RIGHTING MOVEMENT AND XYLEM DEVELOPMENT IN TILTED YOUNG CONIFER TREES

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ABSTRACT

The natural righting movement and the corresponding xylem development in tilted young trees of five conifer species were observed. There were differences in the response to the stimulus of inclination among species. The righting movement in these tilted young trees suggests that the recovery of the vertical position of the stem is initiated at the top of the stem and gradually proceeds to the bottom, with a corresponding increase from top to bottom of compression wood formation. The formation of compression wood on the underside of the inclined stem continues until the normal vertical position is restored, although under prolonged inclination sensitivity to the stimulus of compression wood formation may decline or be lost and effectively suppress additional compression wood formation on the underside of the stem. Compression wood formation may reverse from the underside to the upper side in the slightly inclined stem.

Keywords: Cambium, compression wood, geotropic response, gymnosperms, xylem growth.

INTRODUCTION

The formation of compression wood on the underside of leaning stem in gymnosperms has been thought to be a response to gravity (Onaka 1949; Sinnott 1952; Spurr and Hyvarinen 1954; Scott and Preston 1955; Westing 1965; Wilson and Archer 1977; Yumoto et al. 1982). Compression wood acts to maintain or to restore a genetically determined position of each point of a tree. The forces leading to recovery of the normal position in bent gymnosperm stems are believed to be derived from the one-sided increase of cambial activity accompanied by compression wood formation (Frey-Wyssling 1952; Sinnott 1952; Archer and Wilson 1973; Boyd 1973; Scurfield 1973; Wilson and Archer 1977) caused by the redistribution of auxin within the stem (Onaka 1949; Kennedy and Farrar 1965; Wardrop 1965; Westing 1965).

Our understanding of the stimulus for, and action of, compression wood will be furthered by investigating the longitudinal variation as well as the radial variation of compression wood formation within a growth ring associated with the righting movement of the stem in gymnosperms. Sinnott (1952), Westing (1961), Archer and Wilson (1970, 1973), and Fukazawa (1973) have investigated the compression wood response in tilted young trees. This paper discusses righting movement and xylem development in tilted young trees and some differences in the response to the stimulus of inclination among gymnospermous species.

MATERIALS AND METHODS

The sample trees used in this experiment are described in Table 1. Three trees of each of following species: *Picea jezoensis* var. *hondoensis, Abies firma, Cryptomeria japonica, Chamaecyparis obtusa,* and *Larix leptolepis,* all 3–6 years old, pot-planted, and grown in the nursery of Utsunomiya University, were used. On

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TABLE 1. *Outline of sample trees.*

Species	Sample no.	Age (years)	Height (m)	Diameter (cm)
Picea jezoensis	1		0.72	1.52
var. *hondoensis*	2*	5	0.80	1.35
	3		0.75	1.40
Abies firma	1		1.30	2.65
	2*	6	1.05	2.17
	3		1.05	2.20
Cryptomeria	1*		0.62	1.38
japonica	2	4	0.42	1.30
	3		0.60	1.33
Chamaecyparis	1		1.10	1.63
obtusa	2*	3	1.00	1.22
	3		0.85	1.10
Larix	1		1.15	1.52
leptolepis	2*	5	1.22	1.30
	3		0.90	1.20

* Only asterisked sample trees were cut and used for microscopic observations.

25 May 1983, these sample trees were replanted obliquely at an angle of 45° to the vertical. The natural righting movement of these sample trees was monitored using photographic records taken once a week from the same position. When sample trees for microscopic observations were cut down on 5 October 1983, the ultimate angles of the deviation from the vertical were measured by the method shown in Fig. 1. Only one tree per species was examined microscopically. The diameter growth of the sample trees was also periodically recorded.

Disks 1 cm thick were obtained at an interval of 10 cm from the base of the stems, and were numbered 1, 2, and so on, upward. These disks were obtained from the same point as those used in the measurement of stem deviation. Small wood blocks containing the current growth ring were cut from the disks and immediately fixed with glutaraldehyde.

Unstained transverse sections 20 μm thick were sliced from these blocks and observed under polarizing and fluorescence microscopes. Compression wood tracheids were identified by the lack of the S3 layer and the presence of the excessive lignification in the S2 layer. The proportion of the surface area occupied by the compression wood arc (to the current-year xylem), recognized as bands of heavily lignified cells under a fluorescence microscope, was obtained, to find a relationship between the amount of compression wood and the angle of stem deviation, by the cut-and-weight method using photomicrographs of the transverse sections (Park et al. 1979). The radial sequence of the cell types from normal to compression wood, or vice versa, within a growth ring was determined in detail for ten radial rows in the center of the compression wood arc on each growth ring.

RESULTS AND DISCUSSION

Diameter growth in tilted young trees

In *Larix*, the beginning of bud break was considerably earlier than those in the other species, as reported by Ladeforged (1952). The bud break began in early

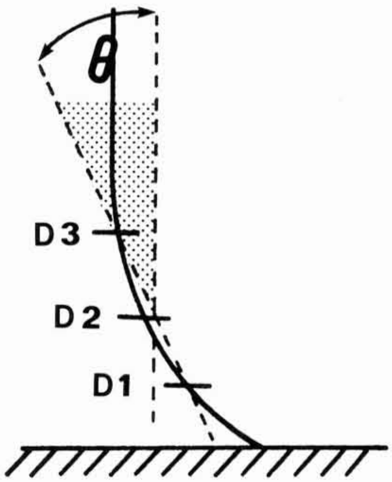

FIG. 1. Measurement of an angle of stem deviation from the vertical in sample trees. The angle of stem deviation at each portion of stem sample, e.g., the angle for disk (2), in this figure was obtained as the angle between the vertical and the tangent line at the position.

April, and the foliage was well developed by mid-April. In the other sample species, the bud break occurred in late April, with foliage development continuing up to early May.

Observations of seasonal diameter growth at the base of each stem revealed that active diameter growth took place from early June through late July in all the sample trees. In *Picea* and *Cryptomeria,* which exhibited an active righting behavior of the stems, diameter growth became slow after early August. In *Abies* and *Chamaecyparis,* it continued up to late September. In *Larix,* it continued up to early October, probably because the stem deviation had not been corrected completely.

Righting movement in tilted young trees

Righting movements in the tilted young trees are shown diagrammatically in Fig. 2. In *Picea* and *Abies,* which have straight young shoots, the recovery from the displacement first took place in the middle portion of the current shoots, during the first 3 days after stem inclination (Yoshizawa et al. 1986). Marked movement at the top of the stems was not observed in the other sample species a little while after stem inclination. From the models of righting movement, it can be said that the stem recovery is most vigorous during June and July, and that the stem recovery initiated at the top proceeds slowly downward to the stem base. These tendencies were in accordance with earlier observations by Sinnott (1952) and Fukazawa (1973). Except for the basal portion of the sample trees, stem recovery was largely completed by August or September in *Picea, Abies,* and *Cryptomeria.* In *Abies,* almost no recovery occurred in the basal portion because of its large diameter. This tendency was more or less similar in the vicinity of the stem base in the other sample species. This would accord with a general trend that geotropic responses usually become modified as trees become older and more massive in size (Scurfield 1973; Brown 1980).

Conversely, in *Chamaecyparis* and *Larix,* the complete recovery of the stem

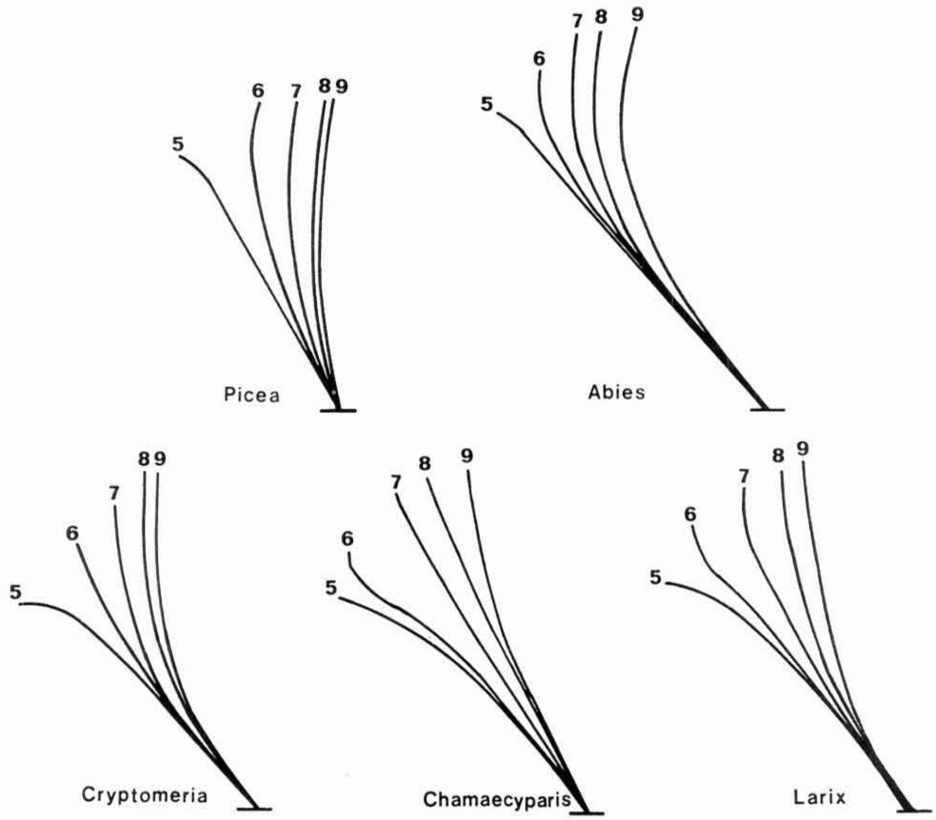

FIG. 2. Diagrammatic model of the righting process of tilted young trees at one-month intervals (5 = May, 6 = June, 7 = July, 8 = August, 9 = September).

could not be observed even by early October (Fig. 2), suggesting that the recovery of the stem in these species proceeds considerably slower. These results suggest a wide range of differences in the geotropic response among species. Brown (1980) pointed out that species of *Picea* and *Abies* are more responsive to geotropic stimulus at maturity than other species. Rapid progression of the stem recovery in *Picea* and *Abies* brought a reverse inclination past the vertical, above the middle portion of the stem, especially near the top. This suggests that the difference in the form of young leader, i.e., straight/drooped form at the top of the stem, by species reflects the difference in the righting activity among species.

Judging from the righting movement in trees used in this study, the righting activity of stems seems to be greater in *Picea* and *Abies* than in *Chamaecyparis* and *Larix*. The righting activity of *Cryptomeria* seems to be intermediate. Whether such a tendency in the differences of the righting movement can be found among genera or not should be further investigated by increasing sample size.

Distribution of compression wood within trees

The angle of stem deviation (ASD) at various points of the stems and the amount of compression wood formed in the corresponding portion are shown in Figs. 3–7. The angle was measured at the time of harvest in early October.

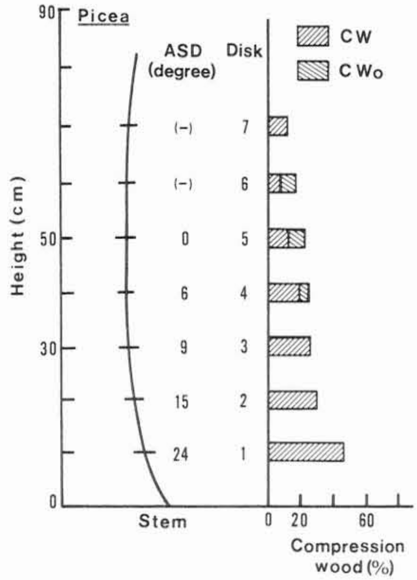

FIG. 3. Angle of stem deviation (ASD) from the vertical, and the amount of compression wood formation within a growth ring at each stem position in *Picea jezoensis*. The negative sign in ASD indicates reverse inclination. CW: Compression wood formation on the original underside. CWo: Compression wood formation on the opposite side.

In each sample tree, compression wood was formed on the underside of the leaning stem. The development of compression wood apparently proceeded from the top of each stem to the base of the stem and the amount of compression wood increased basipetally. The amount of compression wood increased with an increasing angle of stem deviation from the vertical at each stem point of sample

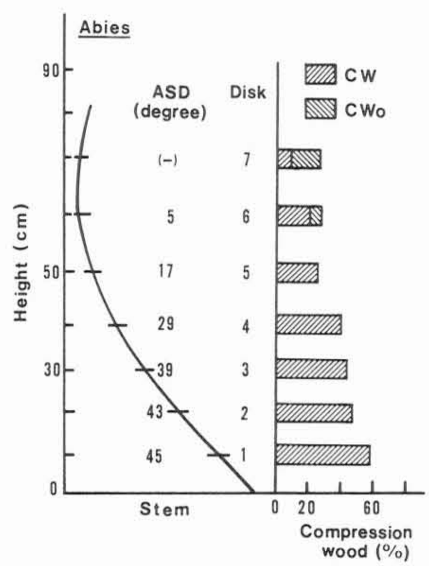

FIG. 4. Angle of stem deviation (ASD) from the vertical and the amount of compression wood formation within a growth ring at each stem position in *Abies firma*. See Fig. 3 as to the details.

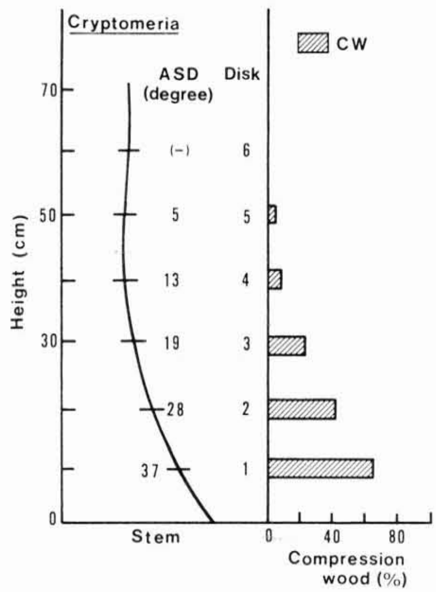

FIG. 5. Angle of stem deviation (ASD) from the vertical and the amount of compression wood formation within a growth ring at each stem position in *Cryptomeria japonica*. See Fig. 3 as to the details.

trees. Judging from the final stem deviation, the formation of compression wood on the original underside in *Picea* and *Cryptomeria* seems to cease early (Fig. 8), especially in the portion above the middle of the stem where the active righting phenomena took place (Figs. 3, 5).*Chamaecyparis* and *Larix* exhibited a slow

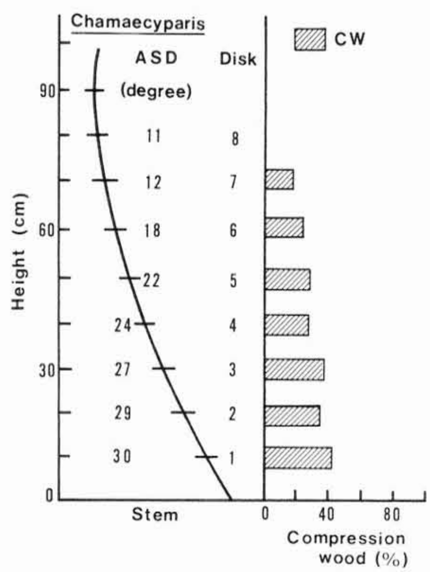

FIG. 6. Angle of stem deviation (ASD) from the vertical and the amount of compression wood formation within a growth ring at each stem position in *Chamaecyparis obtusa*. See Fig. 3 as to the details.

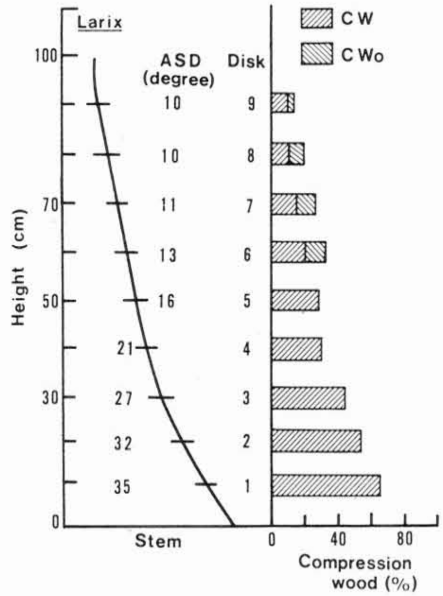

FIG. 7. Angle of stem deviation (ASD) from the vertical and the amount of compression wood formation within a growth ring at each stem position in *Larix leptolepis*. See Fig. 3 as to the details.

righting movement. Although in *Chamaecyparis* compression wood formation ceased early in the upper portion of the stem (Fig. 6), in *Larix* it continued relatively longer (Fig. 7). In *Abies*, which showed a vigorous righting activity, the formation of compression wood stopped relatively early in the upper part of the stem (Fig. 4). However, it continued longer in the lower part of the stem because of its large stem size.

In *Picea* and *Abies*, the reverse inclination of the upper stem resulting from the extensive righting movement caused the formation of compression wood on the opposite side of the stem (new underside) (Figs. 3, 4). The formation of compression wood on the opposite side coincided with the disappearance of compression wood on the original underside. In *Larix*, the compression wood formation reversed to the opposite side of the stem above the middle portion of the stem, but not because the upper stem passed vertical (Fig. 7). Righting of the stem axis of *Larix* remained incomplete (Fig. 2). Sinnott (1952) noted the switching of compression wood from the underside to the opposite side in shoots of *Pinus strobus* in various abnormal positions. Archer and Wilson (1973) reported that in *Pinus strobus* compression wood formation on the upper side occurred when the leader was still 7° to 12° from the vertical. These deviation angles are similar to those of the *Larix* species in this experiment. The mechanism for reversal of compression wood formation seems very complicated. Possibly the redistribution of auxin toward the opposite side may somehow occur prior to the completion of righting movement in the case of *Larix*. Archer and Wilson (1973) pointed out that 1) compression wood formation on the under- and upper side of the stem seems to change location so as to bring the stem into a position where the geotropic stimulus is relatively small, and 2) the reversal in direction of compression wood formation may be due to the undetected lateral or torsional movement of the

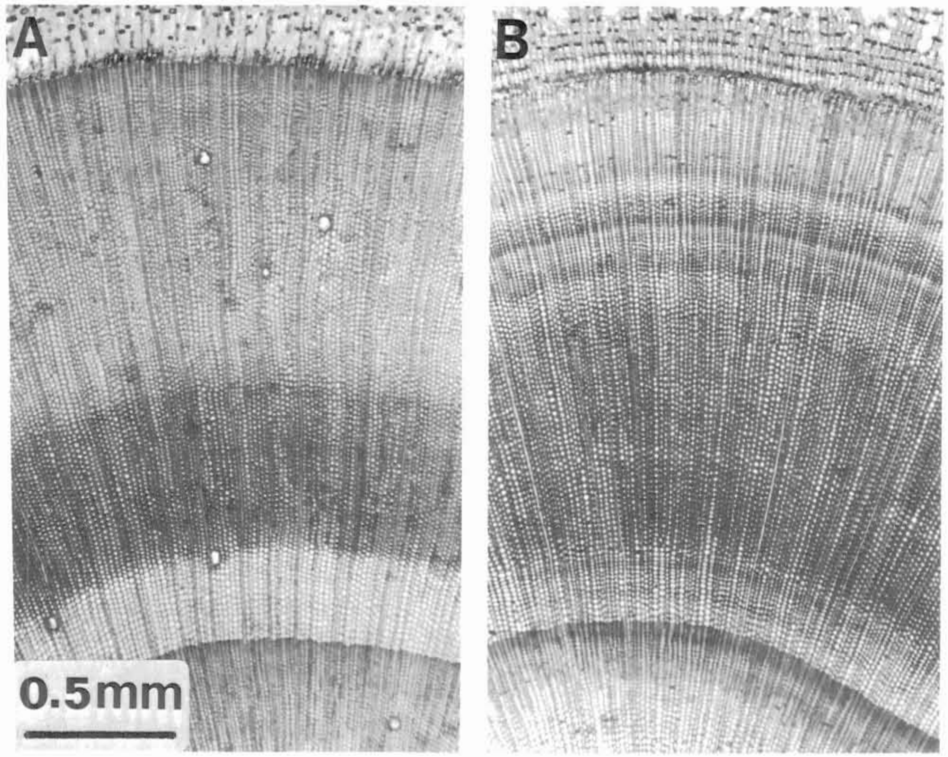

FIG. 8. Compression wood formation on the original underside of the stem. A: *Picea jezoensis* var. *hondoensis*, Disk (6). B: *Cryptomeria japonica*, Disk (3). In the upper part of *Picea* stem compression wood disappears early on the original underside by the reversal of stem inclination. In *Cryptomeria* compression wood gradually disappears toward the latewood region in spite of its still leaning position.

flexible stem. Conversely, no compression wood formation was observed on the opposite side of *Cryptomeria* even after the completion of righting (Fig. 5). This was also true for *Chamaecyparis*, although the stem was still leaning slightly (Fig. 6). Thus, compression wood formation on the opposite side of the stem cannot be predicted from final stem form only.

Xylem development associated with righting was followed in more detail by determining the radial sequence of cell types (normal vs. compression) within the recent growth ring (Fig. 9). Compression wood formation and the stem-righting are basipetal. Except for *Larix*, the nearer the top of the stem the earlier the onset of compression wood formation and corresponding righting movement of the stem.

Auxin transport from the shoot apex is also basipetal (Onaka 1949; Westing 1961, 1965; Wilson and Archer 1977) and this suggests the important participation of auxin in compression wood formation. In the case of *Larix*, production of normal wood cells at the beginning of the growth ring was very brief compared with the other species. This may be related to the conspicuous delay in the time of the inception of cambial division of this species compared to the other sample species used in this experiment (Ladeforged 1952). The formation of compression wood, especially above the middle portion of the stem, ceased early in *Picea*,

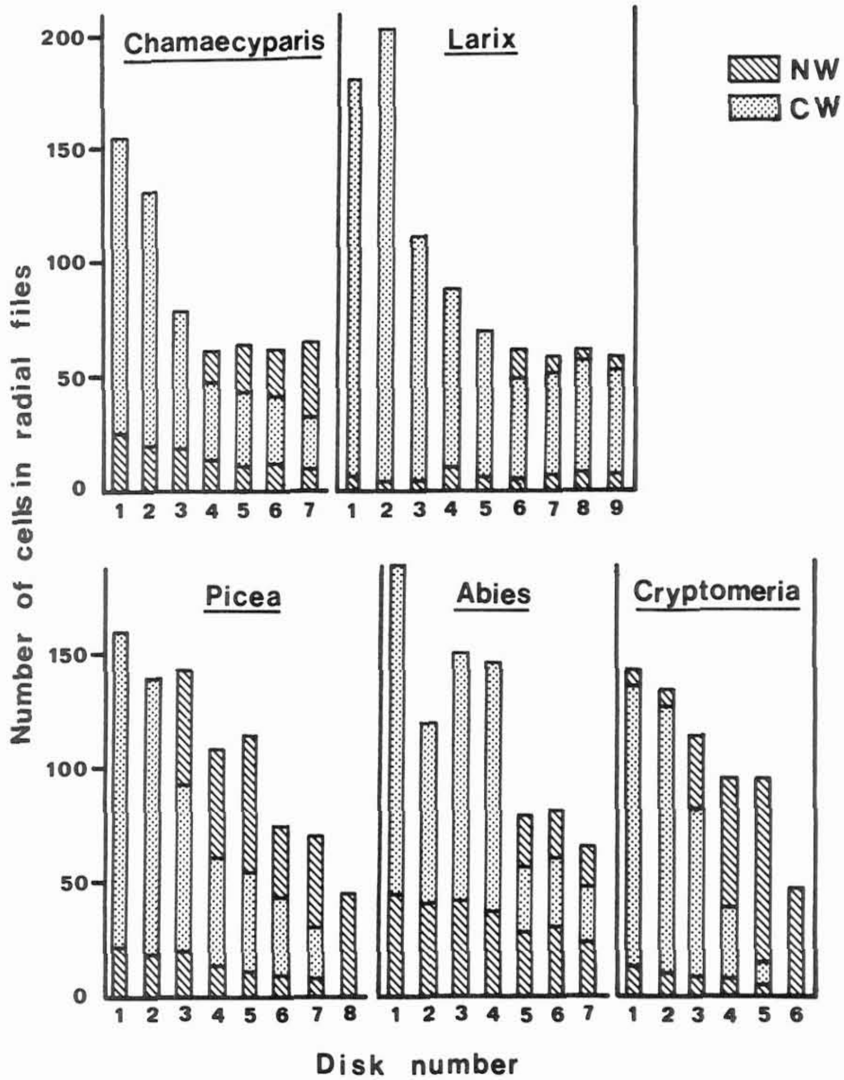

FIG. 9. The radial sequence of normal and compression wood cells on the original underside within a growth ring in each disk of the sample trees. NW: Normal wood cells. CW: Compression wood cells.

Abies, *Cryptomeria*, and *Chamaecyparis* while it continued relatively longer in *Larix* (Fig. 9).

Compression wood formation on the underside near the stem base lasted until the end of this experiment in all sample trees but *Cryptomeria*. Normal wood formation in *Cryptomeria* occurred in the latewood region (Fig. 8), in spite of its still slightly leaning position (Fig. 6). Compression wood formation tends to be restrained in latewood near the growth ring boundary (Timell 1972; Fukazawa 1974; Yoshizawa et al. 1981). This fact suggests that the sensitivity to the stimulus of compression wood formation had been weakened or lost after long-term inclination. Such weakening or loss of sensitivity also was observed in the upper portion of the stem of *Chamaecyparis*, where compression wood disappeared early. Such a phenomenon seems to occur on the underside of a slightly inclined stem with a deviation angle between 10°–20° (Yumoto and Ishida 1982). A similar phenomenon has been reported to take place on the underside of the inclined stem under considerably prolonged inclination (Fukazawa 1974; Yoshizawa et al. 1981). Archer and Wilson (1973) reported that intermittent compression wood formation on the underside or compression wood formation on a flank side of the slightly leaning stem often occurs. Thus, compression wood formation is sensitive to the change of the gravitational stimulus. Decline/loss of sensitivity to the stimulus of compression wood formation on the underside or reversal in direction of compression wood formation may be related to a relocation of auxin within the stem resulting from the undetected stem movement.

SUMMARY AND CONCLUSIONS

Summarizing the observations concerning the righting movement and corresponding compression wood formation, the authors came to the following conclusions. The righting of stems normally proceeds continuously as the stem grows. The recovery of the normal vertical position is initiated at the top of the stem, and proceeds downward to the stem base, as reported by Fukazawa (1973). The forces leading to the righting of the inclined stem are generated in compression wood formation (Frey-Wyssling 1952; Sinnott 1952; Archer and Wilson 1973; Boyd 1973; Scurfield 1973; Wilson and Archer 1977). Compression wood cells appear on the opposite side of the stem in concordance with their disappearance on the original underside at the same height level. This is the result of the reversal of inclination by the excessive righting activity, as pointed out by Fukazawa (1973). The recovery of the vertical position in the upper (younger) portion of the stem is greater than in the lower (older) portion of the stem, which indicates that the righting movement may be related to factors such as stem size and weight, as pointed out by Scurfield (1973). In spite of still leaning, on the other hand, the switching of compression wood formation from the original underside to the upper side at the same height level of the stem occurs. This suggests that the sensitivity of the cambium to respond to the gravitational stimulus declines or is lost on the underside and/or transfers to the upper side of the slightly inclined stem. Apparently this is related to redistribution of auxin within the stem.

Response to the stimulus of inclination occurs faster in *Picea, Abies,* and *Cryptomeria* than in *Chamaecyparis* and *Larix,* suggesting a relationship between differences of the form at the top of the stem and compression wood formation. The transport and production of auxin should be noted with great interest as possibly being a major influence on compression wood formation.

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REFERENCES

ARCHER, R. R., AND B. F. WILSON. 1970. Mechanics of the compression wood response. I. Preliminary analysis. Plant Physiol. 46:550–556.

———, AND ———. 1973. Mechanics of the compression wood response. II. On the location, action, and distribution of compression wood formation. Plant Physiol. 51:777–782.

Boyd, J. D. 1973. Compression wood force generation and functional mechanics. N.Z. J. For. Sci. 3:240–258.

Brown, M. H. 1980. Growth and form. Pages 125–167 *in* M. H. Zimmermann, ed. Trees. Structure and function. Springer-Verlag Press, New York.

Frey-Wyssling, A. 1952. Wachstumsleistungen des Pflanzlichen Zytoplasmas. Ber. Schweiz. Bot. Ges. 62:583–591.

Fukazawa, K. 1973. Process of righting and xylem development in tilted seedlings of *Abies sachalinensis.* Res. Bull. College Exp. Hokkaido Univ. 30:103–123. (In Japanese with English summary.)

———. 1974. The distribution of lignin in compression wood and lateral wood of *Abies sachalinensis* using ultraviolet microscopy. Res. Bull. College Exp. For. Hokkaido Univ. 31:87–114. (In Japanese with English summary.)

Kennedy, R. W., and J. L. Farrar. 1965. Tracheid development in tilted seedlings. Pages 419–453 *in* W. A. Côté, Jr., ed. Cellular ultrastructure of woody plants. Syracuse Univ. Press, Syracuse, NY.

Ladeforged, K. 1952. The periodicity of wood formation. Dan. Biol. Skr. 7:1–98.

Onaka, F. 1949. Studies on compression and tension wood. Mokuzai Kenkyu 1:1–88. (In Japanese with English summary.)

Park, S., H. Saiki, and H. Harada. 1979. Structure of branch wood in akamatsu (*Pinus densiflora* Sieb. et Zucc.). I. Distribution of compression wood, structure of annual ring and tracheid dimensions. Mokuzai Gakkaishi 25:311–317.

Scott, D. R. M., and S. B. Preston. 1955. Development of compression wood in eastern white pine through the use of centrifugal force. For. Sci. 1:178–182.

Scurfield, G. 1973. Reaction wood: Its structure and function. Lignification may generate the force active in restoring the trunks of leaning trees to the vertical. Science 179:647–655.

Sinnott, E. W. 1952. Reaction wood and the regulation of tree form. Am. J. Bot. 39:69–78.

Spurr, S. H., and M. J. Hyvarinen. 1954. Compression wood in conifers as a morphogenetic phenomenon. Bot. Rev. 22:551–560.

Timell, T. E. 1972. Nature of the last-formed tracheids in compression wood. Bull. IAWA 1972/4:10–17.

Wardrop, A. B. 1965. Formation and function of reaction wood. Pages 371–390 *in* W. A. Côté, Jr., ed. Cellular ultrastructure of woody plants. Syracuse Univ. Press, Syracuse, NY.

Westing, A. H. 1961. Changes in radial symmetry in the leaders of eastern white pine following inclination. J. For. 59:17–19.

———. 1965. Formation and function of compression wood in gymnosperms. Bot. Rev. 31:381–480.

Wilson, B. F., and R. R. Archer. 1977. Reaction wood: Induction and mechanical action. Ann. Rev. Plant Physiol. 28:23–43.

Yoshizawa, N., T. Idei, and K. Okamoto. 1981. Structure of inclined grown Japanese black pine (*Pinus thunbergii* Parl.). I. Distribution of compression wood and cell wall structure of tracheids. Bull. Utsunomiya Univ. For. 17:89–105.

———, Y. Tanaka, and T. Idei. 1986. Development of vascular cambium and compression wood formation in the shoot of young spruce (*Picea jizvensis* var. *hondoensis*). IAWA Bull. n.s. 7(1): 21–30.

Yumoto, M., and S. Ishida. 1982. Studies on the formation and structure of the compression wood cells induced by artificial inclination in young trees of *Picea grauca.* III. Light microscopic observation on the compression wood cells formed under five different angular displacements. J. Fac. Agr. Hokkaido Univ. 60(4):337–351.

———, ———, and K. Fukazawa. 1982. Studies on the formation and structure of the compression wood cells induced by artificial inclination in young trees of *Picea grauca.* I. Time course of the compression wood formation following inclination. Res. Bull. College Exp. For. Hokkaido Univ. 39:137–162.