 1973) that microfibril angle is the important factor in tension wood force generation. It is suggested that the generation of tensile growth stress on the upper side of branch containing developed tension wood is affected by the gravitational bending stress due to the self-weight of branch which is responsible for the large spring back strain. In other words, it is explained that the gravity stimulus is responsible for tensile growth stress level in the tension wood. None of the theories suggested as yet have been sufficiently proved to explain the mechanism by which the bent stems straighten.

Figure 4b shows the wall areas of the gelatinous layer and lignified S2 layer of cell wall of the gelatinous fiber-tracheids in the tension wood and the wall areas of the lignified S2 layer of cell wall of the fiber-tracheids in the opposite wood. The percentages of gelatinous layer areas were proportional to the absolute values of the tensile strain values (Fig. 5a). This result agrees 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 position where growth strain was measured.

The occurrence of gelatinous fibers (G-fibers) and frequent correlation of these fibers with increased tension strains and resulting movements of woody axes have been reviewed in detail (Wardrop 1964, Scurfield 1973, Wilson and Archer 1977, 1979). Most workers assume that G-fibers shorten at maturation and induce longitudinal tension strains in the region of the axis in which they occur. These strains are often sufficient to bend the displaced woody axis toward its initial "normal" position within the tree crown. Branches move back to their normal branch angle; the trunk moves back to the vertical. However, some species, such as *Populus* and *Fagus*, form G-fibers within old vertical trunks. Such reaction wood is still associated with internal stresses but not with axis displacement (Kaeiser 1955, Trénard and Guéneau 1975).

Instead of viewing the differentiation of reaction wood as merely as anatomical response to exogenous changes, it could be as a genetically programmed and active part of normal tree development. Experimental studies strongly indicate that a change in relative auxin level in the cambial zone, as related to the direction of gravity, is the mechanism responsible for these histological variations and resulting strains. Boyd (1977) suggested that an initial internal strain might be the active inductive mechanism for reaction wood formation.

## Acknowledgements

This study was funded by the research project (NSC-92-2313-B-002-045) provided from the National Science Council. The Authors wish to thank the NSC for the financial support.

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## Legends

Figure 1. The relationship between released surface growth strains and spring back strains on the upper side of branches.

Figure 2. The occurrence of gelatinous fiber-tracheids and the related released surface growth strains.

Figure 3. (a) Transection of the basal part of a sampling branch. (b) LM of the tension wood stained by phloroglucin-HCl showing the thick gelatinous layer of gelatinous fiber-tracheids surrounded by lignin rich layer. (c) LM of the opposite wood stained by phloroglucin-HCl showing the thick lignified S2 layer. (d) SEM of the tension wood showing the gelatinous fiber-tracheids with the thick non-lignified inner gelatinous layer. (e) SEM of the opposite wood showing the fiber-tracheids with the lignified S2 layer. (f) LM of part of a single gelatinous fiber-tracheid from the tension wood showing the thick gelatinous layer. (g) LM of part of two gelatinous fiber-tracheid from the opposite wood showing the lignified S2 layer with simple pits. (h) The iodine stained microfibrils distributed in the gelatinous layer of fiber-tracheid in the tension wood. (i) The iodine stained microfibrils distributed in the lignified S2 layer of fiber-tracheids in the opposite wood.

Figure 4. (a) The microfibril angle (MFA) in the gelatinous and the lignified S2 cell wall of fiber-tracheid in the tension wood and the lignified S2 wall of the fiber-tracheid in the opposite wood. (b) The percentage averages of gelatinous wall area, lignified S2 wall area and cell lumen of fiber-tracheid in the tension wood and the percentage averages of lignified S2 wall area and cell lumen of the fiber-tracheid in the opposite wood.

Figure 5. (a) Effects of the microfibril angle (MFA) in the gelatinous layer (△) and the lignified S2 layer (▲) of the gelatinous fiber-tracheids of the tension wood and the lignified S2 layer of the fiber-tracheids (●) in the opposite wood on the surface growth strain. (b) Effects of gelatinous layer area of the gelatinous fiber-tracheids of the tension wood on the surface growth strain.

Table 1. Tree and branch number, growth strains and spring back strains at different distances from trunk.

| Tree | Branch | L | $D_1$ | *$D_2$ | Spring back strain ($\mu\varepsilon$) | | Surface growth strain ($\mu\varepsilon$) | |
|---|---|---|---|---|---|---|---|---|
| No | No | (cm) | (cm) | (cm) | Upper side | Lower side | Upper side | Lower side |
| A | 1 | 16.5 | 2.8 | 1.7 | - 518 | 1074 | - 976 | - 83 |
| | | 45.0 | 1.4 | 1.6 | - 1611 | 914 | - 1821 | 537 |
| | | 79.5 | 1.3 | 1.3 | - 923 | 2187 | - 1003 | 469 |
| | | 106.5 | 1.0 | 1.2 | - 1411 | 1366 | - 1962 | 320 |
| A | 2 | 23.4 | 0.7 | 1.1 | - 1802 | 2459 | - 1953 | 1813 |
| | | 46.1 | 0.7 | 0.7 | - 1991 | 3633 | - 1843 | 3102 |
| | | 56.4 | 0.6 | 0.6 | - 2008 | 2674 | - 1836 | 2397 |
| | | 79.4 | 0.6 | 0.6 | - 1736 | 2474 | - 1536 | 2329 |
| B | 3 | 16.5 | 1.8 | 1.9 | - 1455 | 1748 | - 1562 | 977 |
| | | 32.0 | 1.8 | 1.2 | - 1391 | 1868 | - 2185 | 882 |
| | | 61.0 | 1.6 | 0.9 | - 1134 | 1327 | - 1500 | 225 |

*L : Distance from trunk

$D_1$: Vertical axis diameter of branch cross section

$D_2$: Horizontal axis diameter of branch cross section

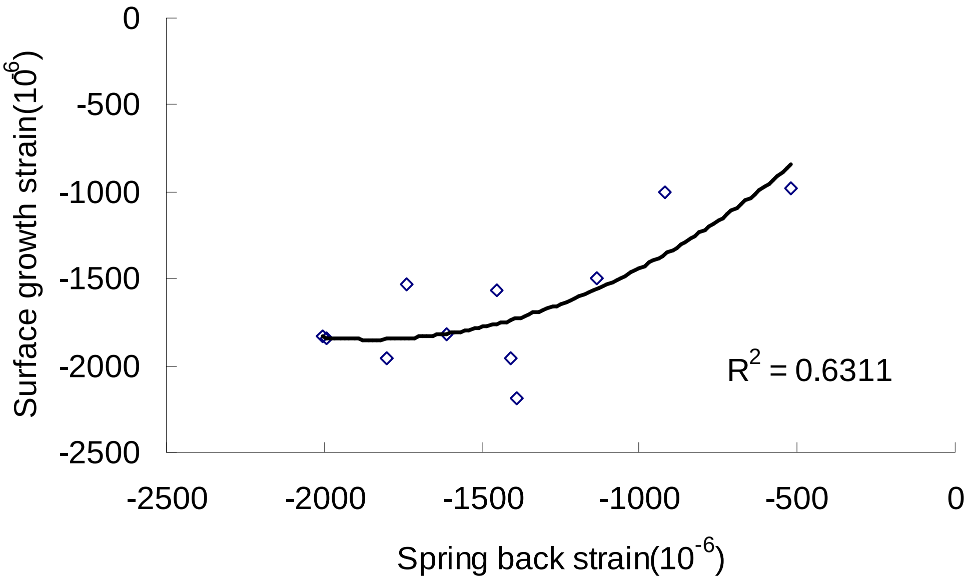

0
-500
-1000
-1500
-2000
-2500
Surface growth strain(10^-6)
-2500
-2000
-1500
-1000
-500
0
Spring back strain(10^-6)
R^2 = 0.6311

Fig. 1

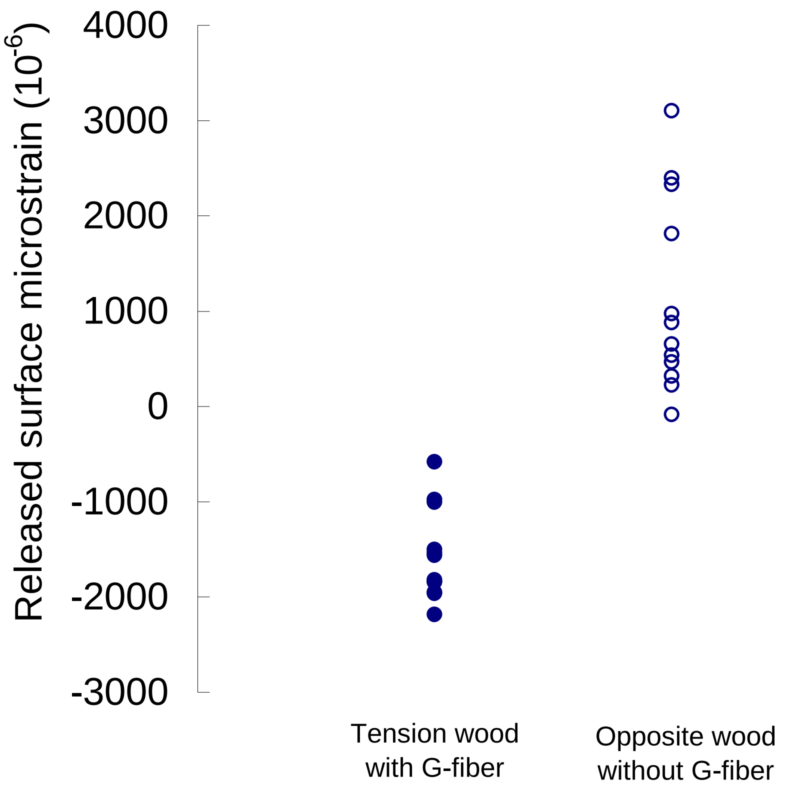
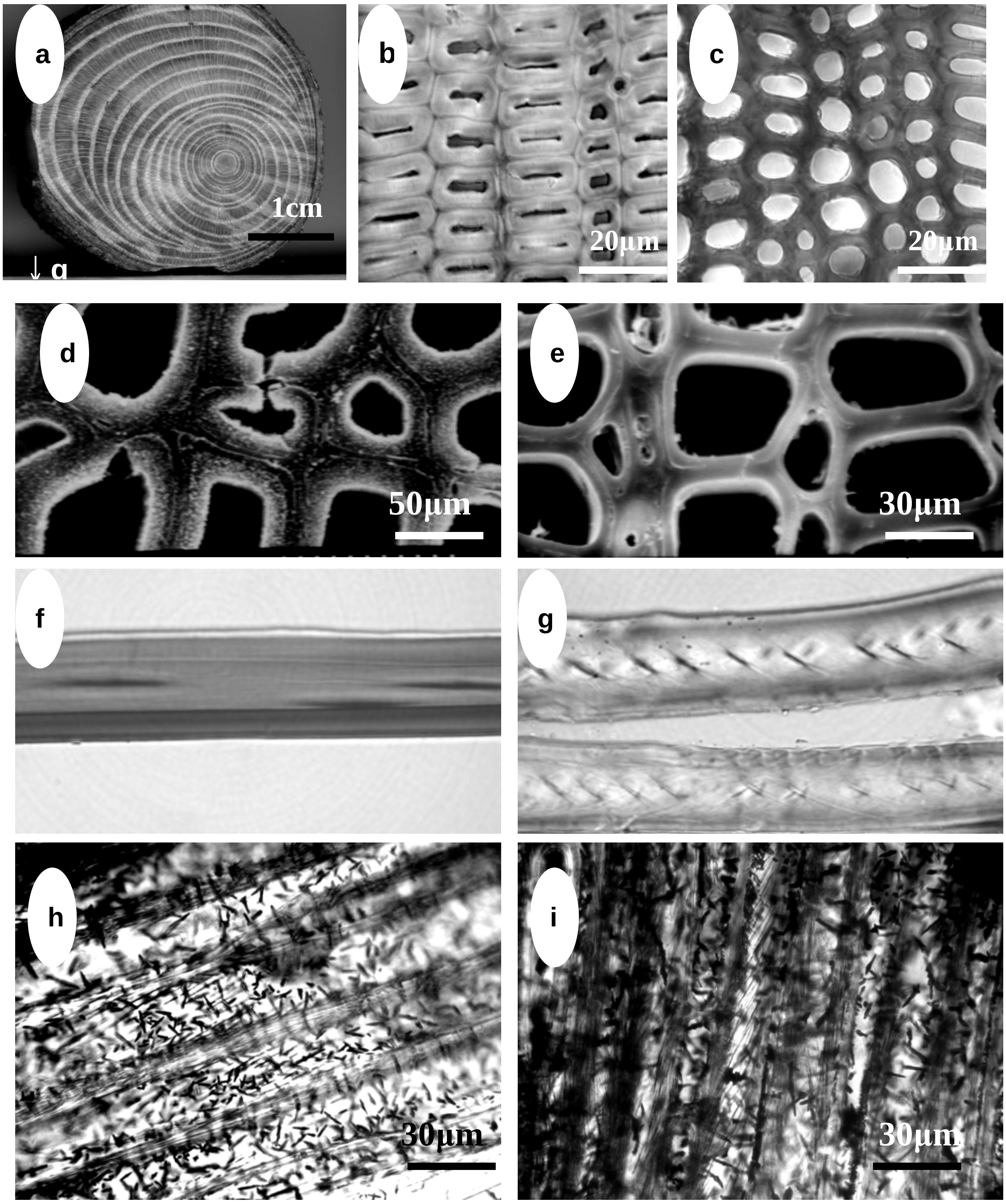

Released surface microstrain ($10^{-6}$)
4000
3000
2000
1000
0
-1000
-2000
-3000
Tension wood with G-fiber
Opposite wood without G-fiber

Fig. 2


a
1cm
↓ g
b
20μm
c
20μm
d
50μm
e
30μm
f
g
h
30μm
i
30μm

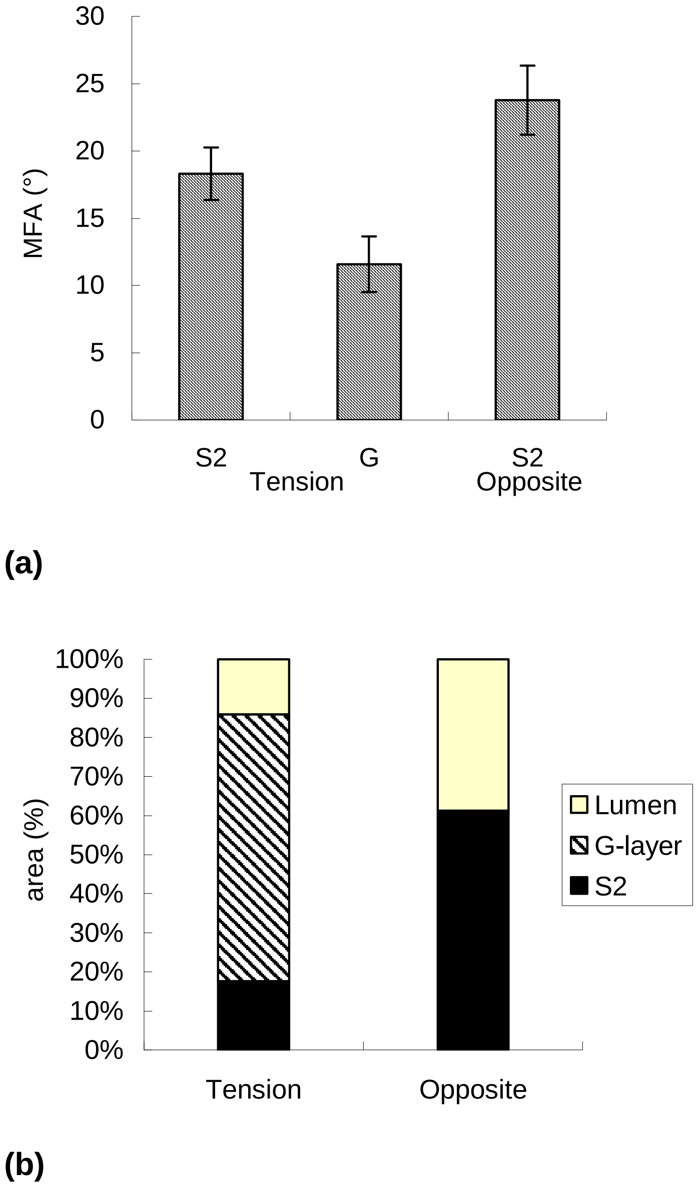
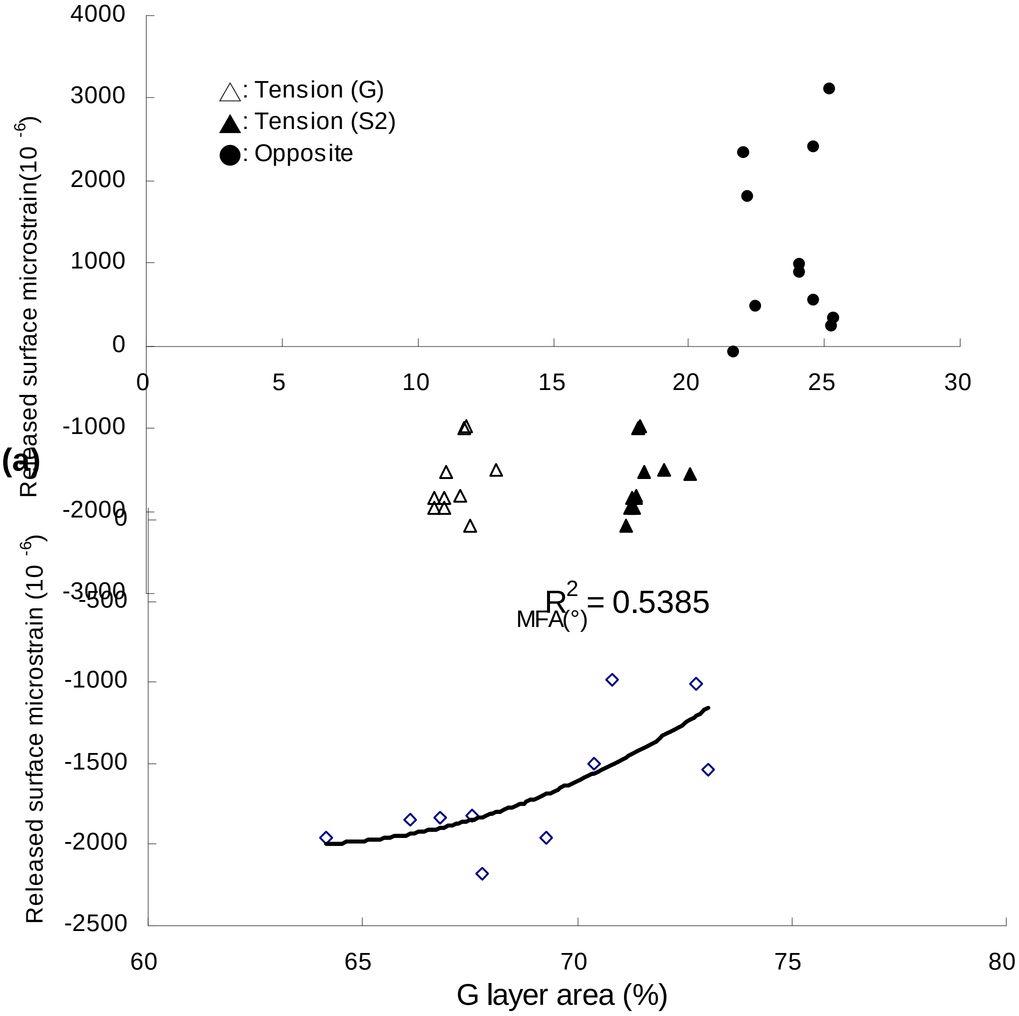

MFA (°)
30
25
20
15
10
5
0
S2
G
S2
Tension
Opposite
(a)
area (%)
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Tension
Opposite
Lumen
G-layer
S2
(b)

Fig. 4


△: Tension (G)
▲: Tension (S2)
●: Opposite
Released surface microstrain(10 -6)
4000
3000
2000
1000
0
-1000
-2000
-3000
0
5
10
15
20
25
30
MFA(°)
R2 = 0.5385
Released surface microstrain (10 -6)
0
-500
-1000
-1500
-2000
-2500
60
65
70
75
80
G layer area (%)

(a)

(b)

Fig. 5