Tree Physiology 25, 1119–1126

Growth strain in the trunk and branches of *Chamaecyparis formosensis* and its influence on tree form

YAN-SAN HUANG,[1] SHIN-SHIN CHEN,[1,2] LING-LONG KUO-HUANG[3] and CHIN-MEI LEE[1]

[1] *Division of Forest Utilization, Taiwan Forestry Research Institute, 53 Nan-Hai Road, Taipei, Taiwan 100*

[2] *Corresponding author (sschen@serv.tfri.gov.tw)*

[3] *Department of Life Science, National Taiwan University, 1 Roosevelt Road, Sec. 4, Taipei, Taiwan 106*

Received October 5, 2004; accepted January 15, 2005; published online July 4, 2005

Summary Distributions of growth strains in branches, straight trunks and basal sweeping trunks of *Chamaecyparis formosensis* Matsum. trees were measured with strain gauges. Microfibril angles (MFAs) of the S_2 layer of the cell wall were measured by the iodine deposition method and their relationships with growth strain examined. The magnitude of the compressive stress on the lower side of trunks with a basal sweep was greater than that of the tensile stress at the surface of straight trunks. However, transverse compressive stress was similar around the trunk regardless of whether normal wood or compression wood was present. The released surface growth strains varied with MFA. At MFAs of 20–25°, growth stress changed from tension to compression, and compressive stress increased dramatically in the compression wood region.

Branches suffer bending stress due to self-loading. This stress is superimposed on the growth stress. Growth strains on the upper or lower sides of branches were larger than those in the trunks, suggesting that generation of growth stress on the lower sides of branches with extensive compression wood is affected by the gravitational bending stress due to self-loading. We conclude that branch form is affected by the interaction between the bending moment due to self-loading and that due to the asymmetric distribution of growth stress. Growth strain distribution in a branch differed depending on whether the branch was horizontal, upward bending or downward bending.

Keywords: compression wood, microfibril angle, residual internal stress, spring-back strain.

Introduction

During growth, tree trunks accumulate growth stresses that are similar to the residual stresses that occur in artificial materials during processing. In coniferous and dicotyledonous trees, secondary growth results from vascular cambial activity, which generates xylem cells inward and phloem cells outward. It has been shown that growth stress accumulates during secondary wall formation of the xylem cells (Boyd 1972, Yamamoto et al. 1991, Guitard et al. 1999).

Heterogeneous growth stress occurs on the surface of the trunk during secondary growth. In response to surface stresses, patterns of residual stress within the trunk arise in longitudinal, radial and tangential directions (Archer and Bynes 1974, Kubler 1987, Fournier et al. 1990). 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 leaning trunks where eccentric stem swelling occurs (Watanabe 1967). Growth stress tends to force the trunk to grow vertically, thereby maximizing exposure to sunlight. In conifers, compression wood is formed on the lower side of a leaning trunk where there is a strong compression stress, whereas in dicotyledonous trees, tension wood is formed on the upper side where there is strong tensile stress (Okuyama et al. 1986, Timell 1986*a*, 1986*b*). Even in a vertically oriented trunk, growth stress forms within the trunk. In response to environmental stress, such as wind, the sapwood is at risk of compression damage. In both coniferous and dicotyledonous trees, the risk of such damage is countered by longitudinal tensile stress at the trunk periphery and compression stress that accumulates within the trunk (Archer 1986).

A high concentration of plant growth regulators has been found on the lower side of leaning trunks or branches of conifers (Savidge et al. 1982, 1983). Doerner (1966) studied the stress and hormone interrelationship during branch growth and observed that maximum bending stress coincides with the highest concentration of growth substances. He also found that auxin concentration was affected more by compressive stress than by tensile stress and concluded that auxin has a role in the formation of compression wood. With the aid of a mechanical model, Yamamoto et al. (2002) studied the interaction between bending moment, due to self-loading of branches, and recovery moment, resulting from asymmetric growth stress distribution around the cross section. They concluded that the growth stress generated in the reaction wood is sufficient to counteract gravitational self-loading of branches. The formation of reaction wood in response to gravity enables the leaning trunk or branch to exhibit the observed growth reorientation. Thus, negative gravitropic movement, manifest as upward-bending of the stem, is assumed to be a result of growth stress generated in reaction wood (Yamamoto et al. 2002).

Most previous studies have focused on growth stresses in trunks, with only a few investigations focusing on growth stress in branches (Ohsak and Yamada 1968, Yoshida et al. 1992*a*, 1992*b*, 1999). Recently, simulation analyses with a biomechanical model were applied to study the effects of growth stresses on the regulation of tree form (Alméras et al. 2002, 2004, Yamamoto et al. 2002, Fourcaud and Lac 2003, Fourcaud et al. 2003). However, experimental data on growth strain in branches and its influence on tree form are still lacking. In this study, we investigated the distribution of microfibril angle (MFA) and its relationship with growth strain in horizontal, upward-bending and downward-bending branches of Taiwan red cypress (*Chamaecyparis formosensis* Matsum.). The correlations between MFA and the released growth strains in branches are discussed and compared with those in trunks.

Materials and methods

Six, 30- to 35-year-old plantation-grown trees of *Chamaecyparis formosensis* at the Chilanshan station (121°15′–121°30′ E, 24°15′–24°45′ N, 1100 m a.s.l.), Forest Conservation Institute, Taiwan, including two with erect stems (C and D) and four with a basal sweep (A, B, E and F), were selected for study. The trees (A, B, C, D, E and F) were 17, 22, 23, 27, 34.5 and 40 cm in diameter at breast height (DBH), and were 15, 16, 16, 17, 18 and 18.5 m tall, respectively. To determine the effect of tree height on growth strain, all the trees were felled. The trunks were cross-cut every 2.0–2.5 m, and both the longitudinal and transverse surface strains on opposite sides of the stem at the mid-point of each segment were measured by the kerf method (Sasaki et al. 1978). After removing the bark at the specified positions, electrical resistance strain gauges were attached with cyanoacrylate adhesive to the xylem in both longitudinal and transverse directions. Measurements were made with a portable digital strain meter (Model UCAM–1A Kyowa, Tokyo, Japan) with a 40-channel scanner. After calibrating the strain gauges to zero, the surface growth strain was released by cutting grooves, 1– 1.5 cm deep, around the strain gauges with a handsaw and chain saw, and recording the released strain immediately. Tree E, which had a typical basal sweep, the trunk reaching a vertical orientation above breast height, was selected for measurement of surface growth strain and MFA around the periphery of the basal sweep, and residual internal stress and other physical properties within the trunk. For internal stress measurement, a radial section, 30 cm long and 2 cm thick, located at a trunk height of 5.3 m, was obtained with a chain saw and hand plane. Strain gauges were glued to the center of the plank at intervals of 1.5 cm in the radial direction and oriented in the longitudinal direction. Longitudinal residual strains on the diametral plank were then measured by cross-cutting the plank with a handsaw at 1 cm above the strain gauges and then ripping among the gauges. In addition, specimens 1 cm wide × 1 cm thick × 18 cm long, matched with the strain measuring positions, were sampled from the plank and used in a static bending test to measure the modulus of elasticity (MOE) which was used to calculate internal stresses (Huang et al. 2001). Bending strength of wood expressed as modulus of rupture (MOR) was also measured (Bodig and Jayne 1982). Specific gravity (oven-dry mass/green volume) was determined for each specimen measured for internal strain to show the within-trunk patterns of variation (Kollmann and Côté 1968). Measurements of the peripheral distributions of growth strains were made on standing tree E at the circumference of the curved portion of the basal sweep between 22.5 and 45°, where the upper side of the trunk was designated 0° and the lower side 180°. Accumulated strain measurements were made along the lower side of the leaning trunk where compression wood had formed (Figure 1). To obtain more information about compression wood, accumulated measurements were made on the lower side of the basal sweeping trunks of trees A, B and F.

Microfibril angles were measured by the iodine-staining method (Kuo-Huang et al. 2004). Ten to fifteen tangential sections, 20 μm in thickness, were cut from the outermost annual ring at each surface growth strain measuring position. The MFAs were measured in about 50 tracheids of each sample, and the mean value for early- and latewood was calculated. Each mean was compared with the magnitude of the released surface growth strain.

Twelve branches comprising three types (horizontal, upward-bending and downward-bending) were selected from young trees with DBHs ranging from 4 to 20 cm to measure growth strains at different distances away from the trunk (see Table 1). The measurements were made on standing trees. After removing the bark, strain gauges were glued in the longitudinal direction on the upper side and the lower side at a specified position on the branch. After zeroing the gauges, the branch was cut down and its spring-back strain due to

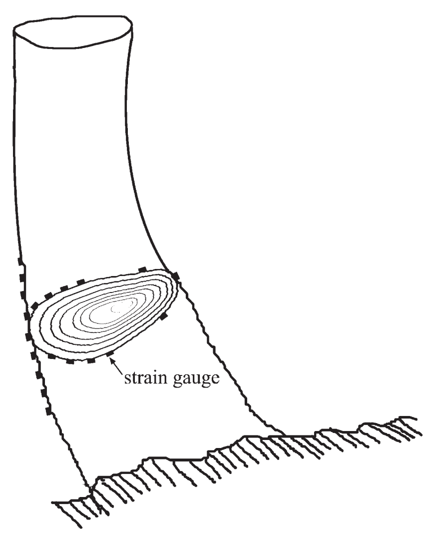

Figure 1. Measurement of released surface growth strain around the periphery of a trunk basal sweep.

Table 1. Branch type, growth strains and spring-back strains after the relief of self-loading at different distances from the trunk. Abbreviations: L = distance from trunk; D_1 = vertical axis diameter of branch cross section; D_2 = horizontal axis diameter of branch cross section; Type I = branch bending upward; Type II = branch horizontal; and Type III = branch bending downward.

Branch no.	Branch type	L (cm)	D_1 (cm)	D_2 (cm)	Spring-back strain (με)		Surface growth strain (με)	
					Upper side	Lower side	Upper side	Lower side
1	I	10	2.90	2.70	–2445	2303	1167	3265
		33	2.50	2.80	–1420	1476	734	2281
		62	2.20	2.40	–126	835	18	1102
		95	1.90	2.20	–777	1337	–454	1459
		121	1.90	1.95	–923	1298	–651	1255
2	I	8	3.10	2.80	–2987	2750	1535	4042
		29	2.50	3.10	–1099	1552	485	1768
		53	2.40	3.00	–1403	1049	338	1092
		77	2.22	2.60	–1224	913	268	28
		97	2.10	2.20	–861	1276	–329	1855
3	I	7	2.40	2.50	–2190	2338	2489	5955
		18	2.40	2.40	–1511	1923	2021	6428
		32	2.20	2.30	–1234	1253	1220	2314
		44	2.10	2.30	–879	395	501	7
		55	2.10	2.10	–817	837	–316	698
4	II	4	1.40	1.30	–4459	4915	–2056	5790
		11	1.40	1.20	–3604	4185	–1942	5160
		19	1.30	1.20	–2760	2815	–1808	3243
		30	1.15	1.10	–877	2926	–99	3584
		41	1.00	1.00	–2571	2704	–1751	3148
5	II	8	1.40	1.40	–3459	4960	–3086	5810
		33	1.40	1.30	–3070	3047	–2182	4015
		53	1.30	1.20	–1857	2327	–855	2979
		80	1.00	1.00	–2141	2275	–1927	2300
		105	0.90	0.90	–1839	2057	–1457	2517
		129	0.90	0.80	–1312	1800	–948	2402
6	II	9	2.20	2.00	–3065	3744	–2539	4214
		41	2.10	1.80	–1648	2197	–1099	2626
		71	2.00	1.60	–1441	1540	–771	1716
		100	1.60	1.40	–1311	1578	–736	1865
		125	1.50	1.10	–1464	1891	–589	2861
		157	1.00	0.80	–1771	2051	–1206	2507
		186	0.70	0.70	–1664	2204	–1916	2129
7	II	13	2.11	2.02	–2920	3866	–1885	4329
		39	2.07	1.65	–1801	2064	–697	3648
		65	1.87	1.52	–1489	1486	–68	2798
		85	1.72	1.46	–1214	1440	–295	2587
		109	1.51	1.31	–1587	1824	–1321	2614
		136	1.36	1.23	–1227	1383	–947	1890
		159	1.29	1.18	–1093	1081	–935	1538
		179	1.19	1.10	–815	805	–960	1168
		205	1.16	1.17	–482	483	–510	690
		244	0.86	0.89	–178	158	–270	126
8	II	10	1.13	1.02	–4196	3536	–2789	4032
		33	1.05	1.10	–1117	2537	–911	3186
		59	0.83	0.89	–1179	1281	–1674	1588
		77	0.78	0.73	–847	1112	–848	1636
9	II	9	1.26	1.07	–3818	4730	–2471	5523
		24	1.13	1.04	–2997	3302	–2330	4107
		45	0.97	0.91	–2831	3348	–1875	3767

Continued overleaf

Table 1 Cont'd. Branch type, growth strains and spring-back strains after the relief of self-loading at different distances from the trunk. Abbreviations: L = distance from trunk; D_1 = vertical axis diameter of branch cross section; D_2 = horizontal axis diameter of branch cross section; Type I = branch bending upwards; Type II = branch horizontal; and Type III = branch bending downward.

Branch no.	Branch type	L (cm)	D_1 (cm)	D_2 (cm)	Spring-back strain (με)		Surface growth strain (με)	
					Upper side	Lower side	Upper side	Lower side
9	II	66	0.86	1.00	–3038	2485	–2961	2542
10	III	5	1.45	1.30	–1445	7608	–525	8734
		25	1.35	1.30	–3165	4133	–1984	4470
		44	1.25	1.20	–2376	2666	–1074	3235
		62	1.10	1.15	–861	2145	–516	2436
		83	1.10	1.05	–1812	2146	–936	2594
11	III	10	2.20	2.00	–4776	7157	–3848	7987
		29	2.30	2.00	–3141	4185	–1827	6622
		44	2.10	2.00	–2899	3434	–1075	4618
		68	2.10	2.00	–2139	2313	–916	3231
		87	1.95	2.00	–2153	2224	–812	3389
12	III	8	2.40	2.80	–1446	1628	–1290	2433
		24	2.00	2.30	–1410	1293	–532	1667
		46	1.90	2.40	–1170	1390	–853	1690
		75	1.50	1.50	–1356	1572	–1509	1318
Mean					–1895	2332	–914	2994
Standard deviation					1042	1432	1191	1807

self-loading determined. Thereafter, growth strains were measured by cross-cutting the branch at a position 5 mm in front or behind the strain gauge. We also measured MFAs on the upper and lower sides of branches at the positions where growth strain was measured.

The anatomical structures of the cross- and radial sections were observed microscopically. The existence of compression wood was confirmed by the presence of thickened cell walls, intercellular spaces due to the formation of tracheids with rounded cross sections and helical fissures in the radial sections of the tracheids (Yamamoto et al. 1991).

Results and discussion

Distribution of physical properties and residual internal growth stresses within the trunk

Radial variation in specific gravity (dry mass/green volume) within the trunk of tree E at 5.3 m height is shown in Figure 2a. The mean value was 0.33 ± 0.03 (SD), with the lowest value occurring near the pith where juvenile wood exists.

The density of a tree trunk is affected by site-related factors, such as precipitation, availability of sunlight and nutrients, wind and temperature. It is also influenced to a large extent by altitude, aspect, slope, latitude, soil type, stand composition and spacing because all these factors can affect the size and wall thickness of cells and thus wood density (Chen et al. 1998). However, species differ greatly in their sensitivities to site factors (Haygreen and Bowyer 1982). Because many of these factors occur in combination, it is difficult to separate the independent effects. There is much literature dealing with these relationships, the inconsistencies of which indicate the complex interactions among the factors. In general, wood density in softwood species is dominated by the percentage of latewood in a growth ring, which is influenced by climate and other ecological variables. The density of heartwood is greatly affected by the amounts of extractives, which may be unrelated to the strength of the wood.

Distribution of the MOE within the trunk is shown in Figure 2b. The mean value was 4.9 ± 1.4 GPa, with the highest MOE at the periphery and the smallest at the pith. The central part of the trunk, which mostly consists of juvenile wood, had a lower stiffness than the outer part. Within the trunk, MOR varied radially (Figure 2c), with a mean value of 44.5 ± 7.3 MPa, and a distribution pattern resembling that of MOE.

Figure 2d shows the distribution of residual internal stress in the longitudinal direction within the erect part of the trunk at a height of 5.3 m in tree E. Contraction strain or tensile stress was found near the periphery, whereas extension strain or compressive stress was found inside. The maximum residual stress was +3.1 MPa near the peripheral surface and –1.5 MPa near the center. This pattern of residual stress distribution is a result of surface growth stress accumulating in the inner portion of the trunk. Surface growth stresses are generated yearly in the outermost layer of a growing trunk. In response to surface growth stress, a stress distribution is established in the inner part of the trunk. In other words, new growth stresses are superimposed on the original stress distribution, resulting in stress redistribution. With growth of the trunk, the process is repeated annually, creating a regular pattern of stress distribution (Okuyama et al. 1986).

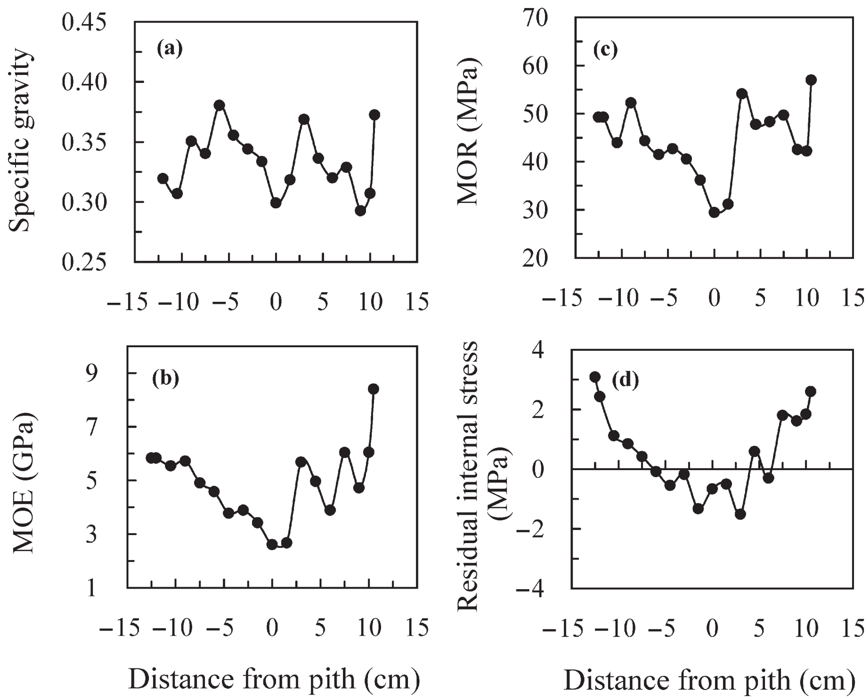

Figure 2. Distribution of (a) specific gravity (dry mass/green volume), (b) modulus of elasticity (MOE), (c) modulus of rupture (MOR) and (d) residual internal growth stress in the longitudinal direction in the trunk of tree E.

Influence of tree height on surface growth strain

Based on measured data for trees E and F as examples, the means of longitudinal and transverse measurements made on opposite sides of the trunk are shown in Figure 3. There was no distinct relationship between tree height and surface growth strain in the longitudinal and transverse directions. Released longitudinal strains were negative, indicating the presence of tensile stress, except for tree F at 5 m height, where compression wood existed. Released transverse strains were positive, indicating the presence of compressive stress. For tree E, maximum strain occurred at 3.3 m height in both the longitudinal and transverse directions, whereas fluctuations in strain value with height were observed for tree F. The mean value of longitudinal surface strain for trees E and F was –245 ± 13 and –180 ± 122 με, respectively. The mean transverse surface strain for trees E and F was 209 ± 150 and 158 ± 118 με, respectively, but there was no significant difference ($P > 0.05$) in growth strains between trees E and F. By comparison, Yao (1979) studied growth stress variation with tree height in shagbark hickory (*Carya ovata* (Mill.) C. Koch), water oak (*Quercus nigra* L.) and white ash (*Fraxinus americana* L.) and found that the longitudinal growth stress for ash reached a peak at a height of 5 m, whereas in oak and hickory, growth stress reached a maximum at a height of 8 m. In a similar study of 39-year-old mountain ash (*Eucalyptus regnans* F.J. Muell.) trees, Chafe (1981) found increases in longitudinal growth strain and stress with increasing height up to 7.5 m. Thus, the relationship between growth stress and tree height warrants further study.

Peripheral distribution of growth strain on leaning trunks

Large released growth strains in the longitudinal direction were detected on the lower side (180°) of the leaning trunk (Figure 4). The strains ranged from +584 to +1100 με. A positive strain value indicates an extension strain, implying that the lower side suffers from compressive stresses. Because only tensile stress is normally found at the surface of erect trunks (Huang et al. 1998), the compressive stress on the lower side of the leaning trunks must have originated from the compression

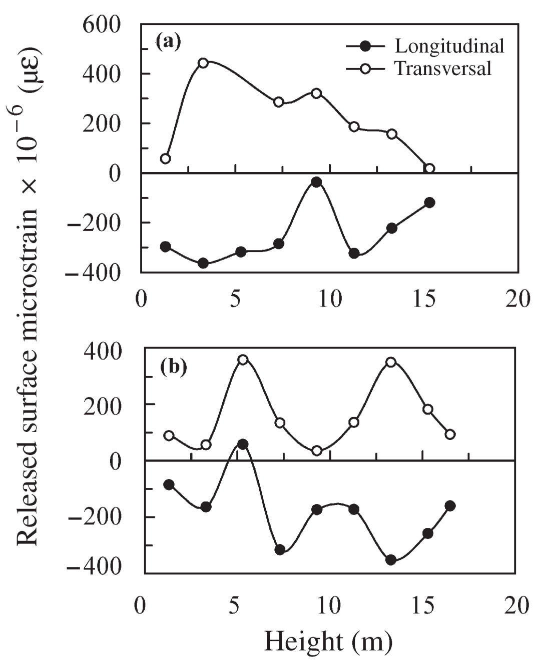

Figure 3. Effects of tree height on released surface growth strain in (a) tree E and (b) tree F.

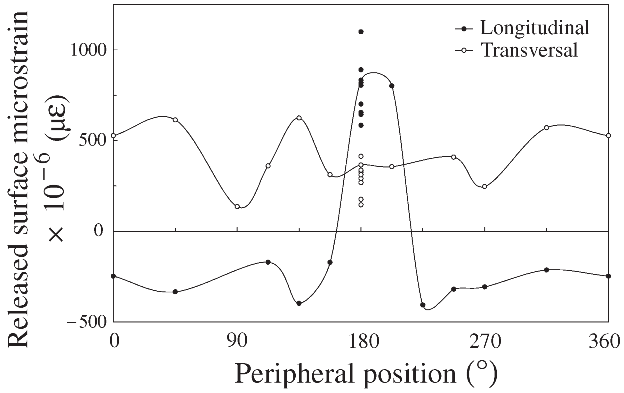

Figure 4. Peripheral distribution of released surface strain in longitudinal and transverse directions in the trunk basal sweep of tree E. Large released growth strains in the longitudinal direction were detected on the lower side (180°) of the leaning trunk.

wood. Boyd (1980) also detected a large extension strain (+1800 με) on the lower side of the leaning trunk of *Pinus radiata* D. Don. Other locations on the trunk periphery showed strain values between –171 and –407 με, indicating the existence of tensile stresses. On the other hand, transverse growth strains showed positive values ranging from +135 to +625 με, indicating the presence of compressive stresses. In Huang et al.'s (2001) study of the growth stress of *Cryptomeria japonica* D. Don, a large negative strain in the transverse direction on the lower side (–924 με) was detected, which contrasts with our observations. However, because of the biaxial character of the surface growth stress, the existence of compressive stress was found (+128 με) after correction with Poisson's ratio. The ability to generate longitudinal compressive stress in compression wood tissue generates a definite mechanical effect, tending to restore the trunk to a vertical orientation. In contrast with hardwood trunks, softwood trunks usually exert both a pulling force from the upper side as well as a pushing force from the lower side in order to reorient the leaning trunk (Archer 1986).

The mechanism of reorientation of a leaning stem has been explained as the expansion of compression wood in the axial direction pushing the trunk into the vertical position (Timell 1986*b*, Niklas 1992, Mattheck and Kubler 1995). However, the mechanism by which the compression wood expands along the grain of the trunk has not been fully clarified. We speculate that the compression stress exerted by the compression wood at the lower side of a leaning trunk introduces a recovery moment. The leaning trunk must bend upward to relieve the compressing stress and attain a mechanical equilibrium. During upward bending, the lower side of the trunk generates tensile stresses and the upper side generates compression stress. These stresses are then superimposed on the original internal growth stress. Thus, the measured internal stress distribution, which is different to that in a normal trunk, is the sum of the original residual stress and the bending stress. This stress distribution is further complicated by the accumulation of newly generated growth stress each year. Additional studies with new techniques are needed to elucidate the physiological significance of stress and strain in the growth of a tree.

Microfibril angle in relation to surface growth strains

Figure 5 shows the relationships between MFA in the S_2 layer of the cell wall and the released longitudinal growth strain at the surface of branches (a) and trunks (b). The released strains tended to increase with increasing MFA. For trunks, the released strain changed from contraction to extension at an MFA of 20–25°, and the extensive strain increased dramatically in the compression wood region. In the normal wood region, growth strains fluctuated with increasing MFA. We observed that mild compression wood showing a small positive growth strain also occurred at low MFAs of 7–17°. This relationship is similar that reported by Yamamoto et al. (1991) in *Chamaecyparis obutusa* Endl., which has a transition angle of 20–25°. Comparing Figure 5a with Figure 5b, it is apparent that the mean MFA of the branches (30.9 ± 5.0°) is larger than that of the trunks (17.3 ± 6.3°) ($P < 0.01$). The mean MFA of the compression wood of trunks (19.9 ± 7.9°) was significantly larger than that of normal wood (14.7 ± 4.7°) ($P < 0.01$). The mean

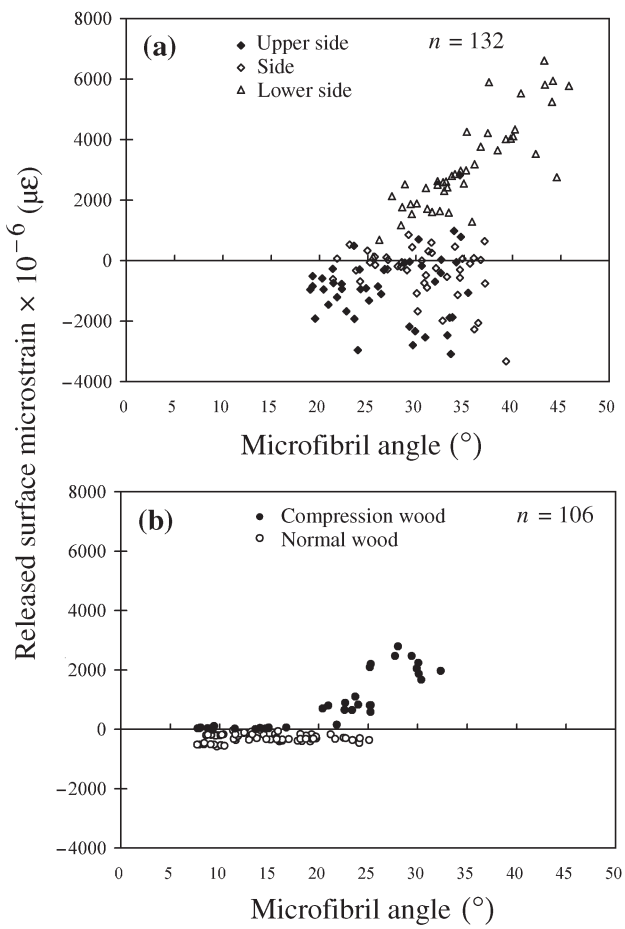

Figure 5. Effects of microfibril angle (MFA) on the surface growth strain in the longitudinal direction of (a) branches and (b) trunks of trees A–F. The MFAs of branches are larger than those of trunks ($P < 0.01$).

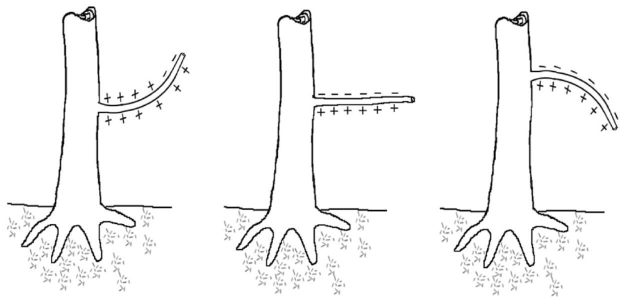

Figure 6. Type of branch in relation to growth strain distribution. Symbols: + = positive released growth strain; and – = negative released growth strain.

MFA on the lower side of the branches (35.2 ± 5.4°) was apparently larger than the mean MFA on the upper side (28.8 ± 5.0°) ($P < 0.01$) because of the existence of compression wood. There is a close relationship between growth stress and MFA (Okuyama et al. 1994, 1986, Yamamoto et al. 1995). Based on the unified hypothesis, Guitard et al. (1999) applied a mechanical model to examine the relationship between growth strain and MFA. They calculated that the critical MFA at which the longitudinal growth stress changed from tension to compression was at about 20–30°. This compressive stress is entirely associated with the specialized tissue of compression wood, suggesting that lignin swelling plays a role 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 taken as a measure of compression wood development.

Longitudinal growth strain distribution in branches

Conifers usually form compression wood on the lower side of branches or leaning trunks (Panshin et al. 1964, Timell 1986*a*). The stress generated from this specialized tissue differs from that of normal wood. Compression wood produces compressive stress in the longitudinal direction, which constrains the extension of the wood. Compression wood forces the branch or the leaning stem of conifers to grow upward or to maintain a definite angle between the main trunk and a branch. Branches also suffer bending stress due to self-loading. This stress is superimposed on the growth stress. In a study of growth stress in branches of *Chamaecyparis obtusa*, Yoshida et al. (1992) reported that the relationships between growth stresses and the physical properties of branches differed from those of stems. They suggested that something was induced in the branch other than growth stress that differs from the normal wood and reaction wood in a stem. Table 1 shows the spring-back strain and surface growth strain at different distances from the trunk of three types of branches: horizontal, upward-bending and downward-bending. The cross sections of the branches were more or less oval with compression wood on the lower side. We found that spring-back strains were contractive on the upper side and extensive on the lower side of branches. Growth strains were larger in the branches than in the stems. Growth strain increased with increasing spring-back strain on the lower side, and the former was larger than the latter ($P < 0.05$). These strains have a strong linear relationship ($r^2 = 0.820$). There is a tendency for growth strain on the upper and the lower sides of the branch to increase with decreasing distance from the trunk. Observations of branch cross sections showed that the pith became more eccentric as its distance from the trunk decreased, indicating intensive development of compression wood that can induce a large compressive stress. It is suggested that the generation of growth stresses on the lower side of branches that developed a large mass of compression wood is affected by gravitational bending stress due to branch self-loading, which in turn is responsible for the large spring-back strain. In other words, the gravitational stimulus is responsible for high growth stress of compression wood. From the data shown in Table 1, the relationship between growth strain and branch type can be deduced graphically as shown in Figure 6. In the case of horizontal and downward-bending branches (Types II and III), growth strains were negative on the upper side and positive on the lower side. With few exceptions, the absolute value of the growth strain on the upper side of the branches was smaller than on the lower side. However, in the upward-bending branches (Type I), the growth strains on both the upper and the lower sides were positive in the bending region near the base, whereas on the more nearly vertical part of the branch near the end, growth strains were negative on the upper side and positive on the lower side. The branch form is related to the equilibrium between the bending stress due to self-loading and that due to growth stress. When the downward-bending moment, due to self-loading, is larger than the upward recovery moment due to the asymmetric growth stress distribution around the branch cross section, the branch bends downward. In contrast, upward-bending branches are an example of the phenomenon of negative gravitropism in the broad sense, as mentioned by Mattheck (1991). We conclude that tree form is adjusted by the large growth stresses generated in reaction wood.

Acknowledgments

This study was funded by the National Science Council through research project NSC-93-2313-B-054-001.

References

Alméras, T., J. Gril and E. Costes. 2002. Bending of apricot tree branches under the weight of axillary growth: test of a mechanical model with experimental data. Trees 16:5–15.

Alméras, T., E. Costes and J.C. Salles. 2004. Identification of biomechanical factors involved in stem shape variability between apricot tree varieties. Ann. Bot. 93:455–468.

Archer, R.R. 1986. Growth stresses and strains in trees. Springer-Verlag, New York, 240 p.

Archer, R.R. and F.E. Bynes. 1974. On the distribution of tree growth stresses. Part l. An anisotropic plane strain theory. Wood Sci. Technol. 8:184–196.

Bodig, J. and B.A. Jayne. 1982. Mechanics of wood and wood composites. VAN Nostrand Reinhold, New York, 712 p.

Boyd, J.D. 1972. Tree growth stresses. V. Evidence of an origin in differentiation and lignification. Wood Sci. Technol. 6:251–262.

Boyd, J.D. 1980. Relationship between fibre morphology, growth strain and physical properties of wood. Aust. For. Res. 10: 337–360.

Chafe, S.C. 1981. Variations in longitudinal growth stress, basic density and modulus of elasticity with height in the tree. Aust. For. Res. 11:79–82.

Chen, Y.S., Y.S. Huang and S.S. Chen. 1998. A study on moisture distribution of green wood and variations of specific gravity in *Cryptomeria japonica* D. Don. Taiwan J. For. Sci. 13:91–100.

Doerner, Jr., K. 1966. Stress and hormone interrelationship in branch growth. Plant Physiol. 41:614–616.

Fourcaud, T. and P. Lac. 2003. Numerical modeling of shape regulation and growth stresses in trees. I. An incremental static finite element formulation. Trees 17:23–30.

Fourcaud, T., F. Blaise, P. Lac, P. Castéra and P. de Reffye. 2003. Numerical modeling of shape regulation and growth stresses in trees. II. Implementation in the AMAPpara software and simulation of tree growth. Trees 17:31–39.

Fournier, M., P.A. Bordonne, D. Guitard and T. Okuyama. 1990. Growth stress patterns in tree stems. Wood Sci. Technol. 24: 131–142.

Guitard, D., H. Masse, H. Yamamoto and T. Okuyama. 1999. Growth stress generation: a new mechanical model of dimensional change of wood cells during maturation. J. Wood Sci. 45:384–391.

Haygreen, J.G. and J.L. Bowyer. 1982. Forest product and wood science: an introduction. The Iowa State University Press, pp 204–217.

Huang, Y.S., S.S. Chen and Y.S. Chen. 1998. Study on the growth stress in tree. I. The growth stress distribution of planted *Cryptomeria japonica*. Quart. J. Chin. For. 31:177–186. In Chinese with English summary.

Huang,Y.S., S.S. Chen, T.P. Lin and Y.S. Chen. 2001. Growth stress distribution in leaning trunks of *Cryptomeria japonica.* Tree Physiol. 21:261–266.

Kollmann, F.F.P. and W.A. Côté, Jr. 1968. Principles of wood science and technology. I. Solid wood. Springer-Verlag, New York, 592 p.

Kubler, H. 1987. Growth stresses in trees and related wood properties. For. Abstr. 48:131–189.

Kuo-Huang, L.L., Y.S. Huang, S.S. Chen and Y.R. Huang. 2004. Growth stresses and related anatomical characteristics in coconut palm trees. IAWA J. 25:297–310.

Niklas, K.J. 1992. Plant biomechanics: an engineering approach to plant form and function. University of Chicago Press, Chicago, IL, 622 p.

Mattheck, C. 1991. Trees: the mechanical design. Springer-Verlag, New York, 121 p.

Mattheck, C. and H. Kubler. 1995. Wood: the internal optimization of trees. Springer-Verlag, New York, 129 p.

Ohsako, Y. and T. Yamada. 1968. Growth stresses in branch of Buna-wood (*Fagus crenata* Blume). Wood Res. 45:36–45. In Japanese with English summary.

Okuyama, T., A. Kawai, Y. Kikata and H. Yamamoto. 1986. The growth stresses in reaction wood. *In* Proc. 18th IUFRO World Congress, Yugoslavia, Div. 5, For. Proc., pp 249–260.

Okuyama, T., H. Yamamoto, M.Yoshida, Y. Hattori and R.R. Archer. 1994. Growth stresses in tension wood: role of microfibrils and lignification. Ann. Sci. For. 51:291–300.

Panshin, A.J., C. deZeeuw and H.P. Brown. 1964. Textbook of wood technology. McGraw-Hill, New York, 722 p.

Sasaki, Y., T. Okuyama and Y. Kikata. 1978. The evolution process of the growth stress in the tree: the surface stress on the tree. Mokuzai Gakkaishi 24:149–157.

Savidge, R.A., J.K. Heald and P.F. Wareing. 1982. Non-uniform distribution and seasonal variation of endogenous indol-3yl-acetic acid in cambial region of *Pinus contorta* Dougl. Planta 155:89–92.

Savidge, R.A., G.M.C. Mutumba, J.K. Heald and P.F. Wareing. 1983. Gas chromatography–mass spectroscopy identification of 1-aminocyclopropane-1-carboxylic acid in compression wood vascular cambium of *Pinus contorta* Dougl. Plant Physiol. 71: 434–436.

Timell, T.E. 1986*a*. Compression wood in gymnosperms. Vol. 1. Springer-Verlag, New York, pp 63–89.

Timell, T.E. 1986*b*. Compression wood in gymnosperms. Vol. 3. Springer-Verlag, New York, pp 1757–1791, 1799–1824.

Watanabe, H. 1967. A study of the origin of longitudinal growth stress in tree stems. Bull. Kyushu Univ. For. 41:169–176.

Yamamoto, H., T. Okuyama, M. Yoshida and K. Sugiyama. 1991. Generation process of growth stresses in cell walls. III. Growth stress in compression wood. Mokuzai Gakkaishi 37:94–100.

Yamamoto, H., T. Okuyama and M. Yoshida. 1995. Generation process of growth stresses in cell walls. VI. Analysis of growth stress generation by using a cell model having three layers (S_1, S_2 and I+P). Mokuzai Gakkaishi 41:1–8.

Yamamoto, H., M. Yoshida and T. Okuyama. 2002. Growth stress controls negative gravitropism in wood plant stems. Planta 216: 280–292.

Yao, J. 1979. Relationships between height and growth stress within and among white ash, water oak and shagbark hickory. Wood Sci. 11:246–251.

Yoshida, M., T. Okuyama and H. Yamamoto. 1992. Tree forms and internal stresses. III. Growth stresses of branches. Mokuzai Gakkaishi 38:663–668.

Yoshida, M., T. Okuyama, H. Yamamoto and K. Sugiyama. 1992. Tree forms and internal stresses. II. Stresses around the base of a branch. Mokuzai Gakkaishi 38:657–662.

Yoshida, M., T. Nakamura, H. Yamamoto and T. Okuyama. 1999. Negative gravitropism and growth stress in GA_3-treated branches of *Prunus spachiana* Kitamura f. *spachiana* cv. *Plenarosea*. J. Wood Sci. 45:368–372.